



# Monograph

urn:lsid:zoobank.org:pub:2412CB4F-4D29-4988-80C1-205D16767678

# ZOOTAXA

3549

## Systematics and Phylogeny of *Leptomorphus* Curtis (Diptera: Mycetophilidae)

CHRISTOPHER J. BORKENT<sup>1</sup> & TERRY A. WHEELER<sup>2</sup>

<sup>1</sup> Plant Pest Diagnostics Center, California Department of Food and Agriculture, 3294 Meadowview Road, Sacramento, CA 95832,  
USA. Corresponding author; email: [chris.borkent@mail.mcgill.ca](mailto:chris.borkent@mail.mcgill.ca)

<sup>2</sup> Dept. Natural Resource Sciences, McGill University, Macdonald Campus, Ste-Anne-de-Bellevue, QC H9X 3V9 CANADA.  
email: [terry.wheeler@mcgill.ca](mailto:terry.wheeler@mcgill.ca)



Magnolia Press  
Auckland, New Zealand

**TERMS OF USE**

**This pdf is provided by Magnolia Press for private/research use.  
Commercial sale or deposition in a public library or website is prohibited.**

CHRISTOPHER J. BORKENT & TERRY A. WHEELER

**Systematics and Phylogeny of *Leptomorphus* Curtis (Diptera: Mycetophilidae)**

(*Zootaxa* 3549)

117 pp.; 30 cm.

15 Nov 2012

ISBN 978-1-77557-014-1 (paperback)

ISBN 978-1-77557-015-8 (Online edition)

FIRST PUBLISHED IN 2012 BY

Magnolia Press

P.O. Box 41-383

Auckland 1346

New Zealand

e-mail: [zootaxa@mapress.com](mailto:zootaxa@mapress.com)

<http://www.mapress.com/zootaxa/>

© 2012 Magnolia Press

All rights reserved.

No part of this publication may be reproduced, stored, transmitted or disseminated, in any form, or by any means, without prior written permission from the publisher, to whom all requests to reproduce copyright material should be directed in writing.

This authorization does not extend to any other kind of copying, by any means, in any form, and for any purpose other than private research use.

ISSN 1175-5326 (Print edition)

ISSN 1175-5334 (Online edition)

## Table of contents

Abstract . . . . .	4
Introduction . . . . .	4
Taxonomic history . . . . .	4
Materials and methods . . . . .	5
Distributions . . . . .	5
Measurements . . . . .	7
Terminology . . . . .	7
Dissections . . . . .	7
Phylogeny . . . . .	7
Systematics . . . . .	7
Genus <i>Leptomorphus</i> Curtis . . . . .	7
Diagnosis . . . . .	7
Description . . . . .	8
Biology . . . . .	10
Key to adults of <i>Leptomorphus</i> species . . . . .	11
Species descriptions . . . . .	13
1. <i>Leptomorphus aliciae</i> Matile . . . . .	13
2. <i>Leptomorphus amorimi</i> Borkent, new species . . . . .	15
3. <i>Leptomorphus babai</i> Sasakawa . . . . .	16
4. <i>Leptomorphus bifasciatus</i> (Say) . . . . .	18
5. <i>Leptomorphus brandiae</i> Borkent, new species . . . . .	20
6. <i>Leptomorphus carnevalei</i> Matile . . . . .	21
7. <i>Leptomorphus chaseni</i> Edwards . . . . .	23
8. <i>Leptomorphus couturieri</i> Matile . . . . .	24
9. <i>Leptomorphus crassipilus</i> Borkent, new species . . . . .	25
10. <i>Leptomorphus crosskeyi</i> Matile . . . . .	27
11. <i>Leptomorphus eberhardi</i> Borkent, new species . . . . .	38
12. <i>Leptomorphus fasciculatus</i> Edwards . . . . .	30
13. <i>Leptomorphus femoratus</i> Edwards . . . . .	31
14. <i>Leptomorphus forcipatus</i> Landrock . . . . .	33
15. <i>Leptomorphus furcatus</i> Borkent, new species . . . . .	35
16. <i>Leptomorphus gracilis</i> Matile . . . . .	36
17. <i>Leptomorphus grjebinei</i> Matile . . . . .	38
18. <i>Leptomorphus hyalinus</i> Coquillett . . . . .	39
19. <i>Leptomorphus magnificus</i> (Johannsen) . . . . .	41
20. <i>Leptomorphus mandelai</i> Borkent, new species . . . . .	43
21. <i>Leptomorphus medleri</i> Matile . . . . .	45
22. <i>Leptomorphus nebulosus</i> (Walker) . . . . .	46
23. <i>Leptomorphus neivai</i> Edwards . . . . .	49
24. <i>Leptomorphus obscurus</i> Matile . . . . .	51
25. <i>Leptomorphus ornatus</i> Brunetti . . . . .	52
26. <i>Leptomorphus panorpiformis</i> (Matsumura) . . . . .	54
27. <i>Leptomorphus perplexus</i> Borkent, new species . . . . .	55
28. <i>Leptomorphus quadrimaculatus</i> (Matsumura) . . . . .	57
29. <i>Leptomorphus stigmatus</i> Borkent, new species . . . . .	58
30. <i>Leptomorphus subcaeruleus</i> (Coquillett) . . . . .	60
31. <i>Leptomorphus subforcipatus</i> Zaitzev & Ševčík . . . . .	62
32. <i>Leptomorphus tabatius</i> Borkent, new species . . . . .	63
33. <i>Leptomorphus tagbanua</i> Borkent, new species . . . . .	64
34. <i>Leptomorphus talyshensis</i> Zaitzev & Ševčík . . . . .	66
35. <i>Leptomorphus titiwangensis</i> Borkent, new species . . . . .	66
36. <i>Leptomorphus walkeri</i> Curtis . . . . .	68
37. <i>Leptomorphus waodani</i> Borkent, new species . . . . .	70
Specimens and species not included . . . . .	71
Phylogenetic analysis of <i>Leptomorphus</i> species relationships . . . . .	72
Characters used . . . . .	72
Monophyly of <i>Leptomorphus</i> . . . . .	74
<i>Leptomorphus ornatus</i> species group . . . . .	76
<i>Leptomorphus grjebinei</i> species group . . . . .	76
<i>Leptomorphus walkeri</i> species group . . . . .	77
<i>Leptomorphus furcatus</i> species group . . . . .	78
Implications of phylogeny for previous classifications . . . . .	79
Acknowledgements . . . . .	79
Literature Cited . . . . .	79
List of figures . . . . .	84

## Abstract

The world fauna of the genus *Leptomorphus* Curtis, 1831 is revised and a phylogeny of species relationships, based on morphological characters, is presented. An updated genus diagnosis and description are given. Species descriptions, diagnoses, illustrations of general habitus, wings, male genitalia and distributions are provided for 37 valid species, along with a key to adults.

Twelve new species are described; *L. amorimi* Borkent, **n. sp.**, *L. brandiae* Borkent, **n. sp.**, *L. crassipilus* Borkent, **n. sp.**, *L. eberhardi* Borkent, **n. sp.**, and *L. waodani* Borkent, **n. sp.**, from the Neotropical realm, *L. furcatus* Borkent, **n. sp.**, and *L. perplexus* Borkent, **n. sp.**, from the Nearctic realm, *L. mandelai* Borkent, **n. sp.**, and *L. stigmatus* Borkent, **n. sp.**, from the Afrotropical realm, and *L. tabatius* Borkent, **n. sp.**, *L. tagbanua* Borkent, **n. sp.**, and *L. titiwangsensis* Borkent, **n. sp.**, from the Oriental realm. Type specimens were studied for all but three species (*L. ornatus*, *L. subforcipatus* and *L. talyshensis*). *Leptomorphus elegans* Matile and *L. lepidus* Matile are considered junior synonyms of *L. gracilis* Matile, **n. syns.**, and *L. ypsilon* Johannsen is a junior synonym of *L. hyalinus* Coquillett, **n. syn.** Lectotypes are designated for *L. magnificus* (Johannsen), *L. neivai* Edwards, and *L. walkeri* Curtis and a neotype is selected for *L. bifasciatus* (Say). This study brings the total number of extant *Leptomorphus* species to 45, including eight, unique (based on figures and descriptions), recently described Oriental and northwestern Australasian species (Papp & Ševčík 2011), for which material was unavailable for this study. The phylogenetic analysis in this study supports the monophyly of *Leptomorphus*. The western Nearctic species, *L. perplexus*, is the sister group to the remaining species, which fell into four major monophyletic species groups (*L. ornatus* Brunetti group, *L. grjebinei* Matile group, *L. walkeri* group, *L. furcatus* group). The monophyletic relationships within each group are also discussed. The clades found in this study do not support the arrangement of species in to the *Leptomorphus* subgenera recognized by previous classifications.

**Keywords:** Taxonomy, Sciophilinae, Sciophilini, new species, morphology, Fungus gnats, distribution, genus revision

## Introduction

The genus *Leptomorphus* Curtis, 1831 (Diptera: Mycetophilidae) is found worldwide, with the exception of Antarctica, and previous to this study, contained 36 extant and three fossil species. The extant species are distributed as follows: ten species are known in the Afrotropical (Matile 1977, 1997), seven in the Palearctic (Matile 1988, Zaitzev & Ševčík 2002), eight in the Oriental (Colless & Liepa 1973, Papp & Ševčík 2011), two in the northwestern Australasian (Papp & Ševčík 2011), three in the Neotropical (Papavero 1978), and six in the Nearctic (Laffoon 1965).

Members of *Leptomorphus* are some of the largest and most robust mycetophilids, ranging in body length from 6–14mm. They also exhibit a range of colour from yellow and orange-red to dark brown or black with bright blue iridescence. They can be easily separated from other Mycetophilidae based on a number of characters (see generic diagnosis below).

## Taxonomic history

*Leptomorphus* was described by Curtis (1831) for a single species (*L. walkeri* Curtis) from the United Kingdom. Shortly thereafter, Walker (1848) erected the genus *Diomonus* for a single new species (*D. nebulosus* Walker) from North America and noted that the wings of *Diomonus* were identical to *Leptomorphus* except that  $R_4$  was present. Over the following 77 years nine species were validly assigned to, or transferred into, these two genera (see below). Though there was some further discussion of the similarity between these genera (Johannsen 1910) they remained separate, and were even placed in different subfamilies of Mycetophilidae by Johannsen (1910, 1912). Two species originally described in *Leptomorphus* during this time were subsequently moved to other genera; *L. parvula* Coquillett (1901: 597) was moved to *Allocotocera* Mik, and *L. elongatus* Walker (1848: 87) was synonymized with *Neuratelia nemoralis* (Meigen).

Edwards (1925) synonymized the two genera because he felt that there was no difference between them, other than the presence of  $R_4$  in *Diomonus*. At the same time, Edwards (1925) placed *Leptomorphus* in the tribe Sciophilini where it has remained since (although some authors have ranked this tribe as the subfamily Sciophilinae s.s. (e.g. Tuomikoski 1966, Väisänen 1984, Chandler 2009)). Most authors have followed this synonymization; however, Matile (1977) gave *Diomonus* subgeneric status and questioned the validity of the synonymization.



In most cases, species have been described in the context of regional monographs on Mycetophilidae, with at most two species being described together, and with little comment on their relationships to other *Leptomorphus* species. The three exceptions to this are the treatment of the four species in the clearly monophyletic *L. quadrimaculatus* species group (Zaitzev & Ševčík 2002), a monograph and update on the *Leptomorphus* of Africa (Matile 1977, 1997) and a recent paper describing eight new species from the Oriental and northwestern Australasian realms (Figs. 138–139, Papp & Ševčík 2011).

Matile (1977, 1997) described ten new species, the first records of the genus from the Afrotropical region. Matile (1977) also divided the genus into four subgenera: *Leptomorphus* (*s.s.*) with nine species from the Holarctic and Neotropical realms, *Diomonus* with five Holarctic species, *Gymnoscutum* Matile with 11 Afrotropical and Oriental species, and the monotypic *Austroleptomorphus* Matile restricted to Madagascar. *Leptomorphus neivai* Edwards was not placed to subgenus as it did not have clear characteristics of any of the subgenera. The limits of the subgenera were based principally on the presence or absence of two wing veins ( $sc_r$  and  $R_4$ ) and the number of setae on the scutum or scutellum. No phylogenetic hypothesis was proposed for the genus or subgenera at that time, as a larger revision was thought necessary before any phylogeny could be considered reliable (Matile 1997).

Additionally, there are three described extinct species of *Leptomorphus*; the oldest, *L. palaeospilus* (Cockerell, 1920), is a compression fossil from the Eocene, showing that this lineage had diverged earlier than 38 million years ago. Having seen the type specimen (USNM) of the latter species, and based on its visible characteristics, we are certain that this species belongs in *Leptomorphus*. The placement in *Leptomorphus* of the other two extinct species (*L. africanus* Meunier, 1907 from Holocene copal and *L. sepultus* (Meunier, 1917) from Baltic amber) is questionable, as the descriptions do not match the general habitus of the genus.

*Leptomorphus* has been included in two published studies of the phylogeny and relationships within the Mycetophilidae or its tribes (Søli 1997, Rindal *et al.* 2009). In these studies, the genus is consistently placed within the subfamily Sciophilinae and tribe Sciophilini. Søli (1997) used morphological characters in his cladistic analysis and showed either *Neuratelia* Rondani or *Allocotocera* as the sister group to *Leptomorphus*. The other study, based on molecular data (Rindal *et al.* 2009), conflicted with morphological hypotheses of relationships across the family. This included suggesting the genus *Manota* Williston as sister group to *Leptomorphus*. In both these studies half or fewer of the genera ascribed to the Sciophilini were included, leaving the placement of a large number of genera unconfirmed and the validity of sister group relationships in question. Ongoing analysis of the phylogeny of Sciophilini, including exemplars of all included genera, strongly suggests that the sister genus to *Leptomorphus* is actually *Eudicrana* Loew (Borkent & Wheeler in press) as shown in the current study.

This paper provides the first world revision of the genus *Leptomorphus* and an identification key for adults. A phylogenetic hypothesis of species relationships is also presented and a revised classification given based on this phylogeny. Forty-five extant species are now recognized in the genus *Leptomorphus*.

## Materials and methods

More than 700 specimens were examined from a number of collections and institutions (Table 1), as well as from collecting in North and Central America. Types for 22 of the 28 known (prior to 2011) extant species were obtained, as well as that of one fossil species. Where possible, the exact label information for primary types is provided, with line breaks indicated with '/' and a change in label with a semi-colon. Any inferred label information is in square brackets. All previously described species with unclear type labels had an additional determination label added with the current status of the species and specimen.

## Distributions

Distributional data was primarily obtained from the material examined. Additional records of specimens not examined were taken from high resolution photographs of specimens in other collections, or recent publications in which species identifications were deemed reliable. Distribution maps were made using Simplemapp (Shorthouse 2010).

**TABLE 1.** Abbreviations for collections and institutions referred to in the text.

Abbreviation	Institution or Collection
ANSP	Academy of Natural Sciences, Philadelphia, PA, USA.
BMNH	Natural History Museum, London, UK.
CAS	California Academy of Sciences, San Francisco, CA, USA.
CMNH	Carnegie Museum of Natural History, Pittsburgh, PA, USA.
CNC	Canadian National Collection, Ottawa, ON, Canada.
CSCA	California State Collection of Arthropods, Sacramento, CA, USA.
CUAC	Clemson University Arthropod collection, Clemson, SC, USA.
CUIC	Cornell University, Ithaca, NY, USA.
DEBU	University of Guelph Insect Collection, Guelph, ON, Canada.
EIHU	Entomological Institute, Hokkaido University, Sapporo, Japan.
HNHM	Hungarian Natural History Museum, Budapest, Hungary.
IEE	A.N. Severtsov Institute of Ecology and Evolution, Moscow, Russia.
IRSNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.
ISUI	Iowa State University Insect Collection, Ames, IA, USA.
LEM	Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, Canada.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA.
MMBC	Moravske Muzeum [Moravian Museum], Brno, Czech Republic.
MNHN	Muséum National d'Histoire Naturelle, Paris, France.
MTD	Museum für Tierkunde, Dresden, Germany.
MVMA	Museum of Victoria, Melbourne, Victoria, Australia.
MZB	Museum Zoologicum Bogoriense, Cibinong, Bogor, Indonesia.
MZHF	Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland.
MZUSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.
NCSU	North Carolina State University Insect collection, Raleigh, NC, USA.
NMSA	Natal Museum, Pietermaritzburg, South Africa.
NZSI	National Zoological Collection, Zoological Survey of India, Calcutta, West Bengal, India.
OMNH	Osaka Museum of Natural History, Osaka, Japan.
RBCM	Royal BC Museum, Victoria, BC, Canada
SEMC	University of Kansas Natural History Museum, Snow Entomological Museum, Lawrence, KS, USA.
SMNS	Staatliches Museum für Naturkunde, Stuttgart, Germany.
SMOC	Silesian Museum (Slezsk zemsk museum), Opava, Czech Republic.
UBCZ	University of British Columbia, Beaty Biodiversity Museum, Spencer Entomological Museum, Vancouver, BC, Canada.
UNHC	University of New Hampshire Arachnid and Insect collection, Durham, NH, USA.
USNM	National Museum of Natural History, Washington DC, USA.
ZMUN	University of Oslo, Zoological Museum, Oslo, Norway.
ZSM	Zoologische Staatssammlung, München, Germany.

### **Measurements**

Wing measurements were taken as the length from the base of the distal median plate to the wingtip. Thorax length was recorded as the distance from the anterior margin of the scutum to the posterior margin of the scutellum when viewed dorsally. For both measurements males and females were measured separately. The average length  $\pm$  95% confidence interval is reported, along with the minimum and maximum lengths and the number of specimens measured (n). When possible, the holotype was included in the series of measured specimens. Specimens that had been reared from the larval stage were not included as they were usually significantly smaller than those collected as pupae, likely due to lack of adequate food supply.

### **Terminology**

Morphological terminology follows Cumming & Wood (2009) in general and Sølvi (1997) for genitalic interpretation. The only exception is in the case of the posterior wing veins CuA<sub>1</sub> and CuA<sub>2</sub> of Cumming & Wood (2009), which are interpreted here as veins M<sub>4</sub> and CuA respectively (Blagoderov & Grimaldi 2004, Saigusa 2006, Amorim & Rindal 2007).

### **Dissections**

Pinned specimens were observed using a Leica Wild MZ8 Stereomicroscope and slide mounted genitalia were observed and drawn with a Leica DMLB compound microscope equipped with a drawing tube. Photographs were taken using a digital camera attached to the MZ8 microscope. Genitalia were prepared by removing the genitalia and posterior 3–4 segments of the abdomen from a specimen. These were then cleared in 85% lactic acid heated for 15-second intervals in a microwave oven three to five times, each separated by cooling periods of one to two minutes. The cleared material was then immersed in two washes of glycerin before being placed on a microscope slide for detailed observation, or being stored in glycerin in a plastic vial pinned below the specimen. The bristles of tergite 9 and the gonocoxite are generally omitted from the drawings as they hid important characters in other parts of the genitalia. Only those bristles that were thought to have diagnostic or phylogenetic importance were included.

### **Phylogeny**

A matrix of characters was constructed using Mesquite 2.74 (Maddison & Maddison 2011) for use in the parsimony analysis. Outgroup taxa were selected based on sister group relationships to *Leptomorphus* found in previous phylogenetic work (Sølvi 1997, Borkent & Wheeler in press), as discussed above. The analysis was performed using TNT 1.1 (Goloboff *et al.* 2003). A heuristic search using parsimony was run with 1000 replicates, saving 100 trees per replicate. The MaxTrees limit was set to 50000 trees. Tree Bisection Reconnection (TBR) branch swapping was used for the search and branches were collapsed when the maximum length was zero. Characters were treated as unordered in the analysis.

Bremer support (Bremer 1994) and Bootstrap (Felsenstein 1985) values were calculated using TNT. Suboptimal trees with 1–20 extra steps were used to calculate Bremer support values. Bootstrap values were calculated using the same parameters as in the heuristic search.

## **Systematics**

### **Genus *Leptomorphus* Curtis**

*Leptomorphus* Curtis, 1831: 365 (Type species: *Leptomorphus walkeri* Curtis, by original designation).

*Diomonus* Walker, 1848: 87 (Type species: *Diomonus nebulosus* Walker, by monotypy).

*Leptomorphus*: Edwards, 1925: 556 (synonymization of *Diomonus*).

### **Diagnosis**

Mycetophilids placed in the Sciophilini include those genera having two fold lines on at least sternites 3–6 and bristles present on the mediotergite and laterotergite (Sølvi 1997, Borkent & Wheeler in press). Species of *Leptomorphus* are distinguished from other Sciophilini by the following combination of characteristics: 3 ocelli; inter-ommatidial bristles absent or very sparse and short; antennal flagellomere 1 with a distinctly dorsally offset

basal stalk; flagellomeres slightly laterally compressed; wing surface with macrotrichia but no microtrichia; costa not produced beyond the apex of  $R_5$ ; point of furcation of posterior fork ( $M_4$  and CuA) before that of medial fork ( $M_1$  and  $M_2$ ); base of  $M_1$  complete, anepimeron and katapisternum bare; antepronotum and proepisternum setose; acrostichal bristles absent (difficult to determine in species with scutum covered in setae); tibial bristles short, no more than half the thickness of tibia in length; vas deferens joining base of aedeagal apodemes rather than fusing and entering aedeagus as a single tube (in all specimens where this was visible, the oriental species may be an exception); gonocoxite III fused or closely associated with gonostylus. The larvae are the only known Mycetophilidae with eight silk spigots anteriorly on the labrum (Plachter 1980) and the pupae are the only mycetophilids, other than cave inhabiting species (e.g. *Speolepta*, Ševčík *et al.* 2012), that are known to hang from a line.

Though not present in all species the following characteristics also appear unique to the genus: gonocoxites placed apically on tergite 9 (mistaken for gonostyli by some authors); all species except *L. perplexus* with ocelli grouped tightly together at vertex, approximating an ocellar triangle; aedeagal apodemes projecting anteriorly into segment VIII and VII; males of some species with comb of bristles on anteroventral margin of foretibia or with apical spine-like process on midfemur.

### Description

Total length 5.5–14.5mm. Wing length 4.0–10.6mm.

**Colour:** (Figs. 1–41) Highly variable even within some species, particularly in the amount of brown on those species with both yellow and brown on scutum and abdomen. Almost completely yellow to partially reddish orange to almost completely dark brown/black, most commonly with head light brown, thorax brown with some yellow markings and abdomen striped yellow and brown. Scutum usually shows most variability in colour within a species with varying amounts of yellow or brown as spots and lines. Antennae usually brown, apical half white in some species. Some adults with adventitious brown spots placed randomly on yellow sclerites.

**Head:** Circular to somewhat dorsoventrally compressed in anterior view. Scape with distinct apicoventral bump, thickly covered with setae; row of setae on apical margin of scape, medial surface bare. Pedicel with 1–6 large bristles and several setae on apicodorsal margin, occasionally with some fine setae on apicoventral margin. Flagellomere 1 with dorsally offset basal stalk, stalk often a different colour than rest of flagellomere. Remaining flagellomeres ranging from square to 2X as long as wide, apical flagellomere tapering to a point apically, all flagellomeres without setae.

Clypeus square or circular to slightly or strongly laterally compressed oval, always longer than face, slightly to strongly protruding anteriorly; surface covered with strong and weak bristles, strong bristles usually densest on ventral portion and directed ventrally. Labrum reduced/not discernible. Face a triangular sclerite with ventral margin somewhat arched; bearing 0–many bristles, when only a few bristles these restricted to ventrolateral corners.

Frons a flat sclerite (no frontal tubercle), typically bare or with a few medioventral bristle, rarely with ventral half covered in bristles; frontal furrow always present though length varying from 1/10 to full length of frons; frontal cleft always present though running from eye margin to either lateral ocelli or just in front of median ocellus. Lacinia present, but small and often hidden behind eye. Palpus with five segments, typically increasing in length from base to apex, segment 1 small and often hidden behind eye, segment 3 with sensillae present and sometimes in a pit or arranged in a distinct patch encircled by dark setae, all segments with setae and trichia with the exception of segment 5 which has setae absent in some species.

Compound eye with small indentation (2–3 ommatidia deep) on medial margin just above level of antennae; inter-ommatidial setulae absent or when present usually only in ¼ of ommatidial junctions and not longer than width of an ommatidia (*L. perplexus* with setulae on all but medial margin). Three ocelli present and close together at vertex on a dark background (except in *L. perplexus*), with lateral ocelli at least 1.5X own diameter from eye margin. Occiput with a number of appressed anteriorly directed setae

**Thorax:** Scutum with acrostichal setae absent, dorsocentral setae present (though often reduced to a few anterior or posterior setae, or very fine setae), lateral setae present; rest of scutum surface ranging from bare to covered with trichia or small setae. Scutellum either with large and small setae or with covering of fine trichia. Mediotergite with several bristles posteriorly and sometimes with small setae or appressed trichia on remainder. Laterotergite with several bristles and setae, sometimes with covering of appressed trichia. Antepronotum and

proepisternum fused (though suture line discernible) and bearing a number of setae; Anepisternum, katepisternum and metepisternum bare. Anapleural suture straight or with slight dorsal curve on anterior portion.

*Legs:* Long and slender. Coxae with setae on dorsal margin, fore- and midcoxae with setae anteriorly. Femora covered with small setae. Tibia with bristles (when numerous in several different rows) and irregularly arranged small setae, bristles no longer than  $\frac{1}{2}$  thickness of tibial apex. Tibial spurs 1:2:2. Foretibia with anteroapical depressed area well developed, semicircular, and with numerous trichia; in some species a comb of setae on anteroventral surface. Those species with a dorsal bare patch on the midtibia have tibia swollen for length of patch (when compared to hind tibia). Tarsi covered with brown macrotrichia. First tarsomere of foreleg longer than foretibia in all species except *L. perplexus*, females usually slightly shorter than males. Tarsal claws with one large and one small basal tooth. Empodium present but highly reduced.

*Wing:* (Figs. 42–77) Hyaline; frequently with apex lightly to darkly shaded and if so then often with medial shaded spot centered around forking of R veins and M. Wing surface covered with irregularly arranged macrotrichia that are decumbent towards apex. C ending at  $R_5$ . Humeral vein joining C close to wing base. Sc ending in C. Vein sc-r usually present though faint or absent in some species, joining R or  $R_1$  within 3X its own length from emergence of  $R_s$ .  $R_4$  absent or present near base of  $R_s$ , sometimes present in one wing of a specimen and missing from the other.  $R_5$  slightly concave or straight with slight posterior turn near apex.  $M_{1+2}$  forking distally of  $M_4$  and CuA fork.  $M_{1+2}$  shorter than  $M_1$  or  $M_2$ . Petiole of posterior fork (bCuA) shorter or longer than either  $M_4$  or CuA. Apices of M veins either reaching wing margin or fading just before. CuA more bent towards wing margin than  $M_4$  resulting in greater divergence between posterior fork veins than between anterior fork veins. CuP present as a darkened crease running just behind posterior fork but not reaching to wing margin.  $A_1$  not reaching wing margin.  $A_2$  absent to faintly present as crease or present as dark vein. Distal median plate setose. Dorsal and ventral surfaces of Sc, all M veins,  $R_1$ ,  $R_5$ , and  $A_1$  with row of setae. Dorsal surface of CuA and humeral vein with row of setae, ventral surface bare.

*Abdomen:* Abdominal segments 1–7 unmodified though segment 1  $\sim\frac{1}{2}$  size of remainder and at least sternites 3–6 with two fold lines. Segment 8 reduced in size in both sexes and partially retracted inside segment 7. Male sternite 8 a setose rounded sclerite, larger than tergite 8, frequently covering basoventral surface of genitalia. Male tergite 8 (erroneously considered sternite 8 by Papp & Ševčík (2011)) broadening towards apex, bare or with setae on apicolateral corners and sometimes 1–2 lines of setae on apical margin. Male genitalia and segment 8 able to rotate by  $90^\circ$  to either side.

*Male genitalia:* Sternite 9 ranging from bare, membranous, or small rounded sclerite ( $<\frac{1}{2}$  width of genitalia), to broad setose sclerite covering most of ventral surface and as broad or broader than tergite 9, apical margin always with membranous or sclerotized attachment to apical half of aedeagus (in Oriental species S9 usually reduced to thin long sclerite that is strongly associated with, and sometimes appears fused to, the aedeagus (Figs 119, 120), = “ejaculatory apodeme” *sensu* Papp & Ševčík (2011)). Tergite 9 setose and ranging in shape from circular to squat or tall rounded rectangle, posterior margin usually with various lobes/processes, usually setose on both dorsal and ventral surfaces (i.e. they are evaginations), some lobes with thickened ventral basoventral margin forming either a concave band or bearing lateral spines that meet with points of gonostyli. Gonocoxite placement on tergite 9 variable from basally to apically, ranging from forming most of ventral surface to only present as apicolateral pyramids less than half length of tergite 9; gonocoxite bearing setae at least on apical half and ranging in shape from simple oval to modified structure with many lobes; gonocoxal apodeme usually fused with parameral apodeme and forming a dorsal pointing hook at base of united apodeme; bearing gonostylus at various levels on medial margin; gonocoxite III present, setose, and always closely associated (sometimes fused) with dorsal margin of gonostylus. Gonostylus with one or two lobes variably pointed or rounded, sometimes with a few setae on surface. Aedeagus usually with large aedeagal apodemes extending anteriorly into abdominal segment 8. Vas deferentia not joining together, running into base of aedeagal apodemes (in all species in which they were visible). Aedeagus usually tapering from apodemes to rounded apex, in a few species apex variously sclerotized and extended into lobes or hooks. Parameres usually as simple single taper, in some species as a swollen lobe or with two lobes, or reduced so only posteriorly attached parameral apodemes remain.

*Female genitalia:* Tergite 8 similar in shape to tergite 7 but slightly shorter. Sternite 8 fused with gonocoxites 8, which are present posteriorly as a rounded lobe on side of median line, these lobes usually bearing several thick bristles apically. Labia and gonapophysis 8 present behind gonocoxite 8, though both reduced and membranous, membrane with numerous small trichia. Gonapophysis 9 (genital fork of Cumming and Wood 2009) clearly present



and extending anteriorly into segment 8. Tergite 9 reduced to thin sclerotized band. Sternite 9 bearing gonopore subapically, apical margin sclerotized and semicircular with medial anteriorly directed thickening. Gonopore with openings of two spermathecal ducts. Gonocoxite 9 present as sclerotized, setose lobes apicolaterally of sternite 9. Tergite 10 surrounding base of cerci, lateral margins almost joining ventrally, covered in long posteriorly directed setae. Sternite 10 present, laterally sclerotized and setose in triangle shape, medially membranous and bare. Hypoproct membranous. Cerci large and unsegmented (most prominent feature in all species).

*Egg:* Few known examples are ovals ~2X long as wide, surface reticulate and covered in long thin spines (Brocher 1931, Eberhard 1970, Santini & Mazzini 1989, Papp & Ševčík 2011).

*Larvae:* (Figs. 127–131) Length 1.0–2.5 cm. In all known examples head capsule with some light-dark brown on margins, lighter medially. Head capsule with eight, pointed, processes on apical margin (labrum) which produce silk strands. Maxillary palps hidden behind labrum in dorsal view. Rest of body ivory in base colour with varying amounts of brown/black spots or lines dorsally and laterally. All segments constricted anteriorly and posteriorly at junction with other segments. Ventral creeping welts of abdomen with two rows of dark spicules.

*Pupae:* (Figs. 132–133) Known examples mottled light and dark brown (darkening with age) and hanging from either a posteriorly attached or ventrally attached (held between developing legs) silk line. Developing antennae clearly visible. Thorax with protruding processes on lateral margins of scutum. Anterior and abdominal spiracles placed on strong protrusions/turrets. Dorsal margin of abdomen straight to strongly arched (concave), bearing either one medial or two mediolateral lines of bumps, developing legs all held together along ventral margin of abdomen.

### **Biology**

Members of the genus *Leptomorphus*, like most Mycetophilidae, inhabit moist and humid woodlands. The larvae can be found on a variety of saproxylic polypore fungi that form sporophores that are either brackets or an encrusting layer on the surface of the wood. Some of these appear to be perennial sporophores. In all *Leptomorphus* species in which the immatures are known, the larvae inhabit the sporulating underside of the fungus, where they spin a fine silk sheet to trap falling spores and to assist their movement (Brocher 1931, Eberhard 1970, Matile 1977, Plachter 1980, Santini 1985). The larvae crawl along the sheet, leaving slime trails and eating small holes in the spore-covered sheet, which they then fill with new silk (Eberhard 1970). They also appear to defend their sheet from other larvae (C. Borkent, unpub. data). When the larva is ready to pupate it runs a silk line, attached at either the posterior end (Plachter 1980, Santini 1985, Ševčík 2006) or both ends (Eberhard 1970), to either the fungus or the underside of the wood near the fungus. The larva pupates on this line by attaching its posterior end to the line (in the case of the single attached line), or by spinning a collar on the line, from which the larva hangs. The larval cuticle, including the head capsule, is shed towards the posterior end of the pupa where it remains on the silk line as a small dried mass (Edwards 1925, Brocher 1931, Madwar 1937, Eberhard 1986). During pupation the line is either fixed to the pupa's posterior or held between the developing legs of the pupa. Pupation takes four to seven days (Madwar 1937, Eberhard 1970), and newly emerged adults hang from the shed pupal cuticle for two to three hours after emergence. The imago hangs from the pupal cuticle by bending the last few abdominal segments as an anchor inside the cuticle (Eberhard 1970, Santini 1985).

Adult males of some species search out female pupae and land on them in preparation for mating when the female emerges. They will defend the pupa from other males that attempt to land on the pupa, with the largest male usually driving off the smaller. Mating occurs as soon as the female is free of the pupal cuticle and can last for several hours (Eberhard 1970). In temperate regions, eggs, which are covered in small spines (Brocher 1931, Eberhard 1970, Santini & Mazzini 1989, Papp & Ševčík 2011), are laid singly on dead wood during the fall and overwinter in this stage (Brocher 1931, Santini 1985). It is not known whether the female is able to detect the presence of polypore host hyphae in the logs chosen when no sporophore is present. Many southern temperate species appear to be polyvoltine or bivoltine (Madwar 1937, Santini 1985) though it is likely that populations in more northern parts of the range are univoltine.

Beyond mating behaviour little is known about the habits of the adults as they are infrequently caught while sweeping and have rarely been observed in the wild. They have functional mouthparts so they probably feed on liquids such as nectar (a few specimens have been collected on flowers). Hymenopteran parasitoids of *Leptomorphus* are known from the Diapriidae and *Orthocentrus* (Ichneumonidae: Orthocentrinae), both of which appear to lay eggs in the developing larva (Séguy 1940, C. Borkent, unpub. data.).

## Key to adults of *Leptomorphus* species

For confirmation of species identification the genitalia of male specimens should be compared to figures. Future additions or revisions to this key (of taxa, characters or images) can be found at <http://sciaroidea.info/Leptomorphus> Key.

This key does not include eight new species recently described from the Oriental and northern Australasian region by Papp & Ševčík (2011) (see 'Specimens and species not included' section below and Figs. 138–139 for distributions). These species should run to *L. tagbanua* with the exception of *L. alienus*, which would run to *L. tabatius*. Papp & Ševčík (2011) provide a key to these eight species.

1. Vein R<sub>4</sub> present (i.e. Figs. 64, 65) ..... 2
- Vein R<sub>4</sub> absent (i.e. Fig. 57) ..... 8
2. (1) Lateral ocelli no more than their own diameter away from eye margin (Fig. 79); foretarsomere slightly shorter than foretibia; male unknown (USA: California, Fig. 148) ..... *L. perplexus* Borkent, n. sp.
- Lateral ocelli more than their own diameter away from eye margin, grouped closely with median ocellus at vertex (Fig. 78); foretarsomere I longer than foretibia ..... 3
3. (2) Vein R<sub>4</sub> joining Rs or junction of Rs and r-m, forming a triangular cell (Fig. 65); genitalia as in Fig. 112 (southeastern South America, Fig. 142) ..... *L. neivai* Edwards.
- Vein R<sub>4</sub> joining Rs beyond junction of Rs and r-m, forming a quadrilateral cell (i.e. Figs. 60, 64) (Nearctic, Palaearctic) .... 4
4. (3) Apex of antennae (at least apical 5 flagellomeres) white, base black or dark brown (e.g. Figs. 24–27, 31) ..... 5
- Antennal flagellomeres (except, rarely, base of first flagellomere) uniformly coloured (e.g. Figs. 1–7) ..... 6
5. (4) Male with large apical spine-like process on midfemur (Fig. 83); male genitalia with two long sickle-like structures curving dorsally (Fig. 111); colour varying from completely black to mostly yellow with dark brown markings on thorax and abdomen (Figs. 24–27) (Canada, northern and eastern USA, Fig. 144) ..... *L. nebulosus* (Walker).
- Male without large apical spine-like process on midfemur; male genitalia as in Fig. 114 without long sickle-like structures; body completely black/ dark brown (Fig. 31) (Japan and far eastern Russia, Fig. 141) ..... *L. panorpiformis* (Matsumura).
6. (4) Male genitalia with two long sickle-like structures curving dorsally (Figs. 108, 117); scutum with setae on entire surface; colour either yellow with brown head, or dark brown/ black (females with tergite 4 red-orange) with yellow coxae and femora (Figs. 21, 36–37) ..... 7
- Male genitalia without sickle-like structures (Fig. 94); scutum with setae restricted to dorsocentral line and margins; thorax varying from dark to light brown, when light brown scutum with two posteriorly converging dark lines; abdomen varying from light to reddish brown, tergites 1–2 often dark brown (Figs. 4–5) (southern Canada, south in eastern USA to NC, Fig. 147) . . .  
..... *L. bifasciatus* (Say).
7. (6) Completely yellow with brown head (Fig. 21) (eastern North America, Fig. 145) ..... *L. magnificus* (Johannsen).
- Thorax and abdomen completely dark brown/black in male, female identical except with tergite 4 reddish-brown; coxae and femora yellow (Fig. 36–37) (central and eastern North America, Fig. 146) ..... *L. subcaeruleus* (Coquillett).
8. (1) Scutum evenly covered with trichia (Fig. 80) or fine setae; male foretibia with 1–2 dense rows (combs) of short anteroventral bristles (spacing between bristles usually less than bristle length) (Figs. 85, 89–90) ..... 9
- Scutal setae or trichia (if present) restricted to dorsocentral and lateral rows (Fig. 81); male foretibia without dense row of anteroventral bristles (Figs. 87–88) . . . . . 22
9. (8) Scutellum with covering of yellow or white fine trichia and without bristles; Neotropical or Afrotropical ..... 10
- Scutellum without covering of fine trichia, but with brown, small or large, bristles (i.e. with sockets); Nearctic or Palaearctic . . . . . 17
10. (9) Palp segment 5 with thick covering of fine, white setulae and with or without a few setae (Fig. 82); vein sc-r present (i.e. Fig. 57); Neotropical ..... 11
- Palp segment 5 without covering of fine, white setulae, but with a few dark setae; vein sc-r absent (Fig. 58); genitalia as in Fig. 105 (eastern Madagascar, Fig. 134) ..... *L. grjebinei* Matile.
11. (10) Scutellum dark brown (rarely yellow), same colour as scutum and mediotergite ..... 12
- Scutellum light brown, yellow or white, distinctly paler than scutum and mediotergite ..... 15
12. (11) Fore- and midfemora and tibia yellow (Figs. 3, 14) ..... 13
- Fore- and midfemora with brown or dark brown spots basally extending from 1/3 to 3/4 towards apex, fore- and midtibia with apical 1/2 or entirely brown or dark brown (Figs. 6, 15) ..... 14
13. (12) At least abdominal segments 2–4 mostly yellow (Fig. 14); metepisternum yellow or white; male genitalia with gonocoxite arising at base of tergite 9 and almost as long as tergite 9, gonocoxite with long thin process, as long as gonocoxite, arising mediobasally and armed with 4 long apical bristles pointed laterally (Fig. 101) (Panama, northern South America and Amazonia, Fig. 142) ..... *L. fasciculatus* Edwards.
- Abdominal segments 2–4 with some brown or dark brown (Fig. 3); metepisternum completely or partially brown; male genitalia with gonocoxite arising 1/4 of length of tergite 9 towards apex, gonocoxite with scalloped edge apicomediaally and hook-like process laterally (Fig. 92) (southern Brazil, Fig. 142) ..... *L. amorini* Borkent, n. sp.
14. (12) Metepisternum brown; male genitalia yellow or white; tergite 9 rounded basally, tapering to a single, long, point posteriorly that extends beyond cerci (Fig. 95) (Costa Rica, Fig. 143) ..... *L. brandiae* Borkent, n. sp.
- Metepisternum yellow or yellow with brown dorsally; male genitalia partially brown; apex of tergite 9 not extending past cerci; tergite 9 posteriorly with some scalloping on apicolateral corner and with 3 rounded medial processes, with central

- shorter than laterals (Fig. 102) (Peru and Bolivia, Fig. 143) ..... *L. femoratus* Edwards.
15. (11) Abdomen mostly yellow, brown posteriorly (posterior half of tergite 5 and all of T6–7, Fig. 39); medial wing spot (macula) only around junction of R and  $M_{1+2}$ , not reaching anterior or posterior wing margin as a complete band (Fig. 77); halter yellow; antennal flagellomere 6 almost square (slightly longer than wide); male genitalia with tergite 9 tapering posteriorly to a point, with short pointed processes laterally at 2/3 of length towards apex; gonocoxite with long projection on medial margin (Fig. 124); female unknown (Ecuador, Fig. 143) ..... *L. waodani* Borkent, n. sp.
- Abdomen striped brown and yellow (Figs. 10, 12); medial wing spot (macula) strong and running from anterior to posterior wing margin as a complete band, though fainter posteriorly (Figs. 50, 52); halter with base of stem yellow, remainder brown; antennal flagellomere 6 1.5–2X longer than wide; male genitalia not as above ..... 16
16. (15) Male genitalia with tergite 9 tridentate posteriorly (medial process laterally compressed); gonocoxite placed posteriorly on tergite 9, gonostylus small (~1/4 length of gonocoxite) with two short, round, apical projections (Fig. 100) (Costa Rica, Fig. 143) ..... *L. eberhardi* Borkent, n. sp.
- Male genitalia with tergite 9 posterior margin rounded laterally and concave medially, lateral process apex with 5 rows of tightly spaced short blunt brown bristles; gonocoxite placed basally on, and subequal in length to, tergite 9; gonostylus ~2/3 length of gonocoxite with two apical processes, medial one most pronounced and tapering to a point, the lateral 1/2 the length of medial, thin and rod-like (Fig. 98); female unknown (northern Argentina (Tucumán province), Fig. 142) ..... *L. crassipilus* Borkent, n. sp.
17. (9) Abdomen brown or dark brown (Fig. 33) ..... 18
- Abdomen mostly yellow, tergite 7 and often posterior margin of other tergites brown (Figs. 16–17, 41) ..... 19
18. (17) . Scutum and mediotergite dark brown; gonocoxite with lateral process of uniform thickness on apical 2/3 (Fig. 116) (far eastern Palaearctic, Fig. 141) ..... *L. quadrimaculatus* (Matsumura).
- Scutum with posterolateral corners yellow; mediotergite yellow with central brown spot; gonocoxite with lateral process swollen at apex (Fig. 118) (north-western Russia and Finland, Fig. 140) ..... *L. subforcipatus* Zaitzev & Ševčík.
19. (17) Wing with apical spot very pale and restricted to apical 1/4 of cell r1; medial spot absent (Fig. 56); male genitalia with sternite 9 bearing a medial invagination for posterior 2/3 and with 2 dark, apical points (Fig. 104) (New Mexico, Arizona and Northern Mexico, Fig. 148) ..... *L. furcatus* Borkent, n. sp.
- Wing with dark apical and medial spots present (Figs. 55, 76); male genitalia with sternite 9 two dimensional (no ventral points or invaginations, Figs. 103, 123) ..... 20
20. (19) Halter yellow; male genitalia with gonocoxite shorter than tergite 9; sternite 9 not reaching lateral margins of tergite 9 (Fig. 123) (Europe, Fig. 140) ..... *L. walkeri* Curtis.
- Halter with stem yellow and knob brown; male genitalia with gonocoxite at least 1.5X length of tergite 9; sternite 9 wider than long, reaching lateral margins of tergite 9 (Figs. 103, 121) ..... 21
21. (20) Gonocoxite straight for 3/4 of length and then angularly bent medially and swollen beyond bend (Fig. 121) (Azerbaijan, Fig. 140) ..... *L. talyshensis* Zaitzev & Ševčík.
- Gonocoxite smoothly curved along entire length, not swollen at apex (Fig. 103) (Europe, Fig. 140) . . . *L. forcipatus* Landrock.
22. (8) Laterotergite and anepisternum brown; anepimeron at least partially brown (Figs. 7, 40); Oriental or Palaearctic. . . . . 23
- Laterotergite, anepisternum and anepimeron yellow (i.e. Figs. 8, 20); Afrotropical or Nearctic . . . . . 28
23. (22) Katepisternum brown; metepisternum at least partially brown or light brown; wing without apical spot (Figs. 48, 73, 74); segments 3–5 of abdomen noticeably swollen relative to other segments (Figs. 35, 40) . . . . . 24
- Katepisternum and metepisternum yellow; wing with pale brown apical wing spot reaching to wing tip (Figs. 44, 67, 75); abdominal segments all relatively the same thickness (Figs. 2, 30, 38) . . . . . 26
24. (23) Scutum dark brown . . . . . 25
- Scutum dark brown with small yellow spots on posterolateral corners; genitalia with tergite 9 bearing two long lateral processes posteriorly, so that tergite 9 is ~2X as long as wide (Fig. 120); female unknown (Sulawesi, Fig. 137) . . . . . *L. tabatius* Borkent, n. sp.
25. (24) Metepisternum brown; antennal flagellomere 1 with base yellow, remainder brown; vein sc-r joining R within its own length of origin of Rs; known only from female holotype (Fig. 7) (northern Borneo, Fig. 137) . . . . . *L. chaseni* Edwards
- Metepisternum brown anteriorly, yellow posteriorly; antennal flagellomere 1 yellow; vein sc-r joining R at ~2X its own length from origin of Rs; genitalia wider than long (Fig. 119); female unknown (Philippines, Fig. 137) . . *L. tagbanua* Borkent, n. sp.
26. (23) Scutellum yellow; pale medial wing spot absent (Figs. 67, 75); genitalia with gonostylus bearing two apical projections (Fig. 122) . . . . . 27
- Scutellum dark brown; pale medial wing spot present (Fig. 44); genitalia with gonostylus a single blunt taper (Fig. 93); female unknown (Japan, Fig. 141) . . . . . *L. babai* Sasakawa.
27. (26) Vein sc-r present (though faint in one specimen); genitalia as in Fig. 122 (Peninsular Malaysia, Fig. 137) . . . . . *L. titiwangsensis* Borkent, n. sp.
- Vein sc-r absent or present; genitalia presumably different from above (male unknown) (eastern India and Nepal, Fig. 137) . . . . . *L. ornatus* Brunetti.
28. (22) Scutellum brown or dark brown . . . . . 29
- Scutellum yellow . . . . . 32
29. (28) Halter with most of stem and knob dark brown; gonostylus with two large lobes (Figs. 99, 106, 113), Afrotropical; *females not currently distinguishable beyond this point* . . . . . 30
- Halter mostly yellow with only tip of knob brown; gonostylus with single large, hook-tipped lobe (Fig. 107) Nearctic (Fig. 149) . . . . . *L. hyalinus* Coquillett.
30. (29) Genitalia with tergite 9 gradually tapering on apical quarter, apex bearing medial spur and often a secondary small bump



- or point, also with strong, ventrally-produced, thin ridge running across ventral surface at approximately 2/3 the distance towards apex, creating a semicircular dorsal margin when viewed caudally (Fig. 113) (central-western Africa, Fig. 136) . . . . . *L. obscurus* Matile.
- Genitalia with tergite 9 ending in more or less blunt apex laterally and with or without small spine-like projection on medial corner (e.g. Figs. 99, 106) . . . . . 31
31. (30) Genitalia with posterolateral projection of tergite 9 either square or with slightly acute angle on medial corner; gonostylus with shortest lobe rounded (Fig. 106); female unknown (Gabon and Central African Republic, Fig. 135) . . . *L. gracilis* Matile.
- Genitalia with posterolateral projection of tergite 9 bearing distinct thin point on medial corner; gonostylus with shortest lobe gradually tapering to thick point (Fig. 99) (central western Africa, Fig. 136) . . . . . *L. crosskeyi* Matile.
32. (28) Abdomen mostly yellow with at most brown bands posteriorly on tergites 3–6, tergite 7 brown or yellow (Figs. 22, 23, 34) . . . . . 33
- Abdomen yellow with varying amounts of brown on tergites 3–5, tergite 6 brown, tergite 7 yellow (Figs. 1, 8, 9), *females not currently distinguishable beyond this point* . . . . . 35
33. (32) Scutum mostly yellow with prealar brown spots (sometimes united as a band) or brown Y-shaped medial marking; abdomen with tergite 7 yellow (Figs. 22, 34) . . . . . 34
- Scutum mostly dark brown with yellow restricted to anterior and lateral margins; abdomen with tergite 7 brown (Fig. 23); genitalia with tergite 9 bearing ventrally-directed fold along most of posterior margin and small point on apicomedial corner (Fig. 109); female unknown (South Africa, Fig. 134) . . . . . *L. mandelai* Borkent, n. sp.
34. (33) Scutum with brown Y-shaped medial marking and prealar brown spots (Fig. 81); genitalia with tergite 9 ending in square lobe bearing small medial point; sternite 9 more or less oval shaped (Fig. 115) (Tanzania, Fig. 134) . . . . . *L. stigmatus* Borkent, n. sp.
- Scutum with prealar brown spots or band only (Fig. 22); genitalia with lateral lobes of tergal evagination gradually tapering to a medial point; sternite 9 a posteriorly directed triangle (Fig. 110) (Guinea and Nigeria, Fig. 136) . . . . . *L. medleri* Matile.
35. (32) Tergite 9 with basal 2/3 of lateral margins parallel; ventrally directed process at base of posterior lobe of tergite 9 forked into two points at apex; apex of posterior lobe blunt and slightly bulbous (Fig. 91) (central and western Africa, Fig. 135) . . . . . *L. aliciae* Matile.
- Tergite 9 with basal 2/3 of lateral margins bulbous tapering posteriorly; ventrally directed process at base of posterior lobe of tergite 9 a single point. (Figs. 96, 97) . . . . . 36
36. (35) Concavity of posterior margin of tergite 9 longer in diameter than width of sternite 9; posterior lobes of tergite 9 tapering to blunt points (Fig. 97) (Ivory Coast and Ghana, Fig. 135) . . . . . *L. couturieri* Matile.
- Concavity of posterior margin of tergite 9 smaller in diameter than width of sternite 9; posterior lobes of tergite 9 tapering first to create a lateral corner and then tapering to a point on medial margin (Fig. 96) (Republic of the Congo and Democratic Republic of the Congo, Fig. 135) . . . . . *L. carnevalei* Matile.

## Species descriptions

### 1. *Leptomorphus aliciae* Matile

(Figures 1, 42, 91, 135, 150, 153)

*Leptomorphus (Gymnoscutum) aliciae* Matile, 1977: 148.

**References:** Crosskey 1980: 1221 (catalogue appendix); Matile 1997: 145, 146, 149, 150 (figures, new records, morphological variation, key).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with following combination of characters: mostly yellow abdomen though tergite 6 brown; male tergite 9 with basal 2/3 of lateral margins parallel, ventrally directed process at base of posterior lobe of tergite 9 forked into two points at apex, apex of posterior tergal evaginations blunt and slightly bulbous (Fig. 91).

This species can most easily be confused with other Afrotropical species with a completely brown tergite 6 (*L. carnevalei*, *L. couturieri*, Figs 1, 8, 9). It can be distinguished from these species based solely on the male genitalia (Fig. 91) which has the basal 2/3 with margins parallel and the apex of the posterior lobes bulbous rather than pointed (Figs 96, 97).

**DESCRIPTION:** *Male.* (Fig. 1) **Head:** yellow, circular in anterior view. Antenna brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 2 large bristles, several setae on apicodorsal margin, a number of fine setae on apicoventral margin; flagellomere 1 brown; flagellomere 6 1.5X as long as broad. Clypeus yellow, dorsoventrally elongate oval; bristles on clypeus yellow, 4–6 strong bristles on ventral margin directed ventrally, a number of bristles on remainder, ventral 3/4 directed medioventrally, remainder directed laterally, clypeus 2X as long as face. Face yellow; shape a just longer than wide

triangle, with few bristles ventrolaterally. Frons yellow; with few bristles medioventrally, frontal furrow running 1/4 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus with segments 1–2 yellow, 3–5 light brown; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length of segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli with median slightly in front of laterals, space between ocelli less than diameter of laterals, lateral ocelli 2.5X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue-green specks. **Thorax:** Length  $1.18 \pm 0.15$  mm (1.07–1.31 mm, n = 9). Dark brown dorsally, yellow laterally. Scutum dark brown/black with blue-green specks, yellow spot anteromedially and on each posterolateral corner; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 4–8 large bristles and many small bristles. Prescutum yellow. Mediotergite light brown to dark brown, darker anteriorly with 6–12 bristles on posterolateral corners, anteromedial patch of small bristles. Laterotergite yellow; anterior margin of laterotergite not reaching katepisternum. Anepimeron yellow. Anepisternum yellow. Katepisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with light brown and yellow trichia respectively. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter stem yellow, knob light brown. **Legs:** principally yellow; hind femur light brown at very apex; extreme anteroapical corner dark brown on all femora; tarsi brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 2/3 of its length, placed basally, shortest midtibial spur subequal to length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 5X apical thickness of hind tibia. Foreleg first tarsomere 1.6X length of foretibia. **Wing** (Fig. 42): Length  $5.2 \pm 0.6$  mm (4.8–5.7 mm, n = 8). Hyaline; apical macula absent or, if present, very light, restricted to apical 1/4 of cell r; medial macula absent. Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining R at 2X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins fading before wing margin. M<sub>4</sub>-CuA fork arising just apical of origin of r-m. A<sub>2</sub> faintly present as crease. **Abdomen:** Tergites 1 and 7 yellow, T2 yellow with posterodorsal triangular brown spot, T3–5 anterior yellow, posterior brown, T6 brown. Tergite 8 smaller than all other abdominal sclerites, with ~15 bristles on each apicolateral corner. **Genitalia** (Fig. 91): yellow. Sternite 9 sclerotized, rounded triangle, 1/3 the width of the genitalia at widest point, overlapping medial margin of gonocoxite. Tergite 9 longer than wide, with basal 2/3 of lateral margins parallel then tapering into two lobes with medial U-shaped indentation, apex of posterior lobes blunt and slightly bulbous, a ventrally extending thin process at base of posterior lobe forked into two points at apex. Gonocoxite placed basally on T9, medial margin reaching medial line, bearing gonostylus on apical 1/3. Gonostylus with two lobes, dorsal lobe shortest and broad, partially hidden behind ventral lobe in ventral view (as in figure), ventral lobe 4X length, but half the width, of dorsal, gonocoxite III fused to dorsolateral margin. Aedeagus 2/3 length of gonocoxite, tapering towards apex, apodemes 1/4 total length. Parameres a simple taper, apodemes ~2X length of parameres.

*Female.* As for male, except as follows. **Thorax:** Length 1.46mm (max: 1.72mm, min: 1.23mm, n = 4). **Wing:** Length 6.4mm (max: 7.5mm, min: 5.3mm, n = 4). **Abdomen:** Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Ivory Coast, Ghana, Nigeria, Cameroon, Central African Republic, and Uganda (Fig. 135), 45–725 masl.

**DISCUSSION:** As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Gymnoscutum* and placed solely in *Leptomorphus*. The holotype for this specimen was incorrectly labelled (see below) with an unrecognized subgenus and different species name. We assume that this label represents Matile's (1977) original thoughts on names for the subgenus and this species (the species was named after Alice Bruneau de Miré) and that he neglected to remove/change the label after finalizing the names.

**MATERIAL EXAMINED:** *Holotype:* adult male, pinned on double mount minuten, genitalia in glass vial on pin, labelled “[Blue paper label] CAMEROUN/ Yaoundé-N’Kolbisson/ p. lum. x.XII.1966/ ----- [‘L. Matile rec.’ crossed out]/ Ph. Bruneau de Miré; [Red label] HOLOTYPE; Leptomorphus/ (Paraleptomorphus)/ mirei n. sp. ♂ht/ L. Matile det. 1974; HOLOTYPE ♂/ Leptomorphus aliciae/ Matile/ Det. C.J. Borkent, 2012” [MNHN].

*Paratypes:* CENTRAL AFRICAN REPUBLIC, Lobaye, M’bale gallery forest, 15.ix.1970, L. Matile (1♀, MNHN); UGANDA, Bwamba, viii.1948, Medical Dept Kenya [coll.], (1♀, BMNH).

*Other material:* GHANA, Western Region, Ankasa game prod. Reserve, 6–12.xii.1993, J. Kjærendsen, T. Andersen. (1♂, ZMUN); Boti Falls, 28.x–4.xi.1994. (2♂, ZMUN); Kakum N.P., 31.x–8.xi.1994. (3♂, ZMUN); IVORY COAST, Taï, 9.v.1980, G. Couturier. (1♂, MNHN); NIGERIA, Ibadan, 25.viii.1962, D.C. Eidt. (1♀, CNC); Illaro Forest, 3.iii.1974, M.A. Cornes. (1♀, MNHN); Sapoba, 11.ix.1962, D.C. Eidt. (1♂, CNC).

## 2. *Leptomorphus amorimi* Borkent, new species

(Figures 3, 43, 92, 142, 150, 155)

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: Scutum and scutellum evenly covered with fine trichia; male foretibia with a dense row (comb) of short anteroventral bristles; palp segment 5 with thick covering of fine, white, setulae; male genitalia with gonocoxite arising ¼ of length of tergite 9 towards apex, gonocoxite with scalloped edge apicomediaally, hook-like process laterally and short basomedial gonocoxal lobe bearing several long setae (Fig. 92).

This species can be distinguished from the other Neotropical species without R<sub>4</sub> by the yellow tibia, brown metepisternum (Fig. 3) and the shape of the gonocoxite (Fig. 92).

**DESCRIPTION:** *Male. Head:* brown spot medially from ocelli to antennal base, remainder yellow, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape yellow, with brown setae in double row at apex extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 2 large bristles, few setae on apicodorsal margin, patch of fine setae apicoventrally; flagellomere 1 with tapered base brown remainder dark brown; flagellomere 6 1.2X as long as broad. Clypeus yellow, slightly laterally compressed oval; bristles on clypeus light brown, strong bristles on ventral half, smaller bristles on entire surface, all directed ventrally or medioventrally, clypeus 2.5X as long as face. Face yellow; shape a slightly wider than tall triangle, bare. Frons dark brown; bare, frontal furrow running 1/2 distance from dorsal margin towards ventral margin, frontal cleft more than 1X diameter of median ocellus anterior of median ocellus. Palpus with segments 1–4 yellow, segment 5 white; segment 1 small but visible below eye, segments increasing in length, segment 5 2X length and 1.5X width of segment 4 with even width from base to apex and covered in fine white setulae, segment 3 with very small lateral patch of fine setae encircled by dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Three ocelli in straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.97 mm (n = 1). Dark brown with yellow lateral spots. Scutum dark brown/black with blue-green specks, pair of small yellow anterolateral spots; surface of scutum covered with trichia; acrostichal setae absent; single dorsocentral seta present anteriorly; two thirds row of lateral setae present; patch of setae on scutum at wing base small. Scutellum dark brown with covering of fine trichia; bristles absent. Prescutum brown. Mediotergite dark brown with 4 bristles on posterolateral corners, and covering of appressed trichia. Laterotergite brown, with covering of appressed trichia; anterior margin of laterotergite abutting katapisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katapisternum brown with posterodorsal corner yellow. Antepnotum and proepisternum brown. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow with light brown dorsal line. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** principally yellow; fore- and midcoxa with anterior surface brown, hind coxa dark brown except for posterior surface; mid- and hind trochanter light brown; hind femur with basal 1/3 dark brown; extreme anteroapical corner yellow on forefemur, on other femora dark brown; midfemur without apical spine-like process. Tibia with covering of yellow macrotrichia, foretibia with strong, double, comb of short setae along length of anteroventral surface, tibial spurs yellow,

foretibial spur length 1.7X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 2/3 of its length, placed basally, shortest midtibial spur 0.9X length of longest, longest midtibial spur 4X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3.4X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 43): Length 7.5 mm (n = 1). Hyaline; apical macula dark brown, running from anterior to posterior wing margin, beginning halfway along R<sub>5</sub> but not reaching wing tip; medial macula extending from R<sub>1</sub> to posterior wing margin (fainter on posterior third). Macrotrichia in all cells, though absent from posterobasal margin of cell a, and very sparse in basal cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end before origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> slightly concave for entire length. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins thinning towards wing margin. M<sub>4</sub>-CuA fork arising before origin of r-m. A<sub>2</sub> faintly present as crease. **Abdomen:** Tergites principally brown to dark brown, T2–5 with parallel yellow lines, T3–5 also with anterior yellow band. Tergite 8 smaller than all other abdominal sclerites, with 1 bristle on each apicolateral corner. **Genitalia** (Fig. 92): brown. Sternite 9 sclerotized anteriorly pointing isocetes triangle with posteromedial indentation, 1/5 the width of the genitalia, not reaching gonocoxal margin. Tergite 9 subcircular with short apicolateral lobe on each side bearing several points and medial U-shaped indentation. Gonocoxite placed 1/4 way toward apex of T9 with scalloped edge apicomediaally, hook like process laterally and gonocoxal lobe emerging mediobasally and bearing several long setae aically, medial margin not reaching medial line, bearing gonostylus on apical 1/3. Gonostylus a single broad-based lobe tapering to a point apically with small setae basally, gonocoxite III fused to dorsolateral margin. Aedeagus equal in length to gonocoxite, tapering to middle and then slightly bulbous apically, apodemes 1/3 total length. Parameres a slightly curved taper, 1.5X length of apodemes, apodemes with a basal hook-shaped spine pointing dorsally.

*Female.* (Fig. 3) As for male, except as follows. **Thorax:** Length 2.01 mm (n = 1). Metepisternum brown. **Wing:** Length 8.3 mm (n = 1). **Legs:** foretibia without strong, double, comb of short setae along length of anteroventral surface. **Abdomen:** Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Southern Brazil (Fig. 142), 25–825 masl.

**ETYMOLOGY:** This species is named for Dr. Dalton de Souza Amorim, in thanks for his help in providing specimens and information, and for his encouragement and many discussions during this study.

**MATERIAL EXAMINED:** *Holotype:* here designated, adult male, pinned with genitalia in plastic vial on pin, labelled “Neudorf, [26.368°S, 48.985°W] Sta/ Catarina/ Brazil, 10–XI; F. Schade/ collector; HOLOTYPE ♂/ *Leptomorphus amorimi*/ Borkent, new species / Det. C.J. Borkent 2012” [MCZ]

*Paratype:* BRAZIL, Santa Catarina, Nova Teutonia, v.1964, F. Plaumann. (1 ♀, CNC).

### 3. *Leptomorphus babai* Sasakawa

(Figures 2, 44, 93, 141, 150, 152)

*Leptomorphus babai* Sasakawa, 1961: 187.

*Leptomorphus (Leptomorphus) babai:* Matile, 1977: 144.

**References:** Matile 1977: 144 (subgeneric placement); Matile, 1988: 234 (catalogue); Matsumoto and Sasakawa, 2006: 16 (type specimens).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite and anepisternum brown; wing with pale brown apical wing spot reaching to wing tip, pale medial wing spot present (Fig. 44); male genitalia with gonostylus a single blunt taper (Fig. 93).

This species can be distinguished from all other Palearctic and Oriental species by the striped abdomen (Fig. 2) and/or the brown scutellum.

**DESCRIPTION:** *Male.* (Fig. 2) **Head:** brown, sometimes with posterior margin yellow, circular in anterior view. Antenna with basal 2 flagellomeres yellow/light brown, brown apically; scape yellow, with light brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 1–2 large bristles, few setae on



apicodorsal margin, none ventrally; flagellomere 1 with tapered base light brown remainder light brown; flagellomere 6 1.0X as long as broad. Clypeus yellow, dorsoventrally elongate oval; bristles on clypeus yellow, 4–6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow; shape a just longer than wide triangle, bare. Frons light brown to brown; bare, frontal furrow running 3/4 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 subequal in length to segment 4 with even width from base to apex, segment 3 with apicolateral patch of fine yellow setae weakly encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput brown on anterior 1/2–2/3, remainder yellow with appressed, anteriorly directed setae. Ocelli with median slightly in front of laterals, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length 1.2 mm (1.19–1.27 mm, n = 2). Mostly brown, with anterolateral area yellow. Scutum dark brown with blue-green specks; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; double row of lateral setae present; patch of setae on scutum at wing base present. Scutellum dark brown; with 6 large bristles and many small bristles. Prescutum brown. Mediotergite brown with 8–10 bristles on posterolateral corners, absent. Laterotergite brown; anterior margin of laterotergite not reaching katepisternum. Anepimeron brown. Anepisternum brown. Katepisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter stem light brown, knob dark brown. **Legs:** principally yellow; hind femur with basal 1/3 and apex light brown; extreme anteroapical corner dark brown on all femora. Midfemur without apical spine-like process. Tibia with covering of yellow macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs light brown, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 3/4 of its length, placed basally, shortest midtibial spur 0.75X length of longest, longest midtibial spur 4.5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 5X apical thickness of hind tibia. Foreleg first tarsomere 1.5–1.6X length of foretibia. **Wing** (Fig. 44): Length 5.3 mm (5.1–5.4 mm, n = 2). Hyaline; apical macula light, reaching wing tip, extending faintly along posterior wing margin into apex of cell  $cua_1$ , cup, not joining with medial macula; medial macula light, extending from  $R_1$  to just beyond fork of  $M_1$  and  $M_2$ . Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R at 2X its own length prior to origin of  $R_s$ .  $R_4$  absent.  $R_5$  straight, slight posterior turn near tip.  $M_1$  reaching apex before  $R_5$ , apices of M veins thinning towards wing margin.  $M_4$ -CuA fork arising at same level as r-m.  $A_2$  absent. **Abdomen:** Tergites principally dark brown, T2–6 with anterolateral yellow spots. Tergite 8 smaller than all other abdominal sclerites and ~15 bristles laterally, centre bare. **Genitalia** (Fig. 93): yellow. Sternite 9 not clearly visible. Tergite 9 longer than wide, rounded margins tapering into two short pointed lobes and shallow medial indentation. Gonocoxite placed basally on T9, medial margins almost touching near base due to triangular projection, a ventromedial lobe covering base of gonostylus, bearing gonostylus halfway to apex. Gonostylus a single broad-based lobe tapering towards rounded apex, gonocoxite III fused to dorsolateral margin. Aedeagus 2/3 length of gonocoxite, slightly tapering towards apex, apodemes 1/5 total length with small dorsally facing hook basally. Parameres a short, wide taper, apodemes ~4X length of parameres.

*Female.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Japan (Fig. 141), 40 masl.

**DISCUSSION:** As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Leptomorphus* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult male, pointed, with wing in separate glass and paper mount, all on same pin, genitalia missing, labelled “[translucent paper] Kurokawa/ Echigo, Japan/ 2.VII.1955/ Col. Kintaro; [pink label] HOLOTYPE ♂/ KPU 0163/ Leptomorphus/ babai/ SASAKAWA” [OMNH].

*Paratype:* labelled as for holotype except 7.VI.1955 (1 ♂, OMNH).

**4. *Leptomorphus bifasciatus* (Say)**

(Figures 4, 5, 45, 94, 147, 150, 154)

*Sciophila bifasciata* Say, 1824: 363.*Diomonus bifasciatus*: Johannsen, 1909: 45.*Leptomorphus bifasciatus*: Procter, 1946: 359.*Leptomorphus (Diomonus) bifasciatus*: Matile, 1977: 146.

**References** : Wiedemann 1828: 62 (re-description); Le Conte 1859: 246 (reprint of original description); Osten Sacken 1878: 10 (catalogue, with note from Loew as to possible placement in *Empheria*); Kertész 1902: 57 (catalogue); Aldrich 1905: 140 (catalogue); Johannsen 1910: 154 (description, key reference, NH); Johnson 1925: 80 (MA, ME, NH, VT); Procter 1938: 310 (ME), 1946: 359 (ME), Shaw & Fisher 1952: 192 (key reference, MA, NH); Laffoon 1965: 223 (catalogue citation), Eberhard 1970 (natural history and behaviour), 1986 (correction to 1970); Matile 1977: 146 (subgeneric placement); Santini 1985: 239, 243–4 (comparison to *L. walkeri*); Poole and Gentili, 1996: 194 (catalogue).

**DIAGNOSIS**: The only extant species of *Leptomorphus* with the following combination of characters: scutum with setae restricted to dorsocentral line and margins;  $R_4$  present and forming a quadrilateral cell; male genitalia with gonocoxites placed apically on tergite 9 and folded dorsally at apex (Fig. 94).

This species can be easily differentiated from other Nearctic species with  $R_4$  by the brown coxae and brown antennae (Fig. 4).

**DESCRIPTION**: *Male*. (Fig. 5) **Head**: light-dark brown, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape light brown, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel brown, with 2–3 large bristles, 2–3 setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base brown remainder brown; flagellomere 6 2.0X as long as broad. Clypeus brown, circular, strongly protruding; bristles on clypeus brown, both strong, smaller bristles on entire surface, all directed ventrally, clypeus 1.5X as long as face. Face yellow to light brown; shape a slightly wider than tall triangle, covered with many strong bristles. Frons brown; bare, frontal furrow running 1/3 distance from dorsal margin towards ventral margin, frontal cleft running to lateral ocellus. Palpus with segments 2–3 light brown remainder yellow; segment 1 small but visible below eye, segments increasing in length, segment 5 1.5X length of segment 4 with even width from base to apex, segment 3 appears to have large lateral patch of fine yellow setae not clearly delimited. Labellum light brown. Eye with a number (in ~1/4 of the ommatidial junctions) of long inter-ommatidial setulae scattered on posterior half. Occiput light-dark brown with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli 1–1.5X diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax**: Length  $2.12 \pm 0.38$  mm (1.89–2.38 mm,  $n = 10$ ). Yellow dorsally with lateral and dorsocentral brown lines, laterally brown, sometimes almost completely brown. Scutum ranging from yellow with posteriorly pointing V of brown and lateral and posterior margins brown, to dark brown with small anteromedial yellow spot; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as complete multiple lines of setae; multiple rows of lateral setae present; patch of setae on scutum at wing base small. Scutellum light to dark brown, darker anteriorly; with 8–12 large bristles and many small bristles. Prescutum brown. Mediotergite brown to dark brown with 8–12 bristles on posterolateral corners, absent. Laterotergite brown; anterior margin of laterotergite not reaching katepisternum. Anepimeron light brown to brown. Anepisternum light brown to brown. Katepisternum brown. Antepnotum and proepisternum light brown to brown. Margin of anterior and posterior spiracles yellow with light brown trichia. Metepisternum dark brown. Anapleural suture straight and clear. Halter stem yellow, knob light to dark brown. **Legs**: Principally yellow to light brown; hind coxa at least 1/2 brown, in northern specimens remaining coxae brown as well as central 4/5 of hind femur and sometimes centre of midfemur; extreme anteroapical corner dark brown on all femora. Midfemur with apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs yellow, foretibial spur length 1.75X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 3/4 of its length, placed basally, shortest midtibial spur 0.7X length of longest, longest midtibial spur 3.5X apical thickness of midtibia, shortest hind tibial spur 0.85X length of longest, longest hind tibial spur 3.5X apical thickness of hind tibia. Foreleg first tarsomere 1.4X length of foretibia. **Wing** (Fig. 45): Length  $8.1 \pm 1.4$  mm (7.1–9.6 mm,  $n = 10$ ). Hyaline; apical

macula dark brown running from anterior to posterior wing margin, beginning halfway along  $R_5$ , but fading towards apex and posterior margin; medial macula extending from Sc to stem of  $M_{1+2}$  with some light brown in cell cua. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long and short for margin of alula, remainder short. Calypter bare. Vein sc-r present, apical end joining R within its own length before or after origin of  $R_s$ .  $R_4$  present.  $R_5$  slightly concave for entire length.  $M_1$  reaching apex before  $R_5$ , apices of M veins clearly reaching wing margin.  $M_4$ -CuA fork arising well before origin of r-m.  $A_2$  faintly present as crease. **Abdomen:** Tergites principally reddish orange, T1 brown, T2 with anteromedial brown spot. Tergite 8 smaller than all other abdominal sclerites and covered in small bristles. **Genitalia** (Fig. 94): orangish yellow. Sternite 9 lightly sclerotized, posteriorly directed triangle covering most of the ventral surface (as wide as genitalia). Tergite 9 subcircular except for gonocoxal indentation and slight apicomedial indentation. Gonocoxite placed apically on T9, apical margin flat with slight dorsally directed fold, medial margin not reaching medial line, bearing gonostylus basally. Gonostylus a single lobe tapering towards apex and bearing several setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus equal in length to T9, tapering towards apex and then swollen and sclerotized at apex, with two short subapicodorsal lobes, apodemes ~1/4 total length. Parameres as long as wide with single lobe slightly swollen and curving laterally with apical surface covered in small spines, apodemes 1/4 length of parameres and strongly united with gonocoxal apodemes.

**Female.** (Fig. 4) As for male, except as follows. **Thorax:** Length  $1.89 \pm 0.39$  mm (1.48–2.13 mm,  $n = 10$ ). **Wing:** Length  $7.4 \pm 1.1$  mm (6.2–8.1 mm,  $n = 10$ ). **Legs:** Midfemur without apical spine-like process. **Abdomen:** Cercus yellow.

**Immatures.** Larva and pupa described by Eberhard (1970). Egg unknown.

**BIOLOGY:** The biology of the immatures and adults is detailed by Eberhard (1970) and is similar to that of *L. subcaeruleus*.

**DISTRIBUTION:** British Columbia east to Maine and south to North Carolina (Fig. 147), 25–1800 masl.

**DISCUSSION:** The original type specimen was collected on Major Long's second expedition (Say 1824), which travelled from Philadelphia through the 'North-west Territory' of the USA (southwest of the Great Lakes) to Lake Winnipeg and then eastward through Lake Superior and Lake Huron. In the description the only distribution data given is that this species 'inhabits North-west Territory' (Say 1824: 363). Unfortunately the collections of Thomas Say were destroyed, with the exception of some syntypes that were sent to colleagues, with some Diptera being sent to Wiedemann (Evenhuis 2006). Wiedemann (1828: 62) described specimens of *L. bifasciata* sent to him by Say, but the depository of these specimens at the end is stated as "Im Museum zu Philadelphia", thus Wiedemann did not keep any but returned them to Philadelphia (Wiedemann, 1828: 62). Given the similarity in general habitus and coloration of *L. bifasciatus* to other *Leptomorphus* species in the region (e.g. *L. subcaeruleus*, *L. nebulosus*), a neotype is designated to fix the identity of the species.

As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Diomonus* and placed solely in *Leptomorphus*.

**MATERIAL EXAMINED:** *Neotype:* (Fig. 5) here designated, adult male, pinned, labelled "CAN:QC: Mont St Hilaire/ Stand 4, flight-intercept trap/ 45°32.22'N, 73°08.91'W/ 1–8.vii.2008, V. Levesque; NEOTYPE ♂/ *Leptomorphus bifasciatus* / (Say) / Det. C.J. Borkent, 2012" [LEM].

*Other material:* CANADA, BC, Kinbasket Reservoir, Bush Arm, 10–11.viii.2009, Cooper, Beauchesne and Associates Ltd. (1♂, RBCM); ON, Coniston, 27.vii, E.S. Parish. (1♂, USNM); Foresters Falls, 14.viii.1991, J.R. Vockeroth. (1♂, CNC); Lake Abitibi, 4.viii.1925, N.K. Bigelow. (1♂, CNC); 7.viii.1925. (1♂, CNC); Tobermory, Dunk's Bay, 26.viii.1996, S.A. Marshall. (1♂, DEBU); Bruce Co., William Henry Marsh, 31.viii.1999, S.A. Marshall. (1♀, DEBU); Carleton Co., 8km S Richmond, 30.viii.2008, D.M. Wood. (1♂, LEM); QC, 2.3km SSW Rapide-Danseur, 29.vi–28.vii.2007, A. Hibbert. (1♂, LEM); 30.vi–29.vii.2007. (2♂, 1♀, LEM); Lake Duparquet Res. and Train. For., 12.vii–1.viii.2006, A. Hibbert. (1♀, LEM); Mont St-Bruno, 24.vi–1.vii.2008, V. Levesque. (1♂, LEM); Mont St-Hilaire, 18–24.ix.2001, E. Fast. (1♂, LEM); 3.viii.2007, C.J. Borkent. (1♂, LEM); 1–8.vii.2008, V. Levesque. (1♂, LEM); 23–30.vi.2008. (1♂, LEM); Old Chelsea, 13.ix.1956, J.R. Vockeroth. (1♂, CNC); Rougemont, 14–21.vii.2008, V. Levesque. (1♂, LEM); 21–28.vii.2008. (2♂, 1♀, LEM); 23–30.vi.2008. (1♂, LEM); 30.vi–7.vii.2008. (1♂, LEM); SK, Belanger, Osten Sacken. (1♂, MCZ); USA, MA, Chester, 5.viii.1911. (1♂, MCZ); ME, York Co., West Lebanon, 28.viii–3.ix.1990, D.W. Barry. (1♂, UNHC); NC, Mason Co., Highlands, 20.vi.1957, J.R. Vockeroth. (1♂,

CNC); 21.vi.1957, J.R. Vockerth. (1♂, CNC); 24.vi.1958, J.L. Laffoon. (1♂, ISUI); NH, Dolly Copp, White Mtns., 13.vii.1931, A.L. Melander. (1♀, USNM); Mt. Washington, A.T. Slosson. (1♂, CUIC, 1♂, USNM); Carr. Co, 1mi. N Wonalancet, E Fk. Spring Brk., 18–23.vii.1985, D.S. Chandler. (1♂, UNHC); 24–30.vii.1985. (1♂, UNHC); 18.ix–1.x.1985. (1♂, UNHC); The Bowl, 2.5mi. NW Wonalancet, 2–10.viii.1984, D.S. Chandler. (1♀, UNHC); 20–26.vii.1984. (2♂, UNHC); 28.vi–4.vii.1984. (1♂, UNHC); 31.vii–6.viii.1985. (1♂, UNHC); Coos Co., 1mi. NE East Inlet Dam, 22.viii–12.ix.1986, D.S. Chandler. (1♂, UNHC); 10–24.vii.1986. (2♂, UNHC); 25.vi–9.vii.1986. (2♂, UNHC); 13–26.ix.1986. (1♀, UNHC); Norton Pool, 3mi. NE East Inlet Dam, 8–21.viii.1986, D.S. Chandler. (1♂, UNHC); 27.ix–17.x.1986. (1♀, UNHC); Straf Co., 1mi. SW Durham, 13.vii.1991, W.J. Morse. (1♀, UNHC); 4mi. W Durham, 23–26.viii.1982, R.M. Reeves. (2♂, UNHC); 13–15.vii.1982. (1♂, UNHC); Spruce Hole, 3mi. SW Durham, 7–20.viii.1987, D.S. Chandler. (1♂, UNHC); NY, Adirondacks, Avalanche Trl, 30.vii.1929, A.L. Melander. (1♀, ANSP); Albany Co., Huyck Preserve, Rensselaerville, 4.vii.1968, W.G., M.J. Eberhard. (1♂, 1♀, MCZ); Greene Co., viii, (1♂, CMNH); Hamilton Co., vic. Jockeybush Outlet, 5.viii.1961, J.L. Laffoon. (1♀, ISUI); PA, Centre Co., Bear Meadows, 6.ix.1979, P.H. Adler. (1♀, USNM); McKean Co, 4.9km S Ludlow, Pigeon Run, 4.viii.1994, M.J. Ricke. (1♂, CMNH); TN, Burrville, 14.vii.1953, Benesh. (1♂, MNHN); VA, Giles Co., Clover Hollow, 9.viii.1967, Ento. Class. (1♂, SEMC); Mt. Lake Biol. Sta., 26.vi.1975, G.W. Byers. (1♀, SEMC); VT, Brattleboro, 1909, H. Kahl. (1♂, CMNH); Morrison, White Mtns. (3♂, USNM).

### 5. *Leptomorphus brandiae* Borkent, new species

(Figures 6, 46, 82, 95, 127, 143, 150, 155)

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: scutum and scutellum evenly covered with fine trichia; male foretibia with a dense row (comb) of short anteroventral bristles; palp segment 5 with thick covering of fine, white, setulae; male genitalia with tergite 9 rounded basally, tapering to a single, long, point posteriorly that extends beyond cerci, gonocoxite without gonocoxal lobe (Fig. 95).

This species can be distinguished from other Neotropical species without  $R_4$  by the distinctive pointed tergite 9 of the large male genitalia (Fig. 95). It also has the darkest legs of any of the species (e.g. hind femur 2/3 dark, Fig. 6).

**DESCRIPTION:** *Male.* (Fig. 6) **Head:** light brown-brown, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 1 large bristle, several setae on apicodorsal margin, patch of fine setae apicoventrally; flagellomere 1 with tapered base yellow, remainder dark brown; flagellomere 6 1.1X as long as broad. Clypeus light brown, slightly laterally compressed oval; bristles on clypeus brown, 6–8 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face light brown; shape a slightly wider than tall triangle, with few bristles ventrolaterally. Frons brown; bare, frontal furrow running 1/10–1/4 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus with segments 1–4 yellow, segment 5 white (Fig. 82); segment 1 small but visible below eye, segments increasing in length, segment 5 2X length and 1.5X width of segment 4 with even width from base to apex and covered in fine white setulae, segment 3 with very small lateral patch of fine setae encircled by dark setae. Labellum light brown. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput brown with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.31 mm ( $n = 1$ ). Dark brown with yellow lateral spots. Scutum dark brown/black with blue-green specks, pair of small yellow anterolateral spots; surface of scutum covered with trichia; acrostichal setae absent; single dorsocentral seta present anteriorly; two thirds row of lateral setae present; patch of setae on scutum at wing base small. Scutellum dark brown with covering of fine trichia; bristles absent. Prescutum yellow. Mediotergite dark brown with 6 bristles on posterolateral corners, and covering of appressed trichia. Laterotergite brown, with covering of appressed trichia; anterior margin of laterotergite abutting katapisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum dark brown. Katapisternum brown with dorsal third yellow. Anteprepronotum and proepisternum brown. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum brown. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion



and knob dark brown. **Legs:** principally dark brown; coxae white except apical margin; fore- and midfemur with apical 1/3–1/2 yellow, hind femur with yellow on third quarter; extreme anteroapical corner brown on forefemur, on other femora dark brown; fore- and midtibia with basal 1/2 yellow. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with comb of short setae along length of anteroventral surface, hind tibial spur dark brown, remainder brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 3/5 of its length, placed basally, shortest midtibial spur 0.84X length of longest, longest midtibial spur 4X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3.75X apical thickness of hind tibia. Foreleg first tarsomere 1.8X length of foretibia. **Wing** (Fig. 46): Length 5.25 mm. Hyaline; apical macula dark brown but fading apically, running from anterior to posterior wing margin, beginning halfway along  $R_5$ ; medial macula extending from Sc to posterior wing margin (fainter on posterior third). Macrotrichia in all cells, though absent from postero-basal margin of cell a and sparse in basal cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length prior to origin of  $R_s$ .  $R_4$  absent.  $R_5$  slightly concave for entire length.  $M_1$  reaching apex before  $R_5$ , apices of M veins thinning towards wing margin.  $M_4$ -CuA fork arising at the same level as r-m.  $A_2$  absent. **Abdomen:** Tergites and sternites principally dark brown, T3–5 with anterolateral yellow spots. Tergite 8 smaller than all other abdominal sclerites, without bristles. **Genitalia** (Fig. 95): basal half brown remainder light yellow/white. Sternite 9 very small, sclerotized, posteriorly directed Y-shape, not reaching to gonocoxal margin. Tergite 9 longer than wide, rounded basally, tapering to a single, long point posteriorly that extends beyond cerci. Gonocoxite placed 1/4 way toward apex of T9, medial margin not reaching medial line, bearing gonostylus on apical 1/3. Gonostylus a single broad-based lobe tapering to a point apically with small setae basally, gonocoxite III fused to dorsolateral margin. Aedeagus equal in length to gonocoxite, tapering to middle and then slightly bulbous apically, apodemes 1/3 total length. Parameres a slightly curved taper, 1.2X length of apodemes, apodemes strongly united with gonocoxal apodemes.

*Female.* As for male, except as follows. **Thorax:** Length 1.56 mm ( $n = 1$ ). **Wing:** Length 6.15 mm ( $n = 1$ ). **Legs:** Foretibia without comb of short setae on anteroventral surface. **Abdomen:** Cercus yellow.

*Immatures.* White/ivory background colour with small, dark, spots covering the dorsal and lateral surfaces. Follows the general habitus for other known species (Fig. 127).

**BIOLOGY:** Larvae and pupae were collected from an encrusting fungus on the underside of wet discarded lumber near La Fortuna, Costa Rica. Larvae had spun sheets and were feeding on the spores that accumulated, as described for other species (Fig. 127). The pupae were suspended from their head and tail.

**DISTRIBUTION:** Costa Rica (Fig. 143), 300–560 masl.

**ETYMOLOGY:** This species is named for my wife Brandi Borkent, as it is a particularly beautiful species, and in thanks for her support and encouragement in all matters relating to life during my doctoral program as well as for her help while I was collecting the paratype specimens.

**MATERIAL EXAMINED:** *Holotype:* here designated, adult male, pinned with genitalia in plastic vial on pin, labelled “COSTA RICA: Prov. Limon. R.B./ Hitoy Cerere, Send. Espavel. 560m./ (9.66°N, 83.03°W) 14–25.iii.2003./ E. Rojas, B. Gamboa, W. Arana/ Tp. Interseccion, sample #73474; HOLOTYPE ♂/ *Leptomorphus brandiae* /Borkent, new species / Det. C.J. Borkent 2012” [LEM].

*Paratypes:* COSTA RICA: Alajeula, 4.3km SSE La Fortuna, 15.viii.2010, C.J. Borkent [with cast off pupal skin] (2♂, 1♀, LEM).

## 6. *Leptomorphus carnevalei* Matile

(Figures 8, 47, 96, 135, 150, 153)

*Leptomorphus (Gymnoscutum) carnevalei* Matile, 1977: 150.

**References:** Crosskey 1980: 1221 (catalogue appendix); Matile 1997: 146, 149, 150 (figures, new records, morphological variation, key).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite, anepisternum and anepimeron yellow; scutellum yellow; abdominal tergite 6 brown, tergite 7 yellow (Fig. 8); male tergite 9 with basal 2/3 of lateral margins bulbous, tapering posteriorly, ventrally directed process at base of

tergal evagination a single point, concavity of posterior margin of tergite 9 smaller in diameter than width of sternite 9, tergal evagination tapering first to create a lateral corner and then tapering to a point on medial margin (Fig. 96).

This species can most easily be confused with other Afrotropical species with a completely brown tergite 6 (*L. aliciae*, *L. couturieri*, Figs 1, 8, 9). It can be distinguished from these species based solely on the male genitalia (Fig. 96) which has the apex of the posterior lobes with a strong step like constriction and then tapering to a point, rather than gradually tapering to a point (Fig. 97) or having a bulbous apex (Fig. 91).

**DESCRIPTION: Male.** (Fig. 8) **Head:** yellow, circular in anterior view. Antenna brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 2 large bristles, several setae on apicodorsal margin, a number of fine setae on apicoventral margin; flagellomere 1 with tapered base dark brown remainder dark brown; flagellomere 6 1.4X as long as broad. Clypeus yellow, dorsoventrally elongate oval; bristles on clypeus yellow, 6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow; shape a subequal triangle, with few bristles ventrolaterally. Frons yellow; with few bristles medioventrally, frontal furrow running 1/4 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus with segments 1–2 yellow, 3–5 light brown; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length of segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length 1.48 mm (n = 1). Dark brown dorsally, yellow laterally. Scutum dark brown/black with blue-green specks, yellow anteromedial triangular spot pointing posteriorly and circle on each posterolateral corner; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 6 large bristles and many small bristles. Prescutum yellow. Mediotergite yellow with anterior brown with 6 bristles on posterolateral corners, anteromedial patch of small bristles. Laterotergite yellow; anterior margin of laterotergite not reaching katapisternum. Anepimeron yellow. Anepisternum yellow. Katapisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter stem yellow, knob light brown. **Legs:** principally yellow; extreme anteroapical corner dark brown on all femora; tarsi brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2.5X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 2/3 of its length, placed centrally, shortest midtibial spur 0.87X length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 47): Length 6.15 mm (n = 1). Hyaline; apical macula absent or, if present, very light, restricted to apical 1/4 of cell  $r_1$ ; medial macula absent. Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining R at 1–2X its own length prior to origin of Rs.  $R_4$  absent.  $R_5$  straight, slight posterior turn near tip.  $M_1$  reaching apex before  $R_5$ , apices of M veins thinning before wing margin.  $M_4$ -CuA fork arising apically of origin of r-m.  $A_2$  faintly present as crease. **Abdomen:** Tergites 1, 2 and 7 yellow, T3–5 yellow with posterodorsal triangular brown spot, T6 dark brown/black. Tergite 8 smaller than all other abdominal sclerites, with 8–10 bristles on each apicolateral corner. **Genitalia** (Fig. 96): yellow. Sternite 9 sclerotized oval, 1/2 the width of genitalia at widest point, overlapping medial margin of gonoxite. Tergite 9 longer than wide, rounded margins tapering to apex first creating a lateral corner subapically and then continuing to taper to a point apically with medial U-shaped indentation, a ventrally extending thin point at base of posterior lobe. Gonocoxite placed basally on T9, medial margin reaching medial line, bearing gonostylus on apical 1/3. Gonostylus with two lobes, dorsal lobe shortest and broad, ventral lobe ~4X as long as dorsal but tapering to point, gonocoxite III fused to dorsolateral margin. Aedeagus 4/5 length of gonocoxite, tapering towards apex (slight central swelling), apodemes 1/3 total length. Parameres a simple taper, apodemes ~3/4 length of parameres.

**Female.** As for male, except as follows. **Thorax:** Length 1.8 mm. **Wing:** Length 7.87 mm. **Abdomen:** Cercus dark yellow.

*Immatures*. Unknown.

**BIOLOGY**: Unknown.

**DISTRIBUTION**: Republic of the Congo and Democratic Republic of the Congo (Fig. 135), 315–475 masl.

**DISCUSSION**: As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Gymnoscutum* and placed solely in *Leptomorphus*

**MATERIAL EXAMINED**: *Holotype*: adult male, pinned on double mount minuten, two legs glued to card on pin below specimen, genitalia in glass vial on pin, labelled “[Republic of the] Congo, Brazzaville/ Meya (Camp ORSTROM)/1.IV,1970/ P. Carnevale rec. [label handwritten]; [Light blue label] MUSEUM PARIS; [Red label] HOLOTYPE; *Leptomorphus*/ (*Gymnoscutum*)/ *carnivalei* n. sp./ ♂ht/ L. Matile det. 1974” [MNHN].

*Paratypes*: DEMOCRATIC REPUBLIC OF THE CONGO, Luebo, II.[19]59, F.J. François. (1 ♀, labelled as ALLOTYPE, IRSN).

## 7. *Leptomorphus chaseni* Edwards

(Figures 7, 48, 137, 150, 152)

*Leptomorphus chaseni* Edwards, 1933a: 229.

*Leptomorphus* (*Gymnoscutum*) *chaseni*: Matile, 1977: 145.

**References**: Colless & Liepa 1973: 454 (catalogue); Matile 1977: 141,145 (subgeneric placement); Papp & Ševčík 2011: 139 (notes on identity).

**DIAGNOSIS**: The only extant species of *Leptomorphus* with the following combination of characters: Laterotergite and anepisternum brown; wing without apical spot (Fig. 48); vein sc-r joining R within its own length of origin of Rs; segments 3–5 of abdomen noticeably swollen relative to other segments. Male unknown.

This species can be distinguished from the other Oriental and eastern Palaearctic species in this manuscript, based on the dark brown colour of the katepisternum and metepisternum (Fig. 7, both completely yellow in *L. babai* (Fig. 2), *L. ornatus* (Fig. 30) and *L. titiwangensis* (Fig. 38); metepisternum light brown in *L. tabatius* (Fig. 35) and half brown/half yellow in *L. tagbanua* (Fig. 40)). The lack of adequate description by Papp & Ševčík (2011) makes it difficult to distinguish this species from theirs, especially as *L. chaseni* is known only from the female.

**DESCRIPTION**: *Female*. (Fig. 7) **Head**: Yellow, circular in anterior view. Antenna with basal flagellomeres lighter brown, darkening apically; scape yellow, with black setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae absent; pedicel yellow, with 3–4 large bristles, several setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base yellow remainder brown; flagellomere 6 1.0X as long as broad. Clypeus yellow, square; bristles on clypeus brown, 2–3 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 1.5X as long as face. Face yellow; shape a slightly wider than tall triangle; bare. Frons yellow; bare, frontal furrow running full distance from dorsal margin towards ventral margin, frontal cleft more than 1X diameter of median ocellus anterior of median ocellus. Palpus with segments 1–4 yellow, segment 5 brown; segment 1 hidden behind eye, segments increasing in length, segment 5 1.3X length of segment 4 with central half thinner than base and apex, segment 3 spherical with apicolateral depressed patch of fine yellow setae partially encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli with median slightly in front of laterals, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax**: Length 1.23 mm (n = 1). Dark brown. Scutum dark brown; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; without large bristles but few small bristles. Prescutum brown. Mediotergite dark brown with 10 bristles on posterolateral corners, few medially. Laterotergite brown; anterior margin of laterotergite abutting katepisternum. Anepimeron brown. Anepisternum brown. Katepisternum brown. Antepronotum and proepisternum brown. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum brown. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs**: principally yellow; extreme anteroapical corner yellow on all femora. Tibia with covering of yellow macrotrichia, tibial spurs

yellow, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, fragmented, dorsal, bare patch of even thickness along its length, shortest midtibial spur subequal to length of longest, longest midtibial spur 4X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3.5X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 48): Length 5.3 mm (n = 1). Hyaline; apical macula absent; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins fading before wing margin. M<sub>4</sub>-CuA fork arising at same level as r-m. A<sub>2</sub> absent. **Abdomen:** Abdominal segments 3–5 swollen relative to other segments; tergites 3–5 with anterior 1/3 yellow, remainder dark brown/black. Cercus yellow.

*Male.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Northern Borneo [Kenokok, Mt Kinabalu] (Fig. 137), 1000 masl.

**DISCUSSION:** It is quite possible that one of the three species described from northern Borneo by Papp & Ševčík (2011) is a synonym of *L. chaseni*, as it is only known from the female. As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Gymnoscutum* and placed solely in *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult female, pinned on double mount, labelled “[Circular label with red edge] HOLO-/ TYPE; B.N. BORNEO/ Mt. Kinabalu,/ Kenok,/ 3,300 ft./ 26<sup>th</sup>.Apr. 1929./ [underside of label] H.M. Pendlebury/ coll./ F.M.S. Museums.; [underside of label] Pres. by/ F.M.S. Museum/ B.M. 1930–510; HOLOTYPE/ Leptomorphus/ chaseni/ Edwards/ det. J.E. Chainey, 1996.; [underside of label] BMNH(E) #/ 257836” [BMNH].

## 8. *Leptomorphus couturieri* Matile

(Figures 9, 49, 97, 135, 150, 153)

*Leptomorphus (Gymnoscutum) couturieri* Matile, 1997: 144.

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite, anepisternum and anepimeron yellow; scutellum yellow; abdominal tergite 6 brown, tergite 7 yellow; male tergite 9 with basal 2/3 of lateral margins bulbous, tapering posteriorly, ventrally directed process at base of tergal evagination a single point, concavity of posterior margin of tergite 9 longer in diameter than width of sternite 9, tergal evagination tapering to blunt points (Fig. 97).

This species can most easily be confused with other Afrotropical species with a completely brown tergite 6 (*L. aliciae*, *L. carnevalei*, Figs 1, 8, 9). It can be distinguished from these species based solely on the male genitalia (Fig. 97) which are as long as wide, with sternite 9 not reaching margins of gonocoxite, and apex of the posterior lobes gradually tapering to a point, rather than having a step like constriction (Fig. 96) or a bulbous apex (Fig. 91).

**DESCRIPTION:** *Male.* (Fig. 9) **Head:** yellow, circular in anterior view. Antenna dark brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 2–3 large bristles, several setae on apicodorsal margin, number of fine setae on apicoventral margin; flagellomere 1 with tapered base yellow remainder dark brown; flagellomere 6 1.5X as long as broad. Clypeus yellow, dorsoventrally elongate oval; bristles on clypeus light brown, 4–6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow; shape a just longer than wide triangle, with few bristles ventrolaterally. Frons yellow; with few bristles medioventrally, frontal furrow running 1/2 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus with segments 1–4 yellow, segment 5 brown; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length of segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow



with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length  $1.33 \pm 0.09$  mm (1.27–1.39 mm,  $n = 8$ ). Dark brown dorsally, yellow laterally. Scutum dark brown/black with blue-green specks, yellow anteromedial triangular spot pointing posteriorly and circle on each posterolateral corner; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base small. Scutellum yellow; with 6 large bristles and few small bristles. Prescutum yellow. Mediotergite yellow to light brown with 6 bristles on posterolateral corners, anteromedial patch of small bristles. Laterotergite yellow; anterior margin of laterotergite not reaching katepisternum. Anepimeron yellow. Anepisternum yellow. Katepisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter stem yellow, knob light brown. **Legs:** principally yellow; hind femur light brown at very apex; extreme anteroapical corner dark brown on all femora; hind tibia light brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2.5X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 3/4 of its length, placed centrally, shortest midtibial spur 0.9X length of longest, longest midtibial spur 4X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 4.5X apical thickness of hind tibia. Foreleg first tarsomere 1.6X length of foretibia. **Wing** (Fig. 49): Length  $5.8 \pm 0.4$  mm (5.5–6.2 mm,  $n = 7$ ). Hyaline; apical macula light, beginning at apex of  $R_1$  and  $M_4$  and reaching wing tip; medial macula absent. Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining R at 2–3X its own length prior to origin of  $R_s$ .  $R_4$  absent.  $R_5$  straight, slight posterior turn near tip.  $M_1$  reaching apex before  $R_5$ , apices of M veins fading before wing margin.  $M_4$ -CuA fork arising apically of origin of r-m.  $A_2$  faintly present as crease. **Abdomen:** Tergites principally yellow. T3–5 with posterior 1/4 dark brown, T6 dark brown. Tergite 8 smaller than all other abdominal sclerites, with ~8 bristles on each apicolateral corner. **Genitalia** (Fig. 97): yellow. Sternite 9 sclerotized oval, 1/3 the width of genitalia at widest point, just reaching medial margin of gonoxite. Tergite 9 as wide as long, rounded margins tapering into two pointed lobes with medial U-shaped indentation, a ventrally extending thin point at base of posterior lobe. Gonocoxite placed basally on T9, medial margin not reaching medial line, bearing gonostylus on apical 1/3. Gonostylus swelling from base into a triangular lobe with apex pointed, gonocoxite III fused to dorsolateral margin. Aedeagus 4/5 length of gonocoxite, tapering towards apex (slight central swelling), apodemes 1/3 total length. Parameres a simple taper, apodemes ~4/5 length of parameres.

*Female.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Ivory Coast and Ghana, (Fig. 135), 120–200 masl.

**DISCUSSION:** As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Gymnoscutum* and placed solely in *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult male, pinned on double mount minuten, genitalia in glass vial on pin, labelled “COTE-D’IVOIRE/ TAI/ 9-II-[19]85/ G. COUTURIER leg.; FORET DENSE/ SEMPERVIRENTE; [Red label] HOLOTYPE; *Leptomorphus* (g.)/ couturieri n. sp./ ♂ holotype/ L. Matile det. 1995” [MNHN].

*Paratype:* labelled as for holotype except 6.v.1980 (1♂, MNHN).

*Other material:* GHANA, Western Region, Ankasa game prod. Reserve, 9.xii.1993, J. Kjærandsen; T. Andersen. (1♂, ZMUN); same except 8–15.xi.1994. (2♂, ZMUN); 31.x–8.xi.1994. (3♂, ZMUN); IVORY COAST, Tai, 6.v.1980, G. Couturier. (1♂, MNHN).

### 9. *Leptomorphus crassipilus* Borkent, new species

(Figures 10, 50, 98, 142, 150, 155)

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: scutum and scutellum evenly covered with fine trichia; male foretibia with a dense row (comb) of short anteroventral bristles;

palp segment 5 with thick covering of fine, white, setulae; male tergite 9 posterior margin rounded laterally and concave medially, lateral process apex with 5 rows of tightly spaced short blunt brown bristles; gonocoxite placed basally on, and subequal in length to, tergite 9, gonostylus  $\sim 2/3$  length of gonocoxite with two apical processes, medial one most pronounced and tapering to a point, the lateral  $1/2$  the length of medial, thin and rod-like (Fig. 98).

This species is distinguished from most other Neotropical species missing  $R_4$  by the yellow or white scutellum and striped abdomen (Fig. 10). It can be distinguished from *L. eberhardi* by the rows of short spines on the posterior margin of tergite 9 (Fig. 98).

**DESCRIPTION:** *Male.* (Fig. 10) **Head:** yellow, circular in anterior view. Antenna brown; scape yellow, with yellow setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 2 large bristles, few setae on apicodorsal margin, patch of fine setae apicoventrally; flagellomere 1 with tapered base yellow remainder brown; flagellomere 6 1.9X as long as broad. Clypeus light brown, slightly laterally compressed oval; bristles on clypeus yellow, 6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face light brown; shape a subequal triangle, bare. Frons light brown; with many bristles covering ventral half, frontal furrow running  $1/10$  distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus yellow; segment 1 small but visible below eye, segments increasing in length, segment 5 not visible, segment 3 without definite patch of fine setae. Labellum brown. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Three ocelli; straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.19 mm ( $n = 1$ ). Dark brown with yellow lateral spots. Scutum dark brown/black with blue-green specks, pair of small yellow posterolateral spots; surface of scutum covered with trichia; acrostichal setae absent; single dorsocentral seta present anteriorly; single row of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; without large bristles but with covering of fine trichia. Prescutum yellow. Mediotergite brown with 4 bristles on posterolateral corners, and covering of appressed trichia. Laterotergite brown, with covering of appressed trichia; anterior margin of laterotergite abutting katepisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum brown with dorsal third yellow. Anteprototum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal  $1/3$  of stem ivory, apical portion and knob dark brown. **Legs:** principally yellow; trochanters light brown; hind femur with basal and apical  $1/4$  brown; extreme anteroapical corner yellow on forefemur, on other femora dark brown; tarsi brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with comb of short setae along length of anteroventral surface, though bristles further apart than in other species, tibial spurs dark brown, foretibial spur length 1.9X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for  $3/4$  of its length, placed basally, shortest midtibial spur 0.8X length of longest, longest midtibial spur 5.3X apical thickness of midtibia, shortest hind tibial spur 0.8X length of longest, longest hind tibial spur 3.5X apical thickness of hind tibia. Foreleg first tarsomere 1.6X length of foretibia. **Wing** (Fig. 50): Length 6.0 mm ( $n = 1$ ). Hyaline; apical macula dark brown running from anterior to posterior wing margin, beginning halfway along  $R_5$ , but fading towards apex and posterior margin; medial macula extending from Sc to posterior wing margin (fainter on posterior third). Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length prior to origin of  $R_s$ .  $R_4$  absent.  $R_5$  straight, slight posterior turn near tip.  $M_1$  reaching apex just before  $R_5$ , apices of M veins clearly reaching wing margin.  $M_4$ -CuA fork arising apically of origin of r-m.  $A_2$  absent. **Abdomen:** Tergites principally dark brown, T3–6 with anterior  $1/3$ – $1/2$  yellow. Tergite 8 smaller than all other abdominal sclerites, with 3–4 bristles on each apicolateral corner. **Genitalia** (Fig. 98): brown. Sternite 9 not clearly visible due to condition of specimen. Tergite 9 as wide as long, margins  $\sim$ parallel, ending apically in broad rounded lobes and shallow medial indentation, rounded lobe bearing 5–6 rows of short, blunt, closely spaced bristles on ventroapical surface. Gonocoxite placed basally on T9, medial margin almost reaching medial line, bearing gonostylus on apical  $1/3$ . Gonostylus with two lobes, basolateral lobe shortest and thin, apicomedial lobe broad based and 2X length of basal but tapering to point, bearing setae along medial margin, gonocoxite III fused to dorsolateral margin. Aedeagus  $3/4$  length of gonostylus, tapering towards apex (slight central swelling), apodemes not observable in specimen. Parameres strongly hooked at apex with apical margin serrated, apodemes  $2/5$  length of parameres.

*Female.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Northern Argentina (Fig. 142), 980 masl.

**ETYMOLOGY:** The species name refers to the rows of thick (*crassi-*) setae (*-pilus*) on the apex of tergite 9, which is a unique characteristic within *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* here designated, adult male, pinned, labelled “Argentina/ Tucuman/ S. Javier [26.783°S, 65.383°W]/ Col. Duret/ [vertically on margin] IV 44; [pink label with genitalia in between two coverslips attached]; 20779; HOLOTYPE ♂/ *Leptomorphus crassipilus*/ Borkent, new species / Det. C.J. Borkent 2012” [MNHN]

## 10. *Leptomorphus crosskeyi* Matile

(Figures 11, 51, 99, 136, 150, 153)

*Leptomorphus (Gymnoscutum) africanus* Matile, 1977: 147. Preoccupied by Meunier, 1907.

*Leptomorphus crosskeyi* Matile, 1980: 1229 (new replacement name for *africanus*).

**References:** Crosskey 1980: 1221 (catalogue appendix as *L. africanus*); Matile 1997: 143, 147–150 (figures, new records, morphological variation, key, *lapsus* as *nom. nov.*).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite, anepisternum and anepimeron yellow; scutellum brown; male genitalia with posterolateral projection of tergite 9 (tergal evagination) bearing distinct thin point on medial corner, gonostylus with shortest lobe gradually tapering to thick point (Fig. 99).

This species can be distinguished from most other Afrotropical species by the brown scutellum and lack of small setae covering the scutum (except along dorsocentral lines). It can be separated from *L. gracilis* by the larger width of the posteromedial concavity of tergite 9 and thin point on the medial corner of the tergal evagination and from *L. obscurus* by the almost square posterior margin of the tergal evaginations (Fig. 99).

**DESCRIPTION:** *Male. Head:* yellow with some brown spots, circular in anterior view. Antenna brown; scape dark yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 2 large bristles, several setae on apicodorsal margin, number of fine setae on apicoventral margin; flagellomere 1 with tapered base brown remainder brown; flagellomere 6 1.8X as long as broad. Clypeus yellow, dorsoventrally elongate oval; bristles on clypeus brown, 6–8 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow; shape a subequal triangle, with few bristles ventrolaterally. Frons ventral half brown rest yellow; with few bristles medioventrally, frontal furrow running full distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus with segments 1–2 yellow, 3–5 light brown; segment 1 hidden behind eye, segments increasing in length, segment 5 2.5X length of segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae encircled by strong dark setae. Labellum yellow. Eye with interommatidial setulae absent. Occiput yellow with some adventitious brown spotting anteriorly, with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown. **Thorax:** Length 1.19 mm (1.15–1.23 mm, n = 4). Dark brown dorsally, yellow laterally. Scutum dark brown/black with blue-green specks, pair of yellow mediolateral and posterolateral spots; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum brown; with 8–10 large bristles and few small bristles. Prescutum yellow. Mediotergite brown, lighter posteriorly with 6–8 bristles on posterolateral corners, anteromedial patch of small bristles. Laterotergite yellow; anterior margin of laterotergite not reaching katepisternum. Anepimeron yellow. Anepisternum yellow. Katepisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with light brown and yellow trichia respectively. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** principally yellow; extreme anteroapical corner dark brown on all femora; midfemur without apical spine-like

process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, hind tibial spur yellow, remainder brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 3/4 of its length, placed centrally, shortest midtibial spur 0.78X length of longest, longest midtibial spur 4.5X apical thickness of midtibia, shortest hind tibial spur 0.8X length of longest, longest hind tibial spur 6.7X apical thickness of hind tibia. Foreleg first tarsomere 1.8X length of foretibia. **Wing** (Fig. 51): Length 5.5 mm (5.3–5.7 mm, n = 4). Hyaline; apical macula absent or, if present, very light, restricted to apical 1/4 of cell r1; medial macula absent. Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining R at 1–2X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins thinning towards margin. M<sub>4</sub>-CuA fork arising just apically of origin of r-m. A<sub>2</sub> faintly present as crease. **Abdomen**: Tergites 1–2 yellow with posterodorsal brown triangle, 3–6 with anterior 1/2 yellow remainder dark brown, T7 yellow. Tergite 8 smaller than all other abdominal sclerites, with 3 bristles on each apicolateral corner. **Genitalia** (Fig. 99): yellow. Sternite 9 sclerotized, circular, 1/3 width of genitalia at widest point, overlapping medial margin of gonocoxite. Tergite 9 longer than wide, margins parallel on apical 2/3 ending in lateral squared off lobe with medially directed spine and medial U-shaped indentation, one thick and one thin, ventrally extending point at base of posterior lobe. Gonocoxite placed basally on T9, medial margin not reaching medial line, bearing gonostylus apically. Gonostylus with two lobes, dorsal lobe a broad based point, ventral lobe half the width of dorsal but 2.5X length and barely tapering until apex, gonocoxite III fused to dorsolateral margin. Aedeagus 2/3 length of T9, tapering towards apex, apodemes ~1/4 total length. Parameres a simple taper, apodemes ~1/2 length of parameres.

*Female*. (Fig. 11) As for male, except as follows. **Thorax**: Length 1.5 mm (1.44–1.56 mm, n = 2). **Wing**: Length 6.5 mm (6.4–6.6 mm, n = 2). **Abdomen**: Tergites 1–6 with anterior 1/3 yellow remainder dark brown, T7 dark brown with pair of small lateral yellow spots. Cercus yellow.

*Immatures*. Unknown.

**BIOLOGY**: Unknown.

**DISTRIBUTION**: Ghana, Central African Republic, and Uganda (Fig. 136), 180–1250 masl.

**DISCUSSION**: As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Gymnoscutum* and placed solely in *Leptomorphus*.

**MATERIAL EXAMINED**: *Holotype*: adult male, pinned on double mount minuten, genitalia in glass vial on pin, labelled “[Blue label] REP. CENTRAFRIC./ LA MABOKE/ 29.IX.1970/ L. MATILE rec.; [Red label] HOLOTYPE; Leptomorphus/ (Afroleptomorphus)/africanus n. sp. ♂ht/ L. Matile det. 1974; HOLOTYPE ♂/ *Leptomorphus crosskeyi*/ Matile/ Det. C.J. Borkent, 2012” [MNHN].

*Paratypes*: Labelled as for holotype (1♀, labelled as Allotype, MNHN); except 2.x.1970 (1♀, MNHN); 20.viii.1967 (1♂, MNHN); UGANDA, Kibale Forest, 12.xii.1971–9.i.1972, R.L. Mason (1#m, BMNH).

*Other material*: CENTRAL AFRICAN REPUBLIC, La Maboke, 20.viii.1967, L. Matile. (1♂, MNHN); same, except 2.x.1970. (1♀, MNHN); GHANA, Kakum N.P., 8–15.x.1994. (1♂, ZMUN); UGANDA, Kibale Forest, 12.xii.1971–9.i.1972, R.L. Masou. (1♂, BMNH).

## 11. *Leptomorphus eberhardi* Borkent, new species

(Figures 12, 13, 52, 100, 143, 150, 155)

**DIAGNOSIS**: The only extant species of *Leptomorphus* with the following combination of characters: scutum and scutellum evenly covered with fine trichia; male foretibia with a dense row (comb) of short anteroventral bristles; palp segment 5 with thick covering of fine, white, setulae; male genitalia with tergite 9 tridentate posteriorly (medial process laterally compressed), gonocoxite placed posteriorly on tergite 9, gonostylus small (~1/4 length of gonocoxite) with two short, round, apical projections (Fig. 100).

This species is distinguished from most other Neotropical species missing R<sub>4</sub> by the yellow scutellum and striped abdomen (Figs 12, 13). It can be distinguished from *L. crassipilus* as it is the only species with a large, laterally compressed posteromedial evagination of tergite 9 (Fig. 100).



**DESCRIPTION:** *Male.* (Fig. 12) **Head:** yellow, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 1 large bristle, several setae on apicodorsal margin, patch of fine setae apicoventrally; flagellomere 1 with tapered base yellow remainder dark brown; flagellomere 6 1.6X as long as broad. Clypeus yellow, slightly laterally compressed oval; bristles on clypeus brown, 6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face light brown; shape a slightly wider than tall triangle. Frons light brown; bare, frontal furrow running 1/4 distance from dorsal margin towards ventral margin, frontal cleft more than 1X diameter of median ocellus anterior of median ocellus. Palpus with segments 1–4 yellow, segment 5 white; segment 1 small but visible below eye, segments increasing in length, segment 5 1.8X length and 0.8X width of segment 4 with even width from base to apex and covered in fine white setulae, segment 3 without definite patch of fine setae. Labellum light brown. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.48 mm (n = 1). Dark brown with yellow lateral spots. Scutum dark brown with blue-green specks; surface of scutum covered with trichia; acrostichal setae absent; single dorsocentral seta present anteriorly; two thirds row of lateral setae present; patch of setae on scutum at wing base small. Scutellum light yellow with covering of fine trichia; bristles absent. Prescutum yellow. Mediotergite dark brown with 4 bristles on posterolateral corners, and covering of appressed trichia. Laterotergite brown, with covering of appressed trichia; anterior margin of laterotergite abutting katepisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum dark brown. Katepisternum brown with dorsal third yellow. Anteprepronotum and proepisternum brown. Margin of anterior and posterior spiracles white with white trichia. Metepisternum white. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** principally yellow; trochanters brown; midfemur with basal 1/3 dark brown, hind femur with basal 1/3 and apex dark brown; extreme anteroapical corner brown on forefemur, on other femora dark brown; tibia with apex brown; tarsi light brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with comb of short setae along length of anteroventral surface, tibial spurs light brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 2/3 of its length, placed basally, shortest midtibial spur 0.78X length of longest, longest midtibial spur 5.1X apical thickness of midtibia, shortest hind tibial spur 0.83X length of longest, longest hind tibial spur 4.1X apical thickness of hind tibia. Foreleg first tarsomere 1.8–1.9X length of foretibia. **Wing** (Fig. 52): Length 6.4 mm (n = 1). Hyaline; apical macula dark brown running from anterior to posterior wing margin, beginning halfway along  $R_5$ , but fading towards apex and posterior margin; medial macula extending from Sc to posterior wing margin (fainter on posterior third). Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining R within its own length prior to origin of  $R_s$ .  $R_4$  absent.  $R_5$  straight, slight posterior turn near tip.  $M_1$  reaching apex before  $R_5$ , apices of M veins reaching wing margin.  $M_4$ -CuA fork arising at same level as r-m.  $A_2$  absent. **Abdomen:** Tergites principally brown, T3–6 with anterior 1/3 yellow. Sternite yellow. Tergite 8 smaller than all other abdominal sclerites, without bristles. **Genitalia** (Fig. 100): basal half brown, remainder light yellow/white. Sternite 9 membranous. Tergite 9 slightly longer than wide, tridentate posteriorly with medial process laterally compressed. Gonocoxite placed apically on T9, medial margin not reaching medial line, bearing gonostylus 1/3 distance from base. Gonostylus small (~1/4 length of gonocoxite) with two short, round, apical bumps (located ventrally and dorsally, dorsal behind ventral in figure) and a single seta, gonocoxite III fused to dorsolateral margin. Aedeagus highly complex with what appear to be 4–6 short apodemes, lateral sclerotized component that is strongly sinusoidal when viewed laterally and tapering sharply in apical half. Parameres a simple taper laterally but apodeme strongly united with both gonocoxal apodeme and aedeagal apodemes/complex, with a basal hook-shaped spine pointing dorsally.

*Female.* As for male, except as follows. Generally darker in colour. **Thorax:** Length 1.48 mm (n = 1). Scutellum light brown. **Wing:** Length 6.5 mm (n = 1). **Legs:** Foretibia without comb of short setae on anteroventral surface. **Abdomen:** Tergites 3–5 with anterior 1/3 yellow, T6 with anterolateral yellow spots, remainder dark brown. Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown, although this is likely the species used in a study of the web spinning behaviour of *Leptomorphus* larvae (Eberhard 1990).

**DISTRIBUTION:** Costa Rica (Fig. 143), 615–1325 masl.

**ETYMOLOGY:** This species is named after Dr. W.G. Eberhard in recognition of his contributions towards the understanding of the immature and adult behaviour of *Leptomorphus*, and his collection of the holotype.

**MATERIAL EXAMINED:** *Holotype:* here designated, adult male, pinned with genitalia in plastic vial on pin, labelled “COSTA RICA: San Jose Region:/ San Antonio de Escazu: vii.1999./ el. 1325 masl. Malaise trap/ W. Eberhard; HOLOTYPE ♂/ *Leptomorphus eberhardi*/ Borkent, new species / Det. C.J. Borkent 2012” [ZMUN].

*Paratypes:* COSTA RICA: La Suiza, x.1923, P. Schild (1♀, USNM).

## 12. *Leptomorphus fasciculatus* Edwards

(Figures 14, 53, 80, 101, 142, 150, 155)

*Leptomorphus fasciculatus* Edwards, 1933b: 305.

*Leptomorphus (Leptomorphus) fasciculatus:* Matile, 1977: 144.

**References:** Edwards 1940: 452–453 (compared to *L. neivai*); Matile 1977: 144 (subgeneric placement); Papavero 1978: 50 (catalogue).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: scutum and scutellum evenly covered with fine trichia; male foretibia with a dense row (comb) of short anteroventral bristles; palp segment 5 with thick covering of fine, white, setulae; gonocoxite with a thin gonocoxal lobe almost equal in length to tergite 9, originating mediobasally and bearing several, long, apical setae, male genitalia unique (Fig. 101).

This species is distinguished from other Neotropical species missing  $R_4$  by the dark brown scutellum, completely yellow fore- and mid legs, and yellow or white metepisternum (Fig. 14). It is also the only species with a basally placed, medial gonocoxal lobe, which is nearly as long as the genitalia (Fig. 101).

**DESCRIPTION:** *Male.* (Fig. 14) **Head:** brown spot medially from ocelli to antennal base, remainder yellow, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape yellow, with brown setae in short row on apicodorsal margin and thick patch covering apicoventral process, remainder bare, anterobasal patch of setulae present; pedicel yellow, with 1–2 large bristles, few setae on apicodorsal margin, patch of fine setae apicoventrally; flagellomere 1 with tapered base yellow remainder dark brown; flagellomere 6 1.3X as long as broad. Clypeus yellow, slightly laterally compressed oval; bristles on clypeus yellow, 4–6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow; shape a slightly wider than tall triangle, bare. Frons brown; bare, frontal furrow running 1/2 distance from dorsal margin towards ventral margin, frontal cleft more than 1X diameter of median ocellus anterior of median ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length and 1.5X width of segment 4 with even width from base to apex and covered in fine white setulae, segment 3 without distinct lateral patch of fine setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2.5X their own diameter from eye margin, ocellar triangle dark brown. **Thorax:** Length  $1.73 \pm 0.3$  mm (1.52–2.01 mm, n = 10). Dark brown with yellow lateral spots. Scutum dark brown/black with blue-green specks, pair of yellow anterolateral spots, one specimen with lateral margins brown and remainder yellow; surface of scutum covered with trichia (Fig. 80); acrostichal setae absent; single dorsocentral seta present anteriorly; two thirds row of lateral setae present; patch of setae on scutum at wing base present. Scutellum dark brown with covering of fine trichia; bristles absent. Prescutum anterior half yellow, posterior half brown. Mediotergite dark brown with 6 bristles on posterolateral corners, and covering of appressed trichia. Laterotergite brown, with covering of appressed trichia; anterior margin of laterotergite abutting katepisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum brown with posterodorsal corner yellow. Antepnotum and proepisternum brown. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter stem yellow, knob light to dark brown. **Legs:** principally yellow; hind coxa with brown spot along length of anterior surface; extreme anteroapical corner yellow on forefemur, on other femora dark brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2X apical thickness of foretibia, midtibia with

strong, dorsal, bare patch of even thickness for 2/3 of its length, placed basally, shortest midtibial spur 0.8X length of longest, longest midtibial spur 4X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.6X length of foretibia. **Wing** (Fig. 53): Length  $6.6 \pm 0.9$  mm (5.8–7.5 mm, n = 10). Hyaline; apical macula dark brown, running from anterior to posterior wing margin, beginning halfway along  $R_5$  but not reaching wing tip; medial macula extending from  $R_1$  to posterior wing margin (fainter on posterior third). Macrotrichia in all cells, though absent from posterobasal margin of cell a and very sparse in basal cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length before or after origin of  $R_s$ .  $R_4$  absent.  $R_5$  slightly concave for entire length.  $M_1$  reaching apex before  $R_5$ , apices of M veins thinning towards wing margin.  $M_4$ -CuA fork arising before origin of r-m.  $A_2$  absent. **Abdomen**: Tergites 1 dark brown, T2–5 yellow, T6–7 brown sometimes with yellow lateral spots, in one specimen completely yellow. Tergite 8 smaller than all other abdominal sclerites, without bristles. **Genitalia** (Fig. 101): light brown. Sternite 9 sclerotized, thin, anteriorly tapered sclerite 2/3 the length of gonocoxite, not reaching gonocoxal margin. Tergite 9 as wide as long, tapering to apex which bears two short apicolateral points on each side and medial shallow V-shaped indentation. Gonocoxite placed basally on T9, with gonocoxal lobe as long as gonocoxite, arising mediobasally and armed with 4 long laterally pointing apical bristles, bearing gonostylus at apex. Gonostylus with two lobes, dorsal lobe short and broad with a number of setae (placed behind ventral lobe in figure), ventral lobe 1/3 the width of dorsal, 2.5X length, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus 1/2 length of T9, tapering to middle and then slightly bulbous apically, apodemes 1/6 total length. Parameres a simple thin taper, apodemes ~1/2 length of parameres.

*Female*. As for male, except as follows. **Thorax**: Length 1.78 mm (1.68–1.89 mm, n = 2). **Wing**: Length 6.4 mm (6.1–6.7 mm, n = 2). **Legs**: Foretibia without comb of short setae on anteroventral surface. **Abdomen**: Cercus yellow.

*Immatures*. Unknown.

**BIOLOGY**: Unknown.

**DISTRIBUTION**: Panama, Ecuador, Peru, Bolivia, Brazil (Sao Paulo, Mato Grosso, Rio de Janeiro) (Fig. 142), 55–700 masl.

**DISCUSSION**: As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Leptomorphus* and placed solely in the genus *Leptomorphus*. This species is the most widely distributed of the Neotropical species and does show some variation in the amount of brown on the abdomen, though the genitalia are identical across the range.

**MATERIAL EXAMINED**: *Holotype*: adult male, pinned with genitalia in plastic vial on pin, labelled “[green label] Bolivia—Mapiri/ 15.III.[19]03/ Sarampioni 700m; Leptomorphus/ fasciculatus Edw./ F.W. Edwards/ det. TYPE. 1933.; Staatl. Museum für/ Tierkunde Dresden/ Coll. W. SCHNUSE, 1911; HOLOTYPE ♂/ *Leptomorphus fasciculatus* /Edwards / Det. C.J. Borkent, 2012” [MTD].

*Paratypes*: PERU, Pichia, Pto Yessup, xii.[19]03 (2♂, MTD and BMNH).

*Other material*: BRAZIL, MT, Maracaju, vi.1937, Serviço Febre Amarela. (1♂, 1, MZUSP); RJ, Nova Iguaçu, Reserva Biológica do Tinguá, 5–8.iii.2002, S.T.P. Amarante. (1♂, MZUSP); SP, R. Parana, Porto Cabral, 1–25.vi.1944, Trav. Fo., Carrera, E. Dente. (1♂, MZUSP); ECUADOR, Orellana, 1km S Onkone Gare Camp, 22.vi.1996, T.L. Erwin. (1♂, LEM); 5.ii.1996. (1♂, LEM); Tiputini Biodiversity Stn., 24.x.1998, T.L. Erwin. (1♂, LEM); PANAMA, Cabima, 23.v.1911, A. Busck. (2♀, USNM); Chilibre, 1.i.1940, G. Fairchild. (1♂, MCZ); Canal Zone, Barro Colorado Isle., 26.vii.1982, R.B. & L.S. Kimsey. (2♂, CNC); Barro Colorado Isle., Dodge. (1♀, USNM); PERU, Pichis River, Puerto de Yessup, 1903. (1♂, BMNH).

### 13. *Leptomorphus femoratus* Edwards

(Figures 15, 54, 102, 143, 150, 155)

*Leptomorphus femoratus* Edwards, 1933b: 306.

*Leptomorphus (Leptomorphus) femoratus*: Matile, 1977: 144.

**References:** Edwards 1940: 452–453 (compared to *L. neivai*); Matile 1977: 144 (subgeneric placement); Papavero 1978: 50 (catalogue).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: scutum and scutellum evenly covered with fine trichia; male foretibia with a dense row (comb) of short anteroventral bristles; palp segment 5 with thick covering of fine, white, setulae; male genitalia with apex of tergite 9 not extending past cerci, tergite 9 posteriorly with some scalloping on apicolateral corner and with 3 rounded medial processes, with central shorter than laterals, gonocoxite with gonocoxal lobe (Fig. 102)

This species is distinguished from other Neotropical species missing  $R_4$  by the dark brown scutellum, fore- and mid legs at least partially brown and an at least partially yellow metepisternum (Fig. 15).

**DESCRIPTION: Male.** (Fig. 15) **Head:** brown spot medially from ocelli to antennal base, remainder yellow, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape yellow, with brown setae in short row on apicodorsal margin and thick patch covering apicoventral process, remainder bare, anterobasal patch of setulae present; pedicel yellow, with 1 large bristle, several setae on apicodorsal margin, patch of fine setae apicoventrally; flagellomere 1 with tapered base yellow remainder dark brown; flagellomere 6 1.1X as long as broad. Clypeus yellow, slightly laterally compressed oval; bristles on clypeus yellow, 4–6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow; shape a slightly wider than tall triangle, bare. Frons brown; bare, frontal furrow running 1/4 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length and 1.5X width of segment 4 with even width from base to apex and covered in fine white setulae, segment 3 without distinct lateral patch of fine setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2.5X their own diameter from eye margin, ocellar triangle dark brown. **Thorax:** Length 2.05 mm (1.56–2.54 mm,  $n = 2$ ). Dark brown with yellow lateral spots. Scutum dark brown/black with blue-green specks, pair of yellow anterolateral spots; surface of scutum covered with trichia; acrostichal setae absent; single dorsocentral seta present anteriorly; two thirds row of lateral setae present; patch of setae on scutum at wing base small. Scutellum dark brown with covering of fine trichia; bristles absent. Prescutum anterior half yellow, posterior half brown. Mediotergite dark brown with 4–6 bristles on posterolateral corners, and covering of appressed trichia. Laterotergite brown, with covering of appressed trichia; anterior margin of laterotergite abutting katepisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum brown with posterodorsal corner yellow. Antepnotum and proepisternum brown. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum light brown dorsal line remainder yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** principally yellow; trochanters brown; midfemur with basal 1/3 dark brown, hind femur with basal 1/5 and apical 2/5 dark brown; extreme anteroapical corner dark brown on all femora; tibia light brown; fore- and midtarsi brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 2/3 of its length, placed basally, shortest midtibial spur 0.85X length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3.5X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 54): Length 6.3 mm (6.0–6.6 mm,  $n = 2$ ). Hyaline; apical macula dark brown but fading towards apex and posterior margin, running from anterior to posterior wing margin, beginning halfway along  $R_5$ ; medial macula extending from  $R_1$  to posterior wing margin (fainter on posterior third). Macrotrichia in all cells, though absent from posterobasal margin of cell a and very sparse in basal cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length prior to origin of  $R_s$ .  $R_4$  absent.  $R_5$  slightly concave for entire length.  $M_1$  reaching apex before  $R_5$ , apices of M veins thinning towards wing margin.  $M_4$ -CuA fork arising before origin of r-m.  $A_2$  absent. **Abdomen:** Tergites principally dark brown, T3–5 with yellow anterior band. Tergite 8 smaller than all other abdominal sclerites, without bristles. **Genitalia** (Fig. 102): light brown. Sternite 9 sclerotized, thin, posteriorly tapered sclerite, almost as long as aedeagus, not reaching gonocoxal margin. Tergite 9 as wide as long, tapering towards apex which flattens and bears some scalloping on the apicolateral corner and with 3 rounded medial processes, with central shorter than laterals. Gonocoxite placed centrally on T9, dorsal gonocoxal lobe scalloped, and bearing setae apically, medial margin not reaching median line, bearing gonostylus halfway along medial



margin. Gonostylus with two lobes, dorsal lobe short point, ventral lobe same width as dorsal but 3–4X length and bearing several setae on medial margin, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus 2/5 length of T9, tapering to middle and then slightly bulbous apically with small points apicolaterally, apodemes 1/4 total length. Parameres a simple taper, apodemes 2/4 length of parameres.

*Female.* As for male, except as follows. **Thorax:** Length 1.56 mm. **Wing:** Length 6.8 mm. **Legs:** Foretibia without comb of short setae on anteroventral surface. **Abdomen:** Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Peru and Bolivia (Fig. 143), 650–1230 masl.

**DISCUSSION:** As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Leptomorphus* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult male, pinned with genitalia in plastic vial on pin, labelled “[green label] Bolivia—Mapiri/ 13.3.[19]03/ Sarampioni 700; Leptomorphus/ femoratus Edw./ F.W. Edwards/ det. TYPE. 1933.; Staatl. Museum für/ Tierkunde Dresden/ Coll. W. SCHNUSE, 1911; HOLOTYPE ♂/ *Leptomorphus femoratus* /Edwards / Det. C.J. Borkent, 2012” [MTD]

*Other material:* PERU, Monson Valley, Tingo Maria, 11.xii.1954, E.I Schlinger, E.S. Ross. (1♂, MZUSP); Huanuco, Rio Monzan, 13.x.1960, J. Schunke. (1♀, SEMC).

#### 14. *Leptomorphus forcipatus* Landrock

(Figures 16, 55, 85, 103, 140, 150, 154)

*Leptomorphus walkeri forcipata* Landrock, 1918: 107.

*Leptomorphus forcipatus:* Séguy, 1940: 86.

*Leptomorphus (Leptomorphus) forcipatus:* Matile, 1977: 144 (as synonym of *L. quadrimaculatus*).

**References:** Okada 1936: 100 (synonymized with *L. quadrimaculatus*); Séguy 1940: 86 (distribution); Matile 1977: 144 (subgeneric placement), 1988: 234 (catalogue); Ostroverkhova & Shtakel'berg 1988: 416, 418 (genitalia figure and key reference); Zaitzev 1994: 157, 161 (key, re-description, male genitalia figure); Yakovlev 1995: 351, 356 (rearing record); Zaitzev and Ševčík, 2002: 204 (removed from synonymy with *L. quadrimaculatus*); Ševčík & Papp 2003: 288 (Hungary); Gammelmo & Sjøli 2006: 60, (Norway); Ševčík 2006: 14 (biology, photo of adults en copula), 2010: 17 (fungal association); Kjærandsen *et al.* 2007: 35 (distribution).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: foretibia with dense row (comb) of short anteroventral bristles; wing with dark apical and medial spots present; male genitalia with gonocoxite smoothly curved along entire length, not swollen at apex and without triangular medial protrusion at base (Fig. 103).

This species can be distinguished from other Palaearctic species by the long gonocoxites (more than half total length of male genitalia, Fig. 103), almost completely dark yellow abdomen (tergite 7 and posterior half of tergite 6, brown, Fig. 16) and scutum evenly covered with small setae. It is the only species with long gonocoxites that has the gonocoxite both smoothly curved (not strongly bent as in *L. talyshensis*, Fig. 121) and without a triangular protrusion mediobasally (Fig. 103).

**DESCRIPTION:** *Male.* (Fig. 16) **Head:** brown dorsally yellow ventrally, somewhat dorsoventrally compressed in anterior view. Antenna brown; scape yellow, with light brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel light brown/yellow, with 3 large bristles, several setae on apicodorsal margin, a few fine setae on apicoventral margin; flagellomere 1 with tapered base brown remainder brown; flagellomere 6 2.0X as long as broad. Clypeus light brown, strongly protruding, slightly laterally compressed oval; bristles on clypeus light brown, both strong, smaller bristles on entire surface, all directed ventrally, clypeus 2X as long as face. Face brown; shape a slightly wider than tall triangle, with fine bristles covering face. Frons brown; with few bristles medioventrally, frontal furrow running 3/4–full distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus yellow; segment 1 small but visible below eye, segments increasing in length, segment 5 1.5X length of segment 4 with even width from base to apex, segment 3

with apicolateral patch of fine yellow setae encircled by strong dark setae. Labellum yellow. Eye with long inter-ommatidial setulae in  $\sim 1/4$  of the ommatidial junctions, scattered on all but medial margin. Occiput brown with appressed, anteriorly directed setae. Ocelli with median slightly in front of laterals, space between ocelli less than diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown. **Thorax:** Length 1.54 mm (1.39–1.64 mm,  $n = 3$ ). Dorsally brown, laterally yellow. Scutum brown on disc with lighter dorsocentral lines, yellow on anterior corners, lateral and posterior margins except for dark spot at wing base; surface of scutum covered with small setae; acrostichal setae absent; dorsocentral setae probably present but not clearly distinguishable from other setae; multiple rows of lateral setae present; patch of setae on scutum at wing base small. Scutellum yellow to light brown; with 6–8 large bristles and many small bristles. Prescutum brown. Mediotergite yellow, darker posteriorly with 8–16 bristles on posterolateral corners, small bristles covering. Laterotergite yellow; anterior margin of laterotergite abutting katepisternum. Anepimeron yellow. Anepisternum yellow. Katepisternum yellow with anteroventral corner brown. Antepronotum and proepisternum light brown to yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture straight and clear. Halter stem yellow, knob light brown. **Legs:** principally yellow; extreme anteroapical corner dark brown on all femora; foretarsi brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with weak comb of short setae along length of anteroventral surface (Fig. 85), tibial spurs yellow, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for  $3/4$  of its length, placed basally, shortest midtibial spur 0.7X length of longest, longest midtibial spur 4.5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 4.5X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 55): Length 7.2 mm (6.6–7.5 mm,  $n = 3$ ). Hyaline; apical macula not reaching wing tip, extending faintly along posterior wing margin into apex of cell  $cua_1$  and cup though not joining with medial macula; medial macula extending from Sc to stem of  $M_{1+2}$ . Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) all the same length. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length prior to origin of Rs.  $R_4$  absent.  $R_5$  straight, slight posterior turn near tip.  $M_1$  reaching apex just before  $R_5$ , apices of M veins thinning towards wing margin.  $M_4$ -CuA fork arising well before origin of r-m.  $A_2$  faintly present as crease. **Abdomen:** Tergites T1–6 yellow, T6 brown posteriorly, T7 brown. Tergite 8 smaller than all other abdominal sclerites, without bristles. **Genitalia** (Fig. 103): light yellow. Sternite 9 lightly sclerotized, posteriorly directed triangle  $1/2$  length of T9 but as wide as genitalia. Tergite 9 subcircular though apical margin somewhat flattened. Gonocoxite placed centrally on T9, much longer than length of T9, medial margin not reaching median line, bearing gonostylus basally. Gonostylus a single lobe tapering to a point apically, strongly bent at halfway point and with several setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus  $3/4$  length of T9, tapering slightly towards apex for basal  $3/4$  and then strongly indented and remainder squarish, apodemes  $\sim 1/2$  total length. Parameres consisting of two lobes, lateral lobe a broad based spine curving laterally, medial lobe 2X length of lateral and very thin, apodemes  $1/2$  length of parameres, strongly united with gonocoxal apodemes and with a dorsal pointing small hook.

*Female.* No specimens examined, but coloration apparently similar to male with female terminalia yellow (Zaitzev & Ševčík 2002).

*Immatures:* Undescribed.

**BIOLOGY:** Larvae are known to feed on the spores of *Stereum* (*S. subtomentosum* and *S. hirsutum*; Zaitzev & Ševčík 2002) and *Trichaptum* (Yakovlev 1995, Jakovlev 2011). Adults copulate soon after emergence from the pupa, and copulation lasts several hours (Ševčík 2006).

**DISTRIBUTION:** Finland, Czech Republic, Slovakia, Sweden, Norway, Hungary, Germany and Switzerland (Fig. 140), 35–780 masl.

**DISCUSSION:** This species was originally described as a subspecies of *L. walkeri*, and was later thought to be a junior synonym of *L. quadrimaculatus* (Okada 1936, Matile 1988). Zaitzev & Ševčík (2002) considered it significantly different from the latter, reinstated it and designated a lectotype from the single type specimen they found. Lectotype information from Zaitzev & Ševčík (2002): adult male, pinned, labelled “Árvaváralja, Kertész, 24.vi.1914, [underside of label] Collectio K. Landrock, K Czižek, D. Jacentkovský” [type depository: MMBC].

As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Leptomorphus* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED:** CZECH REPUBLIC, Bohemia, Josefuv Dul, Jedlový dul, 1–22.ix.2005, J. Preisler & P. Vonička. (1♂, LEM); GERMANY, Saxony, Sachsische Schweiz N.P., 22–23.vi.1989, U. Kallweit. (1♂, MTD); NORWAY, AK, As; Arungen, Syverud, 15.viii–3.ix.2003, E. Rindal, L. Aarvik. (1♂, ZMUN); SLOVAKIA, Polana Biosphere Reserve, 24.v–11.vii.2007, J. Roháček, J. Ševčík. (1♂, LEM).

### 15. *Leptomorphus furcatus* Borkent, new species

(Figures 17, 56, 104, 148, 150, 155)

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: foretibia with dense row (comb) of short anteroventral bristles; wing with apical spot very pale and restricted to apical ¼ of cell r<sub>1</sub>; medial spot absent (Fig. 56); male genitalia with sternite 9 bearing a medial invagination for posterior 2/3 and with 2 dark, apical points (Fig. 104).

This species can be distinguished from most other Nearctic species by the lack of R<sub>4</sub>. It can be separated from *L. hyalinus* based on the yellow scutellum, the presence of small setae on the entire surface of the scutum, and the apically placed gonocoxites (Fig 104).

**DESCRIPTION: Male.** (Fig. 17) **Head:** yellow-orange, circular in anterior view. Antenna brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 1–2 large bristles, several setae on apicodorsal margin, a few fine setae on apicoventral margin; flagellomere 1 with tapered base yellow, remainder brown; flagellomere 6 1.7X as long as broad. Clypeus yellow, slightly laterally compressed oval; bristles on clypeus yellow, both strong, smaller bristles on entire surface, all directed ventrally, clypeus 1.5X as long as face. Face ivory to light brown; shape a subequal triangle, with fine bristles covering face. Frons yellow; with few bristles medioventrally, frontal furrow running 1/2–full distance from dorsal margin towards ventral margin, frontal cleft more than 1X diameter of median ocellus anterior of median ocellus. Palpus light brown; segment 1 small but visible below eye, segments increasing in length, segment 5 1.5X length of segment 4 with even width from base to apex, segment 3 with fine yellow setae laterally but not in distinct patch. Labellum brown. Eye with few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 3X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.24 ± 0.33 mm (0.94–1.39 mm, n = 10). Brown dorsally, yellow laterally. Scutum yellow, some northern specimens light brown with dorsocentral lines and lateral margins yellow; surface of scutum covered with small setae; acrostichal setae vaguely present; dorsocentral setae probably present but not clearly distinguishable from other setae; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; without large bristles and many small bristles. Prescutum yellow. Mediotergite yellow with 8–10 bristles on posterolateral corners, small bristles covering. Laterotergite yellow; anterior margin of laterotergite not reaching katapisternum. Anepimeron yellow. Anepisternum yellow. Katapisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter stem yellow, knob light brown. **Legs:** principally yellow; extreme anteroapical corner brown on hind femur, on other femora yellow. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 2/3 of its length, placed basally, shortest midtibial spur 0.9X length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur 0.85X length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.6X length of foretibia. **Wing** (Fig. 56): Length 5.2 ± 1.2 mm (4.0–6.1 mm, n = 10). Hyaline; apical macula very light, restricted to apical 1/4 of cell r<sub>1</sub>; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex at same level as R<sub>5</sub>, apices of M veins reaching wing margin. M<sub>4</sub>-CuA fork arising apically of origin of r-m. A<sub>2</sub> absent. **Abdomen:** Tergites principally yellow, T2–5 with posterior 1/4–1/3 brown, T6 with posterior 1/3 dark brown, T7 dark brown. Tergite 8 smaller than all other abdominal sclerites, without bristles. **Genitalia** (Fig. 104): yellow.

Sternite 9 sclerotized, mostly circular but with medial invagination on posterior 2/3 and 2 dark apical points, 2/3 the width of genitalia. Tergite 9 slightly longer than wide oval with a subapical dorsal process tapering apically into lateral points and a medial U-shaped indentation. Gonocoxite placed centrally on T9, medial margin not reaching median line, bearing gonostylus halfway along medial margin. Gonostylus a single club-shaped lobe with several setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus 2/3 length of gonocoxite, tapering towards apex, apodemes 1/5 total length. Parameres a laterally curved taper, 1.1X length of apodemes.

*Female.* As for male, except as follows. **Thorax:** Length 1.35 mm (1.31–1.39 mm, n = 2). **Wing:** Length 5.9 mm (5.4–6.3mm, n = 2). **Legs:** Foretibia without comb of short setae on anteroventral surface. **Abdomen:** Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** New Mexico and Arizona south to Northern Mexico (Fig. 148), 915–2255 masl.

**ETYMOLOGY:** The species name refers to the strongly forked nature of sternite 9, particularly the strongly sclerotized apicolateral points, a condition unique within *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* here designated, adult male, pinned, labelled “USA; NM; Grant Co. 14mi N/ Silver City, Cherry Cr. Campgrnd/ 11–14.viii.2007, el 7400’/ (32°54.8’N 108°13.6’W)/ Malaise trap, J.E. O’Hara; HOLOTYPE ♂/ *Leptomorphus furcatus* / Borkent, new species / Det. C.J. Borkent 2012” [LEM]

*Paratypes:* labelled as for holotype (3♂, LEM); except 14–16.viii.2007. (1♂, LEM); MEXICO, SI, 15mi. W El Palmito, 3.viii.1964, W.R.M. Mason. (2♂, CNC); 20.vii.1964. (1♂, CNC); 30.vii.1964. (1♀, CNC); 20mi. E Concordia, 4.viii.1964. (2♂, CNC); Portrerillos, 15mi. W El Palmito, 11.vii.1964, J.F. McAlpine. (4♂, CNC); 16.vii.1964. (3♂, CNC); USA, AZ, 15mi. S Sierra Vista, vii.1967, R.F. Sternitzky. (2♂, CNC); 15mi. S Sierra Vista, 2.vi.1967. (2♂, CNC); Cochise Co., 8km W Portal, 24.ix.1966, P.H. Arnaud, Jr. (1♀, CAS); 14.viii.1985. (1♂, CAS).

## 16. *Leptomorphus gracilis* Matile

(Figures 18, 57, 106, 135, 150, 153)

*Leptomorphus (Gymnoscutum) gracilis* Matile, 1977: 151.

*Leptomorphus (Gymnoscutum) elegans* Matile, 1997: 144. **new synonym.**

*Leptomorphus (Gymnoscutum) lepidus* Matile, 1997: 145. **new synonym.**

**References:** Crosskey 1980: 1221 (catalogue appendix); Matile 1997: 147–149 (figures, new records, morphological variation, key).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite, anepisternum and anepimeron yellow; scutellum brown; male genitalia with posterolateral projection (tg evg) of tergite 9 either square or with slightly acute angle on medial corner, gonostylus with shortest lobe rounded (Fig. 106).

This species can be distinguished from most other Afrotropical species by the brown scutellum and lack of small setae covering the scutum (except along dorsocentral lines). It can be separated from *L. crosskeyi* by the smaller width of the posteromedial concavity of tergite 9 and lack of a thin point on the medial corner of the tergal evagination and from *L. obscurus* by the almost square posterior margin of the tergal evaginations (Fig. 106).

**DESCRIPTION:** *Male.* (Fig. 18) **Head:** yellow, with some brown lateral spots, circular in anterior view. Antenna brown; scape light brown/dark yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel light brown, with 2 large bristles, several setae on apicodorsal margin, a number of fine setae on apicoventral margin; flagellomere 1 completely brown/ dark brown; flagellomere 6 1.6X as long as broad. Clypeus yellow to light brown, dorsoventrally elongate oval; bristles on clypeus brown, 4–6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow to light brown; shape a just longer than wide triangle, with few bristles ventrolaterally. Frons yellow, sometimes with a thin line of brown dorsally; with few bristles medioventrally, frontal furrow running full distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus with segments 1–2 yellow, remainder brown; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length of



segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae encircled by strong dark setae. Labellum yellow. Eye with inter-ommatidial setulae absent. Occiput yellow with dorsolateral brown spots, with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length 1.12 mm (0.98–1.23 mm, n = 3). Brown or dark brown dorsally, yellow laterally. Scutum dark brown/black with blue-green specks, pair of yellow mediolateral and posterolateral spots; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum brown; with 4–10 large bristles. Prescutum yellow. Mediotergite brown/dark brown with 6–8 bristles on posterolateral corners, with anteromedial patch of small setae. Laterotergite yellow; anterior margin of laterotergite not reaching katapisternum. Anepimeron yellow. Anepisternum yellow. Katapisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with brown trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** principally yellow; extreme anteroapical corner dark brown on all femora; tarsi brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2.5X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 3/4 of its length, placed basally, shortest midtibial spur 0.75X length of longest, longest midtibial spur 4.5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3.5X apical thickness of hind tibia. Foreleg first tarsomere 1.8X length of foretibia. **Wing** (Fig. 57): Length 5.1 mm (4.8 – 5.4 mm, n = 3). Hyaline; apical macula absent; medial macula absent. Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length before or after origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins fading near margin but reaching wing margin. M<sub>4</sub>-CuA fork arising apically of origin of r-m. A<sub>2</sub> faintly present as crease. **Abdomen:** Tergite and sternite 1 yellow with posteromedial dark brown square or band, remaining tergites and sternites principally dark brown, 2–5 with anterior 1/3 yellow, 6 with anterior 2/3 yellow, 7 yellow or light brown, sometimes with posterior brown band. Tergite 8 smaller than all other abdominal sclerites, with 4–8 bristles on each apicolateral corner. **Genitalia** (Fig. 106): light brown. Sternite 9 sclerotized, rounded diamond shape, 1/3 the width of genitalia at widest point, overlapping medial margin of gonocoxite. Tergite 9 longer than wide, with lateral margins slightly rounded and tapering apically into lateral ~squared off lobes with medial U-shaped indentation, two ventrally extending spines at base of posterior lobe. Gonocoxite placed basally on T9, medial margin not reaching medial line, bearing gonostylus apically. Gonostylus with two lobes both with rounded tip, dorsal lobe with broad base, ventral lobe 2X length but half the width of dorsal, gonocoxite III fused to dorsolateral margin. Aedeagus 2/3 length of T9, gradual tapering towards apex, apodemes 1/4 total length. Parameres a simple taper, apodemes ~3/4 length of parameres.

*Female.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Central African Republic and Gabon (Fig. 135), 200–520 masl.

**DISCUSSION:** Examination of the holotype specimens of *Leptomorphus elegans* and *L. lepidus* showed no significant differences between these species and *L. gracilis*. *Leptomorphus elegans* and *L. lepidus* are therefore considered new synonyms of *L. gracilis*. As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Gymnoscutum* and placed solely in *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult male, pinned on double mount minuten, genitalia in glass vial on pin, labelled “[Blue label] REP. CENTRAFRIC./ LA MABOKE/ 29.VIII.1967/ L. MATILE rec.; [Red label] HOLOTYPE; Leptomorphus/ (Afroleptomorphus)/ gracilis n. sp. ♂ht/ L. Matile det. 1974; HOLOTYPE ♂/ *Leptomorphus gracilis*/ Matile/ Det. C.J. Borkent, 2012” [MNHN].

*Other material:* GABON, Makokou M’Passa, Bale Affl., 7–16.v.1979, J. Legrand (1♂, MNHN, HT of *L. elegans*); same except 21–28.v.1979, (1♂, MNHN, HT of *L. lepidus*).

**17. *Leptomorphus grjebinei* Matile**

(Figures 19, 58, 105, 134, 150, 153)

*Leptomorphus (Austroleptomorphus) grjebinei* Matile, 1977: 154.**References:** Crosskey 1980: 1221 (catalogue appendix); Matile 1997: 149 (key).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: a thick medial yellow line on the otherwise brown scutum; foretibia with dense row (comb) of short anteroventral bristles; missing wing vein sc-r, male genitalia with gonostylus only a single lobe, apical tergal evaginations present (Fig. 105). This is also the only species known from Madagascar.

This species can be distinguished from other Afrotropical species by the presence of small setae on the entire surface of the scutum (not just restricted to dorsocentral lines and lateral margins).

**DESCRIPTION:** *Male.* (Fig. 19) **Head:** yellow, somewhat dorsoventrally compressed in anterior view. Antenna brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae absent; pedicel yellow, with 1 large bristle, few setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base light brown remainder light brown; flagellomere 6 1.4X as long as broad. Clypeus yellow, square; bristles on clypeus brown, 4–6 strong bristles on ventral margin directed ventrally, a number of bristles on remainder (almost in rows) all directed medioventrally, clypeus 1.1X as long as face. Face yellow; shape a just longer than wide triangle, bare. Frons yellow; with 3–4 bristles medially, frontal furrow running 1/2 distance from dorsal margin towards ventral margin, frontal cleft running to lateral ocellus. Palpus with segments 1–2 yellow, 3–5 light brown; segment 1 hidden behind eye, segments 2–4 subequal, segment 5 1.5X length of segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae weakly encircled by strong dark setae. Labellum yellow. Eye with inter-ommatidial setulae absent. Occiput yellow with appressed, anteriorly directed setae. Ocelli with median slightly in front of laterals, space between ocelli less than diameter of laterals, lateral ocelli 3X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.23 mm (n = 1). Brown dorsally, yellow laterally. Scutum anterior margin and inverted medial triangle yellow/white as well as posterior corners and central lateral spot, two dark brown spots posterolaterally only reaching lateral margin at wing base; surface of scutum covered with small setae; acrostichal setae absent; single dorsocentral seta present anteriorly; single row of lateral setae present; patch of setae on scutum at wing base small. Scutellum yellow; with 2 large bristles and many small bristles. Prescutum yellow. Mediotergite brown with medial line lighter with 6–12 bristles on posterolateral corners. Laterotergite yellow; anterior margin of laterotergite not reaching katepisternum. Anepimeron yellow. Anepisternum yellow. Katepisternum yellow with small brown spot anterodorsally. Anteprepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with light brown and yellow trichia respectively. Metepisternum white. Anapleural suture straight but faint. Halter stem brown, knob white. **Legs:** principally yellow; extreme anteroapical corner yellow on forefemur, on other femora dark brown; hind tibia light brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with remnant of comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 2/3 of its length, placed centrally, shortest midtibial spur subequal to length of longest, longest midtibial spur 4X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3.5X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 58): Length 5.2 mm (n = 1). Hyaline; apical macula absent; medial macula absent. Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r absent. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex just before R<sub>5</sub>, apices of M veins reaching wing margin. M<sub>4</sub>-CuA fork arising after apex of r-m. A<sub>2</sub> absent. **Abdomen:** Tergites 1 brown, T2–6 brown with lateral yellow spots, T7 with anterior 1/2 brown remainder yellow. Tergite 8 smaller than all other abdominal sclerites, with 3–4 bristles on each apicolateral corner. **Genitalia** (Fig. 105): yellow. Sternite 9 not clearly visible possibly due to condition of specimen. Tergite 9 as wide as long, widening apically into lateral process bearing two points and medial square-shaped indentation. Gonocoxite placed basally on T9, medial margin reaching medial line, bearing gonostylus apically. Gonostylus a single broad-based lobe tapering to a point apically, gonocoxite III fused to dorsolateral margin. Aedeagus 4/5 length of gonocoxite, tapering towards apex (slight central swelling), apodemes 1/3 total length. Parameres a simple taper, apodemes ~4/5 length of parameres.

*Female.* As for male, except as follows. **Thorax:** Length 1.19 mm (1.15–1.23 mm, n = 2). **Wing:** Length 5.0 mm (4.6–5.5 mm, n = 2). **Abdomen:** Sternites white/yellow. Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Eastern rainforests of Madagascar (Fig. 134), 1000–1100 masl.

**DISCUSSION:** The female specimen from near Ranomafana has less dark brown on its thorax and tergites than the other specimens. As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Austroleptomorphus* and placed solely in *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult male, pinned on double mount minuten, genitalia in glass vial on pin, labelled “[MADAGASCAR] Madagascar Nord/ Montagne d’Ambre [Ambohitra] 1000m/ det Diego-Suarez/ 23.XI–4.XII.[19]57, B. Stuckenberg; [Red label] HOLOTYPE; Leptomorphus/ (Austroleptomorphus)/ grjebinei n. sp. ♂ht/ L. Matile det. 1974” [MNHN].

*Paratypes:* Same data as holotype (1 ♀, labelled as Allotype, MNHN).

*Other material:* MADAGASCAR, Prov. Fianarantsoa, 7km W Ranomafana, 1100m, 1–7.XI.1988, W.E. Steiner (1 ♀, USNM).

### 18. *Leptomorphus hyalinus* Coquillett

(Figures 20, 59, 107, 126, 132, 149, 150, 152)

*Leptomorphus hyalinus* Coquillett, 1901: 598.

*Leptomorphus ypsilon* Johannsen, 1912: 265. **new synonym.**

**References:** Aldrich 1905: 143 (catalogue); Johnson 1910: 724 (NJ, reported as *L. walkeri* [specimen seen]); Johannsen 1909:72 (catalogue), 1912: 250, 252, 264–266, 323, 327, Fig. 177 (key, re-description, wing); Johnson 1925: 82 (NH); Brimley 1938: 327 (NC); Shaw 1946: 156–7 (comparison to *L. nebulosus*); Shaw & Fisher 1952: 192 (key to species, NH, NJ, NY, RI); Laffoon 1965: 223 (catalogue); Khalaf 1971: 19 (MS, reported as *L. ypsilon*); Matile 1977: 144 (subgeneric placement); Poole and Gentili, 1996: 194 (catalogue); Bertone *et al.* 2008: 674 (exemplar in molecular phylogeny).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite, anepisternum and anepimeron yellow; scutellum brown; gonostylus with single large, hook-tipped lobe (Fig. 107).

This species can be distinguished from most other Nearctic species by the lack of  $R_4$ . It can be separated from *L. furcatus* based on the dark brown scutellum, the lack of setae on the surface of the scutum (with exception of dorsocentral setae) and the basally placed gonocoxites (Fig. 107).

**DESCRIPTION:** *Male.* (Fig. 20) **Head:** brown dorsally yellow ventrally, circular in anterior view. Antenna with basal 2–3 flagellomeres lighter brown, darkening apically; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 1–2 large bristles, few small setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base light brown remainder light brown; flagellomere 6 1.7X as long as broad. Clypeus yellow, slightly laterally compressed oval; bristles on clypeus brown, strong bristles on ventral half, smaller bristles on entire surface, all directed ventrally or medioventrally, clypeus 2X as long as face. Face yellow to brown; shape a just longer than wide triangle, with few bristles ventrolaterally. Frons brown to dark brown; bare, frontal furrow running 3/4–full distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus yellow to brown; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length of segment 4 with central portion somewhat thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput brown with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.19 ± 0.19 mm (0.98–1.35 mm, n = 10). Dark brown dorsally, yellow laterally. Scutum ranging from dark brown with antero- medio- and posterolateral yellow spots, to yellow with spot at wing base and thick Y-shape originating posteriorly both dark brown; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine

setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum dark brown; with 6–8 large bristles and many small bristles. Prescutum yellow. Mediotergite light brown to brown with 16–24 bristles on inverted U, few medially. Laterotergite yellow; anterior margin of laterotergite not reaching katepisternum. Anepimeron yellow. Anepisternum yellow. Katepisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter with tip of knob brown, remainder yellow. **Legs:** principally yellow; extreme anteroapical corner light brown on forefemur, on other femora dark brown. Midfemur without apical spine-like process. Tibia with covering of yellow macrotrichia, foretibia without comb of short setae along length of anteroventral surface, yellow to light brown, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 2/3 of its length, placed basally, shortest midtibial spur 0.75X length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.5X length of foretibia. **Wing** (Fig. 59): Length  $5.3 \pm 0.9$  mm (4.7–6.1 mm, n = 10). Hyaline; apical macula absent or, if present, very light; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R at 2–3X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins thinning towards wing margin. M<sub>4</sub>-CuA fork arising well before origin of r-m. A<sub>2</sub> absent. **Abdomen:** Tergites principally yellow, T1 light to dark brown, T2–7 with posterior 1/3–1/2 ranging from light to dark brown. Tergite 8 smaller than other abdominal sclerites, with 5–15 bristles on each apicolateral corner. **Genitalia** (Fig. 107): light yellow. Sternite 9 membranous. Tergite 9 longer than wide oval tapering apically into two short rounded lobes and shallow medial indentation. Gonocoxite placed basally on T9, medial margins not touching, apicomedial lobe covering base of gonostylus, apicolateral corner with medial facing surface covered in short, thick setae, bearing gonostylus on apical 1/3. Gonostylus a single broad-based lobe tapering towards pointed, dorsally pointing apex, gonocoxite III fused to dorsolateral margin. Aedeagus 4/5 length of gonocoxite, swelling from base to middle and then tapering towards apex, apodemes 1/10 total length. Parameres a simple taper (sometimes with a secondary bump or step at half the length), apodemes ~1.3X length of parameres.

*Female.* As for male, except as follows. **Thorax:** Length  $1.3 \pm 0.22$  mm (1.07–1.48 mm, n = 10). **Wing:** Length  $6.1 \pm 1.5$  mm (4.3–6.9 mm, n = 8). **Abdomen:** Cercus yellow.

*Immatures.* Undescribed.

**BIOLOGY:** Larvae were found feeding under the brackets of *Cerrena unicolor* (Fig. 126), a soft polypore that grows on dead wood. The larvae pupate under these same brackets or adjacent to them on the underside of the dead log. The pupae hang from a line attached near their head and hind end (Fig. 132), usually forming a hammock. Over several hours of observation of the numerous pupae at a single site, no males guarding pupae were found. More than 80 immatures were collected over the course of 1.5 weeks from the fungi on a single log and reared to adulthood. Many of the pupae produced hymenopteran parasitoids (*Orthocentrus* sp. (Ichneumonidae: Orthocentrinae) and a species of Diapriidae).

**DISTRIBUTION:** Alaska and BC east to Maine and Florida (Fig. 149), 5–915 masl.

**DISCUSSION:** The colour of the scutum ranges from completely dark brown to a dark brown background with a yellow Y-shape. This colour difference led to the description of *L. ypsilon* by Johannsen (based on our examination of the type). However all specimens agree in the shape of the components of the male genitalia. There is some variation in the shape of parameres ranging from a single spine to a spine with a secondary rounded lobe arising a third of the distance from the apex. However, this variation was not associated with any other particular morphology, coloration, or distribution.

As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Leptomorphus* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult male, pinned, labelled “White Mts./ Morrison.; [red label] Type/ No. 5451/ U.S.N.M.; *Leptomorphus/ hyalinus/ Coq.*; HOLOTYPE ♂/ *Leptomorphus hyalinus/ Coquillett / Det. C.J. Borkent, 2012*” [USNM].

*Other material:* CANADA, BC, Hixon, 10.viii.1966, E.D.A. Dyer. (1♂, CNC); MB, Aweme, 18.viii.1912, E. Criddle. (1♀, ANSP); ON, 7.5km W Carleton Place, 14.x.2000, L. Masner. (2♀, CNC); Lancaster, 1.vii.2003, R.



Zeran. (1♀, LEM); Ottawa, 1.ix.1968, J.R. Vockeroth. (1♂, CNC); 1.ix.1993. (1♂, CNC); 23.ix.1993. (1♂, CNC); Tobermory, Dunk's Bay, 12.viii.1996, S.A. Marshall. (1♂, DEBU); Bruce Co., Dunk's Bay, 25.viii–1.ix.2005, S.A. Marshall. (1♀, DEBU); QC, 2.3km SSW Rapide-Danseur, 29.vi–28.vii.2007, A. Hibbert. (3♂, 1♀, LEM); 30.vi–29.vii.2007. (3♂, 1♀, LEM); 27.v–29.vi.2007. (1♂, LEM); Lake Duparquet Res. and Train. For., 11–31.vii.2006, A. Hibbert. (1♂, 2♀, LEM); 19.vi–11.vii.2006. (1♀, LEM); Old Chelsea, 2.vii.1959, J.R. Vockeroth. (1♀, CNC); Ste-Anne-de-Bellevue, Morgan Abrtm., 12.vii.2007, C.J. Borkent. (1♂, LEM); 17.vii.2007. (9♂, 4, LEM); 18.vii.2007. (5♂, 7, LEM); 21.ix.2007. (1♀, LEM); 20.viii.2008. (1♀, LEM); Terrasse-Vaudreuil, Molson Reserve, 15–18.vii.1999, S.E. Brooks. (1♂, LEM); USA, AK, 11mi. S Anderson Jct., Rte 3mi. 270, 23.vi–11.viii.1984, S. & J. Peck. (1♀, CNC); FL, Flamingo, 4.vi.1963, G.R. Sutter. (1♂, ISUI); Gainesville, 8–22.xii.1986, W. Mason. (2♂, 1♀, CNC); IA, Ames, 1.xi.1946, D.E. Hardy. (1♂, ISUI); Sioux City, 5.ix.1949, J.L. Laffoon. (1♀, ISUI); 8.ix.1951. (2♂, 1, ISUI); Boone Co., Ledges State Park, 13.x.1950, J.L. Laffoon. (1♂, ISUI); 18.ix.1951. (1♂, ISUI); 3.vii.1961. (1♂, ISUI); Polk Co., Alleman, 27.viii.1952, J.L. Laffoon. (1♂, ISUI); Van Buren Co., Lacey–Keosauqua St. Pk., 9.ix.1949, J. Laffoon, J. Slater. (1♂, ISUI); 10.ix.1949. (1♂, ISUI); IN, La Fayette, 18.viii.1916, J.M. Aldrich. (1♀, USNM); KS, Riley Co., Manhattan, 14.vi.1968, G.F. Hevel. (1♂, USNM); MA, Barre, 16.ix.2008, C. Eiseman. (1♀, LEM); MD, Laurel, 25.vi.1965. (1♂, CNC); Plummers Island, 21.vii.1971, K.V. Krombein. (1♂, USNM); ME, York Co., West Lebanon, 31.vii–6.viii.1990, D.W. Barry. (1♂, UNHC); 11–17.ix.1990. (1♀, UNHC); MN, Clearwater Co., Lake Itasca, 3.ix.1950, J.L. Laffoon. (1♀, ISUI); MO, Wayne Co., Williamsville, x.1987, J. Becker. (3♀, CNC); NC, Looking Glass Rock Nr. Pisgah Forest, 19.vii.1957, J.G. Chilcott. (1♂, CNC); Rainbow Falls, Gr. Sm. Mtns N.P., 28.v.1999, L. Quate. (1♂, CNC); NH, Jefferson Notch, 20.vii.1961, W.W. Wirth. (1♀, USNM); Rock. Co., Seabrook, Backdunes, 7–12.vii.1989, D.S. Chandler. (1♂, UNHC); NJ, Trenton, 23.viii.1909. (1♀, USNM); NY, Ft. Montgomery, 16.ix.1923, F.M. Schott. (1♂, MCZ); Ithaca, (1♂, 1♀, types of *L. ypsilon*, CUIC); Poughkeepsie, 23.viii.1936, H.K. Townes. (1♂, ANSP); OH, Summit Co., 28.viii.1937, L.J. Lipovsky. (1♀, SEMC); SC, Anderson Co., Pendleton, Tanglewood Sprg., x.1987, J. Morse. (2♂, 1♀, CNC); 30.viii.1987. (1♂, CUAC); TN, Sevier Co., Twin Creeks, 14–29.viii.2006, J. Gulbransen. (3♂, 1♀, LEM); 31.vii–15.viii.2006. (2♀, LEM).

### 19. *Leptomorphus magnificus* (Johannsen)

(Figures 21, 60, 86, 108, 145, 150, 154)

*Diomonus magnificus* Johannsen, 1910: 155.

*Leptomorphus subcaeruleus magnificus*: Shaw, 1947: 157.

*Leptomorphus magnificus*: Laffoon, 1965: 223.

*Leptomorphus (Diomonus) magnificus*: Matile, 1977: 146.

**References:** Johnson 1925: 80 (distribution: MA, NH); Shaw & Fisher 1952: 192 (key to species, NY); Laffoon 1965: 223 (catalogue); Cole & Schlinger 1969:120 (distribution: WA); Matile 1977: 146 (subgeneric placement); Poole and Gentili, 1996: 194 (catalogue).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with  $R_4$  that has a completely yellow/orange thorax and abdomen (though abdomen rarely darker on posterior two segments) and foretarsomere I at least 1.5X the length of foretibia.

This species is most easily confused with either the light form of *L. nebulosus* (Fig. 27) or *L. perplexus* (Fig. 32). It can be distinguished from the former by the lack of any dark markings on the scutum and the monochromatic antennae (Fig. 21). It differs from the latter species by the brown head, the slightly concave  $R_5$  wing vein (Fig. 60, rather than sinusoidal, Fig. 69), the presence of wing spots, and the placement of the ocelli in a cluster more than their own diameter away from the eye margin.

**DESCRIPTION: Male.** (Fig. 21) **Head:** dark brown to black, somewhat dorsoventrally compressed in anterior view. Antenna with basal half yellow, brown apically (some with completely brown); scape light to dark yellow, with yellow setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel light brown/yellow, with 3–4 large bristles, several setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base yellow remainder either yellow or brown; flagellomere 6 1.9X as long as broad. Clypeus yellow to light brown, circular, strongly protruding; bristles on clypeus brown, both strong, smaller bristles on entire surface, all directed

ventrally, clypeus 1.5X as long as face. Face yellow to light brown; shape a slightly wider than tall triangle, covered with many strong bristles. Frons dark brown; bare, frontal furrow running 1/4 distance from dorsal margin towards ventral margin, frontal cleft initially running to lateral ocellus then barely in front of median ocellus. Palpus yellow (segments 4–5 lighter); segment 1 small but visible below eye, segments increasing in length, segment 5 subequal in length to segment 4 with even width from base to apex, segment 3 appears to have large lateral patch of fine yellow setae not clearly delimited. Labellum light brown. Eye with a number (in ~1/4 of the ommatidial junctions) of long inter-ommatidial setulae scattered on posterior half. Occiput dark brown with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli 1–1.5X diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length  $2.03 \pm 0.48$  mm (1.64–2.46 mm, n = 10). Scutum yellow; surface of scutum covered with small setae; acrostichal setae absent; dorsocentral setae present as complete multiple lines of setae; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 6–8 large bristles and many small bristles. Prescutum yellow. Mediotergite yellow with 18–24 bristles on posterolateral corners, absent. Laterotergite yellow; anterior margin of laterotergite not reaching katapisternum. Anepimeron yellow. Anepisternum yellow. Katapisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with light brown trichia. Metepisternum yellow. Anapleural suture straight and clear. Halter stem yellow, knob light brown. **Legs:** principally yellow; extreme anteroapical corner dark brown on all femora. Midfemur with apical spine-like process. Tibia with covering of yellow macrotrichia, foretibia without comb of short setae along length of anteroventral surface (Fig. 86), tibial spurs yellow, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 4/5 of its length, placed centrally, shortest midtibial spur 0.75X length of longest, longest midtibial spur 3.5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3.5X apical thickness of hind tibia. Foreleg first tarsomere 1.3X length of foretibia. **Wing** (Fig. 60): Length  $7.7 \pm 1.5$  mm (6.6–9.1 mm, n = 10). Hyaline; apical macula brown, only on anterior third of wing, beginning halfway along  $R_5$  but not reaching wing tip; medial macula extending from Sc to stem of  $M_{1+2}$  with some light brown in cell cua. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) all the same length. Calypter bare. Vein sc-r present, apical end joining R within its own length before or after origin of  $R_s$ .  $R_4$  present.  $R_5$  slightly concave for entire length.  $M_1$  reaching apex before  $R_5$ , apices of M veins clearly reaching wing margin.  $M_4$ -CuA fork arising before origin of r-m.  $A_2$  faintly present as crease. **Abdomen:** Tergites yellow, hind margin of T3–6 dark orange. Tergite 8 smaller than all other abdominal sclerites and covered with many bristles. **Genitalia** (Fig. 108): orangish yellow. Sternite 9 lightly sclerotized, rounded rectangle, 2/3 the length of T9 but wider than genitalia. Tergite 9 as wide as long, with basal half of lateral margins parallel, remainder tapering to rounded medial apex. Gonocoxite placed apically on T9, tapering to a point on apicolateral margin, medial margin not reaching medial line, bearing gonostylus basally. Gonostylus a single lobe tapering towards apex and bearing several setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus 1.5X length of T9, tapering to middle and then bifurcated into two lateral sclerotized sickle-like hooks with serrated tips, apodemes sclerotized and 1/7 total length. Parameres a swollen lobe with apex covered in small spines, apodemes 1/4 length of parameres and strongly united with gonocoxal apodemes.

*Female adult.* As for male, except as follows. **Thorax:** Length  $2.13 \pm 0.62$  mm (1.39–2.46 mm, n = 10). **Wing:** Length  $8.0 \pm 1.1$  mm (7.2–8.7 mm, n = 10). **Legs:** Midfemur without apical spine-like process. **Abdomen:** Cercus dark yellow.

*Immatures:* Unknown.

**BIOLOGY:** Unknown, though likely similar to that of *L. nebulosus* and *L. subcaeruleus*.

**DISTRIBUTION:** Mid-western Quebec and Ontario south to Georgia, and from Maine east to Indiana (Fig. 145), 5–1160 masl.

**DISCUSSION:** None of the specimens (number unknown) from the three locations listed in the original description (Johannsen 1910) were designated as the holotype. A lectotype is therefore designated even though labels indicating holotype etc. were present on the pins when donated to the CUIC (J. Liebherr, Pers. Comm.).

As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Diomonus* and placed solely in *Leptomorphus*.

**MATERIAL EXAMINED:** *Lectotype:* adult male, pinned, labelled “[USA] Ithaca, N.Y.; [left margin with red stripe] ♂ HOLOTYPE/ *Diomonus/ magnificus/* Johannsen; [red label] HOLOTYPE/ Cornell U./ No. 1969; LECTOTYPE ♂/ *Leptomorphus magnificus/* (Johannsen)/ Det. C.J. Borkent, 2012” [CUIC]

*Paralectotypes*: [all with paralectotype labels by C.J. Borkent] labelled as for holotype except 1.vii, (1♀, labelled as allotype, CUIC); OH, Salineville (1♀, labelled as paratype, CUIC); MA, Mt. Greylock, 8.viii.[19]07, O. Bryant (1♂, labelled as cotype, MCZ (originally in the Boston Society of Natural History collection)).

*Other material*: CANADA, ON, Algonquin Park, Swann Lake, 11–21.vii.1994, E.R. Barr. (1♂, DEBU); 15–31.vii.1994. (1♂, DEBU); Bala, 19.vii.1932, A.S. Walley. (1♀, CNC); Rondeau Park, 18.vii.1962, S.M. Clark. (1♀, CNC); Bruce Co., Little Cove, 4.ix.2004, S.A. Marshall. (1♂, DEBU); Elgin Co., Fingal Wildlife Management Area, 21.vi.1992, I. Carmichael. (1♂, CNC); QC, 2.3km SSW Rapide-Danseur, 28.v–30.vi.2007, A. Hibbert. (1♂, LEM); Mont St-Hilaire, 2–8.vii.2001, E. Fast. (1♂, LEM); 18–24.ix.2001. (3♂, LEM); 1–8.vii.2008, V. Levesque. (2♂, LEM); 14–21.vii.2008. (1♂, LEM); 21–28.vii.2008. (1♂, LEM); 22–29.vii.2008. (1♂, LEM); 24.vi–1.vii.2008. (1♂, LEM); 30.vi–7.vii.2008. (1♂, 1♀, LEM); Old Chelsea, 18.vii.1987, L. Masner. (1♀, CNC); Rougemont, 7–14.vii.2008, V. Levesque. (1♂, 1♀, LEM); 14–21.vii.2008. (1♂, LEM); 30.vi–7.vii.2008. (3♂, 2♀, LEM); Masham Twp., Duncan Lake, ix.1977, D.M. Wood. (1♀, CNC); 24–30.viii.2000. (1♂, LEM); USA, CT, Redding, 9.viii.1938, A.L. Melander. (1♀, USNM); GA, Union Co., Neels Gap, 21.vi.1967, G.W. Byers. (1♂, SEMC); IN, LaPorte Co., Michigan City (E. edge), 3.vii.1968, G.W. Byers. (1♂, SEMC); Owen Co., McCormick's Cr., 26.vi.1950, G.W. Byers. (2♂, SEMC); Parke Co., Turkey Run St. Pk., 10.vi.1951, G.W. Byers. (1♀, SEMC); MA, Montgomery, 24.viii.1896. (1♀, USNM); Petersham, vi.1941. (1♀, MCZ); ME, York Co., West Lebanon, 28.viii–3.ix.1990, D.W. Barry. (1♂, UNHC); NC, Highlands, 21.vi.1957, J.R. Vockeroth. (1♀, CNC); NH, Glen House, 19.vii.1915. (1♀, MCZ); Carr. Co., 1mi. N Wonalancet, E Fk., Spring Brk., 18–31.x.1985, D.S. Chandler. (1♂, UNHC); 14–21.viii.1985. (2♂, UNHC); 22–28.viii.1985. (1♂, 1♀, UNHC); 18.ix–1.x.1985. (1♂, UNHC); 2.5mi. NW Wonalancet, 21–27.vi.1984, D.S. Chandler. (1♂, UNHC); 12–19.vii.1984. (4♂, 1♀, UNHC); 27.vii–1.viii.1984. (1♂, UNHC); 2–10.viii.1984. (1♂, UNHC); 11–16.viii.1984. (2♂, UNHC); 17–22.viii.1984. (2♂, UNHC); 23.viii–1.ix.1984. (3♂, UNHC); 2–17.ix.1984. (2♂, UNHC); 14–21.vi.1985. (1♂, UNHC); 11–17.vii.1985. (1♂, UNHC); 18–23.vii.1985. (1♂, UNHC); 24–30.vii.1985. (3♂, UNHC); 31.vii–6.viii.1985. (2♂, UNHC); Grafton Co., Bridgewater, Newfound Lk., Whitmore Pt., 23–25.vii.1994, S.D. Gaimari. (1♂, CSCA); Rock. Co., 1mi. W Odiorne Pt., 22–24.vi.1983, D.S. Chandler. (1♂, UNHC); Odiorne Pt, 16–20.ix.1983, D.S. Chandler. (1♂, UNHC); Straf Co., 1mi. SW Durham, 24.vii–6.viii.1987, D.S. Chandler. (1♂, UNHC); 30.ix.1987. (1♂, UNHC); 8.x.1990, W.J. Morse. (1♂, UNHC); 4mi. W Durham, 2–5.viii.1982, R.M. Reeves. (1♂, UNHC); Durham, 29.viii.1978, W.J. Morse. (1♂, UNHC); Spruce Hole, 3mi. SW Durham, 24.vii–6.viii.1987, D.S. Chandler. (1♂, UNHC); 15.x–4.xi.1987, D.S. Chandler. (1♂, UNHC); NY, Accord, viii.1959, F. Hough. (1♂, USNM); Beaver Creek, McLean Res., 30.viii.1924. (1♀, CUIC); Hamburg, 8.vi.1908, M.C. VanDuzee. (1♂, CAS); Irving, 30.vi.1918, M.C. VanDuzee. (1♂, CAS); Ithaca, 16.viii.1898. (1♀, CUIC); 2.vii.1915. (1♀, CUIC); 15.viii.1928, A.L. Melander. (1♀, ANSP); 17.ix.1936, H.K. Townes. (1♂, ANSP); O.A. Johannsen. (1♀, CUIC); S. Wales, 9.vii.1911, M.C. VanDuzee. (1♀, CAS); West Point, 4.ix.1927, W. Robinson. (1♂, 1♀, USNM); Albany Co., Huyck Preserve, Rensselaerville, 3.vii.1968, W.G. M.J. Eberhard. (3♂, MCZ); 9.vii.1968, W.G. M.J. Eberhard. (1♀, MCZ); Greene Co., Onteora Mt., 26.vii.1929, L.O. Howard. (1♂, USNM); Greene Co., viii.1910. (1♀, CMNH); PA, Hazleton, 12.ix.1917, Dietz. (1♀, ANSP); Allegheny Co., Pittsburgh, Mt Troy, 18.vi.1970, J. Bauer. (1♂, CMNH); Centre Co., Bear Meadows, 11.ix.1979, P.H. Adler. (1♂, USNM); Forest Co., 5km SE Marienville, 22.ix.1993, J. Rawlins, W. Zanol. (2♂, SEMC); Warren Co., 2.2km NW Truemans, 12.vii.1994, M. Ricke. (3♂, CMNH); 12.vii.1994, M. Ricke. (1♂, SEMC); 4.6km ESE Donaldson, Tionesta Scenic Area, 27.ix.1994, W. Metheny. (2♂, CMNH); Westmor. Co. (1♂, CMNH); SC, Oconee Co., Coley Cr., 15–16.vi.1987, Hamilton; Hoffman. (1♂, CUAC); TN, Sevier Co., Twin Creeks, 31.vii–15.viii.2006, J. Gulbransen. (1♀, LEM); VT, Dorset, vii.1962, C. Parsons. (1♀, MCZ); WV, Cheat River. (1♂, CMNH).

## 20. *Leptomorphus mandelai* Borkent, new species

(Figures 23, 61, 87, 109, 134, 150, 153)

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite, anepisternum and anepimeron yellow; scutellum yellow; scutum mostly dark brown with yellow restricted to anterior and lateral margins; abdomen with tergite 7 brown (Fig. 23); male genitalia with tergal evagination bearing ventrally-directed fold along most of posterior margin and small point on apicomedial corner (Fig. 109).

This species can be distinguished from other Afrotropical species by the yellow scutellum, brown tergite 7 (Fig. 23), and lack of small setae covering the scutum (except along dorsocentral lines).

**DESCRIPTION:** *Male.* (Fig. 23) **Head:** yellow, somewhat dorsoventrally compressed in anterior view. Antenna brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae absent; pedicel yellow, with 2 large bristles, several setae on apicodorsal margin, a few fine setae on apicoventral margin; flagellomere 1 with tapered base light brown remainder brown; flagellomere 6 1.5X as long as broad. Clypeus ivory, slightly laterally compressed oval; bristles on clypeus light brown, 6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2.5X as long as face. Face ivory; shape a slightly wider than tall triangle, with few bristles ventrolaterally. Frons yellow; with few bristles medioventrally, frontal furrow running full distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus yellow; segment 1 small but visible below eye, segments increasing in length, segment 5 2X length of segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae weakly encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.52 mm (n = 1). Dark brown dorsally, yellow laterally. Scutum dark brown with blue-green specks, anteromedial spot and pair of mediolateral and posterolateral spots yellow; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as complete multiple lines of setae; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 8 large bristles and many small bristles. Prescutum yellow. Mediotergite yellow with 12 bristles on posterolateral corners, anteromedial patch of small bristles. Laterotergite yellow; anterior margin of laterotergite not reaching katepisternum. Anepimeron yellow. Anepisternum yellow. Katepisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with light brown trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter yellow. **Legs:** principally yellow; extreme anteroapical corner dark brown on all femora. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface (Fig. 87), hind tibial spur yellow, remainder brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 3/4 of its length, placed centrally, shortest midtibial spur 0.85X length of longest, longest midtibial spur 4.7X apical thickness of midtibia, shortest hind tibial spur 0.8X length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 61): Length 6.5 mm (n = 1). Hyaline; apical macula absent; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining R within its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins thinning towards wing margin. M<sub>4</sub>-CuA fork arising before origin of r-m. A<sub>2</sub> faintly present as crease. **Abdomen:** Tergites 1 yellow, T2 yellow with posterodorsal triangular brown spot, T3-6 anterior 1/2-3/4 yellow, remainder brown. Sternites yellow. Tergite 8 smaller than all other abdominal sclerites, with ~10 bristles on each apicolateral corner. **Genitalia** (Fig. 109): yellow. Sternite 9 sclerotized rounded square, 1/2 the width of genitalia at widest point, just overlapping medial margin of gonoxite. Tergite 9 longer than wide, margins ~parallel except for slight taper at apex, ending apically in lateral squared off dorsoventrally flattened lobe with small ventrally directed fold and short medially placed spine and medial U-shaped indentation, a ventrally extending point at base of posterior lobe. Gonocoxite placed basally on T9, medial margin not reaching medial line, bearing gonostylus apically. Gonostylus with two lobes, dorsal lobe a broad based point, ventral lobe half the width of dorsal but 2.5X length and barely tapering until apex, gonocoxite III fused to dorsolateral margin. Aedeagus 0.9X length of gonocoxite, tapering towards apex (slight central swelling), apodemes 1/5 total length. Parameres a simple taper, apodemes ~3/4 length of parameres.

*Female adult.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** South Africa (Fig. 134), 1325 masl.

**ETYMOLOGY:** This species is named in honour of former South African President Nelson R. Mandela, in recognition of his role in ending apartheid in South Africa and for his advocacy of peace, reconciliation and social justice.



**MATERIAL EXAMINED:** *Holotype*: here designated, adult male, pinned with genitalia in plastic vial on pin, labelled “RSA [South Africa]: KwaZulu-Natal/ Howick district, Karkloof Range/ Geekie’s Farm (28.16°S, 30.21°E):/ 29.11–9.111.2000. Malaise trap./ W. BARKEMEYER; HOLOTYPE ♂/ *Leptomorphus mandelai* / Borkent, new species / Det. C.J. Borkent 2012” [NMSA].

## 21. *Leptomorphus medleri* Matile

(Figures 22, 62, 110, 136, 150, 153)

*Leptomorphus (Gymnoscutum) medleri* Matile, 1977: 152.

**References:** Crosskey 1980: 1221 (catalogue appendix); Matile 1997: 146, 148, 149 (figures, new records, morphological variation, key).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite, anepisternum and anepimeron yellow; scutum with prealar brown spots or band only (Fig. 22); scutellum yellow; male genitalia with lateral lobes of tergal evagination gradually tapering to a medial point; sternite 9 a posteriorly directed triangle (Fig. 110).

This species can be distinguished from other Afrotropical species by the mostly yellow scutum (brown prealar spots or band present), yellow scutellum and tergite 7 (Fig. 22), and lack of small setae covering the scutum (except along dorsocentral lines).

**DESCRIPTION:** *Male.* (Fig. 22) **Head:** yellow, circular in anterior view. Antenna brown; scape yellow, with yellow setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae absent; pedicel yellow, with 1 large bristle, several setae on apicodorsal margin, several fine setae on apicoventral margin; flagellomere 1 with tapered base yellow remainder brown; flagellomere 6 1.4X as long as broad. Clypeus yellow, dorsoventrally elongate oval; bristles on clypeus yellow, 6–8 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow; shape a just longer than wide triangle, with few bristles ventrolaterally. Frons yellow; bare, frontal furrow running 1/3 distance from dorsal margin towards ventral margin, frontal cleft usually running to lateral ocellus though some with unconnected portion crossing frontal furrow just in front of median ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 2.5X length of segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length  $1.01 \pm 0.2$  mm (0.9–1.19 mm, n = 10). Yellow with two posterolaterodorsal brown spots. Scutum yellow with a central transverse brown band (sometimes split into two lateral spots); surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 6–8 large bristles and many small bristles. Prescutum yellow. Mediotergite yellow with 8–12 bristles on posterolateral corners, few medially. Laterotergite yellow; anterior margin of laterotergite not reaching katepisternum. Anepimeron yellow. Anepisternum yellow. Katepisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter yellow. **Legs:** principally yellow; extreme anteroapical corner dark brown on all femora. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs yellow, foretibial spur length 2.5X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 3/4 of its length, placed centrally, shortest midtibial spur 0.72X length of longest, longest midtibial spur 6X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 4.5X apical thickness of hind tibia. Foreleg first tarsomere 1.5X length of foretibia. **Wing** (Fig. 62): Length  $4.9 \pm 0.8$  mm (4.2–5.4 mm, n = 10). Hyaline; apical macula absent or, if present, very light, restricted to apical 1/4 of cell  $r_1$ ; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short.

Calypter with group of macrotrichia. Vein sc-r present, apical end joining R at 2X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins fading before wing margin. M<sub>4</sub>-CuA fork arising well before origin of r-m. A<sub>2</sub> faintly present as crease. **Abdomen:** Tergites principally yellow. T3–6 with posterior 1/5–1/4 brown. Tergite 8 smaller than all other abdominal sclerites, with 6–8 bristles on each apicolateral corner. **Genitalia** (Fig. 110): yellow. Sternite 9 sclerotized, rounded triangle, 1/3 the width of the genitalia at widest point, overlapping medial margin of gonocoxite. Tergite 9 longer than wide, with basal 3/4 of lateral margins parallel then tapering into two pointed lobes with medial U-shaped indentation, a ventrally extending point at base of posterior lobe. Gonocoxite placed basally on T9, medial margin just not reaching medial line, bearing gonostylus on apical 1/3. Gonostylus with two lobes, dorsal lobe shortest and broad, ventral lobe prominent but half the width of dorsal, gonocoxite III fused to dorsolateral margin. Aedeagus 0.85X length of gonocoxite, tapering towards apex (slight central swelling), apodemes 1/4 total length. Parameres a simple taper, apodemes ~3/4 length of parameres.

*Female adult.* As for male, except as follows. **Thorax:** Length  $1.22 \pm 0.17$  mm (1.11–1.34 mm, n = 5). **Wing:** Length  $5.7 \pm 0.7$  mm (5.3–6.1 mm, n = 5). **Abdomen:** Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Guinea and Nigeria (Fig. 136), 215–750 masl.

**MATERIAL EXAMINED:** *Holotype:* adult male, in Ethanol (this portion of specimen not seen), genitalia pinned separately in genitalia vial “[Red label] HOLOTYPE/ reste—coll. Alcool.; HOLOTYPE ♂/ Leptomorphus medleri/ Matile/ Det. C.J. Borkent, 2012” [MNHN]. Type locality: NIGERIA, W.State, Ile Ife, v.1973, J.T. Medler (Matile 1977).

*Paratypes:* NIGERIA, W.State, Ile Ife, viii.1974, J.T. Medler. (6♂, 1♀, MNHN); Ibadan, 3.vii.1922 (1♀, BMNH).

*Other material:* GUINEA, Mt. Nimba, 18–19.vi.1991, Girard et Legrand. (1♀, MNHN); NIGERIA, Ibadan, 23.vii.1962, D.C. Eidt. (2♀, CNC); same except 31.viii.1962 (1♂, CNC); 3.ix.1962 (1♂, CNC); 18.ix.1962 (1♂, CNC); 1962 (1♂, CNC).

## 22. *Leptomorphus nebulosus* (Walker)

(Figures 24–27, 63–64, 83, 111, 125, 128, 129, 131, 144, 150, 154)

*Diomonus nebulosus* Walker, 1848: 87.

*Leptomorphus nebulosus:* Edwards, 1925: 556

*Leptomorphus subcaeruleus gurneyi* Shaw, 1947: 155 **new synonym.**

*Leptomorphus (Diomonus) nebulosus:* Matile, 1977: 146.

*Leptomorphus nebulosus:* Papavero, 1978 (lapsus).

**References:** Osten Sacken 1878: 9 (catalogue); Kertész 1902: 49 (catalogue); Aldrich 1905: 141 (catalogue); Johannsen 1909: 45 (catalogue), 1910: 155 (description, key reference, MA), 1926: 51 (notes on type); Coquillett 1910: 533 (type designations); Alexander 1924: 55 (compared to *L. panorpiformis*); Procter 1946: 359 (ME); Shaw 1947: 156–7 (compared to *L. s. gurneyi*); Shaw & Fisher 1952: 192 (key to species, NH); Laffoon 1965: 223 (catalogue); Matile 1977: 141, 146 (subgeneric placement); Vockeroth 1981: 231 (wing figure in generic key), 2009: 270 (wing figure in generic key); Poole and Gentili, 1996: 194 (catalogue, synonymy); Sjøli *et al.* 2000: 66 (wing figure in generic key).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: apical half of the antennae white (base dark brown); scutum with setae on entire surface; males with a midfemoral spine-like process; R<sub>4</sub> present; male genitalia with two long sickle-like structures (aedeagus) curving dorsally (Fig. 111).

This species is most easily confused, in its light form, with *L. magnificus* or *L. perplexus*. It can be distinguished from the former by the presence of dark markings on the scutum and the bicoloured antennae (Fig. 27). It differs from the latter species by the slightly concave R<sub>5</sub> wing vein (Figs 63, 64, rather than sinusoidal Fig. 69) and the placement of the ocelli in a cluster more than their own diameter away from the eye margin. The dark form (Figs 24, 25, 26) is most similar to *L. panorpiformis*, *L. bifasciatus* and *L. subcaeruleus* and differs from the first in having a Nearctic distribution, by the presence of the midfemoral spine in the male, and the shape male

genitalia. The dark form differs from the latter two species in having bicoloured antennae and from *L. subcaeruleus* in having the coxae and at least one set of femurs dark brown or black. The shape of the male genitalia of *L. nebulosus* (Fig. 111) and *L. bifasciatus* (Fig. 94) is very different, particularly the shape of the aedeagus.

**DESCRIPTION:** *Male.* (Figs. 25, 27) **Head:** yellow with dark brown band posterodorsally to completely dark brown/black, somewhat dorsoventrally compressed in anterior view. Antenna with basal 5 flagellomeres dark brown/black, white apically; scape yellow to dark brown, with brown to black setae in short row on apicodorsal margin and thick patch covering apicoventral process, remainder bare, anterobasal patch of setulae present; pedicel brown, with 2–3 large bristles, several setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base brown remainder brown; flagellomere 6 1.6X as long as broad. Clypeus brown, circular, strongly protruding; bristles on clypeus light brown, both strong, smaller bristles on entire surface, all directed ventrally, clypeus 2X as long as face. Face brown; shape a slightly wider than tall triangle, covered with many fine bristles. Frons light to dark brown; bare, frontal furrow running 1/2–3/4 distance from dorsal margin towards ventral margin, frontal cleft initially running to lateral ocellus then barely in front of median ocellus. Palpus ranging from yellow to brown; segment 1 small but visible below eye, segments increasing in length, segment 5 subequal in length to segment 4 with even width from base to apex, segment 3 without distinct lateral patch of fine setae. Labellum brown. Eye with a number (in ~1/4 of the ommatidial junctions) of long inter-ommatidial setulae scattered on posterior half. Occiput dark brown with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli 1.0–1.5X diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length  $2.34 \pm 0.47$  mm (2.01–2.71 mm, n = 10). Dark brown, sometimes with dorsal yellow spots. Scutum ranging from completely dark brown/black, to dark brown with pair of mediolateral yellow spots and anteriorly placed V of yellow, rarely brown with yellow anteromedial triangle and lateral margins yellow; surface of scutum covered with small setae; acrostichal setae absent; dorsocentral setae present as multiple lines of very short, thin setae for anterior half and longer setae on posterior; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum dark brown; with 6–8 large bristles and many small bristles. Prescutum yellow. Mediotergite dark brown with 10–20 bristles on posterolateral corners, absent. Laterotergite brown; anterior margin of laterotergite not reaching katepisternum. Anepimeron brown. Anepisternum dark brown. Katepisternum dark brown. Antepronotum and proepisternum dark brown. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum dark brown (a few specimens from Kansas and Iowa yellow with central dark spot). Anapleural suture straight and clear. Halter dark brown in northwest of range, to light brown and yellow in southeast. **Legs:** principally dark brown; trochanters white or yellow; fore- and midfemora typically yellow, though sometimes brown, hind femur with base and apex yellow; extreme anteroapical corner dark brown on all femora. Midfemur with apical spine-like process (Fig. 83). Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs yellow, foretibial spur length 1.7X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 5/7 of its length, placed basally, shortest midtibial spur 0.75X length of longest, longest midtibial spur 3.5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3X apical thickness of hind tibia. Foreleg first tarsomere 1.2X length of foretibia. **Wing** (Figs. 63–64): Length  $8.2 \pm 1.5$  mm (7.5–9.6 mm, n = 10). Hyaline; apical macula dark brown but fading towards apex and posterior margin, running from anterior to posterior wing margin, beginning halfway along  $R_5$ ; medial macula extending from Sc to near fork of  $M_1$  and  $M_2$ . Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long and short for margin of alula, remainder short. Calypter bare. Vein sc-r present, apical end joining R within its own length before or after origin of Rs.  $R_4$  present.  $R_5$  slightly concave for entire length.  $M_1$  reaching apex before  $R_5$ , apices of M veins clearly reaching wing margin.  $M_4$ -CuA fork arising well before origin of r-m.  $A_2$  faintly present as crease. **Abdomen:** Tergite 1 always dark brown/black, remainder ranging from completely reddish brown to completely dark brown/black, when dark often with T3–4 dark reddish brown. Tergite 8 smaller than all other abdominal sclerites and covered with many bristles. **Genitalia** (Fig. 111): orangish yellow to dark brown. Sternite 9 light-darkly sclerotized, rounded rectangle, 2/3 the length of T9 but wider than genitalia. Tergite 9 as wide as long, with basal half of lateral margins parallel, remainder tapering to rounded medial apex. Gonocoxite placed apically on T9, tapering to a point on apicolateral margin, medial margin not reaching medial line, bearing gonostylus basally. Gonostylus a single lobe tapering towards apex and bearing several setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus ~1.2X length of T9, tapering to middle and then becoming a lateral sclerotized sickle-like hook with serrated tip (smaller

than in *L. subcaeruleus* or *L. magnificus*), apodemes sclerotized and 1/7 total length. Parameres a swollen lobe with apex covered in small spines, apodemes 1/4 length of parameres and strongly united with gonocoxal apodemes.

**Female adult.** (Figs. 24, 26) As for male, except as follows. **Thorax:** Length  $2.34 \pm 0.70$  mm (1.85–2.95 mm,  $n = 10$ ). **Wing:** Length  $8.0 \pm 2.1$  mm (6.5–9.8 mm,  $n = 10$ ). **Legs:** Midfemur without apical spine-like process. **Abdomen:** Cercus yellow to black.

**Immatures.** Similar in general appearance to *L. subcaeruleus* (Figs. 128, 129, 131, 133).

**BIOLOGY:** Immatures of *L. nebulosus* were found feeding under the sporophores of *Fomitopsis pinicola*, a woody bracket fungus (Figs. 125, 128, 129). The behaviour of the larvae agreed closely with that found by Eberhard (1970). Larvae spun pupation lines under or near the fungus, moved to the middle of the line, and pupated there (Figs. 131, 133).

**DISTRIBUTION:** Nearctic, particularly Canada and the eastern USA (Fig. 144), 20–1800 masl.

**DISCUSSION:** *Leptomorphus s. gurneyi* was originally described as a subspecies of *L. subcaeruleus* (Shaw 1947) based on similar genitalia (shared by *L. magnificus*, *L. nebulosus* and *L. subcaeruleus*), and then synonymized with *L. subcaeruleus* by Poole & Gentili (1996). However it is actually a lighter form of *L. nebulosus* (differs from *L. subcaeruleus* in having bicoloured antennae and distinct body colouration). *Leptomorphus nebulosus*' colour ranges from lighter (yellowish with some dark spots) in the southwest part of the range to completely black in the north. Since no discrete boundaries are seen between the lighter and darker forms, we do not recognize a distinct subspecies.

As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Diomonus* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult male, glued to card on pin. Wing glued to separate card, labelled "[Circular label with red edge] HOLO-/ TYPE; [Circular label with green edge] Type; Diomonus/ nebulosus/ Walker/ (type); 686/ Sciophila/ nebulosa; One of Walkers/ series so named/ EAW; a. St. Martin's Falls,/ [underside] lines; [label upside down] BMNH(E) #/ 257830; [circular label] 44/ 17/ [underside] Hudson's/ Bay; HOLOTYPE ♂/ *Leptomorphus nebulosus* / (Walker) / Det. C.J. Borkent 2012" [BMNH]. This specimen was apparently collected by G. Barnston along the Albany River, Ontario, Canada (Walker 1848), probably at the Martin Falls Fort of the Hudson's Bay Co. (51.53°N, 86.5°W).

*Other material:* CANADA, BC, 14km E Coal River, 14.vi–3.ix.1984, S. & J. Peck. (1♂, CNC); 23km NE Nelson, 10.vii.2008, A. Borkent. (1♂, LEM); 2km W Little Slovan Lk. Cmpgnd., 1.vii.2008, A. Borkent. (3♂, 1♀, LEM); 3.8mi. S Steamboat, 22.vi.1989, P.H. Arnaud, Jr. (1♂, CAS); 6km E Salmon Arm, 13.vi.2009, A. Borkent. (1♂, LEM); Kaslo, 18.vii, A.N. Caudell. (1♀, USNM); Likely, 6.vii.1938, G.S. Walley. (1♂, CNC); Robson, 14.vi.1948, H.R. Foxlee. (1♂, CNC); Rosebery, 11.vii.2008, A. Borkent. (1♂, 1♀, LEM); Quesnel, 26.vi.1948, G.J. Spencer, (1♂, UBCZ); Salmon Arm, 1.vi.2006, A. Borkent. (1♀, LEM); 10.vi.2006. (1♀, LEM); 12.vi.2006. (1♀, LEM); 26.vi.2006. (1♀, LEM); 7.vii.2007. (1♀, LEM); 9.vii.2007. (1♂, LEM); 14.ix.2008. (1♂, LEM); 12.vi.2008, C.J. Borkent. (1♂, 2♀, LEM); Trinity Valley, 13.vii.1937, K. Graham. (1♂, CNC); ON, Algonquin Park (South of Shirley Lake), 21–28.vii.1984, K. Pendreigh. (1♂, CNC, 1♂, DEBU); 16–24.vi.1984. (1♂, DEBU); 18–26.v.1984. (2♂, CNC); 18–26.v.1984. (3♂, DEBU); Fathom 5 N.P., N Cove Isl., 25.vi.1995, S.A. Marshall. (1♂, DEBU); Finland, 8.vii.1960, S.M. Clark. (1♂, CNC); Macdiarmid, 6.vii.1922, Bigelow. (1♂, CNC); Orwell, 14.vi.1978, W.A. Attwater. (1♀, DEBU); Kent Co., Rondeau Prov.Pk., Spicebush Trail, Carolinian Forest, 15.viii–7.ix.2003, Marshall *et al.* (1♀, DEBU); Rondeau Park, 14.viii–7.ix.2003, Buck & Marshall. (1♀, DEBU); 15.viii–7.ix.2003, Marshall *et al.* (1♀, DEBU); QC, 2.3km SSW Rapide-Danseur, 27.v–29.vi.2007, A. Hibbert. (1♂, LEM); Laniel, 12.vi.1944, A.R. Brooks. (1♂, CNC); Masham Twp., Duncan Lake, 13.ix.1975, D.M. Wood. (2♂, 1♀, CNC); 17.ix.1975. (1♀, CNC); 1.ix.1985. (1♂, 3♀, CNC); 8.ix.1985. (1♂, CNC); 11.ix.1985. (1♂, 2♀, CNC); 16.ix.1985. (1♀, CNC); 16.ix.1985. (1♂, 1♀, CNC); 10–12.ix.1986. (1♂, CNC); 12.ix.1986. (1♂, CNC); 7.x.1985. (4♂, CNC); 10.x.1985. (3♂, 1♀, CNC); USA, IA, Boone Co., Ledges State Park, 13.x.1950, J.L. Laffoon. (1♂, ISUI); 18.ix.1951. (1♀, ISUI); Winneshiek Co., Kendallville, 14.vii–4.viii.2008, M.J. Hatfield. (1♂, LEM); KS, Douglas Co., U. Kansas Nat. Hist. Res., 13.vi.1974, C.W. Young. (1♂, CMNH); 10–20.vi.2005, Z.H. Falin. (1♀, SEMC); 20.vi.2005. (1♂, SEMC); 19–24.vii.2005. (1♂, SEMC); 7–16.ix.2005. (1♀, SEMC); 16.ix–1.x.2005. (2♂, SEMC); MD, Cabin John, R.M. Fouts. (1♂, USNM); Patuxent Refuge, Bowie, 4.vii.1945. (1♀, USNM); Plummer's Island, 1906, D.H. Clemons, H.S. Barber. (1♀, USNM); 27.vi.1909, W.L. McAtee. (1♀, USNM); 8.viii.1917, Schwarz & Barber. (1♂, USNM); Calvert Co., Port Republic, 12–15.x.1996, D.M. Wood.



(1♀, CNC); Prince George Co., Camp Springs, 20.ix.1979, G.F. Hevel. (1♀, USNM); Wash. Co., 5km NE Boonsboro, Greenbrier St. Pk., 12–14.viii.1989, M.E. Steiner *et al.* (1♂, USNM); ME, Houlton, 5.vii. (1♀, USNM); MI, Isle Royale, 3–7.viii.1936, C.W. Sabrosky. (1♂, USNM); MO, Camp Crowder, 7.x.1942, A.B. Gurney. (2♂, 1♀, USNM, Type specimens of *L. s. gurneyi*); MS, Oxford, 20.vi.1966, F.M. Hull. (1♀, CNC); NH, Carriage Road, Mt. Washington, G. Dimmock. (1♀, USNM); Carr. Co., 1mi. N Wonalancet, E Fk., Spring Brk., 18–23.vii.1985, D.S. Chandler. (1♂, UNHC); The Bowl (2.5mi. NW Wonalancet), 8–14.vi.1984, D.S. Chandler. (2♂, UNHC); The Bowl (2.5mi. NW Wonalancet), 15–20.vi.1984. (3♂, UNHC); The Bowl (2.5mi. NW Wonalancet), 28.vi–4.vii.1984. (1♂, UNHC); The Bowl (2.5mi. NW Wonalancet), 20–26.vii.1984. (2♂, UNHC); The Bowl (2.5mi. NW Wonalancet), 2–10.viii.1984. (1♂, UNHC); The Bowl (2.5mi. NW Wonalancet), 11–16.viii.1984. (3♂, 2♀, UNHC); The Bowl (2.5mi. NW Wonalancet), 18.ix–3.x.1984. (2♂, UNHC); The Bowl (2.5mi. NW Wonalancet), 20.x–7.xi.1984. (1♂, UNHC); NJ, Stockton, 1–15.vii.1906. (1♀, USNM); NY, 7mi. south town of Long Lake, 26.viii.1956, J.L. Laffoon. (1♂, 1♀, ISUD); Essex Co., foot Cliff Mtn, 26.vii.1920, J. Bequaert. (1♂, MCZ); PA, North Mt., 1.ix.1917. (1♀, USNM); Warren Co., 2.2km NW Truemans, 4.viii.1994, M.J. Ricke. (1♂, CMNH); SC, Anderson Co., Pendleton, Tanglewood Sprg., x.1987, J. Morse. (1♀, CNC); 22.vii.1987. (1♂, CUAC); 30.ix.1987. (1♀, CUAC); VA, Fairfax Co., Dead Run, 22.vi.1915, R.C. Shannon. (1♀, USNM); Turkey Run, mouth, 24.vi.2006, W.N. Mathis, T. Zatwarnicki. (1♀, USNM); WA, Pierce Co., 6.5km W Ashford, 8.vii.2008, C.J. Borkent. (1♂, LEM); 9.vii.2008. (1♂, LEM); 10.vii.2008. (3♀, LEM); WV, Hampshire Co., 8km NW Capon Bridge (Buffalo Gap Camp), 12–14.ix.1986, W.E. Steiner; J.M. Swearingen. (1♀, USNM).

### 23. *Leptomorphus neivai* Edwards

(Figures 29, 65, 112, 142, 150, 155)

*Leptomorphus neivai* Edwards, 1940: 452.

**References:** Lane 1958: 150 (distribution list); Matile 1977: 144 (subgeneric placement); Papavero 1978: 50 (catalogue).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with  $R_4$  present and forming a triangular cell (rather than rectangular, Fig. 65), and with lateral lobes of parameres longer than tergite 9 and bending sharply dorsally (Fig. 112). This is the only species in the neotropics with  $R_4$ .

**DESCRIPTION:** *Male.* (Fig. 29) **Head:** yellow, circular in anterior view. Antenna brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with two rows of strong setae on apicodorsal margin, a few small setae on apicoventral margin; flagellomere 1 with tapered base yellow remainder dark brown; flagellomere 6 1.7X as long as broad. Clypeus yellow, slightly laterally compressed oval; bristles on clypeus brown, all similar sized, principally on lateral, ventral margins, ventral bristles directed ventrally, clypeus 2.5X as long as face. Face yellow; shape a slightly wider than tall triangle, bare. Frons brown; bare, frontal furrow running 1/3 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus with segments 1–4 yellow, segment 5 white; segment 1 hidden behind eye, segments 2–3 subequal (1/2 as long as segment 4), segment 5 2X length and 1.5X width of segment 4, segment 3 without apicolateral patch of setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli with median slightly in front of laterals, space between ocelli less than diameter of laterals, lateral ocelli 2.5X their own diameter from eye margin, ocellar triangle black. **Thorax:** Length  $1.4 \pm 0.22$  mm (1.23–1.56 mm, n = 10). Dark brown with a few yellow spots. Scutum dark brown/black, occasionally with two paler lines beginning just behind anterior margin and converging just before posterior margin; surface of scutum covered with trichia; acrostichal setae absent; single dorsocentral seta present anteriorly; single row of lateral setae present; patch of setae on scutum at wing base absent. Scutellum yellow with covering of fine trichia; bristles absent. Prescutum light brown. Mediotergite brown with 8–12 bristles on posterior third, and covering of appressed trichia. Laterotergite brown, with covering of appressed trichia; anterior margin of laterotergite abutting katapisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katapisternum brown with dorsal third white. Anteprepronotum and proepisternum brown. Margin of anterior and posterior spiracles white with white trichia. Metepisternum light yellow with light brown

line on ventral margin. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** principally yellow; trochanters with brown margins; midfemur with basal 1/4 brown, hind femur with basal and apical 1/4 brown; extreme anteroapical corner dark brown on all femora; midtibia with apex light brown, hind tibia brown; tarsi brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with comb of short setae along length of anteroventral surface, foretibial spur dark brown, remainder brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 2/3 of its length, placed basally, shortest midtibial spur 0.75X length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur 0.8X length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 65): Length  $5.9 \pm 0.8$  mm (5.3–6.5 mm, n = 10). Hyaline; apical macula reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell *cua*<sub>1</sub>, cup, not joining with medial macula; medial macula extending from R<sub>1</sub> to fork of CuA and M<sub>4</sub>. Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining R within its own length prior to origin of Rs. R<sub>4</sub> present, forming a triangular cell by originating at, or close to, the junction of Rs and r-m. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins reaching wing margin. M<sub>4</sub>-CuA fork arising just apical of origin of r-m. A<sub>2</sub> absent. **Abdomen:** Tergites and sternites 3–5 with anterior 1/3 yellow, remainder dark brown/black. Tergite 8 smaller than all other abdominal sclerites, without bristles. **Genitalia** (Fig. 112): basal half brown remainder yellow. Sternite 9 sclerotized, posteriorly pointing triangle with slight bifurcation at apex, as long as aedeagus and 1/2 the width of genitalia. Tergite 9 longer than wide, lateral margins ~parallel, posterior margin ~flat with small point laterally. Gonocoxite placed centrally on T9, medial margin not reaching median line, bearing gonostylus apically. Gonostylus a single apically blunt lobe with several setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus mostly membranous and fused with sternite 9, 4/5 length of gonocoxite, tapering towards apex, apodemes 1/5 total length. Parameres with two lobes, lateral lobes longer than T9, sharp bend dorsally after reaching apical margin of T9, medially lobes long and thin, but shorter than lateral and placed dorsally behind aedeagus; basal bridge between apodeme lobes with dorsally directed pair of hooks; joined basally with aedeagus.

*Female adult.* As for male, except as follows. **Head: Thorax:** Length 1.49mm ( $\pm 0.28$ , max: 1.72mm, min: 1.27mm, n = 10). **Wing:** Length  $6.2 \pm 0.8$  mm (5.5–6.8 mm, n = 10). **Legs:** Foretibia without comb of short setae on anteroventral surface. **Abdomen:** Sternites yellow. Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Brazilian states of Sao Paulo, Parana, and Santa Catarina, and adjacent areas of north-eastern Argentina (Lane 1958) and south-eastern Paraguay (Fig. 142), 150–925 masl.

**MATERIAL EXAMINED:** *Lectotype*, here designated, adult male, pinned, labelled “Brasilien [BRAZIL]/ [Santa Catarina,] Nova Teutonia/ 27°11’ B [S], 52°23’ L. [W]/ Fritz Plaumann/ 18.XII.1937; [circular label with blue ring] SYNTYPE; Leptomorphus/ neivai Edw./ F.W. Edwards; SYNTYPE/ Leptomorphus/ neivai/ Edwards/ det. J.E. Chainey, 1996.; LECTOTYPE ♂ / *Leptomorphus neivai*/ Edwards/ Det. C.J. Borkent 2012” [BMNH]. This specimen was chosen as it was in the best condition of the five syntypes available (some minor leg damage).

*Paralectotypes* labelled as for lectotype except without F.W. Edwards determination label and: 21-IX-1938. (sex ? (broken abdomen)); 26.VIII.1937 (1♀); 16.VI.1937 (sex ? (broken abdomen)); 8.VI.1937 (1♀), All paralectotypes in BMNH. In the original description Edwards (1940) lists seven type specimens. We are only aware of these five specimens, with the remaining two considered lost.

*Other material:* All in CNC except where noted. BRAZIL, [Santa Catarina], Nova Teutonia. XI.1966, F. Plaumann. (1♂, 1♀); same data except IX.1966 (3♂, 1♀); V.1966 (1♂, 1♀); I.1965 (1♂); XII.1964 (1♂); IX.1964 (2♂, 1♀); X.1963 (1♂); IX.1963 (1♀); VIII.1963 (1♂); VI.1963 (6♂); XII.1962 (1♂); 30.XI.1962 (1♂); 15.XI.1962 (1♂); 9.XI.1962 (1♀); 6.XI.1962 (1♂, 1♀); 22.X.1962 (1♂); 26.IX.1962 (1♂); 21.IX.1962 (1♂); 3.VIII.1961 (1♂); 5.VI.1961 (1♂); 4.VI.1961 (1♂); 8.V.1961 (1♂); 9.XI.1960 (1♀); 4.XI.1960 (1♂); 8.VIII.1960 (1♂); 9.I.1960 (1♀); 6.I.1960 (1♀); 29.XII.1959 (1♀); 23.XI.1959 (1♀); 24.X.1959 (1♂); 20.IX.1959 (1♂); 29.XI.1958 (1♀); 7.V.1957 (1♂); 12.IX.1944 (1♀); Sao Paulo, Embu. VI.1953, J.P. Duret (1♂, MNHN); Parana, Curitiba, 20–31.I.1969, L. Strange (1♂, MNHN); PARAGUAY, [Guairá] Villarrica, VII.1937, F. Schade (1♂, USNM).

## 24. *Leptomorphus obscurus* Matile

(Figures 28, 66, 113, 136, 150, 153)

*Leptomorphus (Gymnoscutum) obscurus* Matile, 1977: 152.

**References:** Crosskey 1980: 1221 (catalogue appendix); Matile 1997: 147–149 (figures, new records, morphological variation, key).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite, anepisternum and anepimeron yellow; scutellum brown, male genitalia with tergite 9 gradually tapering on apical quarter (tergal evagination), apex bearing medial spur and often a secondary small bump or point, also with strong, ventrally-produced, thin ridge running across ventral surface at the anterior margin of the tergal evagination, creating a semicircular dorsal margin when viewed caudally (Fig. 113).

This species can be distinguished from most other Afrotropical species by the brown scutellum and lack of small setae covering the scutum (except along dorsocentral lines). It can be separated from *L. crosskeyi* and *L. obscurus* by the gradually tapering shape of the tergal evaginations (Fig. 113) rather than the almost square posterior margin in these two other species.

**DESCRIPTION:** *Male.* (Fig. 28) **Head:** yellow with some brown spots, circular in anterior view. Antenna brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae absent; pedicel light brown/yellow, with 2 large bristles, several setae on apicodorsal margin, a few fine setae on apicoventral margin; flagellomere 1 with tapered base either brown or yellow remainder brown; flagellomere 6 1.1X as long as broad. Clypeus yellow, slightly laterally compressed oval; bristles on clypeus brown, 4–6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow; shape a just longer than wide triangle, with few bristles ventrolaterally. Frons yellow; with few bristles medioventrally, frontal furrow running 1/2 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus with 1–3 yellow, remainder brown; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length of segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae encircled by strong dark setae. Labellum light brown. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with some adventitious brown spotting anteriorly, with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length  $1.08 \pm 0.14$  mm (0.98–1.23 mm, n = 10). Dark brown dorsally, yellow laterally. Scutum dark brown/black with blue-green specks, pair of yellow mediolateral and smaller posterolateral spots; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; single row of lateral setae present; patch of setae on scutum at wing base present. Scutellum brown; with 8–10 large bristles and many small bristles. Prescutum yellow. Mediotergite dark brown with 6–8 bristles on posterolateral corners, anteromedial patch of small bristles. Laterotergite yellow; anterior margin of laterotergite not reaching katapisternum. Anepimeron yellow. Anepisternum yellow. Katapisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with light brown trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** principally yellow; hind femur light brown at very apex; extreme anteroapical corner dark brown on all femora. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, hind tibial spur yellow, remainder brown, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 1/3 of its length, placed basally, shortest midtibial spur 0.8X length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.8X length of foretibia. **Wing** (Fig. 66): Length  $5.1 \pm 0.7$  mm (4.5–5.7 mm, n = 10). Hyaline; apical macula absent or very light at R<sub>5</sub> apex; medial macula absent. Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining R at 2X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins fading before wing margin. M<sub>4</sub>-CuA fork arising before origin of r-m. A<sub>2</sub> faintly

present as crease. **Abdomen:** Tergites principally dark brown, T2–6 with lateral yellow spots. Tergite 8 smaller than all other abdominal sclerites, with 2–3 bristles on each apicolateral corner. **Genitalia** (Fig. 113): yellow. Sternite 9 sclerotized, oval/rounded diamond, 3/5 the width of genitalia at widest point, overlapping medial margin of gonoxite. Tergite 9 longer than wide, lateral margins widening slightly to apex and then tapering sharply into pointed lobes with medial U-shaped indentation, a ventrally extending sclerotized band running along the base of posterior lobes. Gonocoxite placed basally on T9, medial margin just not reaching medial line, bearing gonostylus apically. Gonostylus with two lobes, dorsal lobe a broad based point, ventral lobe half the width of dorsal but 2.5X length and barely tapering until apex, gonocoxite III fused to dorsolateral margin. Aedeagus 2/3 length of gonocoxite, tapering towards apex, apodemes 2/5 total length. Parameres a simple taper, apodemes ~1/2 length of parameres.

*Female adult.* As for male, except as follows. **Thorax:** Length  $1.32 \pm 0.20$  mm (1.19–1.48 mm, n = 9). **Wing:** Length  $6.1 \pm 0.9$  mm (5.3 – 6.8 mm, n = 9). **Abdomen:** Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Guinea, Ivory Coast, Ghana, Gabon, the Central African Republic and the Republic of the Congo (Fig. 136), 120–750 masl.

**DISCUSSION:** As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Gymnoscutum* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult male, pinned on double mount minuten, genitalia in glass vial on pin, labelled “[Blue label] REP. CENTRAFRIC./ LA MABOKE/ 29.IX.1970/ L. MATILE rec.; [Red label] HOLOTYPE; *Leptomorphus/ (Afroleptomorphus)/ obscurus* n. sp. ♂<sup>ht</sup>/ L. Matile det. 1974; HOLOTYPE ♂/ *Leptomorphus obscurus/ Matile/ Det. C.J. Borkent, 2012*” [MNHN].

*Paratypes:* labelled as for holotype (3♂, 4♀ (1 labelled allotype)); except 24.IX.1970 (1♀); 26.IX.1970 (1♂); 27.IX.1970 (2♂, 1♀). All paratypes in MNHN.

*Other material:* CENTRAL AFRICAN REPUBLIC, La Maboque, 26.ix.1970, L. Matile. (1♂, MNHN); same except 27.ix.1970. (2♂, MNHN); 29.ix.1970. (3♂, MNHN); GABON, Makokou m'passa, Bale Affl., 7–16.v.1979, J. Legrand. (2♂, MNHN); GHANA, Kakum National Park, 8.xi.1994 (2♂, ZMUN); 31.x–8.xi.1994 (2♂, ZMUN); 8–15.xi.1994 (1♂, ZMUN); 8–15.x.1994 (1♀, ZMUN); Western Region, Ankasa game prod. reserve, 8.xii.1993, J. Kjørandsen, T. Anderson (1♂, 1♀, ZMUN); GUINEA, Mt. Nimba, 18–29.vi.1991, Girard et Legrand. (1♂, MNHN); IVORY COAST, Taï, 5.v.1980, G. Couturier. (1♂, MNHN); REPUBLIC OF THE CONGO, Mayombe Dimonika, 14.xi.1975, L. Matile. (1♂, MNHN).

## 25. *Leptomorphus ornatus* Brunetti

(Figures 30, 67, 137, 150, 152)

*Leptomorphus ornatus* Brunetti, 1912: 85. Plate II.

*Leptomorphus (Gymnoscutum) ornatus:* Matile, 1977: 145.

**References:** Edwards 1933a: 229–30 (comparison to *L. chaseni*); Colless & Liepa 1973: 454 (catalogue); Matile 1977: 141,145 (subgeneric placement); Papp & Ševčík 2011: 139 (notes on identity).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite and anepisternum brown; wing with pale brown apical wing spot reaching to wing tip, pale medial wing spot absent (Fig. 67); male genitalia presumably different from other species with these characters (male unknown).

This species can be distinguished from most other Oriental and eastern Palearctic species (including those in Papp & Ševčík 2011) based on the yellow katepisternum and metepisternum (Fig. 30, both brown in all other species in these regions except *L. babai*, and *L. titiwangsensis*). It can be distinguished from *L. babai* by its yellow scutellum (brown in *L. babai*) and from *L. titiwangsensis* by *L. ornatus*' occurrence only in Nepal and India and presumably different male genitalic morphology.

**DESCRIPTION:** *Female.* (Fig. 30) **Head:** yellow, circular in anterior view. Antenna with basal flagellomeres lighter brown, darkening apically; scape yellow, with brown setae in single apical row extending from dorsum



laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 1–2 large bristles, few setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base yellow remainder either light brown or brown; flagellomere 6 1.1X as long as broad. Clypeus yellow, dorsoventrally elongate oval; bristles on clypeus yellow, 6–8 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 1.5X as long as face. Face yellow; shape a just longer than wide triangle, with few bristles ventrolaterally. Frons yellow; with few bristles medioventrally, frontal furrow running 3/4 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length of segment 4 with central half thinner than base and apex, segment 3 appears to have apicolateral patch of fine yellow setae weakly encircled by strong dark setae (difficult to see in specimens). Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length 1.31 mm (1.27–1.35 mm, n = 3). Mostly brown, with anterolateral area yellow. Scutum dark brown with blue-green specks; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae on posterior two thirds; two thirds row of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 6 large bristles and many small bristles. Prescutum brown. Mediotergite dark brown with 4 bristles on posterolateral corners, absent. Laterotergite brown; anterior margin of laterotergite abutting katapisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katapisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter stem yellow, knob light brown. **Legs:** principally yellow; hind coxa with brown spot along length of anterior surface; hind femur with apex and basal 1/3 light brown; extreme anteroapical corner yellow on forefemur, on other femora dark brown; midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 3/4 of its length, placed basally, shortest midtibial spur 0.5X length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3X apical thickness of hind tibia. Foreleg first tarsomere 1.4X length of foretibia. **Wing** (Fig. 67): Length 5.5 mm (5.0–5.7 mm, n = 3). Hyaline; apical macula light, beginning at apex of R<sub>1</sub> and M<sub>4</sub> and reaching wing tip; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r absent, faint, or present, when present joining R at 2–3X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins thinning towards wing margin. M<sub>4</sub>-CuA fork arising apically of origin of r-m. A<sub>2</sub> absent. **Abdomen:** Tergites 3–5 and sometime 6 with anterior 1/3 yellow, T7 light to dark brown, remainder dark brown/black. Cercus yellow.

*Male.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Bangladesh, India (Assam) and Nepal (Fig. 137), 30–2070 masl.

**DISCUSSION:** The holotype is in the collection of the Zoological Survey of India (NZSI), though I was unable to borrow the specimen. The type location given for the female holotype is “[Bangladesh] Sylhet, 3.ii.[19]05 (Hall). [30m elevation]” The specimen is labelled as TYPE, FEMALE, and has three legs and one wing damaged (A. Chattopadhyay, (NZSI) pers. comm.). This species was previously known only from the female holotype. I assigned three female specimens to this species as they were collected close to the type locality and agreed closely with the original description. The only differences noted were: tergite 7 lighter brown in the Nepalese specimens; one Nepalese specimen with a slightly darker head; one Nepalese and the Indian specimen with vein sc-r absent (presence of this wing vein seems to be variable in the Oriental region, see *L. titiwangsensis*). It is possible that these females are actually different species, as females are typically very similar between related species. However, I refrained from naming them, as male specimens are needed to confirm genitalic differences.

As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Gymnoscutum* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED:** INDIA, Assam, Above Tura, Garo hills, vii.1917, S. Kemp. (1♀, BMNH); NEPAL, Kathmandu, Godavaril [= Godawari?], 21.vii.1967, Can. Exp. (1♀, CNC); Pulchauki, 14.vii.1967, Can. Exp. (1♀, CNC).

## 26. *Leptomorphus panorpiformis* (Matsumura)

(Figures 31, 68, 114, 141, 150, 154)

*Mycomyia panorpiformis* Matsumura, 1915: 54.

*Diomonus esakii* Alexander, 1924: 54. (junior synonym, Matile 1977: 146).

*Mycomyia panorpaeformis*: Matsumura, 1931: 405 (*lapsus*).

*Diomonus panorpiformis*: Okada, 1938: 92.

*Leptomorphus* (*Diomonus*) *panorpiformis*: Matile, 1977: 146.

**References:** Matsumura 1916: 439–40, Pl. XXIV (English description, habitus); Matile 1977: 146 (subgeneric placement); Zaitzev 1981: 123–4 (re-description, male genitalia figures, far-eastern Russia); Krivosheina *et al.* 1986: 133–4 (key, male genitalia figure); Matile, 1988: 234 (catalogue); Zaitzev 1999: 170–1 (key, male genitalia figure); Krivosheina & Zaitzev 2008: 611 (larval habitat, larval mandible figure).

**DIAGNOSIS:** The only extant species of *Leptomorphus* found in the eastern Palaearctic with  $R_4$  present and with apical 4–5 flagellomeres white (remainder dark brown). Males without an apical spine-like process. Male genitalia with aedeagal lobes bifurcate (Fig. 114).

**DESCRIPTION:** *Male.* (Fig. 31) **Head:** dark brown to black, somewhat dorsoventrally compressed in anterior view. Antenna with basal flagellomeres dark brown/black, apical 5 flagellomeres white; scape medium to dark brown, with black setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel brown, with 3–4 large bristles, several setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base dark brown remainder dark brown; flagellomere 6 1.5X as long as broad. Clypeus dark brown, circular, strongly protruding; bristles on clypeus dark brown, both strong, smaller bristles on entire surface, all directed ventrally, clypeus 1.2X as long as face. Face dark brown; shape a slightly wider than tall triangle, covered with many strong bristles. Frons dark brown; bare, frontal furrow running full distance from dorsal margin towards ventral margin, frontal cleft running to lateral ocellus. Palpus dark brown; segment 1 small but visible below eye, segments increasing in length, segment 5 2X length of segment 4 with even width from base to apex, segment 3 without distinct lateral patch of fine setae. Labellum dark brown. Eye with a number (in ~1/4 of the ommatidial junctions) of long inter-ommatidial setulae scattered on posterior half. Occiput dark brown with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown. **Thorax:** Length 2.62mm (2.21–3.03 mm, n = 4). Dark brown. Scutum dark brown/black with blue-green specks; surface of scutum covered with small setae; acrostichal setae absent; dorsocentral setae probably present but not clearly distinguishable from other setae; double row of lateral setae present; patch of setae on scutum at wing base present. Scutellum dark brown; with 10–14 large bristles and many small bristles. Prescutum brown. Mediotergite dark brown with 18–24 bristles on posterolateral corners, absent. Laterotergite brown; anterior margin of laterotergite not reaching katapisternum. Anepimeron brown. Anepisternum dark brown. Katapisternum dark brown. Antepronotum and proepisternum dark brown. Margin of anterior and posterior spiracles brown with brown trichia. Metepisternum dark brown. Anapleural suture straight and clear. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** principally dark brown; trochanters white; basal tip of femora white; extreme anteroapical corner dark brown on all femora. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 4/5 of its length, placed centrally, shortest midtibial spur 0.8X length of longest, longest midtibial spur 3X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3.5X apical thickness of hind tibia. Foreleg first tarsomere 1.3X length of foretibia. **Wing** (Fig. 68): Length 9.7 mm (8.3–10.6 mm, n = 4). Hyaline; apical macula very dark, reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell  $cua_1$ ,  $cup$ ,  $a_1$ , not joining with medial macula; medial macula very dark, extending from Sc

to just beyond fork of  $M_1$  and  $M_2$ , lighter between apex of CuA, CuP, and  $A_1$ . Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) all the same length. Calypter bare. Vein sc-r present, apical end joining R within its own length before or after origin of Rs.  $R_4$  present.  $R_5$  slightly concave for entire length.  $M_1$  reaching apex before  $R_5$ , Apices of M veins reaching wing margin.  $M_4$ -CuA fork arising well before origin of r-m.  $A_2$  faintly present as crease. **Abdomen:** Tergites all dark brown to black. Tergite 8 smaller than all other abdominal sclerites, with many bristles but tapering to single row medially. **Genitalia** (Fig. 114): dark brown. Sternite 9 lightly sclerotized, posteriorly directed triangle covering most of the ventral surface, wider than genitalia. Tergite 9 wider than long, triangle-shaped pointing posteriorly with apex rounded with slight medial indentation. Gonocoxite placed apically on T9, tapering to a point on apicolateral margin, medial margin not reaching medial line, bearing gonostylus basally. Gonostylus a single broad-based lobe tapering towards apex and bearing setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus 2X length of S9, lateral margin sclerotized, tapering to middle and then with lateral lobe ending in rounded tip with fine serrations, medially tapering to apex, apodemes 1/4 total length. Parameres as broad lobes with rounded apex, apodemes ~1/2 length of parameres.

*Female.* As for male, except as follows. **Thorax:**  $2.56 \pm 0.57$  mm (2.13–3.03 mm, n = 8). **Wing:** Length  $8.9 \pm 1.9$  mm (7.2–10.2 mm, n = 8). **Abdomen:** Cercus yellow.

*Immatures.* Pupa similar to *L. bifasciatus* (T. Saigusa, pers. comm.). Larva described by Krivosheina & Zaitzev (2008). Egg unknown.

**BIOLOGY:** The larvae are known to feed on the spores of wood encrusting and tinder fungi (Krivosheina & Zaitzev 2008). The pupae hang from a line that is attached anteriorly and posteriorly, and are sometimes guarded by adult males, as in *L. subcaeruleus* (T. Saigusa, pers. comm.).

**DISTRIBUTION:** Japan (Hokkaido, Honshu (Okada 1938)) and far eastern Russia (Fig. 141), 30–1400 masl.

**DISCUSSION:** Though Matile (1977) considered *Diomonus esakii* Alexander to be a synonym of *L. panorpiformis*, he did not discuss his reasons for the synonymization. I was unable to compare the type of *D. esakii* (originally at the USNM but now considered lost, F.C. Thompson pers. comm.) to the holotype of *L. panorpiformis*. However, I agree with his synonymization based on the similarity of Alexander's (1924) description to the holotype of *L. panorpiformis*.

As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Diomonus* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED:** *Holotype:* adult male, pinned, labelled "Sapporo; 57; [red label] type/ Matsumura; Sciophila/ panorpiformis/ n. sp./ det. Matsumura; [two Japanese characters in red ink on left margin] Mycomyia/ panorpiformis/ Mats./ [line of Japanese text]; [folded paper] Mycomyia/ [line of Japanese text]/ panorpiformis/ Mats.; HOLOTYPE ♂/ *Leptomorphus/ panorpiformis* (Matsumura) / Det. C.J. Borkent 2012" [EIHU].

*Other material:* JAPAN, 12.viii (1♀, OMNH); Hokkaido, Karibu, 22.viii.1966, P. Savolainen. (1♀, MZHF); Honshu, Hyogo Pref., Haga, 4.vi.2003, R. Matsumoto. (1♂, OMNH); Nagano Pref., Matsumoto, 15.vii.1997, R. Matsumoto. (1♀, OMNH); Shinano Noziji, 10.vii.1941, T. Nakatane. (1 specimen of unknown sex (damaged), OMNH); Okayama Pref., Niimi: Nishio, 19.viii.1998, R. Matsumoto. (1♀, LEM); Yamanashi Pref., Hirogawara: Fuefuki, 19.vii.1997, R. Matsumoto. (1♀, OMNH); Kyushu, Fukuoka, Hiko-san Biol. Lab., 10–11.viii.1980, K. Mikkola. (1♀, MZHF); Kumamoto Pref., Kikuchisuigen, 2.vii.1976, Y. Yoshiyasu. (1♂, LEM); Miyazaki Pref., Takakuma, 14.vii.1960, A. Nagatomi. (1 specimen of unknown sex (damaged), OMNH); Oita Pref., Yufu, 21.vi.1997, R. Matsumoto. (1♀, OMNH); Shikoku, Ehime Pref., Ishizuchi Mt N. P., 11–18.viii.1980, S. Peck. (1♂, 1♀, CNC).

## 27. *Leptomorphus perplexus* Borkent, new species

(Figures 32, 69, 79, 148, 150, 151)

**DIAGNOSIS:** The only extant species of *Leptomorphus* with  $R_4$  that has foretarsomere I shorter in length than the forefemur, the lateral ocelli placed less than their own diameter from the eye margin (Fig. 79), and no dark wing spot (Fig. 69).

This species is most easily confused with either the light form of *L. nebulosus* (Fig. 27) or *L. magnificus* (Fig. 21). It can be distinguished from the former by the lack of any dark markings on the scutum and the monochromatic antennae (Fig. 32). It differs from the latter species by the yellow head, the sinusoidal  $R_5$  wing vein (Fig. 69) and the placement of the lateral ocelli approximately their own diameter away from the eye margin and the median ocellus (Fig. 79).

**DESCRIPTION:** *Female.* (Fig. 32) **Head:** (Fig. 79) yellow-orange, circular in anterior view. Antenna brown; scape yellow, with yellow setae on entire surface except basal 1/4, anterobasal patch of setulae present; pedicel yellow, with 1–2 large bristles, few setae on apicodorsal margin, patch of fine setae apicoventrally; flagellomere 1 with tapered base yellow remainder brown; flagellomere 6 1.3X as long as broad. Clypeus yellow, circular, strongly protruding; bristles on clypeus light brown, both strong, smaller bristles on entire surface, all directed ventrally, clypeus 2X as long as face. Face yellow; shape a slightly wider than tall triangle, with fine bristles covering face. Frons yellow; with many bristles covering ventral half, frontal furrow running 1/10–1/4 distance from dorsal margin towards ventral margin, frontal cleft faint running to lateral ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 1.5X length of segment 4 with even width from base to apex, segment 3 appears to have large lateral patch of fine yellow setae not clearly delimited and interspersed with dark setae. Labellum yellow. Eye with many long inter-ommatidial setulae (in most inter-ommatidial junctions) on all but medial margin. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli 1–1.5X diameter of laterals, lateral ocelli 0.5X their own diameter from eye margin, ocellar triangle brown ring around each ocelli but not overlapping other ocelli. **Thorax:** Length 1.82 mm (1.72–1.89 mm,  $n = 4$ ). Yellow. Scutum yellow; surface of scutum covered with small setae; acrostichal setae vaguely present; dorsocentral setae probably present but not clearly distinguishable from other setae; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 8–10 large bristles and many small bristles. Prescutum yellow. Mediotergite yellow with 22–28 bristles on posterior third, absent. Laterotergite yellow; anterior margin of laterotergite not reaching katapisternum. Anepimeron yellow. Anepisternum yellow. Katapisternum yellow. Anteprepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture straight and clear. Halter yellow. **Legs:** principally yellow; extreme anteroapical corner light brown on hind femur, on other femora yellow. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, tibial spurs yellow to light brown, foretibial spur length 2.5X apical thickness of foretibia, shortest midtibial spur subequal to length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur 0.85X length of longest, longest hind tibial spur 5X apical thickness of hind tibia. Foreleg first tarsomere 0.9X length of foretibia. **Wing** (Fig. 69): Length 6.6 mm (6.0–6.9 mm,  $n = 4$ ). Hyaline; apical macula absent; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining  $R_1$  at least 3X its own length after origin of Rs.  $R_4$  present.  $R_5$  slightly sinusoidal.  $M_1$  reaching apex at same level as  $R_5$ , apices of M veins clearly reaching wing margin.  $M_4$ -CuA fork arising well before origin of r-m.  $A_2$  present. **Abdomen:** Tergites principally yellow, T1 light brown. Cercus yellow.

*Male.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** California, USA (Tuolumne Co., Amador Co.) (Fig. 148), 750 masl.

**DISCUSSION:** Even though this species exhibits a number of plesiomorphic characteristics (*i.e.* ocelli not forming an ocellar triangle, inter-ommatidial setulae covering most of eye, acrostichal setae present), it fits within the current limits of the genus. This placement should be confirmed when male specimens are found. It should be noted that the cell created by  $R_4$  is longer than that found in other *Leptomorphus* species. The sinusoidal shape of  $R_5$  is also unique within *Leptomorphus*, though this condition is seen in other Sciophilini genera such as *Neuratelia* and *Polylepta* Winnertz.

**ETYMOLOGY:** The species name refers to the confounding thought process that went into determining that this species was placed within *Leptomorphus*, due to both the number of plesiomorphic characters and lack of male material.

**MATERIAL EXAMINED:** *Holotype:* here designated, adult female, pinned, labelled “[USA] CAL.: Tuolumne Co./ Basin Creek Cmpgd./ 31.v.1963/ P.H. Arnaud, Jr.; HOLOTYPE ♀/ *Leptomorphus perplexus* / Borkent, new species / Det. C.J. Borkent 2012” [USNM]



*Paratypes*: labelled as for holotype (3♀, USNM). USA, Amador Co., Indian Grinding Rock State Park, dry wash nr. S. Nature trail. MT#2, 38°25' N, 120°8' W, 715masl, 24.v–10.vi.2007, 07LOT096, P. Kerr & M. Hauser / 07Y771 (1♀, CSCA).

## 28. *Leptomorphus quadrimaculatus* (Matsumura)

(Figures 33, 70, 116, 141, 150, 154)

*Boletina 4-maculata* Matsumura, 1916: 440.

*Coelosia (Boletina) 4-maculata*: Matsumura, 1931: 404.

*Lepitomorphus 4-maculata*: Okada, 1936: 99 (lapsus).

*Lepitomorphus 4-maculatus*: Okada, 1939: 302.

*Leptomorphus (Leptomorphus) quadrimaculatus*: Matile, 1977: 144.

**References**: Okada 1938: 93 (Japan: Hokkaido, South Kuril Islands); Matile 1977: 144 (subgeneric placement); Zaitzev 1984 (details and figure of the digestive tract), 1994: 157, 160 (key, re-description, male genitalia figure), 1999: 170–171 (key, male genitalia figure); Krivosheina *et al.* 1986: 134, 137 (key, genitalia figure [given as *L. forcipatus* though genitalia = *L. quadrimaculatus*]); Matile, 1988: 234 (catalogue); Krivosheina & Zaitzev 2008: 608 (larval habitat).

**DIAGNOSIS**: Other than *L. subforcipatus* this is the only extant species of *Leptomorphus* with both the gonocoxite longer than, and placed apically on, tergite 9, and a triangular, basal, medial-projecting process (Fig. 116). This species is darker in colour on the thorax than *L. subforcipatus* and does not have a slightly bulbous tip to the gonocoxite. See discussion under *L. subforcipatus* for more information. This species can be distinguished from the other Palaearctic species by the dark brown or black body with yellow legs (Fig. 33) and scutum evenly covered with small setae.

**DESCRIPTION**: *Male*. (Fig. 33) **Head**: brown to dark brown, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape brown with some yellow spots, with dark brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel light brown/yellow, with 3–4 large bristles, several setae on apicodorsal margin, a few of fine setae on apicoventral margin; flagellomere 1 with tapered base light brown remainder brown; flagellomere 6 1.8X as long as broad. Clypeus brown, strongly protruding, slightly laterally compressed oval; bristles on clypeus brown, both strong, smaller bristles on entire surface, all directed ventrally, clypeus 2X as long as face. Face brown; shape a subequal triangle, with fine bristles covering face. Frons from brown to dark brown; with few bristles medioventrally, frontal furrow running 3/4-full distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 subequal in length to segment 4 with even width from base to apex, segment 3 without distinct apicolateral patch of fine setae. Labellum brown. Eye with a number (in ~1/4 of the ommatidial junctions) of long inter-ommatidial setulae scattered on all but medial margin. Occiput brown with appressed, anteriorly directed setae. Ocelli with median slightly in front of laterals, space between ocelli less than diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax**: Length  $1.94 \pm 0.41$  mm (1.64 – 2.13 mm, n = 5). Dark brown. Scutum dark brown/black with blue-green specks; surface of scutum covered with small setae; acrostichal setae absent; dorsocentral setae probably present but not clearly distinguishable from other setae; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum dark brown; with 8–10 large bristles and many small bristles. Prescutum brown. Mediotergite dark brown with 16–20 bristles on posterolateral corners, anteromedial patch of small bristles. Laterotergite brown; anterior margin of laterotergite not reaching katapisternum. Anepimeron brown. Anepisternum brown. Katapisternum brown. Anteprototum and proepisternum brown. Margin of anterior and posterior spiracles yellow with brown trichia. Metepisternum dark brown. Anapleural suture straight and clear. Halter stem yellow, knob light to dark brown. **Legs**: principally yellow; coxa with basal margin dark brown; trochanters sometime light brown; extreme anteroapical corner dark brown on all femora; tarsi changing from yellow to brown from tarsi I to V. Midfemur without apical spine-like process. Tibia with covering of yellow macrotrichia, foretibia with comb of short setae along length of anteroventral surface, foretibial spur yellow, remainder brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of

even thickness for 2/3 of its length, placed basally, shortest midtibial spur 0.75X length of longest, longest midtibial spur 3.75X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 70): Length 7.9 mm (6.9–8.8 mm, n = 4). Hyaline; apical macula dark, reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell  $cua_1$ ,  $cup$ ,  $a_1$ , not joining with medial macula; medial macula extending from Sc to stem of  $M_{1+2}$ . Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) all the same length. Calypter bare. Vein sc-r present, apical end joining R within its own length prior to origin of  $R_s$ .  $R_4$  absent.  $R_5$  straight, slight posterior turn near tip.  $M_1$  reaching apex at same level as  $R_5$ , apices of M veins clearly reaching wing margin.  $M_4$ -CuA fork arising before origin of r-m.  $A_2$  faintly present as crease. **Abdomen**: Tergites dark brown. Tergite 8 smaller than all other abdominal sclerites, with 3 bristles on each apicolateral corner. **Genitalia** (Fig. 116): brown. Sternite 9 sclerotized medially as rounded square, 1/4 the width of T9, membranous margins reaching gonocoxal margin. Tergite 9 a slightly wider than long oval. Gonocoxite placed centrally on T9, much longer than length of T9, medial margin not reaching median line, bearing gonostylus basally. Gonostylus a single lobe tapering to a point apically, slightly curved and with several setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus 2/3 length of T9, tapering towards apex for basal 3/4 and then strongly indented and remainder squarish, apodemes ~1/2 total length. Parameres consisting of two lobes, lateral lobe a broad based spine curving laterally, medial lobe 2X length of lateral and very thin, apodemes 1/4 length of parameres, strongly united with gonocoxal apodemes and with a dorsal pointing small hook.

**Female**. As for male, except as follows. **Thorax**: Length  $1.85 \pm 0.37$  mm (1.68–2.17 mm, n = 6). **Wing**: Length  $7.4 \pm 1.1$  mm (6.7–8.1 mm, n = 6). **Legs**: Foretibia without comb of short setae on anteroventral surface. **Abdomen**: Cercus yellow.

*Immatures*. Undescribed.

**BIOLOGY**: Larvae have been recorded consuming spores on the underside of *Stereum* sp. fungi (Krivosheina & Zaitzev 2008).

**DISTRIBUTION**: Far Eastern Russia and Japan (Fig. 141) 30–1050 masl. Records from Western Europe are probably *L. forcipatus*, which was previously synonymized with *L. quadrimaculatus*.

**DISCUSSION**: As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Leptomorphus* and placed solely in the genus *Leptomorphus*. See also discussion under *L. subforcipatus*.

**MATERIAL EXAMINED**: *Holotype*: adult female, pinned, labelled “[illegible handwriting over top of printed label] Sapporo/ Matsum; Boletina/ 4-maculata; [red label] Type/ Matsumura; [folded large label] Boletina/ 4-maculata/ Mats/ [line of Japanese text]; Lepitomorphus/ 4-maculatus/ (Matsumura)/ det. I. Okada; HOLOTYPE ♀/ *Leptomorphus/ quadrimaculatus* (Mats.)/ Det. C.J. Borkent, 2012” [EIHU].

*Other material*: JAPAN, Hokkaido, Tokachi, Ashoromura, 5.viii.1949, R. Matsuda. (1♂, OMNH); Honshu, Kyoto, Ashiu, 7.vi.1964, M. Sasakawa. (1♀, OMNH); Yamanashi Pref., Hirogawara, Ashiyasu, 19.vii.1997, R. Matsumoto. (1♂, OMNH); 20.vii.1997, R. Matsumoto. (1♂, OMNH); 13.vii.1996, T. Saigusa. (1♂, OMNH); Kitazawa, Senjodake, 25.vii.1961, T. Saigusa. (1♀, LEM); RUSSIA, Far East, Primorskiy, Lazo, 11.vii.1979, A. Zaitzev. (1♂, 2♀, CNC); Lazo, Sokolchi, 12.viii.1979, A. Zaitzev. (1♀, BMNH).

## 29. *Leptomorphus stigmatus* Borkent, new species

(Figures 34, 71, 81, 115, 134, 150, 153)

**DIAGNOSIS**: The only extant species of *Leptomorphus* with the following combination of characters: laterotergite, anepisternum and anepimeron yellow; scutellum yellow; scutum with brown Y-shaped medial marking and prealar brown spots (Fig. 81); ; male genitalia with tergite 9 ending in square lobe (tergal evagination) bearing small medial point, sternite 9 more or less oval shaped (Fig. 115).

This species can be distinguished from other Afrotropical species by the mostly yellow scutum (brown Y-shape and prealar spots, Fig. 81) and abdomen (small posteromedial brown spots on tergites 4, 5), yellow scutellum (Fig. 34), and lack of small setae covering the scutum (except along dorsocentral lines).

**DESCRIPTION**: *Male*. (Fig. 34) **Head**: yellow, somewhat dorsoventrally compressed in anterior view. Antenna brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick

patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 2–3 large bristles and several setae on apicodorsal margin, a few fine setae on apicoventral margin; flagellomere 1 with tapered base brown remainder brown; flagellomere 6 1.6X as long as broad. Clypeus ivory, dorsoventrally elongate oval; bristles on clypeus light brown, 6–8 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 1.5X as long as face. Face ivory; shape a subequal triangle, with few bristles ventrolaterally. Frons yellow; with few bristles medioventrally, frontal furrow running full distance from dorsal margin towards ventral margin, frontal cleft initially running to lateral ocellus then barely in front of median ocellus. Palpus yellow; segment 1 small but visible below eye, segments increasing in length, segment 5 2.5X length of segment 4 with central half thinner than base and apex, segment 3 with apicolateral patch of fine yellow setae weakly encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.8 mm (n = 1). Yellow with dorsal brown spots. Scutum yellow, with spot at wing base and Y-shape originating posteriorly and thickening after split both dark brown (Fig. 81); surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 8 large bristles and few small bristles. Prescutum yellow. Mediotergite yellow with 6–10 bristles on posterolateral corners, anteromedial patch of small bristles. Laterotergite yellow; anterior margin of laterotergite not reaching katapisternum. Anepimeron yellow. Anepisternum yellow. Katapisternum yellow. Anteprepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with light brown and yellow trichia respectively. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter yellow. **Legs:** principally yellow; trochanters with brown margins; extreme anteroapical corner dark brown on all femora; tarsi brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, hind tibial spur yellow, remainder brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 3/4 of its length, placed basally, shortest midtibial spur 0.8X length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur 0.85X length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.6X length of foretibia. **Wing** (Fig. 71): Length 6.2 mm (n = 1). Hyaline; apical macula absent; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with group of macrotrichia. Vein sc-r present, apical end joining R at 2X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex just before R<sub>5</sub>, apices of M veins reaching wing margin. M<sub>4</sub>-CuA fork arising before origin of r-m. A<sub>2</sub> present. **Abdomen:** Tergites principally yellow, T3–5 with small, posteromedial dark brown spot. Tergite 8 smaller than all other abdominal sclerites, with 2–3 bristles on each apicolateral corner. **Genitalia** (Fig. 115): yellow. Sternite 9 sclerotized oval, 1/2 the width of genitalia at widest point, overlapping medial margin of gonoxite. Tergite 9 longer than wide, margins rounded ending in lateral squared off lobe with spine on medial margin and medial U-shaped indentation, one thick and one thin, a ventrally extending thin process at base of posterior lobe forked into two points at apex. Gonocoxite placed basally on T9, medial margin not reaching medial line, bearing gonostylus apically. Gonostylus with two lobes, dorsal lobe a broad based point, ventral lobe half the width of dorsal but 2X length and barely tapering to rounded apex, gonocoxite III fused to dorsolateral margin. Aedeagus equal in length of gonocoxite, tapering towards apex, apodemes 1/4 total length. Parameres a simple taper laterally with a small medial bump, apodemes 3/4 length of parameres.

*Female.* As for male, except as follows. **Thorax:** Length 1.8 mm. **Wing:** Length 7.2 mm. **Abdomen:** Cercus dark yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Tanzania (Fig. 134), 460–1740 masl.

**ETYMOLOGY:** The species name refers to the dark spots (stigmata) present on the scutum (Fig. 81).

**MATERIAL EXAMINED:** *Holotype:* here designated, adult male, pinned, labelled “TANZANIA: Tanga region, / E. Usambara Mts. Amani/ Botanical Gardens: 2.xii.1990/ ZMB’s Tanzania Exp. 1990:/ Sweep net, el. 460m.; HOLOTYPE/ *Leptomorphus stigmatatus* / Borkent, new species / Det. C.J. Borkent 2012” [ZMUN].

*Paratypes:* Labelled as for holotype (1 ♀, ZMUN).

**30. *Leptomorphus subcaeruleus* (Coquillett)**

(Figures 36–37, 72, 84, 117, 130, 146, 150, 154)

*Sciophila subcaerulea* Coquillett, 1901: 595.*Sciophila pulchra* Johannsen, 1903: 14. Synonymized by Shaw (1947).*Diomonus subcaeruleus*: Johannsen, 1909: 45.*Diomonus pulcher*: Johannsen, 1909: 45.*Leptomorphus subcaeruleus pulcher*: Shaw, 1947: 157.*Leptomorphus subcaeruleus subcaeruleus*: Shaw, 1947: 157.*Leptomorphus (Diomonus) subcoeruleus*: Matile, 1977: 146 (*lapsus*).

**References:** Johannsen 1910: 154–157 (description, key reference, NH); Johnson 1925: 80 (distribution; MA, ME, NH, RI, VT); Brimley 1938: 326 (NC); Procter 1946: 359 (ME); Shaw & Fisher 1952: 192 (key to species, MA, ME, NH, NY, RI, VT); Laffoon 1965: 223 (catalogue); Cole & Schlinger 1969: 120 (distribution: AB); Wray 1967: 75 (North Carolina); Eberhard 1970 (complete natural history and behaviour), 1986 (correction to 1970); Matile 1977: 146 (subgeneric placement); Santini 1985: 239, 243–4 (comparison to *L. walkeri*); Poole and Gentili, 1996: 194 (catalogue).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: scutum with setae on entire surface; thorax completely dark brown/black and the legs completely yellow, scutum with setae on entire surface;  $R_4$  present; male genitalia with two long sickle-like structures (aedeagus) curving dorsally (Fig. 117).

This species can easily be distinguished from other species with  $R_4$  present, based on the completely dark brown or black body (sometimes tergite 4 light brown or reddish in female, Fig. 37), yellow legs (including the coxae) and completely brown antennae (Fig. 36).

**DESCRIPTION:** *Male.* (Fig. 36) **Head:** dark brown to black, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape medium to dark brown, with brown to black setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel brown, with 2–3 large bristles, several setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base dark brown remainder dark brown; flagellomere 6 1.6X as long as broad. Clypeus dark brown, circular, strongly protruding; bristles on clypeus dark brown, both strong, smaller bristles on entire surface, all directed ventrally, clypeus 1.5X as long as face. Face dark brown; shape a slightly wider than tall triangle, covered with many strong bristles. Frons dark brown; bare, frontal furrow running 1/3 distance from dorsal margin towards ventral margin, frontal cleft initially running to lateral ocellus then barely in front of median ocellus. Palpus with segments 1–3 light brown, remainder brown; segment 1 small but visible below eye, segments increasing in length, segment 5 1.5X length of segment 4 with even width from base to apex, segment 3 without distinct lateral patch of fine setae. Labellum brown. Eye with a number (in ~1/4 of the ommatidial junctions) of long inter-ommatidial setulae scattered on posterior half. Occiput dark brown with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli 1–1.5X diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax:** Length  $2.12 \pm 0.56$  mm (1.72–2.54 mm,  $n = 10$ ). Dark brown. Scutum dark brown/black with blue-green specks; surface of scutum covered with small setae; acrostichal setae absent; dorsocentral setae present as complete multiple lines of setae; double row of lateral setae present; patch of setae on scutum at wing base present. Scutellum dark brown; with 8–10 large bristles and many small bristles. Prescutum brown. Mediotergite dark brown with 18–24 bristles on posterolateral corners, absent. Laterotergite brown; anterior margin of laterotergite not reaching katapisternum. Anepimeron brown. Anepisternum dark brown. Katapisternum dark brown. Anteprototum and proepisternum dark brown. Margin of anterior and posterior spiracles brown with brown trichia. Metepisternum anterior ventral corner yellow remainder dark brown. Anapleural suture straight and clear. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** Principally yellow; femora with apex brown; extreme anteroapical corner dark brown on all femora; foretibia with apical 1/2 brown, midtibia with apex brown, hind tibia brown except for base; tarsi brown. Midfemur with apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface (Fig. 84), yellow to light brown, foretibial spur length 1.7X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 3/4 of its length, placed basally, shortest midtibial spur 0.8X length of longest,



longest midtibial spur 3X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3X apical thickness of hind tibia. Foreleg first tarsomere 1.4X length of foretibia. **Wing** (Fig. 72): Length  $8.0 \pm 1.7$  mm (6.9–9.4 mm,  $n = 10$ ). Hyaline; apical macula brown, only on anterior half of wing, beginning halfway along  $R_5$  but not reaching wing tip; medial macula extending from Sc to stem of  $M_{1+2}$  with some light brown in cell cua. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) all the same length. Calypter bare. Vein sc-r present, apical end joining R within its own length prior to origin of  $R_s$ .  $R_4$  present.  $R_5$  slightly concave for entire length.  $M_1$  reaching apex before  $R_5$ , apices of M veins clearly reaching wing margin.  $M_4$ -CuA fork arising well before origin of r-m.  $A_2$  faintly present as crease. **Abdomen**: Tergites all dark brown to black. Tergite 8 smaller than all other abdominal sclerites and covered with many bristles. **Genitalia** (Fig. 117): dark brown. Sternite 9 sclerotized, rounded rectangle,  $2/3$  the length of T9 but wider than genitalia. Tergite 9 as wide as long, with basal half of lateral margins parallel, remainder tapering to rounded medial apex. Gonocoxite placed apically on T9, tapering to a point on apicolateral margin, medial margin not reaching medial line, bearing gonostylus basally. Gonostylus a single lobe tapering towards apex and bearing several setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus 1.5X length of T9, tapering to middle and then becoming a lateral sclerotized sickle-like hook with serrated tip, apodemes sclerotized and  $1/7$  total length. Parameres a swollen lobe with apex covered in small spines, apodemes  $1/4$  length of parameres and strongly united with gonocoxal apodemes.

**Female**. (Fig. 37) As for male, except as follows. **Thorax**: Length  $2.03 \pm 0.34$  mm (1.8–2.3 mm,  $n = 10$ ). **Wing**: Length  $7.8 \pm 1.2$  mm (6.8–8.6 mm,  $n = 10$ ). **Legs**: Midfemur without apical spine-like process. **Abdomen**: Tergite 4 often light brown or reddish. Cercus dark brown.

**Immatures**. Pupa, larva (Fig. 130) and egg are described by Eberhard (1970).

**BIOLOGY**: A detailed description of immature and adult behaviour is given by Eberhard (1970). The larvae feed on the underside of polypore fungi where they spin a silken sheet that traps the fungal spores, which they then eat and fill in the hole in the sheet. Larvae pupate by anchoring a line underneath or adjacent to the fungus. They then crawl to the middle of this line and pupate attached to the line hammock-style. Adult males are known to find and guard female pupae from other males. The guarding male fights off challengers using his forelegs while hanging on with his four hind legs. The ability of the male to hang on while under attack is probably aided by the presence of the midfemoral apical process (Fig. 84) which is placed in such a way that it interacts with the tibia to lock the joint. This applies to the other species with the midfemoral apical process as well.

**DISTRIBUTION**: Nearctic; South Dakota east to New Brunswick, and from Ontario south to North Carolina (Fig. 146), 5–1830 masl.

**DISCUSSION**: After studying the type of *L. pulcher* we agree with the previous synonymization with *L. subcaeruleus*. Males and females were associated based on the collection of a mated pair.

As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Diomonus* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED**: *Holotype*: adult male, pinned on paper point, genitalia in glass vial on pin, labelled "FRANCONIA, N.H.; Mrs Slosson/ Collector; [Red label] Type/ No. 5444/ U.S.N.M; Sciophila/ subcaerulea/ Coq.; HOLOTYPE ♂/ *Leptomorphus/ subcaeruleus* (Coquillett) /Det. C.J. Borkent, 2012" [USNM].

*Other material*: CANADA, NB, Newcastle, 6.vii.1971, B.V. Petersen. (1♀, CNC); ON, 6mi. W Richmond, 6.vii.1971, J.E.H. Martin. (1♀, CNC); Algonquin Park, Swann Lake, 1–10.vii.1994, E.R. Barr. (1♂, DEBU); Bouck's Hill, 18.vi.2003, R. Zeran. (3♂, LEM); Greenbush, 10.vii.1999, R. Hainault. (1♂, CNC); Hall's Lake, 19.vii.1961, G.K. Morris. (1♂, DEBU); Innisville, 5.vii.1963, W.R.M. Mason. (1♀, CNC); 16.vii.1963. (1♂, CNC); Lancaster, 1.vii.2003, R. Zeran. (4♂, LEM); Morrisburg, 18.vi.2003, R. Zeran. (1♂, LEM); Niagara Falls, 10.ix.1910, M.C. VanDuzee. (1♀, CAS); One sided Lake, 12.vii.1960, S.M. Clark. (1♂, CNC); Ottawa. (1♂, USNM); Bruce Co., Little Cove, 4.ix.2004, S.A. Marshall. (1♂, DEBU); Dunks Bay, 22.viii.2003, S.A. Marshall. (1♂, DEBU); Carleton Co., 8km S Richmond, 30.viii.2008, D.M. Wood. (1♂, LEM); Dufferin Co., nr. Mansfield, 19–20.ix.1992, J Skevington, A Goering. (1♀, CNC); Lanark Co., N. Burgess Twp., 1.viii.1970, D.M. Wood. (2♀, CNC); 24.viii.1972. (1♀, CNC); QC, 2.3km SSW Rapide-Danseur, 30.vi–29.vii.2007, A. Hibbert. (1♂, 1♀, LEM); 28.v–30.vi.2007. (1♂, LEM); Aylmer, 15.vii.1924, C.H. Curran. (1♂, CNC); Kirk's Ferry, 22.viii.1924, E.P. Ide. (1♀, CNC); Lake Duparquet Res. and Train. For., 12.vii–1.viii.2006, A. Hibbert. (3♂, 1♀, LEM); Mont St-Bruno, 1–8.vii.2008, V. Levesque. (2♂, LEM); 24.vi–1.vii.2008. (3♂, LEM); Mont St-Hilaire, 11–18.ix.2001,

E. Fast. (1♂, LEM); 18–24.ix.2001. (2♂, LEM); 15–22.vii.2008, V. Levesque. (1♂, LEM); 17–23.vi.2008. (2♂, LEM); 30.vi–7.vii.2008. (2♂, LEM); 23–30.vi.2009. (1♂, LEM); Norway Bay, 30.viii.1938, G.E. Shewell. (1♀, CNC); Rougemont, 16–23.vii.2008, V. Levesque. (1♂, LEM); Ste-Anne-de-Bellevue, Morgan Abtrm., 31.vii.2007, C.J. Borkent. (1♂, LEM); 3.vii.2010. (4♂, 5♀, LEM); 30.vi.2010. (4♂, 2♀, LEM); USA, CT, Redding, 17.vii.1931, A.L. Melander. (1♀, USNM); Stamford, 3.vii.1944. (1♂, USNM); MA, Holliston, 2.vii, N. Banks. (1♂, MCZ); Petersham, vii.1926, A.L. Melander. (1♂, ANSP); Petersham, vi.1941. (1♀, MCZ); MD, Garrett Co., New Germany St. Pk., 7.vi.1977, Byers, May, Young. (1♂, SEMC); ME, York Co., West Lebanon, 5–9.vii.1990, D.W. Barry. (1♂, UNHC); MI, Isle Royale, 3–7.viii.1936, C.W. Sabrosky. (1♀, USNM); Berrien Co., St Joseph, 15.vi.1975, D.D. Wilder. (1♂, CAS); NC, Highlands, 26.vi.1957, W.R.M. Mason. (1♂, 1♀, CNC); Sunburst, 6.v.1912. (1♂, NCSU); NH, Dover, 30.vi.1974, A.H. Mason. (1♀, UNHC); Hampton, 25.vii.1903, S.A. Shaw. (1♀, CUIC); Carr. Co., 1mi. N Wonalancet, E Fk., Spring Brk., 29.viii–5.ix.1985, D.S. Chandler. (1♀, UNHC); 2.5mi. NW Wonalancet, 28.vi–4.vii.1984, D.S. Chandler. (1♂, UNHC); Rock. Co., 1mi. W Odiorne Pt., 22–24.vi.1983, D.S. Chandler. (1♂, UNHC); Straf Co., 1mi. SW Durham, 24.vii–6.viii.1987, D.S. Chandler. (1♂, UNHC); 4mi. W Durham, 14–20.ix.1982, R.M. Reeves. (1♂, UNHC); Durham, 14.viii.1957, W.J. Morse. (1♂, 1♀, UNHC); 22.vii.1984. (1♂, UNHC); 10.vii.1989. (1♂, UNHC); NY, Axton, 12–22.vi.1901, A.D. MacG, C.O.H. (1♀, CUIC); Beaver Creek, McLean Res., 30.viii.1924. (1♀, CUIC); 1.ix.1925. (1♂, CUIC); East Aurora, 30.vii.1922, M.C. Van Duzee. (1♂, CAS); Erie Co., Protection, 18.vii.1915, M.C. Van Duzee. (1♀, CAS); PA, Ohiopyle, viii.1907, H. Kahl. (1♂, CMNH); State College, 6.viii.1949, C.W. Sabrosky. (1♂, USNM); Clarion Co., Cook Forest St Pk., 11.viii.1961, J.L. Laffoon. (1♂, ISUI); Forest Co., nr. Marienville, 27.ix.1994, W. Metheny. (1♀, CMNH); Huntingdon Co., Cornpropstsmills, 28.vi.1973, D.J. Shetlar. (1♂, CAS); Moreland Co., Powdermill Nature Reserve, 20.vii.1956, H.K. Clench, N. Richmond. (1♂, CMNH); SD, Harney Peak, Harney Nat. For., 24.vii.1951, G.W. Byers. (1♂, SEMC); Lawrence Co., 6.2mi. SW Lead, 10.vii.1959, G.W. Byers. (1♂, SEMC).

### 31. *Leptomorphus subforcipatus* Zaitzev & Ševčík

(Figures 118, 140)

*Leptomorphus subforcipatus* Zaitzev & Ševčík, 2002: 208.

**DIAGNOSIS:** Other than *L. quadrimaculatus* this is the only extant species of *Leptomorphus* with both the gonocoxite longer than, and placed apically on, tergite 9, and a triangular, basal, medial-projecting process (Fig. 118). This species is lighter in colour on the thorax than *L. quadrimaculatus* and has a slightly bulbous tip to the gonocoxite. See discussion below for more information. This species can be distinguished from the other Palaearctic species by the dark brown or black body with yellow legs (Fig. 33) and scutum evenly covered with small setae.

**DESCRIPTION:** *Male. Head:* dark brown. Antenna dark brown; scape yellow, with yellow setae; flagellomere 6 2X as long as broad. Clypeus yellow to light brown. Palpus yellow. Ocellar triangle light brown. **Thorax:** Dark brown dorsally, yellow laterally. Scutum dark brown with yellow posterolateral corners. Scutellum brown. Mediotergite yellow with central brown spot. Laterotergite light brown. Halter knob brown. **Legs:** yellow. Foretibia with strong, double comb of short setae along length of anteroventral surface. Foreleg first tarsomere 1.5X length of foretibia. **Wing:** Length 7 mm (6–8 mm). Hyaline; apical macula reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell  $cua_1$ , cup, not joining with medial macula; medial macula present from Sc to M fork.  $M_4$ -CuA fork arising before origin of r-m. **Abdomen:** Tergites brown. **Genitalia** (Zaitzev & Ševčík 2002: 205, figs. 2, 6): Tergite 9 light brown, circular with posterior margin flat except for small medial bump. Gonocoxite placed apicoventrally on T9, lateral margin straight for 3/4 of length then sharply curved medially, almost twice as thick beyond bend than at bend, interior margin flat from base until bend. Gonostylus single geniculate lobe covered in setae.

*Female.* As for male, except as follows. **Legs:** Foretibia without comb of short setae on anteroventral surface. **Abdomen:** Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** NW Russia and SE Finland (Fig. 140), 125–200 masl.

**DISCUSSION:** The description here is based on the original description (Zaitzev & Ševčík 2002), as no material was available for study. This species is very similar to *L. quadrimaculatus*, with the perceived difference in the genitalia (Zaitzev & Ševčík 2002) being very slight (slightly more bulbous apex of gonocoxite in *L. subforcipatus*) and likely due to the membranous nature of the gonocoxite. The species is also lighter in colour on the thorax. Because colour can vary within a species of *Leptomorphus*, we suspect that *L. subforcipatus* is a synonym of *L. quadrimaculatus*. However, until types can be compared we treat the two species as distinct.

**MATERIAL KNOWN:** *Holotype:* Adult male, not examined. Label data is given as: RUSSIA, Moscow Reg., Pavlovskaya Sloboda, 10.VII.1982, Zaitzev leg. [IEE].

*Paratypes:* 4 ♂ and 1 ♀ from type locality, 4 ♂ from other locations in northwestern Russia and 1 ♂ from Finland (IEE, Zaitzev & Ševčík 2002).

### 32. *Leptomorphus tabatius* Borkent, new species

(Figures 35, 73, 78, 120, 137, 150, 152)

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite and anepisternum brown; wing without apical spot; segments 3–5 of abdomen noticeably swollen relative to other segments; male genitalia with tergite 9 bearing two long lateral processes posteriorly, so that tergite 9 is ~2X as long as wide (Fig. 120).

This species can be distinguished from the other Oriental and eastern Palaearctic species either by the brown katepisternum and metepisternum (Fig. 35, both completely yellow in *L. babai*, *L. ornatus* and *L. titiwangsensis*), or by the posterolateral yellow spots on the scutum and the long evaginations (more than half the length of the genitalia) at the posterior margin of the male genitalia (Fig. 120).

**DESCRIPTION:** *Male.* (Fig. 35) **Head:** (Fig. 78) light yellow, somewhat dorsoventrally compressed in anterior view. Antenna with basal 2–3 flagellomeres lighter brown, darkening apically; scape yellow, with black setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae absent; pedicel light brown, with 5–6 setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base light brown remainder brown; flagellomere 6 1.1X as long as broad. Clypeus light yellow, dorsoventrally elongate oval; bristles on clypeus brown, 4 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 1.6X as long as face. Face light yellow; shape a slightly wider than tall triangle, with few bristles ventrolaterally. Frons yellow; bare, frontal furrow running full distance from dorsal margin towards ventral margin, frontal cleft more than 1X diameter of median ocellus anterior of median ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length of segment 4 with apex slightly swollen, segment 3 spherical with apicolateral depressed patch of fine yellow setae partially encircled by strong dark setae. Labellum yellow. Eye with inter-ommatidial setulae absent. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle black. **Thorax:** Length 1.19 mm (n = 1). Dark brown. Scutum dark brown with a pair of small yellow posterolateral spots; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; multiple rows of lateral setae present; patch of setae on scutum at wing base present. Scutellum light yellow; without large bristles but few small bristles. Prescutum light brown. Mediotergite dark brown with 8 bristles on posterolateral corners, anteromedial patch of small setae. Laterotergite brown; anterior margin of laterotergite not reaching katepisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum brown. Antepnotum and proepisternum brown. Margin of anterior spiracle brown and posterior spiracle yellow, both with light brown trichia. Metepisternum light brown. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** Light yellow except for joint of hind femur and tibia which is brown; extreme anteroapical corner dark brown on all femora. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, foretibial and anterior midtibial spurs brown, remainder yellow, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 2/3 of its length,

placed basally, shortest midtibial spur subequal to length of longest, longest midtibial spur 4X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3.5X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 73): Length 5.0 mm (n = 1). Hyaline; apical macula absent; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a group of macrotrichia. Vein sc-r present, apical end joining R at 2X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins fading before wing margin. M<sub>4</sub>-CuA fork arising apically of origin of r-m. A<sub>2</sub> absent. **Abdomen**: Abdominal segments 3–5 swollen to 2X thickness of other segments; tergites 3–5 with anterior 1/3–1/2 yellow, remainder brown. Tergite 8 smaller than all other abdominal sclerites, with 8 bristles on each apicolateral corner and few bristles along posterior margin but not as complete row (missing from medial 1/4). **Genitalia** (Fig. 120): light yellow. Sternite 9 reduced to long thin sclerite attached to aedeagus. Tergite 9 longer than wide, basal 1/3 rounded and then spreading apically into strongly pointed lateral lobes and deep V-shaped medial notch, mediobasal corner of lobes with two sclerotized points ventrally. Gonocoxite strongly fused with T9 but visible due to difference in sclerotization, placed centrally on T9, medial margin not reaching median line, bearing gonostylus apically. Gonostylus a single broad-based lobe tapering to apex which is bifurcated into two short sclerotized points, gonocoxite III fused to gonostylus basally. Aedeagus 1/4 length of genitalia, broad, rounded base tapering to apex, strongly united basally with S9, apodemes highly reduced. Parameres squared off so essentially only apodemes remain (posterior margin flat), apodemes strongly united with gonocoxal apodemes.

*Female adult*. Unknown.

*Immatures*. Unknown.

**BIOLOGY**: Unknown.

**DISTRIBUTION**: Sulawesi, Indonesia (Fig. 137), 820 masl.

**DISCUSSION**: This species appears to have male genitalia similar to, but sufficiently distinct from, those of *L. alienus* Papp & Ševčík. We were unable to examine specimens of that species for comparison and cannot comment further on the relationship.

**ETYMOLOGY**: This species name is derived from the Tolaki for ‘fat’ (taba) ‘belly’ (tia), in reference to the swollen abdomen. Tolaki is the language spoken by the people of the Mekongga Mountains of Sulawesi, where the holotype was collected.

**MATERIAL EXAMINED**: *Holotype*: here designated, adult male, pinned with genitalia in plastic vial on pin, labelled “Indonesia, se Sulawesi, North Kolaka / Rante Angin, Tinukari, Mekongga Mt. / 23.vi–1.vii.2010, ICBG team, 401 masl / 3.639444°S, 121.151111°E / CSCA11L042; HOLOTYPE ♂ / *Leptomorphus tabatius* / Borkent, new species / Det. C.J. Borkent 2012” [MZB]. The holotype was collected as part of the International Cooperative Biodiversity Group: Indonesia study of this biodiversity hotspot. This study was funded by the National Institute of Health (NIH) with the support of the Indonesian Institute of Sciences (LIPI). We thank them for providing us with this specimen for our study.

### 33. *Leptomorphus tagbanua* Borkent, new species

(Figures 40, 74, 88, 119, 137, 150, 152)

**DIAGNOSIS**: The only extant species of *Leptomorphus* with the following combination of characters: laterotergite and anepisternum brown; wing without apical spot; vein sc-r joining R at ~2X its own length from origin of Rs; segments 3–5 of abdomen noticeably swollen relative to other segments; male genitalia wider than long (Fig. 119).

This species can be distinguished from the other Oriental and eastern Palaearctic species either by the brown katepisternum (Fig. 40, yellow in *L. babai*, *L. ornatus* and *L. titiwangsensis*), or by the wider than long male genitalia with uniquely shaped tergal evaginations at the posterior margin (Fig. 119).

**DESCRIPTION**: *Male*. (Fig. 40) **Head**: yellow, taller than wide in anterior view. Antenna with basal 2–3 flagellomeres lighter brown, darkening apically; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third, entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 2 large bristles, few of setae on apicodorsal margin, none



ventrally; flagellomere 1 with tapered base yellow remainder yellow; flagellomere 6 1.0X as long as broad. Clypeus light brown, slightly laterally compressed oval; bristles on clypeus light brown, 4 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 1.5X as long as face. Face light brown; shape a just longer than wide triangle, with few bristles ventrolaterally. Frons yellow; bare, frontal furrow running 3/4 distance from dorsal margin towards ventral margin, frontal cleft more than 1X diameter of median ocellus anterior of median ocellus. Palpus yellow; segments increasing in length, segment 3 appears spherical (difficult to tell in specimen). Labellum yellow. Eye with inter-ommatidial setulae absent. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.03 mm (n = 1). Dark brown. Scutum dark brown with blue-green specks; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae for most of length; two thirds row of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 6–8 large bristles and few small bristles. Prescutum brown. Mediotergite dark brown with 6 bristles on posterolateral corners, few medially. Laterotergite brown; anterior margin of laterotergite not reaching katapisternum. Anepimeron brown. Anepisternum dark brown. Katapisternum dark brown. Antepronotum and proepisternum dark brown. Margin of anterior and posterior spiracles yellow with light brown trichia. Metepisternum anterior half brown posterior yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs:** principally yellow; extreme anteroapical corner light brown on all femora; tarsi brown. Midfemur without apical spine-like process. Tibia with covering of yellow macrotrichia, foretibia without comb of short setae along length of anteroventral surface (Fig. 88), tibial spurs yellow, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 3/4 of its length, placed basally, shortest midtibial spur subequal to length of longest, longest midtibial spur 3.5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 3X apical thickness of hind tibia. Foreleg first tarsomere 1.6X length of foretibia. **Wing** (Fig. 74): Length 4.0 mm (n = 1). Hyaline; apical macula absent; medial macula absent. Macrotrichia in all cells, though absent from posterobasal margin of cell a. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R at 2X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex just before R<sub>5</sub>, apices of M veins fading before wing margin. M<sub>4</sub>-CuA fork arising apically of origin of r-m. A<sub>2</sub> absent. **Abdomen:** Abdominal segments 3–5 swollen relative to other segments; principally dark brown, T3–5 with anterior 1/3–1/2 yellow. Tergite 8 smaller than other abdominal sclerites and 2 rows of bristles on posterior margin and large patches (~30) laterally. **Genitalia** (Fig. 119): orangish yellow. Sternite 9 reduced to long thin sclerite attached to aedeagus. Tergite 9 wider than long oval, posterior margin with a shallow medial indentation and an intricate strongly sclerotized process with many points on lateral corner. Gonocoxite strongly fused with T9 but visible due to difference in sclerotization, placed centrally on T9, medial margin not reaching median line, bearing gonostylus apically. Gonostylus a single broad-based lobe tapering to apex which is bifurcated into two short sclerotized points, gonocoxite III fused to gonostylus basally but forming its own lobe. Aedeagus ~1/2 length of genitalia, broad, rounded base tapering to apex, strongly united basally with S9, apodemes highly reduced. Parameres squared off so essentially only apodemes remain (posterior margin flat), apodemes strongly united with gonocoxal apodemes.

*Female adult.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Coron Island, Philippines (Fig. 137), 215 masl.

**DISCUSSION:** This species was compared to the descriptions and figures of the recently described Oriental and Australasian species (Papp & Ševčík 2011), and is clearly different from all of them and not a junior synonym.

**ETYMOLOGY:** This species is named for the Tagbanua people, who are the ancestral and current inhabitants of Coron Island where this species was found.

**MATERIAL EXAMINED:** *Holotype:* here designated, adult male, pinned, labelled “Coron,/ Busuanga,/ Phil. Is.; Coll. J. Laffoon/ VI-21-1945; HOLOTYPE ♂/ *Leptomorphus tagbanua* / Borkent, new species / Det. C.J. Borkent 2012” [ISUI].

**34. *Leptomorphus talyshensis* Zaitzev & Ševčík**

(Figures 121, 140)

*Leptomorphus talyshensis* Zaitzev & Ševčík, 2002: 210.

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: foretibia with dense row (comb) of short anteroventral bristles; wing with dark apical and medial spots present; male genitalia with outer margin of the gonocoxite straight, and with the gonocoxite longer than, and placed apically on, tergite 9 (Fig. 121).

This species can be distinguished from other Palaearctic species by the long gonocoxites (more than half total length of male genitalia, Fig. 121), striped abdomen and scutum evenly covered with small setae. It is the only species with long gonocoxites that has the gonocoxite strongly bent at two-thirds of its length (Fig. 121).

**DESCRIPTION:** *Male.* **Head:** yellow. Antenna; flagellomere 6 2X as long as broad. Clypeus yellow. Palpus yellow. Ocellar triangle light brown. **Thorax:** Dark brown dorsally, yellow laterally. Scutum dark brown with yellow lateral parts. Scutellum yellow. Mediotergite yellow. Laterotergite yellow with ventral margin brown. Anepisternum yellow. Katepisternum yellow. Halter knob brown. **Legs:** yellow. Foretibia with comb of short setae along length of anteroventral surface. Foreleg first tarsomere 2X length of foretibia. **Wing:** Length 7 mm. Hyaline; apical macula reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell cua, cup, not joining with medial macula; medial macula present from Sc to M fork. M<sub>4</sub>-CuA fork arising at same level as r-m. **Abdomen:** Tergites 1–5 yellow with posterior margin dark brown, T6 dark brown with anterior margin yellow. **Genitalia** (Zaitzev & Ševčík 2002: 205, figs. 4–5): Tergite 9 yellow, circular with posterior margin flat to slightly concave. Gonocoxite placed apicoventrally on T9, lateral margin smoothly curved medially with slight thickening at apex, interior margin with basal triangular projection covered in setae. Gonostylus small dorsal lobe and large sickle shaped ventral lobe, both covered with setae.

*Female.* As for male, except as follows. **Legs:** Foretibia without comb of short setae on anteroventral surface.

**Abdomen:** Cercus yellow.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Azerbaijan (Fig. 140), -3 masl.

**DISCUSSION:** The description here is based solely on the original description (Zaitzev & Ševčík 2002), as no material was available for study.

**MATERIAL KNOWN:** *Holotype:* Adult male, not examined. Label data is given as: AZERBAIJAN, Avrora, 13.V.1980, Zaitzev leg. [IEE]. Paratypes have the same data (1♂, 1♀, IEE).

**35. *Leptomorphus titiwangensis* Borkent, new species**

(Figures 38, 75, 122, 137, 150, 152)

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: laterotergite and anepisternum brown; wing with pale brown apical wing spot reaching to wing tip, pale medial wing spot absent; male genitalia with gonocoxite as long as tergite 9 with margins distinguishable, apex of gonostylus bifurcated, aedeagal apodemes present (Fig. 122).

This species can be distinguished from most other Oriental and eastern Palaearctic species (including those in Papp & Ševčík 2011) based on the yellow katepisternum and metepisternum (Fig. 38, both brown in all other species in these regions except *L. babai*, and *L. ornatus*). It can be distinguished from *L. babai* by its yellow scutellum (brown in *L. babai*) and from *L. ornatus* by its occurrence only in peninsular Malaysia and presumably different male genitalic morphology.

**DESCRIPTION:** *Male.* **Head:** yellow, somewhat dorsoventrally compressed in anterior view. Antenna brown; scape yellow, with brown setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 1–2 large bristles, few of setae on apicodorsal margin, none ventrally; flagellomere 1 with tapered base brown remainder brown; flagellomere 6 1.1X as long as broad. Clypeus ivory, dorsoventrally elongate oval; bristles on clypeus yellow, 6–8 strong bristles on ventral margin directed ventrally, remaining setae directed

medioventrally, clypeus 2X as long as face. Face ivory; shape a subequal triangle, bare. Frons yellow; bare, frontal furrow running 3/4-full distance from dorsal margin towards ventral margin, frontal cleft running to lateral ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 ~1.5X length of segment 4, segment 3 spherical with apicolateral depressed patch of fine yellow setae partially encircled by strong dark setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Ocelli in a straight line, space between ocelli 1–1.5X diameter of laterals, lateral ocelli 3X their own diameter from eye margin, ocellar triangle dark brown/black with electric blue green specks. **Thorax** : Length 1.04 mm (0.90–1.23 mm, n = 3). Mostly dark brown with anterolateral area yellow. Scutum dark brown/black with blue-green specks, pair of small yellow anterolateral spots; surface of scutum bare; acrostichal setae absent; dorsocentral setae present as fine setae on posterior two thirds; two thirds row of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 2–4 large bristles and few small bristles. Prescutum brown. Mediotergite dark brown with 2 bristles on posterolateral corners, absent. Laterotergite brown; anterior margin of laterotergite abutting katepisternum. Anepimeron brown. Anepisternum brown. Katepisternum yellow. Anteprepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter with basal 1/3 of stem ivory, apical portion and knob dark brown. **Legs**: principally yellow; hind coxa with brown spot along length of anterior surface; hind femur with apex and basal 1/4 light brown; extreme anteroapical corner light brown on forefemur, on other femora dark brown; tarsi light brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia without comb of short setae along length of anteroventral surface, tibial spurs light brown, foretibial spur length 2X apical thickness of foretibia, midtibia with faint, dorsal, bare patch of even thickness for 4/5 of its length, placed basally, shortest midtibial spur 0.6X length of longest, longest midtibial spur 5X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.8X length of foretibia. **Wing** (Fig. 75): Length 4.5 mm (4.4–4.5 mm, n = 3). Hyaline; apical macula light brown, reaching wing tip, but fading towards posterior margin; medial macula absent. Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present (sometimes very light), apical end joining R at 2X its own length prior to origin of Rs. R<sub>4</sub> absent. R<sub>5</sub> straight, slight posterior turn near tip. M<sub>1</sub> reaching apex before R<sub>5</sub>, apices of M veins fading before wing margin. M<sub>4</sub>-CuA fork arising just apically of origin of r-m. A<sub>2</sub> absent. **Abdomen**: Tergites 3–5 with anterior 1/3 yellow, remainder dark brown. Tergite 8 smaller than all other abdominal sclerites, with 4–5 bristles on each apicolateral corner. **Genitalia** (Fig. 122): yellow. Sternite 9 reduced to thin rectangular sclerite attached to aedeagus. Tergite 9 longer than wide, rounded margins tapering into two short rounded lobes and medial indentation. Gonocoxite placed basally on T9, medial margins not reaching median line, a ventromedial lobe covering base of gonostylus, bearing gonostylus halfway to apex. Gonostylus a single lobe tapering towards middle and then bifurcated into two points and bearing several basal setae, gonocoxite III separate from gonostylus dorsomedially. Aedeagus 2/3 length of gonocoxite, tapering towards apex (slight central swelling), apodemes 1/4 total length. Parameres as a broad lobe with rounded apex and medial bump, apodemes 1.8X length of parameres and strongly bent dorsally at base.

*Female adult*. (Fig. 38) As for male, except as follows. **Thorax**: Length 1.29 mm (1.27–1.31 mm, n = 2).

**Wing**: Length 5.6 mm (5.4–5.7 mm, n = 2). **Abdomen**: Cercus yellow.

*Immatures*. Unknown.

**BIOLOGY**: Unknown.

**DISTRIBUTION**: Peninsular Malaysia (Fig. 137), 1220–1280 masl.

**DISCUSSION**: This species was compared to the descriptions and figures of the recently described Oriental and Australasian species (Papp & Ševčík 2011), and is clearly different from all of them and not a junior synonym.

**ETYMOLOGY**: This species is named for the Titiwangsa mountain range of peninsular Malaysia where the type specimens were collected.

**MATERIAL EXAMINED**: *Holotype*: here designated, adult male, pinned on double mount minute with genitalia in plastic vial on main pin, labelled “Malay Penin [MALAYSIA]:/ Pahang, F.M.S./ Fraser’s Hill/ 4200’/ May 20<sup>th</sup> 1932/ [underside of label] H.M. Pendlebury/ F.M.S./ Museums.; HOLOTYPE ♂ / *Leptomorphus titiwangsensis* Borkent / Det. C.J. Borkent 2012” [BMNH]

*Paratypes*: labelled as for holotype except 29.i.1929 (1♂, 1♀); 29.v.1932 (1♀); viii.1926, B. Gater (1♂). All paratypes in BMNH.

**36. *Leptomorphus walkeri* Curtis**

(Figures 41, 76, 89, 123, 140, 150, 154)

*Leptomorphus walkeri* Curtis, 1831: plate 365.*Leptomorphus (Leptomorphus) walkeri*: Matile, 1977: 144.*Leia apicalis* Roser, 1840: 51. Synonymized by Landrock, 1917: 39.

**References:** Grzegorzek 1875: 7 (description of female, wing figure); Mik 1887: 35–6 (Poland, Austria); Röder 1892: 170 (Switzerland); Strobl 1897: 15 (Germany); Kertész 1902: 72 (catalogue); Johannsen 1909:72 (catalogue); Coquillett 1910: 560 (type designations); Landrock 1917: 39 (synonymization of *Leia apicalis*), 1940: 39–40 (key, description, wing figure); Edwards 1925: 555–6, 652, Pl. LIX-193 (key, description, biology, wing figure), 1933a: 230 (compared to *L. chaseni* and *L. ornatus*), 1933b: 306 (venation compared to *L. fasciculatus*); Brocher 1931: 73–6 (description of larva, egg, and immature behaviour); Enderlein 1936: 13 (key reference); Okada 1936: 100 (compared to *L. quadrimaculatus*); Lackschewitz 1937: 13 (Latvia); Madwar 1937: 52, 54–57, 98–100 (description of larval morphology, biology, numerous figures); Kessel & Kessel 1939: 81 (fungal host record); Séguy 1940: 86–7 (description, biology, figures of egg, larval habitus, and male genitalia); Shaw 1947: 156–157 (comparison to *L. nebulosus*); Eberhard 1970: 361, 365, 367, 369, 377–8 (compared to *L. bifasciatus* and *L. subcaeruleus*); Plassmann 1971: 62–3 (Germany, this might be *L. forcipatus*); Matile 1977: 141–144 (biology, subgeneric placement); Cole & Chandler 1979: 51 (faunal list); Hutson *et al.* 1980: 23, 46–47, 85, 96 (distribution, description, key, figures of wing and genitalia); Plachter 1980 (immature morphology and behaviour, figures, SEM photos); Santini 1983 (biology), 1985 (biology, figures of all life stages); Krivosheina *et al.* 1986: 133–4 (key, genitalia figure); Ostroverkhova & Shtakel'berg 1988: 416, 418 (genitalia figure and key reference); Santini & Mazzini 1989 (SEM study of the egg); Zaitzev 1994: 157, 160 (key, re-description, male genitalia figure); Dahl *et al.* 1995: 17 (Italy); Yakovlev 1995: 356 (rearing record); Poole and Gentili, 1996: 194 (catalogue); Sjøli 1997: 6, 9, 10, 14, 32, 34, 46–47 (figure of head, palp, and genitalia, phylogenetic matrix exemplar); Sjøli *et al.* 2000: 52 (figure of palp); Kurina 2003: 61 (Germany); Kurina *et al.* 2005: 483 (Sweden); Gammelmo & Sjøli 2006: 60, 65 (Norway); Kjærandsen *et al.* 2007: 35 (distribution); Papp & Ševčík 2011: 139 (as type species of genus).

**DIAGNOSIS:** The only extant species of *Leptomorphus* with the following combination of characters: foretibia with dense row (comb) of short anteroventral bristles (Fig. 89); wing with dark apical and medial spots present; male genitalia with gonocoxite shorter than tergite 9, sternite 9 not reaching lateral margins of tergite 9 (Fig. 123).

This species can be distinguished from other Palaearctic species principally based on the bulbous, almost spherical, male genitalia, and the gonocoxites shorter than and placed apically on, tergite 9.

**DESCRIPTION:** *Male.* (Fig. 41) **Head:** yellow, somewhat dorsoventrally compressed in anterior view. Antenna with basal 3–4 flagellomeres lighter brown, darkening apically; scape yellow, with yellow setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare, anterobasal patch of setulae present; pedicel yellow, with 4–5 large bristles, several setae on apicodorsal margin, patch of fine setae apicoventrally; flagellomere 1 with tapered base light brown remainder light brown; flagellomere 6 1.8X as long as broad. Clypeus yellow, strongly protruding, slightly laterally compressed oval; bristles on clypeus yellow, both strong, smaller bristles on entire surface, all directed ventrally, clypeus 2X as long as face. Face yellow; shape a subequal triangle, with fine bristles covering face. Frons yellow; with few bristles medioventrally, frontal furrow running 1/4 distance from dorsal margin towards ventral margin, frontal cleft just anterior of median ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 subequal in length to segment 4 with even width from base to apex, segment 3 without distinct apicolateral patch of fine setae. Labellum yellow. Eye with a number (in ~1/4 of the ommatidial junctions) of long inter-ommatidial setulae scattered on posterior margin. Occiput yellow with appressed, anteriorly directed setae. Ocelli with median slightly in front of laterals, space between ocelli less than diameter of laterals, lateral ocelli 1.5X their own diameter from eye margin, ocellar triangle dark brown/black. **Thorax:** Length 1.65 ± 0.41 mm (1.19–1.97 mm, n = 10). Mediodorsally brown, remainder yellow. Scutum brown with lighter dorsocentral lines, yellow on anterior corners and posterior and lateral margins, occasionally brown reduced to triangle in center of disc with remainder yellow; surface of scutum covered with small setae; acrostichal setae vaguely present; single dorsocentral seta present anteriorly though remainder could be intermixed with small setae; double row of lateral setae present; patch of setae on scutum at wing base present. Scutellum yellow; with 2–6 large bristles and many



small bristles. Prescutum yellow. Mediotergite yellow with 10–20 bristles on posterolateral corners, small bristles covering. Laterotergite yellow; anterior margin of laterotergite not reaching katapisternum. Anepimeron yellow. Anepisternum yellow. Katapisternum yellow. Antepronotum and proepisternum yellow. Margin of anterior and posterior spiracles yellow with light brown and yellow trichia respectively. Metepisternum yellow. Anapleural suture straight and clear. Halter yellow. **Legs:** principally yellow; extreme anteroapical corner yellow on forefemur, on other femora dark brown. Midfemur without apical spine-like process. Tibia with covering of light brown macrotrichia, foretibia with comb of short setae along length of anteroventral surface (Fig. 89), tibial spurs yellow, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 3/4 of its length, placed basally, shortest midtibial spur 0.8X length of longest, longest midtibial spur 4.5X apical thickness of midtibia, shortest hind tibial spur 0.8X length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 76): Length  $7.1 \pm 2.2$  mm (4.8–8.2 mm,  $n = 10$ ). Hyaline; apical macula dark brown but fading towards apex and posterior margin, running from anterior to posterior wing margin, beginning halfway along  $R_5$ ; medial macula extending from  $R_1$  to stem of  $M_{1+2}$ . Macrotrichia in all cells. Setae on basal posterior margin of wing (along base of cell a) all the same length. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length prior to origin of  $R_s$ .  $R_4$  absent.  $R_5$  straight, slight posterior turn near tip.  $M_1$  reaching apex just before  $R_5$ , apices of M veins clearly reaching wing margin.  $M_4$ -CuA fork arising before origin of r-m.  $A_2$  faintly present as crease. **Abdomen:** Tergites principally yellow, T1–5 with posterior brown band, T6 with posterior 1/2–3/4 dark brown, T7 dark brown. Tergite 8 smaller than all other abdominal sclerites, without bristles. **Genitalia** (Fig. 123): yellow. Sternite 9 sclerotized, more or less circular with apicomedial indentation, 1/2 width and length of T9. Tergite 9 circular with posterior margin concave. Gonocoxite placed apically on T9, medial margins not reaching median line, apex with two short rounded points, bearing gonostylus halfway to apex. Gonostylus swelling from base into a square lobe with medial margin bearing dorsally directed point and bearing several setae, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus 3/4 length of T9, tapering to apex and then swollen at apex with extra sclerotized bumps dorsally, apodemes ~1/4 total length. Parameres strongly sclerotized and complex though main lobe bent and directed dorsally for apical 1/3, apodemes 1/2 length of parameres, strongly united with gonocoxal apodeme.

**Female.** As for male, except as follows. **Thorax:** Length  $1.71 \pm 0.26$  mm (1.48–1.89 mm,  $n = 10$ ). **Wing:** Length  $7.0 \pm 1.2$  mm (6.2–8.0 mm,  $n = 10$ ). **Legs:** Foretibia without comb of short setae on anteroventral surface. **Abdomen:** Tergite 7 light brown; Cercus yellow.

**Immatures.** Pupa described by Plachter (1980), Santini (1985). Larva described by Madwar (1937), Plachter (1980), Santini (1985). Egg described by Santini & Mazzini (1989).

**BIOLOGY:** This species overwinters as eggs that hatch in the early spring. The larvae spin a fine silk sheet under the sporulating surface of various wood inhabiting fungi, which collects the falling spores. The larvae then feed on the spore-covered sheet. Larvae feed on spores of Polyporaceae (*Anthrodia radula*, *Coriolus versicolor*, *Inonotus hispidus*, *Poria vaporaria*, *Schizophora paradoxa*, *Trametes gibbosa*), Stereaceae (*Stereum ochroleucum*) and Auriculariaceae (*Auricularia mesenterica*) (Madwar 1937, Santini 1985). This species is also reported as being reared from *Discina gigas* (Ascomycota: Discinaceae, Yakovlev 1995), though this may have been from an individual that had migrated from the host fungus. Pupation occurs underneath or near the host fungus, with the pupa hanging, head down, from a single line attached to the posterior end of their abdomen (Edwards 1925, Landrock 1940). The final larval skin remains attached to the anchor line behind the pupa (Madwar 1937). The species is thought to be multivoltine, the number of generations varying depending on the length of the season (Madwar 1937, Santini 1985). *Orthocentrus* sp. (Ichneumonidae: Orthocentrinae) have been recorded as parasitoids of the immatures (Séguy 1940). During the autumn females lay light coloured eggs (which gradually darken in colour to brown) on or near the host fungus (Santini 1985, Santini & Mazzini 1989).

**DISTRIBUTION:** Europe (Fig. 140), 35–1400 masl. Previous records of *L. walkeri* from the Nearctic were due to misidentification of *L. hyalinus*.

**DISCUSSION:** As discussed below in the phylogeny section, the placement of *Leptomorphus* species in subgenera (Matile 1977) is not supported by our phylogenetic results. This species is therefore removed from the subgenus *Leptomorphus* and placed solely in the genus *Leptomorphus*.

**MATERIAL EXAMINED:** *Lectotype:* Here designated, photographs of the specimen and author's notebook were examined (available from MVMA): adult female, pinned, labelled "1173a." corresponding information in notebooks (as given in the original description (Curtis 1831)): "1173: taken in July on the windows at Arno's Grove

[type locality], and off a hedge by a wood at Southgate, by my friend Francis Walker, Esq., to whom I have the pleasure of dedicating this fine addition to our fauna.” [MVMA]

*Paralectotype*: The Southgate specimen is missing from the Curtis collection at MVMA and Walker collection at BMNH, presumed lost (originally recorded as being ‘in the cabinets of Mr. F. Walker’ (Curtis 1831).

*Other material*: AUSTRIA, Langua, 8.viii.1981. (1♀, ZSM); Tirol, Igls, 8.vii.1953, J.R. Vockeroth. (2♂, CNC); CZECH REPUBLIC, Lanzhot, Ranspurk, 7–9.viii.1991, L. Masner. (1♂, CNC); BOHEMIA, Josefuv Dul, Jedlový dul, 1–22.ix.2005, J. Preisler & P. Vonička. (1♂, LEM); BOHEMIA, viii.1900. (1♂, MTD); FRANCE, 15.xi.1966. (1♂, MNHN); 30.x.1966. (1♂, MNHN); Centre, Indre-et-Loire, Richelieu, 24.viii.1963. (1♂, MNHN); 25.viii.1963. (1♂, MNHN); Île-de-France, Seine-et-Marne, Fontainebleau, 14.vii.1992, G. Hodebert. (1♀, MNHN); Saint-Augustin, vii.1969, L. Matile. (1♂, MNHN); Poitou-Charentes, Deux-Sèvres, Saint-Martin-de-Sanzay, 14 1971, G. Couturier. (1♂, MNHN); Provence-Alpes-Côte d'Azur, Bouches-du-Rhône, St-Braume, 1919, A. de Perrin. (1♀, MNHN); Hautes-Alpes, Saint-Bonnet-en-Champsaur, vii.1975, C. Girard. (1♀, MNHN); Seine et Marne, Bois-le-Roi, 25.viii.1984, P.H. Arnaud, Jr. (1♂, CAS); GERMANY, Jungfernhardt, Siebengebirge, 27.ix.1957, E. Schmidt. (1♂, CNC); Markgröningen, 21.ix.1970. (1♀, SMNS); Baden-Württemberg, 23km NW Freiburg, 26.x.1984, FVA-Abt. Ws Freiburg. (1♀, ZSM); Bavaria, Eltmann, Naturpark Steigerwald, 12.viii.1995, A. Floren. (1♂, ZSM); Schöngesing, 12.vii.1986. (1♂, ZSM); North Rhine-Wesphalia, Cologne, 2.v–15.xi.1995, A.G.W. Topp. (1♂, MTD); Saxony, Sächsische Schweiz, (1♀, MTD); Württemberg. (1♂, SMNS); NORWAY, AK, Nesodden, Skoklefall, 27.vi–9.vii.2005, O. Lønnue. (1♂, LEM); SLOVAKIA, Polana Biosphere Reserve, 24.v–11.vii.2007, J. Roháček, J. Ševčík. (1♂, LEM); SWITZERLAND, Cheserex, 28.viii.1931, E. Roman. (1♀, MNHN); Lugano, vi.1906, W. Schnuse. (1♂, MTD); UK, Anderson Co., Northwood, 4.x.1924, E.E. Austen. (1♂, BMNH); Hampshire, Minstead, 30.vii.1963, L.W. Siggs. (1♀, BMNH); New Forest, 2.x.1901, F.C. Adams. (1♀, BMNH); 25.viii.1901. (1♂, MNHN); 13.ix.1905. (1♀, MNHN); 29.viii.1910, B. Sharp. (1♂, BMNH); New Forest, Gorley, 12.viii.1972, Cranston, Dear. (1♂, BMNH); Hertfordshire, Hitch Wood, 22.ix.1918, F.W. Edwards. (2♀, BMNH); 22.ix.1918. (1♂, CNC); ix.1918. (1♀, BMNH); Monmouthshire, Monnow Valley, 8.vii.1912, J.H. Wood. (1♂, BMNH); Surrey, Old Coulsdon, 19.ix.1934. (1♂, BMNH).

### 37. *Leptomorphus waodani* Borkent, new species

(Figures 39, 77, 90, 124, 143, 150, 155)

**DIAGNOSIS**: The only extant species of *Leptomorphus* with the following combination of characters: scutum and scutellum evenly covered with fine trichia; male foretibia with a dense row (comb) of short anteroventral bristles (Fig. 90); palp segment 5 with thick covering of fine, white, setulae; male genitalia with tergite 9 tapering posteriorly to a point, with short pointed processes laterally at 2/3 of length towards apex; gonocoxite with large gonocoxal lobe on medial margin (Fig. 124).

This species is distinguished from most other Neotropical species missing  $R_4$  by mostly yellow abdomen (tergites 6, 7 brown) and having the scutellum lighter brown than the scutum or mediotergite (Fig. 39). It can be distinguished from *L. amorimi* and *L. fasciculatus* by the posteromedial margin of tergite 9 being pointed rather than concave (Fig. 124).

**DESCRIPTION**: *Male*. (Fig. 39) **Head**: brown spot medially from ocelli to antennal base, remainder yellow, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape yellow, with brown setae in short row on apicodorsal margin and thick patch covering apicoventral process, remainder bare, anterobasal patch of setulae present; pedicel yellow, with 1–2 large bristles, few setae on apicodorsal margin, patch of fine setae apicoventrally; flagellomere 1 with tapered base yellow remainder dark brown; flagellomere 6 1.3X as long as broad. Clypeus yellow, slightly laterally compressed oval; bristles on clypeus yellow, 4–6 strong bristles on ventral margin directed ventrally, remaining setae directed medioventrally, clypeus 2X as long as face. Face yellow; shape a slightly wider than tall triangle, bare. Frons brown; bare, frontal furrow running 1/2 distance from dorsal margin towards ventral margin, frontal cleft more than 1X diameter of median ocellus anterior of median ocellus. Palpus yellow; segment 1 hidden behind eye, segments increasing in length, segment 5 2X length and 1.5X width of segment 4 with even width from base to apex and covered in fine white setulae, segment 3 without distinct lateral patch of fine setae. Labellum yellow. Eye with very few, short inter-ommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Three ocelli, in a straight line, space between ocelli less than diameter of laterals, lateral ocelli 2.5X

their own diameter from eye margin, ocellar triangle dark brown. **Thorax:** Length 1.64 mm ( $n = 1$ ). Dark brown with yellow lateral spots. Scutum dark brown/black with blue-green specks, pair of yellow anterolateral spots, one specimen with lateral margins brown and remainder yellow; surface of scutum covered with trichia; acrostichal setae absent; single dorsocentral seta present anteriorly; two thirds row of lateral setae present; patch of setae on scutum at wing base present. Scutellum dark brown with covering of fine trichia; bristles absent. Prescutum anterior half yellow, posterior half brown. Mediotergite dark brown with 6 bristles on posterolateral corners, and covering of appressed trichia. Laterotergite brown, with covering of appressed trichia; anterior margin of laterotergite abutting katepisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum brown with posterodorsal corner yellow. Anteprototum and proepisternum brown. Margin of anterior and posterior spiracles yellow with yellow trichia. Metepisternum yellow. Anapleural suture with anterior portion slightly curved dorsally. Halter stem yellow, knob light to dark brown. **Legs:** principally yellow; hind coxa with brown spot along length of anterior surface; extreme anteroapical corner yellow on forefemur, on other femora dark brown. Midfemur without apical spine-like process. Tibia with covering of brown macrotrichia, foretibia with comb of short setae along length of anteroventral surface (Fig. 90), tibial spurs brown, foretibial spur length 2X apical thickness of foretibia, midtibia with strong, dorsal, bare patch of even thickness for 2/3 of its length, placed basally, shortest midtibial spur 0.8X length of longest, longest midtibial spur 4X apical thickness of midtibia, shortest hind tibial spur subequal to length of longest, longest hind tibial spur 4X apical thickness of hind tibia. Foreleg first tarsomere 1.7X length of foretibia. **Wing** (Fig. 90): Length 6.7 mm ( $n = 1$ ). Hyaline; apical macula dark brown but fading towards apex and posterior margin, running from anterior to posterior wing margin, beginning halfway along  $R_5$ ; medial macula extending from  $R_1$  to stem of  $M_{1+2}$ . Macrotrichia in all cells, though absent from posterobasal margin of cell a, and sparse in basal cells. Setae on basal posterior margin of wing (along base of cell a) alternating long, short. Calypter with a few short setae. Vein sc-r present, apical end joining R within its own length prior to origin of Rs.  $R_4$  absent.  $R_5$  slightly concave for entire length.  $M_1$  reaching apex before  $R_5$ , apices of M veins reaching wing margin.  $M_4$ -CuA fork arising before origin of r-m.  $A_2$  absent. **Abdomen:** Tergites principally yellow, T1 and 6–7 dark brown, T5 with posterior 1/2 dark brown. Tergite 8 smaller than all other abdominal sclerites, without bristles. **Genitalia** (Fig. 124): mostly brown with apex yellow. Sternite 9 sclerotized, thin, posteriorly tapered sclerite, almost as long as aedeagus, not reaching gonocoxal margin. Tergite 9 longer than wide, rounded basally, tapering into long point at apex with small point 2/3 way to apex. Gonocoxite placed centrally on T9, medial margins not reaching median line, apicolateral margin a short point, apicoventral margin extended into long (2X remainder of gonocoxite) tapering point, bearing gonostylus centrally. Gonostylus a single broad-based lobe tapering to a point apically and slightly curved dorsally with setae on basal half, gonocoxite III associated with dorsal margin of gonostylus but not fused to it. Aedeagus ~1.2X length of S9, tapering to middle and then swelling to apex which ends in a pointed lobe on each lateral corner and a medial rounded bump, apodemes sclerotized and 1/4 total length. Parameres a simple thin taper with a swollen base, apodemes ~1/2 length of parameres.

*Female.* Unknown.

*Immatures.* Unknown.

**BIOLOGY:** Unknown.

**DISTRIBUTION:** Ecuador (Fig. 143), 215 masl.

**ETYMOLOGY:** This species is named in honour of the Waodani (also spelled Waorani or Huaorani) people of Amazonian Ecuador, as the holotype was collected in their territories. The name is proposed as a noun in apposition.

**MATERIAL EXAMINED:** *Holotype:* here designated, adult male, pinned with genitalia in vial on pin, labelled "ECUADOR: Orellana, Res. Ethnica/ Waorani, 1 km S. Onkone Gare Cmp/ Trans. Ent. 216.3m, 00°39'26"S, / 076°27'11"W, 21.vi.1996, fogging/ terre firme forest, T. L. Erwin *et al.*/ Trans. 4 Sta. 1 Proj. MAXUS # 1551; HOLOTYPE ♂/ *Leptomorphus waodani* / Borkent, new species / Det. C.J. Borkent 2012" [USNM].

### Specimens and species not included

There were several specimens that were not determined to species or described as new, as they did not include sufficient label data, were in particularly poor condition, or had only females found in a particular location. These specimens are listed below with associated notes.

**MATERIAL EXAMINED:** CUBA, Pico Turquino, vi.1936, Darlington [almost completely yellow except for V-shape on scutum and posterior margin of tergites both brown,  $R_4$  absent] (2♀, MCZ); MEXICO, Chiapas, San Cristobal de las Casas, 17–21.vii.1964, P.J. Spangler [mostly brown with abdomen striped with yellow, legs partially yellow,  $R_4$  present] (1♀, USNM); DEMOCRATIC REPUBLIC OF THE CONGO, Pawa, viii.1938, Dr. Radna [abdomen broken off and specimen covered in fungus, near *L. obscurus* group] (1?. BMNH); Luebo, ii.1950, F.J. Francois [female near *L. obscurus* group] (1♀, IRSNB/MNHN); SIERRA LEONE, Daru, 31.vii.1912, J.J. Simpson [abdomen broken, near *L. aliciae* group] (1?, BMNH); UNKNOWN COUNTRY, La Rastra, 22–26.iv.1956 [These two specimens are badly shrivelled and it is unclear where they were collected, as there is a ‘La Rastra’ in Colombia, Mexico and Argentina. They may have been collected by H. Sturm who collected in Colombia around this time and sent specimens to J. Lane at MZUSP (Lane & Sturm 1958). The male genitalia are similar to *L. amorimi* and *L. waodani* but appear unique] (1♂, 1♀, MZUSP).

We were also unable to include the recently described Oriental species (Papp & Ševčík 2011) as the material was not made available to us. However, we closely compared the descriptions and figures in Papp & Ševčík (2011) with our new species. None of their species agree with ours, and we are therefore confident that our new species are not junior synonyms of any of their species. Unfortunately the descriptions and figures of these eight species were inadequate to provide characters for use in the species key or the phylogenetic analysis of our study. However, the general habitus of their *L. ascutellatus* group is clear enough to place them in the apical clade (*L. titiwangsensis* and above) of the *L. ornatus* group of this study (Fig. 152). As noted in the phylogeny section below the subgenera erected by Matile (1977) are not supported and the suggestion that the eight new species belong in the subgenus *Gymnoscutum* is abandoned. They are now placed solely in the genus *Leptomorphus* and in the *L. ornatus* species group. The use of the term ‘*L. ascutellatus* species group’ should be abandoned as the group appears paraphyletic in relation to the apical species of the *L. ornatus* group.

The eight species of Papp & Ševčík (2011) are listed below along with the museums where the holotype (HT) and any paratypes (PT) are deposited:

*Leptomorphus alienus* Papp & Ševčík, 2011: 141. HT ♂ (BMNH).

*Leptomorphus ascutellatus* Papp & Ševčík, 2011: 141. HT ♂ (HNHM), PT: 1♀ (HNHM).

*Leptomorphus baramensis* Papp & Ševčík, 2011: 146. HT ♂ (BMNH).

*Leptomorphus gunungmuluensis* Papp & Ševčík, 2011: 147. HT ♂ (BMNH), PT: 4♂ 1♀ (BMNH); 3♂ (HNHM); 1♂ SMOC).

*Leptomorphus longipes* Papp & Ševčík, 2011: 149. HT ♂ (BMNH).

*Leptomorphus matilei* Papp & Ševčík, 2011: 149. HT ♂ (MNHN).

*Leptomorphus papua* Papp & Ševčík, 2011: 152. HT ♂ (BMNH), PT: 1♂ (HNHM).

*Leptomorphus utarensis* Papp & Ševčík, 2011: 152. HT ♂ (BMNH), PT: 1♀ (BMNH); 1♂ (HNHM); 1♂ (MNHN).

## Phylogenetic analysis of *Leptomorphus* species relationships

### Characters used

The phylogenetic analysis was based on 73 characters (46 binary, 27 multistate), of which 29 were male genitalic characters. The consistency index (C.I.) and retention index (R.I.) are given for each character. Character states coded as ‘0’ are considered to be plesiomorphic.

1. Head colour: brown (0), yellow with some brown (1), yellow (2) (C.I. = 0.25, R.I. = 0.68).
2. Scape with apicoventral process: absent (0), present (1), (C.I. = 1.00, R.I. = 1.00).
3. Scape setae: on entire surface (0), in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare (1), in short row on apicodorsal margin and thick patch covering apicoventral process, remainder bare (2) (C.I. = 0.67, R.I. = 0.86).
4. Pedicel colour: yellow (0), brown (1) (C.I. = 0.50, R.I. = 0.86).
5. Pedicel vestiture: setae and/or bristles on both ventral and dorsal apex (0), setae and/or bristles only on dorsal apex (1) (C.I. = 0.50, R.I. = 0.91).
6. Clypeus shape: slightly wider than tall oval (0), circular (1), dorsoventrally elongate oval or square (2) (C.I. = 0.29, R.I. = 0.74).
7. Clypeus in lateral view: flat or slightly curved (0), strongly protruding (1) (C.I. = 0.50, R.I. = 0.88).



8. Clypeus bristles location: strong and smaller bristles on half or more of surface (0), 2–8 strong bristles only along ventral margin (1) (C.I. = 0.25, R.I. = 0.81).
9. Bristles on face: many (0), few or fine (1), absent (2), (C.I. = 0.22, R.I. = 0.59).
10. Frons: yellow (0), brown (1) (C.I. = 0.20, R.I. = 0.78).
11. Inter-antennal bristles on frons: many, long (Fig. 79) (0), few, short, often difficult to see (1), absent (Fig. 78) (2) (C.I. = 0.33, R.I. = 0.78).
12. Palp segment 3 shape: conical (0), spherical (1) (C.I. = 1.00, R.I. = 1.00).
13. Palp segment 5 width: even width [same thickness as segment 4] (0), central portion thinner than apex and base (1), broad [1.5X width of segment 4] (2) (C.I. = 0.40, R.I. = 0.83).
14. Palp segment 5 surface with covering of white setulae: absent (0), present, Fig. 82 (1) (C.I. = 1.00, R.I. = 1.00).
15. Inter-ommatidial setulae: covering eye in every ommatidial junction (0), a number of long setulae in ~1/4 of junctions (1), absent or very few very short (easily missed) setulae (2) (C.I. = 1.00, R.I. = 1.00).
16. Space between ocelli: more than diameter of laterals, Fig. 79 (0), less than diameter of laterals (1) (C.I. = 0.33, R.I. = 0.78).
17. Lateral ocellus X own diameter from eye margin:  $0 > X = 0.5$ , Fig. 79 (0),  $0.5 > X = 1.5$  (1),  $1.5 > X = 3$  (2) (C.I. = 0.40, R.I. = 0.75).
18. Ocellar triangle colour and placement: separated, with basal colour not joined between ocelli, Fig. 79 (0), all ocelli on same dark patch, forming ocellar triangle (Fig. 78) (1) (C.I. = 1.00, R.I. = 1.00).
19. Surface of scutum with covering of setae: present (0), absent (1) (C.I. = 0.25, R.I. = 0.77).
20. Surface of scutum with covering of fine trichia: absent (0), present, Fig. 80 (1) (C.I. = 1.00, R.I. = 1.00).
21. Acrostichal setae: present (0), absent (1) (C.I. = 1.00, R.I. = 1.00).
22. Dorsocentral setae present as: multiple lines of closely spaced strong setae (sometimes obscured by scutal setae) (0), single or double line of fine setae, usually spaced ~their own length apart (1), a single, anterior, large seta (2) (C.I. = 0.50, R.I. = 0.91).
23. Scutellum: brown (0), yellow (1) (C.I. = 0.13, R.I. = 0.59).
24. Scutellum with covering of fine trichia: absent (0), present (1) (C.I. = 1.00, R.I. = 1.00).
25. Large socketed scutellar bristles: present (0), absent (1) (C.I. = 0.50, R.I. = 0.90).
26. Mediotergite with medial or anteromedial patch of small bristles/setae: present (0), absent (1) (C.I. = 0.13, R.I. = 0.61).
27. Mediotergite with covering of appressed fine trichia: absent (0), present (1) (C.I. = 1.00, R.I. = 1.00).
28. Laterotergite with covering of appressed fine trichia: absent (0), present (1) (C.I. = 1.00, R.I. = 1.00).
29. Laterotergite meeting katapisternum ventrally (anepimeron obscured ventrally by meeting of these two sclerites): no (0), yes (1) (C.I. = 0.25, R.I. = 0.70).
30. Male foretibial comb of bristles (Fig. 85–90): absent (0), present (1) (C.I. = 0.50, R.I. = 0.91).
31. Foreleg first tarsomere length: tibia length:  $< 1X$  (0),  $1–1.5X$  (1),  $> 1.5X$  (2) (C.I. = 0.40, R.I. = 0.67).
32. Male mid-femoral apical process: absent (0), present (Fig. 83–84) (1) (C.I. = 1.00, R.I. = 1.00).
33. Apical wing spot: present as a strong dark spot or band (0), absent or very faintly present in apical 1/4 of r (1) (C.I. = 0.14, R.I. = 0.65).
34. Median wing spot: absent (0), present (1) (C.I. = 0.25, R.I. = 0.83).
35. Macrotrichia in cell  $a_2$ : present (0), absent (1) (C.I. = 0.25, R.I. = 0.79).
36. Macrotrichia in basal third of wing: densely and evenly distributed, *i.e.* Fig. 55 (0), sparsely distributed, though denser near wing veins, *i.e.* Fig. 53 (1) (C.I. = 1.00, R.I. = 1.00).
37. Surface of alula: with macrotrichia (0), without macrotrichia (1) (C.I. = 0.14, R.I. = 0.33).
38. Setae on basal posterior margin of wing (distal of alula, along base of cell  $a_2$ ): alternating long and short (0), single length (1) (C.I. = 0.50, R.I. = 0.90).
39. Calypter surface with macrotrichia: present (0), absent (1) (C.I. = 0.33, R.I. = 0.75).
40. Vein C: extending beyond tip of  $R_5$  (0), ending at  $R_5$  (1) (C.I. = 1.00, R.I. = 1.00).
41.  $R_4$ : present (0), absent (1) (C.I. = 0.25, R.I. = 0.63).
42.  $R_5$  (relative to anterior wing margin): convex (straight with a posterior turn at tip) (0), concave (1) (C.I. = 0.50, R.I. = 0.88).
43. Apices of M veins: reaching wing margin (0), thinning apically and not reaching wing margin (1) (C.I. = 0.33, R.I. = 0.71).
44. Abdominal segments 3–5: similar in thickness to adjacent segments (0), Swollen relative to adjacent segments (1) (C.I. = 1.00, R.I. = 1.00).
45. Bristles on tergite 8: covering surface (0), restricted to apicolateral corners (1), absent (2) (C.I. = 0.29, R.I. = 0.71).
46. Sternite 9: absent or membranous (0), not more than 2/3 the width of tergite 9 (1), ~equal to width of tergite 9 (2) (C.I. = 0.33, R.I. = 0.67).
47. Sternite 9: absent or membranous (0), anterior margin convex or flat (1), anterior margin concave (2) (C.I. = 0.33, R.I. = 0.43).
48. Lateral margins of sternite 9: reaching or overlapping medial margin of gonocoxite (0), not reaching medial margin of gonocoxite (1) (C.I. = 0.50, R.I. = 0.93).
49. Tergite 9 with posterolateral lobes (evaginations): absent (0), present (1) (C.I. = 0.33, R.I. = 0.82).
50. Number of lobes on posterior margin of tergite 9: none (0), one (1), two (2), three (3) (C.I. = 0.50, R.I. = 0.77).
51. Tergite 9 with posterolateral lobes (evaginations): absent (0), broad for at least half of length, rounded or square apically (sometimes with multiple points) (1), tapering for entire length (2) (C.I. = 0.25, R.I. = 0.67).
52. Tergite 9 with medioposterior lobe (evagination): absent (0), present (1) (C.I. = 0.33, R.I. = 0.33).
53. Tergite 9 with ventrobasal margin of posterior lobes: of similar thickness and sclerotization to remainder of tergite 9 margin (0), thickened and sclerotized, often bearing one or more ventrally extending points laterally (1) (C.I. = 0.50, R.I. = 0.91).
54. Fusion of tergite 9 and gonocoxite: not fused (0), sclerite margins at least partially fused but discernible as a crease (1), strongly fused margin only discernible as a thickening (2) (C.I. = 1.00, R.I. = 1.00).

55. Gonocoxite placement on tergite 9: basally or difficult to distinguish due to fusion (0), distally or apically (1) (C.I. = 1.00, R.I. = 1.00).
56. Ratio of gonocoxite length to medial tergite 9 length: >1.8 (0), 1.3–1.79 (1), 0.8–1.29 (2), <0.8 (3) (C.I. = 0.43, R.I. = 0.75).
57. Gonocoxal lobe: absent (0), present (1) (C.I. = 0.50, R.I. = 0.75).
58. Gonocoxite bearing gonostylus: on apical two thirds (0), basally (1) (C.I. = 1.00, R.I. = 1.00).
59. Gonostylus: a single lobe (0), with two lobes (1) (C.I. = 0.33, R.I. = 0.82).
60. Ratio of ventral gonostylar lobe length to length of dorsal (smaller) lobe: absent (0), <2.0 (1), > 2.0 (2) (C.I. = 0.50, R.I. = 0.80).
61. Main gonostylar lobe: three dimensional pointed or rounded lobe (0), laterally compressed into almost two dimensional flange (1) (C.I. = 1.00, R.I. = 1.00).
62. Apex of gonostylar main lobe: single point or knob (0), bifurcated into 2 points (1) (C.I. = 1.00, R.I. = 1.00).
63. Apex of gonostylar dorsal (smaller) lobe: absent (0), flange-like (1), tapered to point (2) (C.I. = 0.50, R.I. = 0.78).
64. Gonostylus: with at least a few setae (0), bare (1) (C.I. = 1.00, R.I. = 1.00).
65. Gonocoxite III: separate from gonostylus (0), fused to gonostylus (1) (C.I. = 0.33, R.I. = 0.86).
66. Aedeagus shape: tapering towards apex (sometimes with slight central swelling) (0), initially tapered but then swelling and bulbous at apex (1), initially tapered but ending in sclerotized apex with one or more lateral lobes/flanges of various lengths and ornamentation (2) (C.I. = 0.50, R.I. = 0.88).
67. Sclerotized apex of aedeagus: simple rounded taper (0), with lateral lobes and with medial apex apparent (1), as lateral lobes only [medial apex absent/indiscernible] (2) (C.I. = 0.67, R.I. = 0.91).
68. Aedeagal lateral lobes: absent (0), short taper/flange (1), long, thick, sickle-like taper (2), forked apically (3) (C.I. = 0.60, R.I. = 0.80).
69. Aedeagus with: 2 apodemes (0), apodemes reduced to a single lobe and united with sternite 9 (1) (C.I. = 1.00, R.I. = 1.00).
70. Anterior margin of fusion of parameral and gonocoxal apodemes: indistinguishable from surrounding area of apodeme (0), with a sclerotized, thickened area (1), forming a sclerotized hook (2) (C.I. = 0.50, R.I. = 0.82).
71. Paramere shape: straight taper (0), curved taper (1), broad or bulbous at apex sometimes with serrated margin or covering of small spines (2), reduced (3) (C.I. = 0.27, R.I. = 0.56).
72. Apex of longest paramere relative to apex of aedeagus (when anterior margin of apodemes are at same level): shorter (0), at same level (1), longer (2), reduced (3) (C.I. = 0.60, R.I. = 0.90).
73. Paramere: a single lobe (0), with two lobes (1), reduced (2) (C.I. = 0.50, R.I. = 0.50).

### Monophyly of *Leptomorphus*

The phylogenetic analysis based on 35 ingroup taxa and 4 outgroups (Table 2) resulted in three equally parsimonious trees (length = 259, C.I. = 0.40, R.I. = 0.80). Tree support values (Bremer (Br) and bootstrap >50%) are shown on the branches of the strict consensus tree (Fig. 150). One of the three equally parsimonious trees was selected for discussions of species relationships, classification, and character evolution within the genus. Character state changes are shown on the branches of this tree (Figs. 151–155).

The monophyly of *Leptomorphus* is supported (Br = 4, Fig. 150) by two uniquely-derived synapomorphies (Fig. 151): scape with apicoventral process present (character 2: state 1, hereafter *e.g.* 2:1), and wing vein C ending at R<sub>5</sub> (40:1), and by three homoplasious character states: head yellow (1:2), very few, fine bristles on face (9:1), and scutellum yellow (23:1).

*Leptomorphus perplexus* came out as the sister group to the rest of the genus (Figs. 150, 151); however, this species is only known from the female, so no male genitalic characters were included in the analysis. If and when males are found additional genitalic characters may change the arrangement within the remaining species. Although *L. perplexus* seems to share a number of characters with the *L. walkeri* group it does exhibit a large number of plesiomorphic character states, so would likely retain its basal position. The remaining species form a clade, supported by three uniquely-derived synapomorphies (Br = 5, bootstrap = 67): inter-ommatidial setulae only present in ~1/4 of junctions (15:1), ocelli closely associated, forming an ocellar triangle with a dark background (18:1), and acrostichal setae absent (21:1). Eleven homoplasious character states also support this clade: scape setae in single apical row extending from dorsum laterally into thick patch covering apicoventral process, basal third and entire medial surface bare (3:1), inter-antennal bristles on frons few, short, often difficult to see (11:1), space between ocelli less than diameter of lateral ocelli (16:1), lateral ocellus between 1.5 and 3X own diameter from eye margin (17:2), foreleg first tarsomere length >1.5X tibia length (31:2), R<sub>4</sub> absent (41:1), sternite 9 not more than 2/3 the width of tergite 9 (46:1), sternite 9 with anterior margin convex or flat (47:1), tergite 9 with posterolateral lobes (evaginations) present (49:1), posterior margin of tergite 9 with two lobes (50:2), and tergite 9 with posterolateral lobes (evaginations) broad for at least half of length, rounded or square apically (sometimes with multiple points) (51:1).

**TABLE 2.** Character state matrix used for *Leptomorphus* phylogenetic analysis. All taxa described in this manuscript are included except *L. subforcipatus* and *L. talyshensis* (see text). Missing character state data are indicated by a “?”.

	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777
	123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123
<b>Ingroup Taxa</b>							
<i>L. perplexus</i>	210001101	0000000000	0001001000	?0?1000100	10000?????	???????????	????
<i>L. ornatus</i>	211012011	0101021211	0111001000	?1?0000100	11000?????	???????????	????
<i>L. babai</i>	011012012	1200021211	0110001000	0200100000	11000100?1	2100102000	0000110000
<i>L. hyalinus</i>	111010001	1201021211	0110000000	0201000000	1100010011	2100102000	0000110000
<i>L. titiwangsensis</i>	211012012	0211020211	0111001001	0200000100	1101011111	2100102000	0010110000
<i>L. tagbanua</i>	2?1010011	021?021211	0111000000	0201000100	1101101111	2101203000	0010110001
<i>L. tabatius</i>	211112011	0211021211	0111010000	0201000000	1101111111	2201203000	0010110001
<i>L. chaseni</i>	211012012	0210021211	0111010001	?2?1000100	11011?????	???????????	????
<i>L. grjebinei</i>	211002012	0101021210	0121001000	0201010100	11000100?1	3101102000	0000110000
<i>L. stigmatus</i>	211002011	0101021211	0111000000	0201000100	1100011101	2101102001	1002110000
<i>L. mandelai</i>	211000011	0101021111	0101000000	0201000000	1100011101	2101102001	1002110000
<i>L. obscurus</i>	111002011	0101021211	0110000000	0201010100	1101011101	2101102001	2002110000
<i>L. crosskeyi</i>	111002011	0101021211	0110000000	0201010100	1100011101	2101102001	2002110000
<i>L. gracilis</i>	111002011	0101021211	0110000000	0201010100	1100011101	2101102001	2002110000
<i>L. carnevalei</i>	211002011	0101021211	0111000000	0201010100	1100011101	2201102001	1001110000
<i>L. couturieri</i>	211002011	0101021211	0111000000	0200010100	1101011101	2201102001	1001110000
<i>L. medleri</i>	211002011	0201021211	0111000000	0201000100	1101011201	2201102001	1001110000
<i>L. aliciae</i>	211002011	0101021211	0111000000	0201010100	1101011201	2201102001	1001110000
<i>L. walkeri</i>	211000101	0100011110	0101000000	1200100010	1100021111	2100012010	0000002110
<i>L. quadrimaculatus</i>	011100101	1100011110	0100000000	1200100011	1100012100	0000011010	0000001000
<i>L. forcipatus</i>	111100101	1100011110	0101000001	1200100010	1100022100	0000011010	0000001000
<i>L. panorpiformis</i>	011111100	1200011110	0100001000	0100100011	1010002100	0000013010	0000002230
<i>L. bifasciatus</i>	011111100	1200010111	0100001000	0110100111	1010002100	0000013010	0000002230
<i>L. subcaeruleus</i>	011111100	1200010110	0100001000	0110100111	1010002100	0000013010	0100002220
<i>L. nebulosus</i>	012111101	1200010110	0100001000	0110100111	1010002100	0000013010	0100002220
<i>L. magnificus</i>	011111100	1200010110	0101001000	0110100111	1010002100	0000013010	0100002220
<i>L. furcatus</i>	211000001	0100021210	0101010010	1201000100	1100021111	2200013000	0000001000
<i>L. neivai</i>	211000002	1202121211	1121111111	1200110100	1000021211	2100013000	0000002110
<i>L. eberhardi</i>	211000012	1200121211	1121111111	1200110100	1100020111	3210013000	0000012120
<i>L. crassipilus</i>	211000012	100?121211	1121111111	1200110100	110001??11	2100??2001	200201???0
<i>L. brandiae</i>	011000011	1202121211	1120111111	1200111100	1100021110	1010013000	0000012110
<i>L. amorimi</i>	111000002	1202121211	1120111111	1200111100	1110011111	2100013100	0000012110
<i>L. fasciculatus</i>	112000012	1202121211	1120111111	1200111100	1110021111	2100012100	0000002110
<i>L. femoratus</i>	112000012	1202121211	1120111111	1200111100	1110021111	3110013100	0000002110
<i>L. waodani</i>	112000012	1202121211	1120111111	1200111100	1110021111	3210013100	0000002110
<b>Outgroup taxa</b>							
<i>Polylepta</i>	000000000	1000000100	0000001000	0101000111	0000001110	000?000100	000000000?
<i>Allocotocera</i>	000000000	0000000100	0001000000	0001000011	01000000?0	000?000001	10020?1000
<i>Neuratelia</i>	000001000	1000000000	0000001000	0101000111	01000000?0	000?000001	100?00100?
<i>Eudicrana</i>	000000000	0000000000	0000000000	0100100000	00000000?0	000?002000	00000?000?

The remaining species fall into four monophyletic species groups (Fig. 151); the *L. ornatus* group (7 spp., Fig. 152), *L. grjebinei* group (10 spp., Fig. 153), *L. walkeri* group (10 spp., Fig. 154), and *L. furcatus* group (9 spp., Fig. 155). The *L. ornatus* and *L. grjebinei* groups form a monophyletic clade supported by two uniquely-derived synapomorphies (Br = 4, bootstrap = 62): tergite 9 and gonocoxite margins at least partially fused but discernible as a crease (54:1), gonostylus bare (64:1), and by six homoplasious character states: clypeus dorsoventrally elongate oval or square (6:2), clypeus with 2–8 strong bristles only along ventral margin (8:1), palp segment 5 with central portion thinner than apex and base (13:1), dorsocentral setae present as single or double line of fine setae, usually spaced ~their own length apart (22:1), bristles on tergite 8 restricted to apicolateral corners (45:1), and gonocoxite III fused to gonostylus (65:1).

The *L. walkeri* and *L. furcatus* groups also form a clade supported by one uniquely-derived synapomorphy (Br = 4): gonocoxite placed distally or apically on tergite 9 (55:1), and four homoplasious character states: male foretibial comb of bristles present (30:1), tergite 8 bare (45:2), aedeagus initially tapered but ending in sclerotized apex with one or more lateral lobes/flanges of various lengths and ornamentation (66:2), and paramere a curved taper (71:1).

### ***Leptomorphus ornatus* species group**

The monophyly of the *L. ornatus* group is weakly supported (Br = 1) by a single homoplasious character state: pedicel with setae and/or bristles only on dorsal apex (5:1) (Figs. 150–152). This group includes species from the Oriental, northeastern Australasian, eastern Palearctic, and Nearctic regions. *Leptomorphus ornatus* is the sister group to the remaining species, though this may be due to a lack of information on male genitalic characters, so this placement should be confirmed if and when males are found for this species. The remaining species in this clade are weakly united by a single homoplasious character state (Br = 1): no inter-antennal bristles on frons (11:2).

*Leptomorphus babai* and *L. hyalinus* form a well-supported clade (Br = 3), based on six homoplasious character states: frons brown (10:1), scutellum brown (23:0), alula with macrotrichia (37:0), sternite 9 absent or membranous (46:0, 47:0), and anterior margin of fusion of parameral and gonocoxal apodemes with a sclerotized, thickened area (70:1).

The monophyly of the remaining four species is supported by two uniquely-derived synapomorphies (Br = 2): palp segment 3 spherical (12:1), apex of gonostylar main lobe bifurcated into 2 points (62:1), and one homoplasious character state: apices of M veins thinning apically and not reaching wing margin (43:1). The three species found in the Malay Archipelago (*L. tagbanua*, *L. tabatius*, *L. chaseni*) form a well-supported monophyletic group supported by five uniquely-derived synapomorphies (Br = 2): abdominal segments 3–5 swollen relative to adjacent segments (44:1), fusion of tergite 9 and gonocoxite strongly fused, margin only discernible as a thickening (54:2), aedeagus with apodemes reduced to a single lobe and united with sternite 9 (69:1), apex of paramere shorter than apex of aedeagus due to reduction/loss of paramere (72:3), paramere reduced (73:2), and five homoplasious character states: mediotergite with medial or anteromedial patch of small bristles/setae absent (26:0), apical wing spot absent or faintly present in apical 1/4 of r (33:1), tergite 9 with ventrobasal margin of posterior lobes thickened and sclerotized, often bearing one or more ventrally extending points laterally (53:1), length of gonocoxite <0.8X medial length of tergite 9 (56:3), and paramere shape unknown due to reduction (71:3).

The relationship between *L. tabatius* and *L. chaseni* should be regarded as tentative, as it is only supported by one homoplasious character state (Br = 1): large-socketed scutellar bristles absent (25:1), and *L. chaseni* is missing information for many characters because it is only known from the female.

None of the eight species recently described from the Malay Archipelago by Papp & Ševčík (the *L. ascutellatus* group, 2011) were included in the phylogenetic analysis, due to a lack of material and incomplete description of characters relevant to the analysis. However, based on the illustrations of male genitalia in the original descriptions, they all appear to belong to the apical group of species in the *L. ornatus* group (*L. titiwangsensis* and relatives).

### ***Leptomorphus grjebinei* species group**

The *L. grjebinei* species group is supported by one uniquely-derived synapomorphy (Br = 1): apex of longest paramere at same level as apex of aedeagus (when anterior margin of apodemes are at the same level, 72:1), and 3 homoplasious character states: apical wing spot absent or faintly present in apical 1/4 of r (33:1), macrotrichia absent from cell a (35:1), and tergite 9 with ventrobasal margin of posterior lobes thickened and sclerotized, often



bearing one or more ventrally extending points laterally (53:1) (Figs. 150, 151, 153). This species group is restricted to the Afrotropical region. The Malagasy species *Leptomorphus grjebinei* is the sister species to the nine continental African species. These nine species are a monophyletic group supported by one uniquely-derived synapomorphy (Br = 2): ventral gonostylar lobe <2X length of dorsal (smaller) lobe (60:1), and three homoplasious character states: mediotergite with medial or anteromedial patch of small bristles/setae (26:0), lateral margins of sternite 9 reaching or overlapping medial margin of gonocoxite (48:0), and gonostylus with two lobes (59:1).

*Leptomorphus carnevalei*, *L. couturieri*, *L. medleri*, and *L. aliciae* form a monophyletic clade supported by one uniquely-derived synapomorphy (Br = 1): apex of gonostylar dorsal (smaller) lobe flange-like (63:1), and one homoplasious character state: tergite 9 with posterolateral lobes (evaginations) tapering for entire length (51:2). The latter three species form a clade supported by one homoplasious character state (Br = 1): apices of M veins thinning apically and not reaching wing margin (43:1). *Leptomorphus medleri* and *L. aliciae* are sister species supported by one homoplasious character state (Br = 1): sternite 9 with anterior margin concave (47:2).

The remaining five species form a weakly supported clade based on a single homoplasious character state: apex of gonostylar dorsal (smaller) lobe tapered to point (63:2). Within this group *L. obscurus*, *L. crosskeyi*, and *L. gracilis* form a clade based on three homoplasious character states (Br = 2, bootstrap = 67): head yellow with some brown (1:1), scutellum brown (23:0), and ventral gonostylar lobe >2X length of dorsal (smaller) lobe (60:2). The sister-group relationships between the three species within this clade is not clear, though the apices of the M veins reach the wing margin in *L. crosskeyi* and *L. gracilis* but not in *L. obscurus*. *Leptomorphus stigmatus* and *L. mandelai* are sister species based on one weak homoplasious character state (Br = 1): macrotrichia present in cell a (35:0).

#### ***Leptomorphus walkeri* species group**

The monophyly of the Holarctic *L. walkeri* species group is strongly supported by three uniquely-derived synapomorphies (Br = 4): inter-ommatidial setulae absent or present as very few, very short (easily missed) setulae (15:2), setae on basal posterior margin of wing (distal of alula, along base of cell a) all a single length (38:1), gonocoxite bearing gonostylus basally (58:1), and four homoplasious characters: (7:1), lateral ocellus between 0.5 and 1.5X own diameter from eye margin (17:1), median wing spot present (34:1), and alula with microtrichia (37:0) (Figs. 150, 151, 154).

*Leptomorphus walkeri* is the sister species to the rest of this group. The remaining species form a strongly supported clade based on one uniquely-derived synapomorphy (Br = 4): sternite 9 ~equal to width of tergite 9 (46:2), and eight homoplasious character states: head brown (1:0), pedicel brown (4:1), frons brown (10:1), calypter with macrotrichia/setae absent (39:1), lateral margins of sternite 9 reaching or overlapping medial margin of gonocoxite (48:0), tergite 9 with posterolateral lobes (evaginations) absent (49:0), and posterior margin of tergite 9 without lobes (50:0, 51:0).

*Leptomorphus quadrimaculatus* and *L. forcipatus* form a sister clade to the remaining species. This monophyletic group is supported by one uniquely-derived synapomorphy (Br = 1): length of gonocoxite 1.3–1.79X medial length of tergite 9 (56:1), and four homoplasious character states: aedeagus initially tapered but then swelling and bulbous at apex (66:1), Anterior margin of fusion of parameral and gonocoxal apodemes forming a sclerotized hook (70:2), apex of longest parameral lobe reaching well beyond apex of aedeagus (when anterior margin of apodemes are at same level (72:2), and paramere with two lobes (73:1). Although previously published descriptions of *L. subforcipatus* and *L. talyshensis* are included in this manuscript no material was available for study and character coding. These species were initially included in the analysis, but the large amount of missing character data caused polytomies in the tree, so they were omitted to allow greater resolution of species relationships. However, when included in preliminary analyses these species were consistently placed close to *L. quadrimaculatus* and *L. forcipatus*. The illustrations of genitalia in the original descriptions support this, as they share the uniquely-derived synapomorphy that unites this clade. Furthermore, *L. subforcipatus* may be conspecific with *L. quadrimaculatus* (see taxonomic discussion under these species).

The final five species in this species group comprise the species previously assigned to the subgenus *Diomonus* (Matile 1977), and make up the second most strongly supported clade in the tree (Br = 7, bootstrap = 92). This lineage is supported by one uniquely-derived synapomorphy: sclerotized apex of aedeagus present

as lateral lobes only (medial apex absent/indiscernible, 67:2), and 12 homoplasious character states: pedicel with setae and/or bristles only on dorsal apex (5:1), clypeus circular (6:1), many bristles on face (9:0), no inter-antennal bristles on frons (11:2), scutellum brown (23:0), no comb of bristles on male foretibia (30:0), foreleg first tarsomere length 1–1.5X tibia length (31:1),  $R_4$  present (41:0),  $R_5$  concave relative to anterior wing margin (42:1), bristles covering tergite 8 (45:0), length of gonocoxite <0.8X medial length of tergite 9 (56:3), and length of gonocoxite <0.8X medial length of tergite 9 (68:3). *Leptomorphus panorpiformis* is the sister species to the remaining four (Nearctic) species, which are united by one uniquely-derived synapomorphy (Br = 2): male mid-femur with an apical process (Figs. 83–84, 32:1), and two homoplasious character states: space between ocelli more than diameter of laterals (16:0), and alula without microtrichia (37:1).

*Leptomorphus bifasciatus* is the sister species to the rest of the Nearctic clade. The remaining three species (*L. magnificus*, *L. subcaeruleus* and *L. nebulosus*) are united by two uniquely-derived synapomorphies (Br = 2, bootstrap = 53): main gonostylar lobe laterally compressed into almost two-dimensional flange (61:1), and aedeagal lateral lobe present as long, thick, sickle-like taper (68:2). These three species (the *L. nebulosus* group) also have almost identical male genitalia (Figs. 108, 111, 117), so relationships between the three species are uncertain. However, *L. nebulosus* does have two homoplasious character states not present in the other two: scape setae in short row on apicodorsal margin and thick patch covering apicoventral process, remainder bare (3:2), and face without bristles (9:1).

### ***Leptomorphus furcatus* species group**

The monophyly of the *L. furcatus* group is supported by one uniquely-derived synapomorphy (Br = 1): laterotergite with covering of appressed fine trichia (28:1), and four homoplasious character states: no large-socketed scutellar bristles (25:1), length of gonocoxite <0.8X medial length of tergite 9 (56:3), anterior margin of fusion of parameral and gonocoxal apodemes with a sclerotized, thickened area (70:1), and apex of longest paramere reaching well beyond apex of aedeagus (when anterior margin of apodemes are at same level, 72:2) (Figs. 150, 151, 155).

*Leptomorphus furcatus*, the only Nearctic member of this clade (with an extension into northwest Mexico), is the sister species to the remainder of the group, all of which are Neotropical. The Neotropical clade is the most strongly supported clade in the tree, with four uniquely-derived synapomorphies (Br = 11, bootstrap = 94): palp segment 5 surface with covering of white setulae (14:1), surface of scutum covered with trichia (Fig. 80, 20:1), scutellum with covering of fine trichia (24:1), mediotergite with covering of appressed trichia (27:1), and ten homoplasious character states: face without bristles (9:2), frons brown (10:1), no inter-antennal bristles on frons (11:2), surface of scutum without covering of setae (19:1), dorsocentral setae present as a single, anterior, large seta (22:2), laterotergite abutting katapisternum (29:1), median wing spot present (34:1), no macrotrichia in cell  $a_2$  (35:1), sclerotized apex of aedeagus with lateral lobes and with medial apex apparent (67:1), and aedeagal lateral lobes present as short taper/flange (68:1).

*Leptomorphus neivai* is the sister species to the remainder of the Neotropical species, which form a clade based on two homoplasious character states (Br = 1): clypeus with strong bristles only along ventral margin (8:1), and gonocoxite III fused to gonostylus (65:1). It is uncertain whether *L. eberhardi* or *L. crassipilus* is the sister species to the remaining five species, probably due to the missing male genitalic characters for *L. crassipilus* (the genitalia of the male holotype are crushed). The clade of five species is supported by one uniquely-derived synapomorphy (Br = 1): few macrotrichia in basal third of wing (36:1) and one homoplasious character state: scutellum brown (23:0). *Leptomorphus brandiae* is the sister species to *L. amorimi*, *L. fasciculatus*, *L. femoratus* and *L. waodani*. These four species form a monophyletic clade based on one strong uniquely-derived synapomorphy (Br = 2): gonocoxal lobe present (57:1), and two homoplasious character states: head yellow (1:0), and  $R_5$  concave relative to anterior wing margin (42:1).

The relationships between the remaining species are based on homoplasious character states, with *L. amorimi* as sister species to the remaining three species based on three characters (Br = 3, bootstrap = 58): scape setae in short row on apicodorsal margin and thick patch covering apicoventral process, remainder bare (3:2), gonocoxite III separate from gonostylus (65:0), and paramere a straight taper (71:0). At the apex of the *L. furcatus* clade *L. fasciculatus* is the sister species to *L. femoratus* and *L. waodani*, supported by two character

states (Br = 2): tergite 9 with medioposterior lobe (evagination) present (52:1), and posterior margin of tergite 9 with three lobes (50:3).

### Implications of phylogeny for previous classifications

Matile (1977) recognized four subgenera within *Leptomorphus* (*Austroleptomorphus*, *Diomonus*, *Gymnoscutum*, and *Leptomorphus*) based on a study of the Afrotropical species, a handful of specimens from other regions, and prior species descriptions. Each subgenus was based on a set of assumed synapomorphies, though these were not tested with a phylogenetic analysis. Our analysis found no phylogenetic support for any of these subgenera with the possible exception of *Gymnoscutum*. However, even the limits of this subgenus would be changed to include *L. grjebinei*, which is basal to the group and was previously placed in a monotypic *Austroleptomorphus*. Because the previous subgenera are mostly non-monophyletic, we consider them synonyms of *Leptomorphus*. We prefer the use of species groups, as defined in this analysis, to subgenera.

In her unpublished, but occasionally cited, thesis, Tozoni (1998) treated *Leptomorphus* and *Diomonus* as separate genera in a preliminary phylogeny of the Mycetophilidae. However, the characters supporting that decision were incorrectly interpreted (*Leptomorphus* has both the mediopleural suture complete and pseudotrachea present), so separation of the genera based on those characters is unfounded.

This revision brings together all current systematic and biological information on *Leptomorphus*. There are now 45 extant species recognized in this genus. We expect that new species will continue to be discovered in this genus, especially given the number of new species described here and in Papp & Ševčík (2011) from only a handful of specimens. More sampling of mycetophilids in general, and from under-represented regions in particular, will certainly continue to increase this number and provide further interesting stories about the phylogeny, natural history and ecology of this genus.

### Acknowledgements

We thank the following individuals for their help in obtaining specimens: D.S. Amorim (USP); B. Blinn, Z. Falin (NCSU); A. Borkent (RBCM); S.E. Brooks, J.M. Cumming, B. Sinclair (CNC); M. Buck, S.A. Marshall (DEBU); D.S. Chandler (UNHC); C. Copley (RBCM); G. Courtenay (ISUD); S. Cover (MCZ); C. Daugeron, E. Delfosse (MNHN); T. Erwin, F.C. Thompson (USNM); C. Griswold, D. Kavanaugh (CAS); U. Kallweit, B. Rulik (MTD); P. Kerr (CSCA); L.S. Kimsey (UCDC); M. Kotrba (ZSM); C. Lamas (MZUSP); J. Liebherr (CUIC); R. Matsumoto (OMNH); M. Mostovski (NMSA); K. Needham (UBCZ); E. Rindal (ZMUN); R. Ubaidillah (MZB); I. Stocks (CUAC); H. Tschorsnig (SMNS); P. Vilcama (FMNH); J. Weintraub (ANSP); N. Wyatt (BMNH); K. Yoshizawa (EIHU); C. Young (CMNH), M. Zumbado (INBIO). C. Eiseman and M.J. Hatfield also donated specimens from their personal collections.

I also thank A. Borkent, W.E. Gross, and C. Regnier for their help in the field and the lab, and T. Saigusa and J. Ševčík for discussions on Japanese and Oriental *Leptomorphus* species respectively. The manuscript was much improved by reviews from Dr. Neal Evenhuis, Dr. Dalton S. Amorim, Sarah S. Oliveira and Dr. Peter Kerr. Finally, I would like to thank my wife, Brandi, for her emotional, physical and financial support and for her help in the field, the lab and the writing of the manuscript.

This study was done as part of a PhD thesis under the supervision of TAW at McGill University. Funding was provided by an NSERC Postgraduate Scholarship, Margaret DuPorte Fellowship, Dipterology Fund Student Research and Travel Grant, Williston Fund Grant, to CJB, and by an NSERC Discovery Grant to TAW. The Willi Hennig Society provided free access to TNT (Goloboff *et al.* 2003).

### Literature Cited

- Aldrich, J.M. (1905) *A catalogue of North American Diptera. Smithsonian Miscellaneous Collections* 46 [no. 1444], Smithsonian Institution, Washington D.C., 680 pp.
- Alexander, C.P. (1924) Undescribed species of Nematocera from Japan. *Insector Inscitiae Menstruus*, 12, 49–55.
- Amorim, D.S. & Rindal, E. (2007) Phylogeny of the Mycetophiliformia, with proposal of the subfamilies Heterotrichinae,

- Ohakuneinae, and Chiletrichinae for the Rangomaramidae (Diptera, Bibionomorpha). *Zootaxa*, 1535, 1–92.
- Bertone, M.A., Courtney, G.W. & Wiegmann, B.M. (2008) Phylogenetics and temporal diversification of the earliest true flies (Insecta: Diptera) based on multiple nuclear genes. *Systematic Entomology*, 33, 668–687.
- Blagoderov, V. & Grimaldi, D. (2004) Fossil Sciaroidea (Diptera) in Cretaceous ambers, exclusive of Cecidomyiidae, Sciaridae, and Keroplatidae. *American Museum Novitates*, 3433, 1–76.
- Borkent, C.J. & Wheeler, T.A. (in press) Phylogeny of the tribe Sciophilini (Diptera: Mycetophilidae: Sciophilinae). *Systematic Entomology*.
- Bremer, K. (1994) Branch support and tree stability. *Cladistics*, 10, 295–304.
- Brimley, C.S. (1938) *The Insects of North Carolina*. North Carolina Department of Agriculture, Raleigh, 560 pp.
- Brocher, F. (1931) Observations biologiques sur la larve du *Delopsis aterrima* Zett. et sur celle du *Leptomorphus walkeri* Curt. (Diptères mycétophiles). *Revue Suisse de Zoologie*, 38, 67–76.
- Brunetti, E. (1912) Diptera Nematocera (excluding Chironomidae and Culicidae). In: Shipley, A.E. and Marshall, G.A.K. (eds.), *Fauna of British India, including Ceylon and Burma*. Taylor and Francis, London, 581 pp., 12 pls.
- Chandler, P.J. (2009) The fungus gnats (Diptera: Bolitophilidae, Keroplatidae, Mycetophilidae) of Sardinia, with description of six new species. *Zootaxa*, 2318, 450–506.
- Cockerell, T.D.A. (1920) Eocene insects from the Rocky Mountains. *Proceedings of the United States National Museum*, 57, 233–260.
- Cole, F.R. & Schlinger, E.I. (1969) *The Flies of western North America*. University of California Press. Berkeley and Los Angeles. 693 pp.
- Cole, J.H. & Chandler, P.J. (1979) The Fungus Gnats (Diptera, Mycetophilidae) of Monk's Wood National Nature Reserve, Cambridgeshire. *Entomologist's Gazette*, 30, 47–55.
- Colless, D.H. & Liepa Z. (1973) Superfamily Myceptophiloidea, family Mycetophilidae. In: Delfinado, M.D. and Hardy, D.E. (eds.) 1973. *A catalog of the Diptera of the Oriental Region. Vol. 1. Suborder Nematocera*. University Press of Hawaii, Honolulu, pp. 444–463.
- Coquillett, D.W. (1901) New Diptera in the U.S. National Museum. *Proceedings of the United States National Museum*, 23, 593–618.
- Coquillett, D.W. (1910) The type-species of the North American genera of Diptera. *Proceedings of United States National Museum*, 37, 499–647, Washington D.C.
- Crosskey, R.W. (ed.) (1980) *Catalogue of the Diptera of the Afrotropical Region*. British Museum of Natural History, London, 1437 pp.
- Cumming, J.M. & Wood, D.M. (2009) Adult Morphology and Terminology. In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. and Zumbado, M.A. (eds.) *Manual of Central American Diptera, Vol. 1*. NRC Research Press, Ottawa, pp. 9–50.
- Curtis, J. (1831) Plate 365. *Leptomorphus walkeri*. In: Curtis, J. *British entomology; Being illustrations and descriptions of the genera of insects found in Great Britain and Ireland. Vol. 8*. Privately published, London, 439pp.
- Dahl, C., Krivosheina, N.P., Krzeminska, E., Lucchi, A., Nicolai, P., Salamanna, G., Santini, L., Skuhrava, M. & Zwick, P. (1995) Diptera Blephariceromorpha, Bibionomorpha, Psychodomorpha, Ptychopteromorpha. In: Minelli, A., Ruffo, S. and La Posta, S. (eds.), *Checklist delle specie della fauna italiana, 64*. Calderini, Bologna, pp. 1–39.
- Eberhard, W.G. (1970) The natural history of the fungus gnats *Leptomorphus bifasciatus* (Say) and *L. subcaeruleus* (Coquillett) (Diptera: Mycetophilidae). *Psyche* (Cambridge), 77, 361–383.
- Eberhard, W.G. (1986) Pupation in mycetophilid flies: a correction. *Psyche* (Cambridge) 93, 117–119.
- Eberhard, W.G. (1990) Imprecision in the behavior of *Leptomorphus* sp. (Diptera, Mycetophilidae) and the evolutionary origin of new behavior patterns. *Journal of Insect Behavior*, 3, 327–357.
- Edwards, F.W. (1925) British fungus-gnats (Diptera, Mycetophilidae). With a revised generic classification of the family. *Transactions of the Entomological Society of London* (1924), 71, 505–670, pls. 44–51.
- Edwards, F.W. (1933a) Diptera Nematocera from Mount Kinabulu. *Journal of the Federated Malay States Museums*, 17, 223–296.
- Edwards, F.W. (1933b) New Neotropical Mycetophilidae II (Diptera). *Revista de Entomologia Rio de Janeiro*, 3, 303–322.
- Edwards, F.W. (1940) New Neotropical Mycetophilidae IV (Diptera). *Revista de Entomologia Rio de Janeiro*, 11, 440–465.
- Enderlein, G. (1936) 22. Ordnung: Zweiflügler, Diptera. In: Brohmer, P., Ehrmann, P., & Ulmer, G. *Die Tierwelt Mitteleuropas Band 6, Lief. 2, Insekten: III Teil, Vol. 16, Quelle & Meyer, Leipzig*, pp. 1–259.
- Evenhuis, N.L. (2006) Catalog of the Keroplatidae of the world (Insecta: Diptera). *Bishop Museum Bulletin in Entomology*, 13, 1–177.
- Felsenstein, J. (1985) Confidence limits on phylogenies: an approach using bootstrap. *Evolution*, 39, 783–791.
- Gammelmo, Ø. & Sjøli, G. (2006) Norwegian fungus gnats of the family Mycetophilidae (Diptera, Nematocera). *Norwegian Journal of Entomology*, 53, 57–69.
- Goloboff, P., Farris, J. & Nixon, K. (2003) T.N.T.: Tree Analysis using New Technology. Program and documentation available from <http://www.zmuc.dk/public/phylogeny/tnt>. (accessed August 11, 2011)
- Grzegorzec, A. (1875) Neue Pilzmücken aus der Sanclerzer Gegend. *Verhandlungen der Kaiserlich-Königlichen Zoologisch-Botanischen Gesellschaft in Wien*, 25 (Abhandlungen), 1–8.
- Hutson, A.M., Ackland D.M., & Kidd L.N. (1980) Mycetophilidae (Bolitophilinae, Ditomyiinae, Diadocidiinae, Keroplatinae,



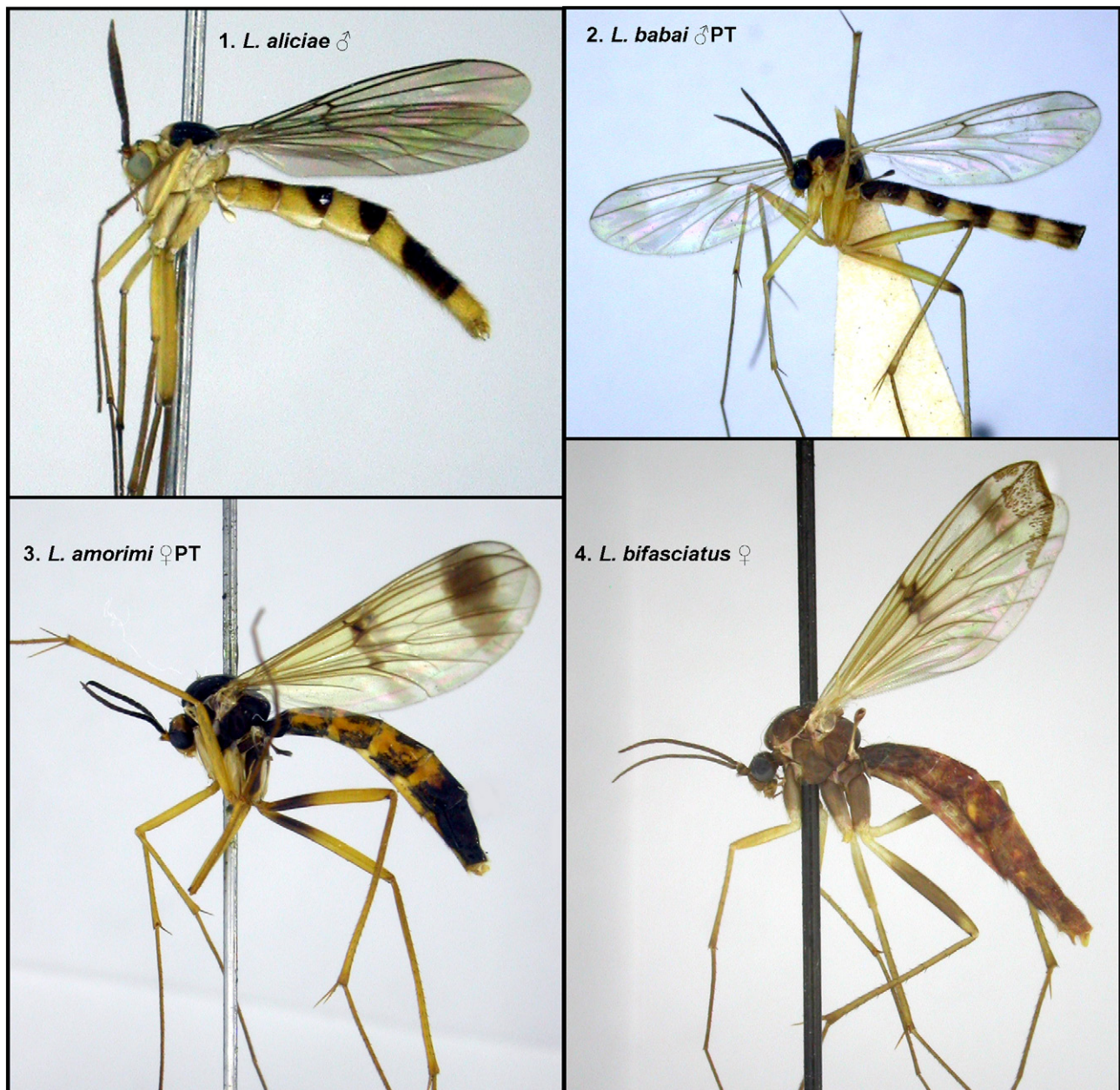
- Sciophilinae and Manotinae) (Diptera, Nematocera). *Handbooks for the Identification of British Insects*, 9, 1–111.
- Jakovlev, J. (2011) Fungus gnats (Diptera: Sciarioidea) associated with dead wood and wood growing fungi: new rearing data from Finland and Russian Karelia and general analysis of known larval microhabitats in Europe *Entomologica Fennica*, 22, 157–189.
- Johannsen, O.A. (1903) Notes on some Adirondack Diptera collected by Messrs. MacGillivray and Houghton. *Entomological News*, 14, 14–17.
- Johannsen, O.A. (1909) Diptera, Family Mycetophilidae. *Genera Insectorum*, 93, 1–141. 7pls.
- Johannsen, O.A. (1910) The fungus gnats of North America. The Mycetophilidae of North America. Part II. The Sciophilinae. *Bulletin of the Maine Agricultural Experiment Station*, 180, 125–192, 4 pls.
- Johannsen, O.A. (1912) The fungus gnats of North America. The Mycetophilidae of North America. Part III. The Mycetophilinae. *Bulletin of the Maine Agricultural Experiment Station*, (1911) 196, 249–328, 5 pls.
- Johannsen, O.A. (1926) Notes on Walker's types of North American Mycetophilidae (Diptera). *Canadian Entomologist*, 58, 51–52.
- Johnson, C.W. (1910) Order Diptera. In: Smith, J. B., *Annual Report of the New Jersey State Museum, Including a Report of the Insects of New Jersey 1909*. MacCrellish & Quigley, Trenton, pp. 703–814.
- Johnson, C.W. (1925) Fauna of New England. 15. List of the Diptera or two-winged flies. *Occasional Papers of the Boston Society of Natural History*, 7, 3–326.
- Kertész, K. (1902) *Catalogus dipterorum hucusque descriptorum Vol. 1*. Museum Nationale Hungaricum, Budapest, 339 pp.
- Kessel, E.L. & Kessel, B.B. (1939) Diptera associated with fungi. *The Wasmann Collector*, 3, 73–92.
- Khalaf, K.T. (1971) Keroplatinae and Sciophilinae from Louisiana and Mississippi (Diptera: Mycetophilidae). *Florida Entomologist*, 54(1), 13–20.
- Kjærandsen, J., Hedmark, K., Kurina, O., Polevoi, A., Økland, B. & Götmark, F. (2007) Annotated checklist of fungus gnats from Sweden (Diptera: Bolitophilidae, Diadocidiidae, Ditomyiidae, Keroplatidae and Mycetophilidae). *Insect Systematics and Evolution, Supplement*, 65, 1–128.
- Krivosheina, N.P., Zaitzev, A.I. & Yakovlev, E.B. (1986) [*Insect-pests of fungi in the forests of the European parts of the USSR*]. Nauka, Moscow, 307pp. [in Russian].
- Krivosheina, N.P. & Zaitzev, A.I. (2008) Trophic relationships and main trends in morphological adaptations of larval mouthparts in sciaroid dipterans (Diptera, Sciarioidea). *Biology Bulletin*, 35, 606–614.
- Kurina, O. (2003) Fungus gnats from the tribe Schiophilini [Sciophilini] (Diptera, Mycetophilidae) in the collection of the Swedish Museum of Natural History in Stockholm. *Entomologisk Tidskrift*, 124, 59–63.
- Kurina, O., Polevoi, A., Götmark, F., Økland, B., Frank, N., Norden, B. & Hedmark, K. (2005) Fungus gnats (Diptera: Sciarioidea excl. Sciariidae) in the Swedish boreonemoral forests. *Studia dipterologica*, 11, 471–488.
- Lackschewitz, P. (1937) Die Fungivoriden des Ostbaltischen Gebietes. *Arbeiten des Naturforscher-Vereins zu Riga (N.F.)*, 21, 1–47.
- Laffoon, J.L. (1965) Family Mycetophilidae (Fungivoridae). In: Stone, A., Sabrosky, C.W., Wirth, W.W., Foote, R.H. and Coulson J.R. *A catalog of the Diptera of America north of Mexico*. U.S. Department of Agriculture, Handbook, 276, 196–229 pp.
- Landrock, K. (1917) Die Typen der Piltzmücken der von Roserchen Sammlung in Stuttgart. *Wiener Entomologische Zeitung*, 36, 36–39.
- Landrock, K. (1918) Tabellen zum Bestimmen europäischer Piltzmücken. II. *Wiener Entomologische Zeitung*, 37, 107–120.
- Landrock, K. (1940) 38. Zweiflügler oder Diptera. VI. Piltzmücken oder Fungivoridae (Mycetophilidae). In: Dahl, F. *Die Tierwelt Deutschlands und der angrenzenden Meeresteile nach ihren Merkmalen und nach ihrer Lebensweise*. Verlag von Gustav Fischer, Jena, 166 pp.
- Lane, J. (1958) Mycetophilidae, chiefly from Argentina. *Proceedings of the 10th International Congress of Entomology Montreal, 1956*. 1, 143–162.
- Lane, J. & Sturm, H. (1958) A new genus of "Ditomyiinae". Description of two new species with bionomical notes (Diptera, Mycetophilidae). *Revista Brasileira de Biologia*, 18, 199–207.
- Le Conte, J.L. (ed.) (1859) *The complete writings of Thomas Say on the entomology of North America, Vol. 1*. Baillière, New York. 412 pp.
- Maddison, W.P. & Maddison, D.R. (2011) Mesquite: a modular system for evolutionary analysis. Version 2.75 available from <http://mesquiteproject.org> (accessed October 15, 2011)
- Madwar, S. (1937) Biology and Morphology of the Immature Stages of Mycetophilidae (Diptera, Nematocera). *Philosophical Transactions of the Royal Society of London. Series B. Biological Sciences*, 227, 1–110.
- Matile, L. (1977) Notes sur le genre *Leptomorphus* et description de taxa nouveaux de la region éthiopienne (Diptera, Mycetophilidae). *Bulletin de l'Institut Fondamental de Afrique Noire (A)*, 38 (1976), 141–155.
- Matile, L. (1980) 15. Family Mycetophilidae. In: Crosskey, R.W. (ed.). *Catalogue of the Diptera of the Afrotropical region*. British Museum of Natural History, London, pp. 216–230.
- Matile, L. (1988) Tribe Sciophilini. In: Soós, A. and Papp, L. *Catalogue of Palaearctic Diptera: Volume 3: Ceratopogonidae – Mycetophilidae*. Elsevier, Amsterdam, pp. 231–241.
- Matile, L. (1997) Nouvelles données sur les *Leptomorphus* Afrotropicaux (Diptera, Mycetophilidae). *Revue Française d'Entomologie (Nouvelle Série) 1996*, 18(4), 143–150.

- Matsumoto, R. and Sasakawa, M. (2006) A list of the holotype-specimens of Diptera described by Dr. M. Sasakawa and co-workers, and deposited in the Osaka Museum of Natural History. *Bulletin of the Osaka Museum of Natural History*, 60, 13–30.
- Matsumura, S. (1915) *Konchu-Bunruigaku*, 2, Keiseisha shoten, Tokyo, 316pp. [In Japanese]
- Matsumura, S. (1916) *Thousand insects of Japan*. Additamenta. Vol. 2 (Diptera). Keisei-sha, Tokyo, 2, 185–474, pls. 16–25. [In Japanese]
- Matsumura, S. (1931) *6,000 Illustrated insects of Japan-Empire*. Toko Shoin, Tokyo. 1694 pp. [In Japanese]
- Mik, J. (1887) Dipterologische Miscellen. IV. *Wiener Entomologische Zeitung*, 6, 33–36.
- Okada, I. (1936) Einige Nematocera aus den Süd-Kurilen (Diptera). *Insecta Matsumurana*, 10, 99–103.
- Okada, I. (1938) Einige Fungivoriden vom Daisetsu-Gebirge in Hokkaido (Dipt., Nematocera). *Insecta Matsumurana*, 12, 91–98.
- Okada, I. (1939) Studien über die Pilzmücken (Fungivoridae) aus Hokkaido (Diptera, Nematocera). *Journal of the Faculty of Agriculture Hokkaido Imperial University*, 42, 267–336, pls. 15–18.
- Osten Sacken, C.R. (1878) *Catalogue of the described Diptera of North America. 2nd Edition. Smithsonian miscellaneous collections 270*, Smithsonian Institution, Washington D.C., 276 pp.
- Ostroverkhova, G.P. & Shtakel'berg A.A. (1988) 24. Family Mycetophilidae (Fungivoridae). In: Bei-Bienko G., (Ed.) *Keys to the Insects of the European Part of the USSR. Volume 5: Diptera and Siphonaptera Part 1*. Smithsonian Institution Libraries & National Research Foundation, Washington D.C., pp. 404–487.
- Papavero, N. (1978) Family Mycetophilidae (Fungivoridae). *A Catalogue of the Diptera of the Americas South of the United States*, 19E, 1–78.
- Papp, L. & Ševčík, J. (2011) Eight new oriental and Australasian species of *Leptomorphus* (Diptera: Mycetophilidae). *Acta Zoologica Academiae Scientiarum Hungaricae*, 57, 139–159.
- Plachter, H. (1980) Eidonomie und Gespinstbau der Juvenilstadien von *Leptomorphus walkeri* Curtis 1831 (Diptera, Mycetophilidae). *Spixiana*, 3, 11–24.
- Plassmann, E. (1971) Über die Fungivoriden-Fauna (Diptera) des Naturparkes Hoher Vogelsberg. *Oberhessische Naturwissenschaftliche Zeitschrift*, 38, 53–87.
- Poole, R.W. and Gentili, P. (1996) *Nomina Insecta Nearctica*. Vol. 3. Diptera, Lepidoptera, Siphonaptera. Entomological Information Services, Inc., Rockville, Maryland, 1120 pp.
- Procter, W. (1938) *Biological Survey of the Mount Desert Region. Part VI. The Insect Fauna*. The Wistar Institute of Anatomy and Biology, Philadelphia, 496 pp.
- Procter, W. (1946) *Biological Survey of the Mount Desert Region. Part VII. The Insect Fauna*. The Wistar Institute of Anatomy and Biology, Philadelphia, 566 pp.
- Rindal, E., Søli, G.E.E. & Bachmann, L. (2009) Molecular phylogeny of the fungus gnat family Mycetophilidae (Diptera, Mycetophiliformia). *Systematic Entomology*, 34, 524–532.
- Röder, V. von. (1892) Ein neuer Fundort des *Leptomorphus Walkeri* Curt. *Wiener Entomologische Zeitung*, 11, 170.
- Roser, C.F.L. von. (1840) Erster Nachtrag zu dem im Jahre 1834 bekannt gemachten Verzeichnisse in Wuttemberg vorkommender zweiflügliger Insekten. *Correspondenzblatt des Württembergischen Landwirthschaftlichen Vereins*, (N.S.) 17(1), 49–64.
- Saigusa, T. (2006) *Homology of wing venation of Diptera*. Privately published by the author, Fukuoka, Japan, 26 pp.
- Santini, L. (1983) Contributo alla conoscenza dei micetofili italiani. 1. Osservazioni preliminari sull'etologia di *Keroplatus testaceus* Dalm., *Keroplatus tipuloides* Bosc, *Cerotelion lineatus* F. (Diptera, Keroplatinae) e *Leptomorphus walkeri* Curtis (Diptera, Sciophilinae). *Atti del XII Congresso Nazionale Italiano di Entomologia, Roma, 1980*, 2, 469–471.
- Santini, L. (1985) Contributi alla conoscenza dei micetofili italiani. IV. Sulla biologia di *Leptomorphus walkeri* Curtis (Diptera, Mycetophilidae) nell'Italia centrale. *Frustula Entomologica*, 6, 239–254.
- Santini, L. & Mazzini M. (1989) Contributo alla conoscenza dei micetofili italiani. 11. Le sculture corionidee dell'uovo di *Leptomorphus walkeri* Curtis (Diptera, Mycetophilidae) al microscopio elettronico a scansione. *Redia*, 72, 205–213.
- Sasakawa, M. (1961) Japanese Fungivoridae. II. New or little known fungus gnats, with descriptions of five new species. *Kontyu*, 29, 186–194.
- Say, T. (1824) Appendix. Part I-Natural History. 1. Zoology. E. Class Insecta. In: Keating, W. H. *Major Long's second expedition. Vol. 2*. H.C. Carey & I. Lea, Philadelphia, pp. 268–378.
- Séguy, E. (1940) Diptères nématocères (Fungivoridae, Lycoriidae, Hesperinidae, Bibionidae, Scatopsidae, Phrynidae, Pachyneuridae, Blepharoceridae). *Faune de France*, 36, 1–386.
- Ševčík, J. (2006) Diptera associated with fungi in the Czech and Slovak Republics. *Časopis Slezského Zemského Muzea Série A Vědy Přírodní*, 55 (supplement 2), 1–84.
- Ševčík, J. (2010) *Czech and Slovak Diptera associated with fungi*. Slezské Zemské Muzeum, Opava. 112 pp.
- Ševčík, J. & Papp, L. (2003) New Mycetophilidae (Diptera) and additions to the Hungarian checklist. *Folia Entomologica Hungarica*, 64, 285–295.
- Ševčík, J., Kjørandsen, J. & Marshall S.A. (2012) Revision of *Speolepta* (Diptera: Mycetophilidae), with descriptions of new Nearctic and Oriental species. *Canadian Entomologist* 144, 93–107.
- Shaw, F.R. (1947) Some observations on the genus *Leptomorphus* with a description of a new subspecies. *Bulletin of the Brooklyn Entomological Society (1946)*, 41, 155–157.

- Shaw, F.R. & Fisher, E.G. (1952) Fungivoridae (Mycetophilidae). In: *Guide to the Insects of Connecticut. Part VI. The Diptera or true flies. Fifth Fascicle: Midges and gnats*. Connecticut State Geological and Natural History Survey, Bulletin 80, pp. 177–231.
- Shorthouse, D.P. (2010) SimpleMappr, a web-enabled tool to produce publication-quality point maps. Available from <http://www.simplemappr.net>. (accessed October 10, 2011).
- Søli, G.E.E. (1997) The adult morphology of Mycetophilidae (s.str.), with a tentative phylogeny of the family (Diptera, Sciaroidea). *Entomologica Scandinavica Supplement*, 50, 5–55.
- Søli, G.E.E., Vockeroth, R.J. & Matile, L. (2000) A.4. Families of Sciaroidea. In: Papp, L. and Darvas, B. (eds). *Contribution to a Manual of Palaearctic Diptera. Appendix*. Science Herald, Budapest, pp. 49–92.
- Strobl, P.G. (1897) Siebenbürgische Zweiflügler. *Verhandlungen und Mitteilungen des Siebenbürgischen Vereins für Naturwissenschaften zu Hermannstadt*, 46, 11–48.
- Tozoni, S.H.S. (1998) Morfologia de cápsula cefálica, tórax e asa e uma análise filogenética da família Mycetophilidae (Diptera: Bibionomorpha). Unpublished Ph.D. Thesis, Universidade Federal do Paraná.
- Tuomikoski, R. (1966) Generic taxonomy of the Exechiini (Dipt., Mycetophilidae). *Annales Entomologici Fennici*, 32, 159–194.
- Väisänen, R. (1984) A monograph of the genus *Mycomya* Rondani in the Holarctic region (Diptera, Mycetophilidae). *Acta Zoologica Fennica*, 177, 1–346.
- Vockeroth, J.R. (1981) Family Mycetophilidae. In: McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. and Wood, D.M. (coord.), *Manual of Nearctic Diptera. Vol. 1*, Research Branch, Agriculture Canada, Monograph 27, pp. 223–246.
- Vockeroth, J.R. (2009) Mycetophilidae (Fungus Gnats). In: Brown, B.V., Borkent, A., Cumming, J.M., Wood, D.M., Woodley, N.E. and Zumbado, M.A. (eds.) *Manual of Central American Diptera, Vol. 1*. NRC Research Press, Ottawa, pp. 267–278.
- Walker, F. (1848) *List of the specimens of dipterous insects in the collection of the British Museum. Part 1*. British Museum, London, 229 pp.
- Wiedemann, C.R.W. (1828) *Aussereuropäische zweiflügelige Insekten. Erster Theil*. Schulzischen Buchhandlung, Hamm, Germany. xxxii + 608 pp., 7 pls.
- Wray, D.L. (1967) *Insects of North Carolina: Third Supplement*. North Carolina Department of Agriculture, Division of Entomology, Raleigh, 181 pp.
- Yakovlev, E.B. (1995) Species diversity and abundance of fungivorous Diptera in forests and city parks of Russian Karelia. *An International Journal of Dipterological Research*, 6, 335–362.
- Zaitzev, A.I. (1981) New and little-known species of Mycetophilidae, tribe Sciophilini (Diptera from the Far East and Central Asia. *Entomologicheskoe Obozreniye*, 60, 395–400 [in Russian, English translation in *Entomological Review*, 60, 123–128 (1981)].
- Zaitzev, A.I. (1984) [Trends in morphological specialization of the digestive tract in higher mycetophiloid dipteran larvae (Diptera, Mycetophiloidea)]. *Biologicheskije nauki* 1984, 38–44. [in Russian]
- Zaitzev, A.I. (1994) *Fungus gnats of the fauna of Russia and adjacent regions. Part 1*. Nauka, Moscow, 288 pp. [in Russian]
- Zaitzev, A.I. (1999) 20. Mycetophilidae. In: Ler, P.A. and Belov, V.V. *Key to the insects of Russian Far East. Vol. 6. Diptera and Siphonaptera. Pt 1*. Dalnauka, Vladivostok, pp. 151–239. [in Russian]
- Zaitzev, A.I. & Ševčík J. (2002) A review of the Palaearctic species of the *Leptomorphus quadrimaculatus* (Matsumura) group (Diptera: Mycetophilidae). *Acta Zoologica Academiae Scientiarum Hungaricae*, 48, 203–211.

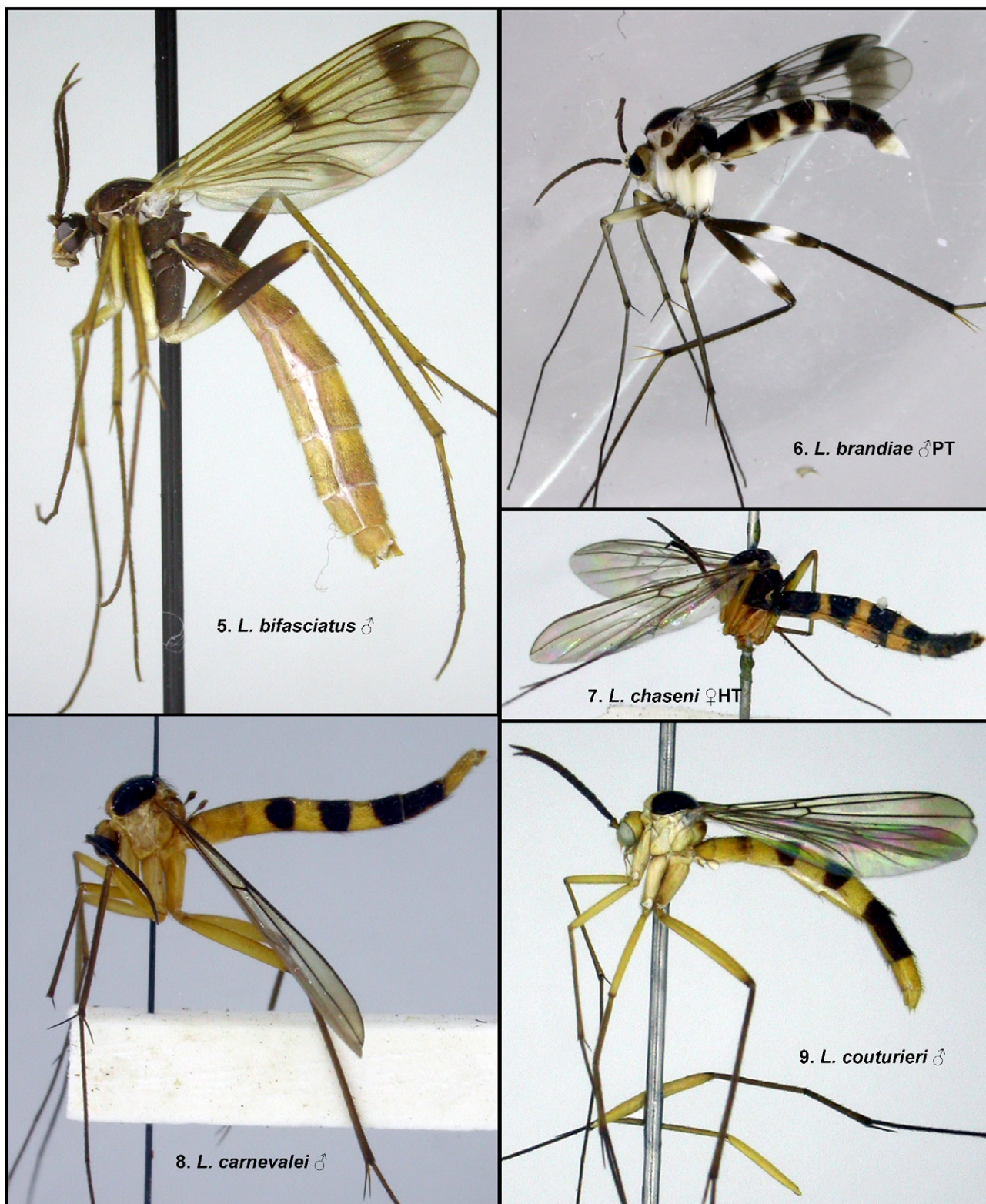


List of figures



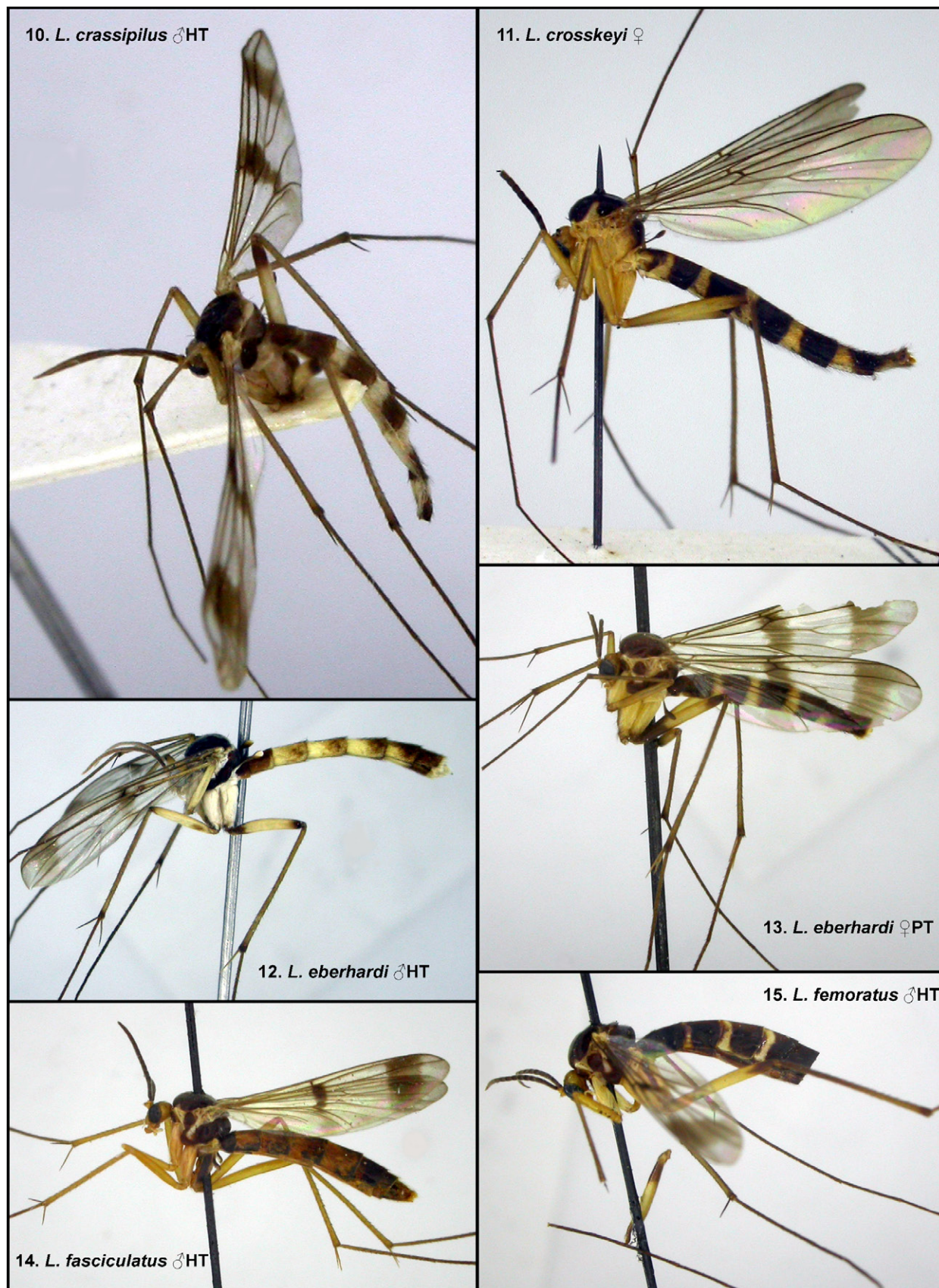
FIGURES 1–4. *Leptomorphus habitus*. 1. *L. aliciae*, male. 2. *L. babai*, paratype male. 3. *L. amorimi*, paratype female. 4. *L. bifasciatus*, female.





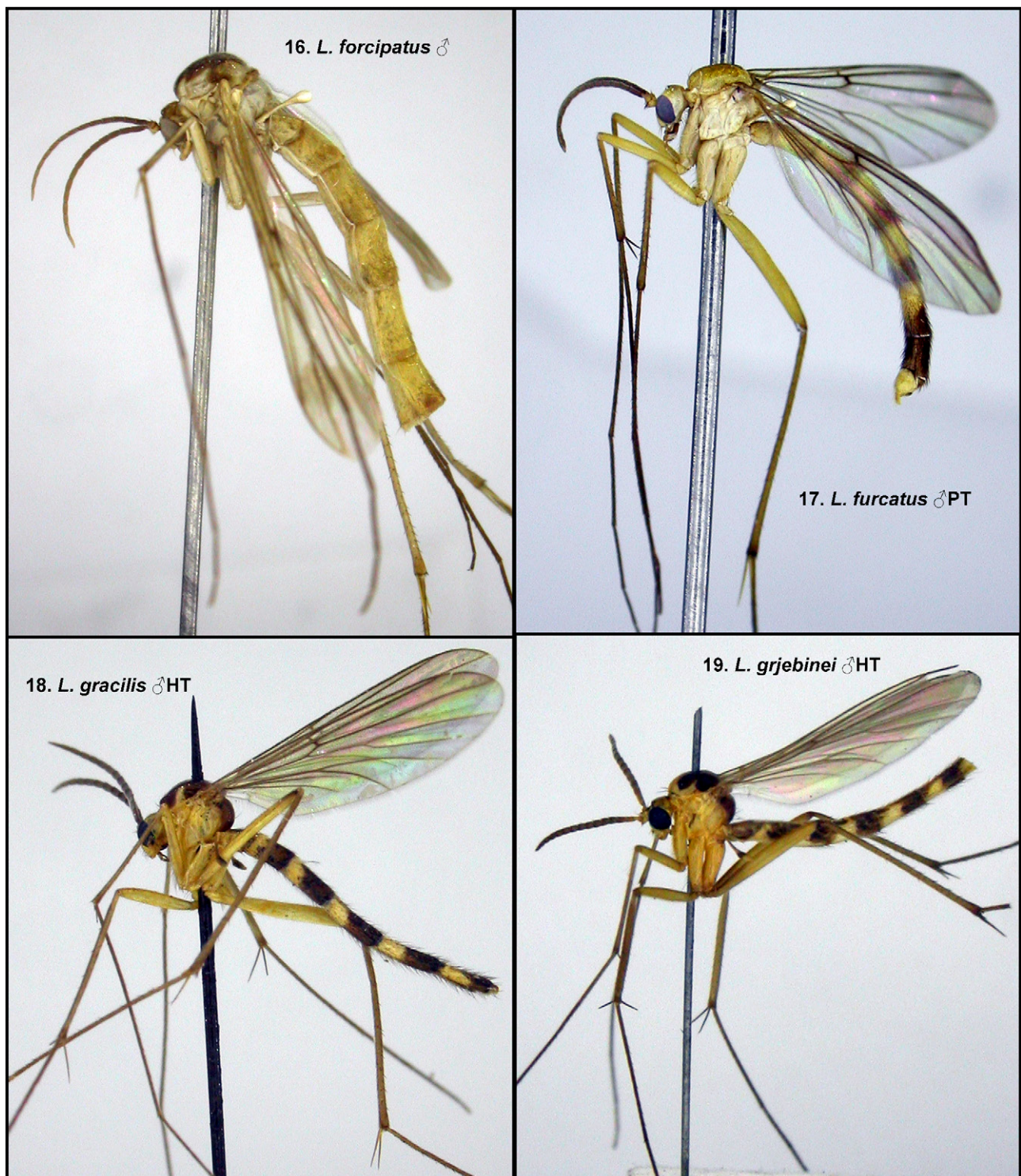
FIGURES 5–9. *Leptomorphus habitus*. 5. *L. bifasciatus*, neotype male. 6. *L. brandiae*, paratype male (in ethanol). 7. *L. chaseni*, holotype female. 8. *L. carnevalei*, male. 9. *L. couturieri*, male.





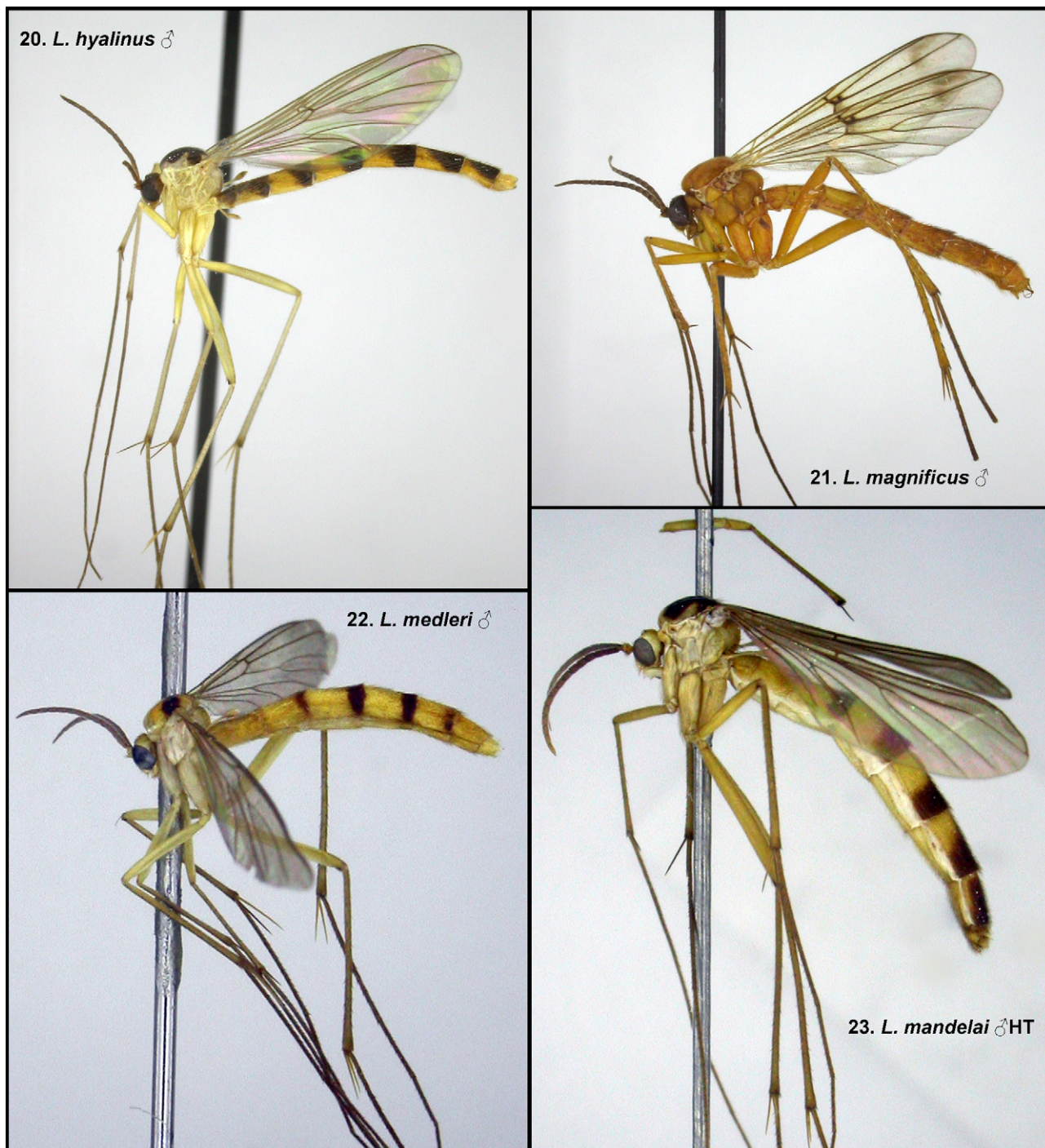
FIGURES 10–15. *Leptomorphus habitus*. 10. *L. crassipilus*, holotype male. 11. *L. crosskeyi*, female. 12. *L. eberhardi*, holotype male. 13. *L. eberhardi*, paratype female. 14. *L. fasciculatus*, holotype male. 15. *L. femoratus*, holotype male.





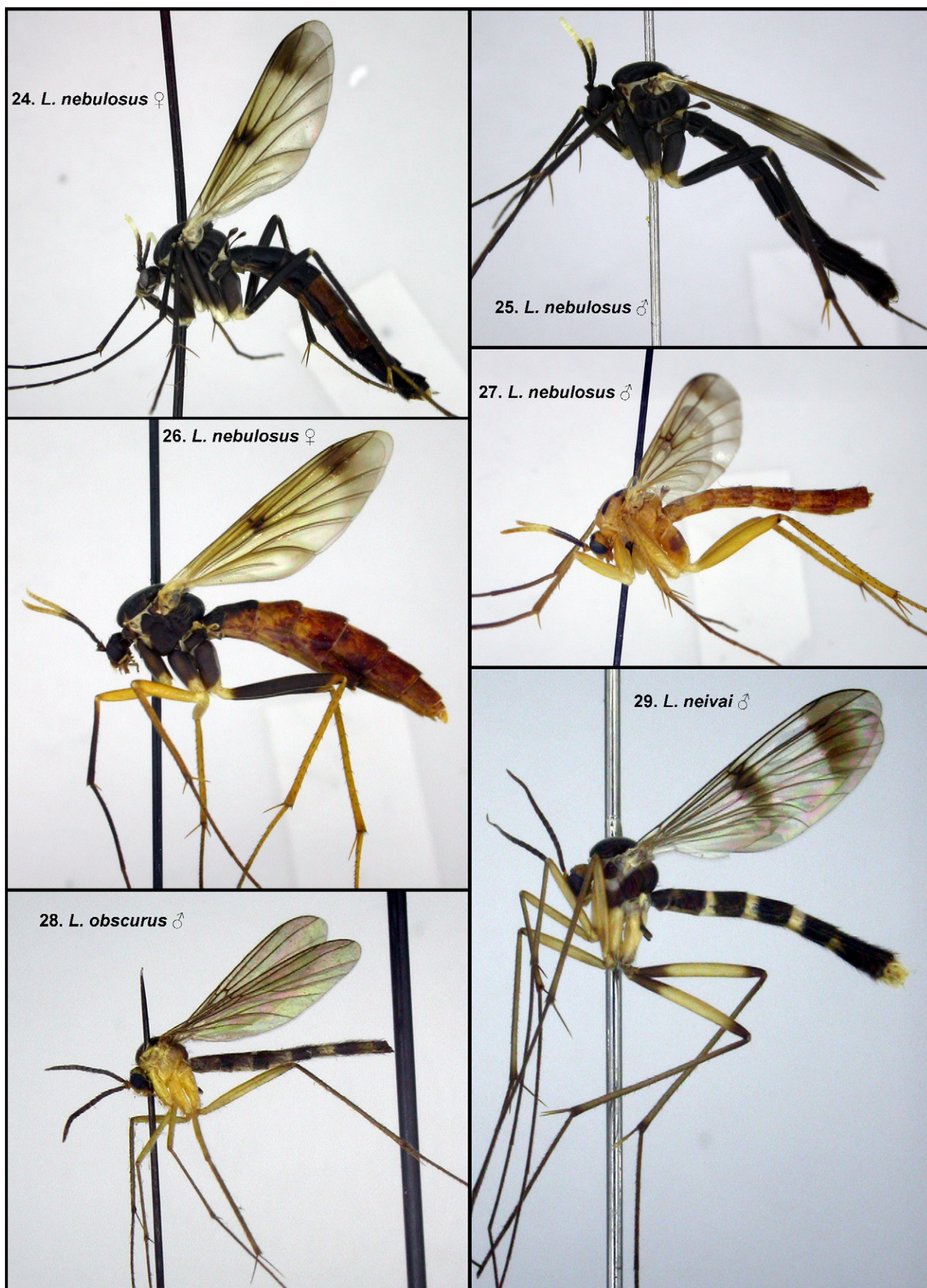
FIGURES 16–19. *Leptomorphus* habitus. 16. *L. forcipatus*, male. 17. *L. furcatus*, paratype male. 18. *L. gracilis*, holotype male. 19. *L. grjebinei*, holotype male.





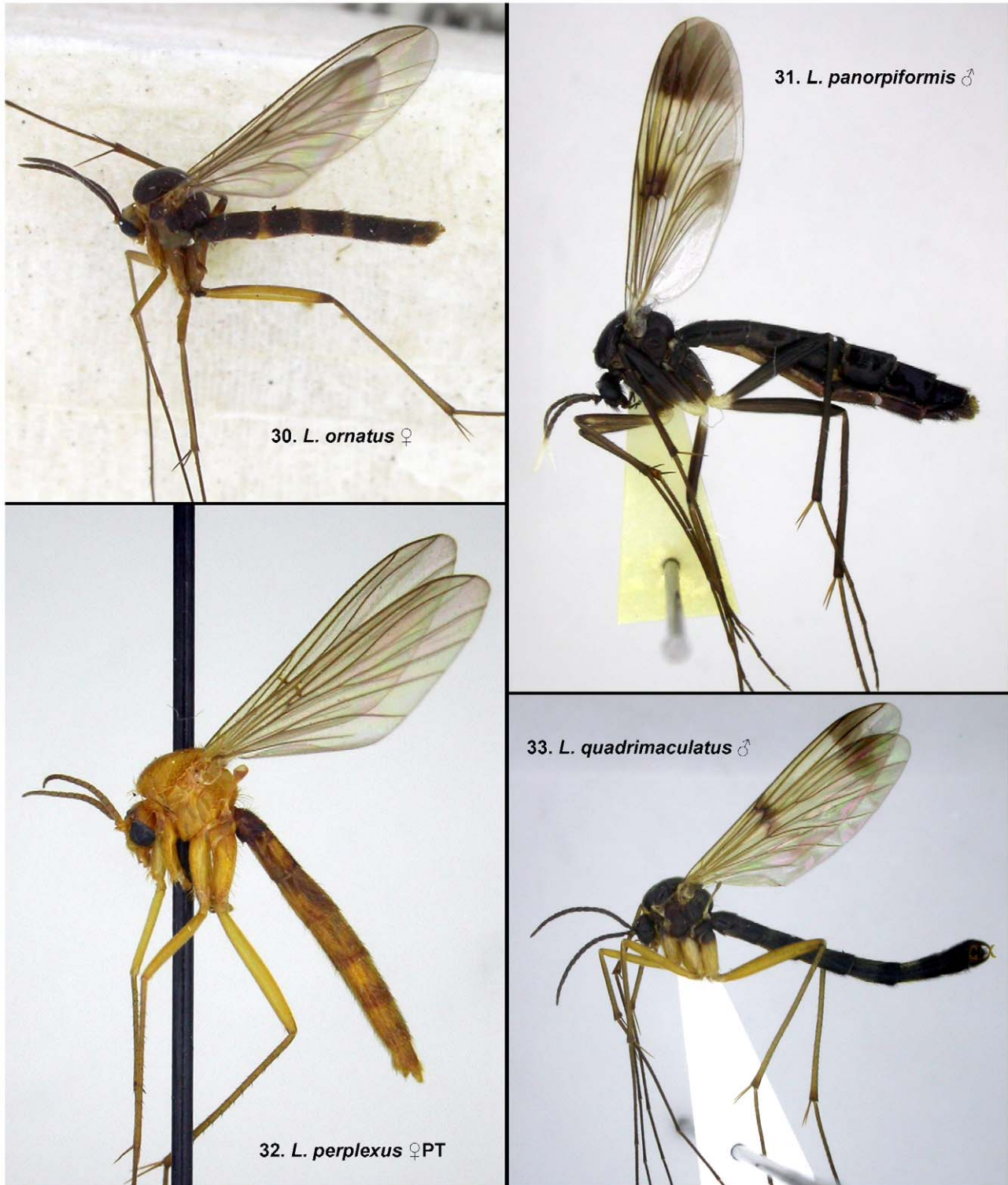
FIGURES 20–23. *Leptomorphus* habitus. 20. *L. hyalinus*, male. 21. *L. magnificus*, male. 22. *L. medleri*, male. 23. *L. mandelai*, holotype male.





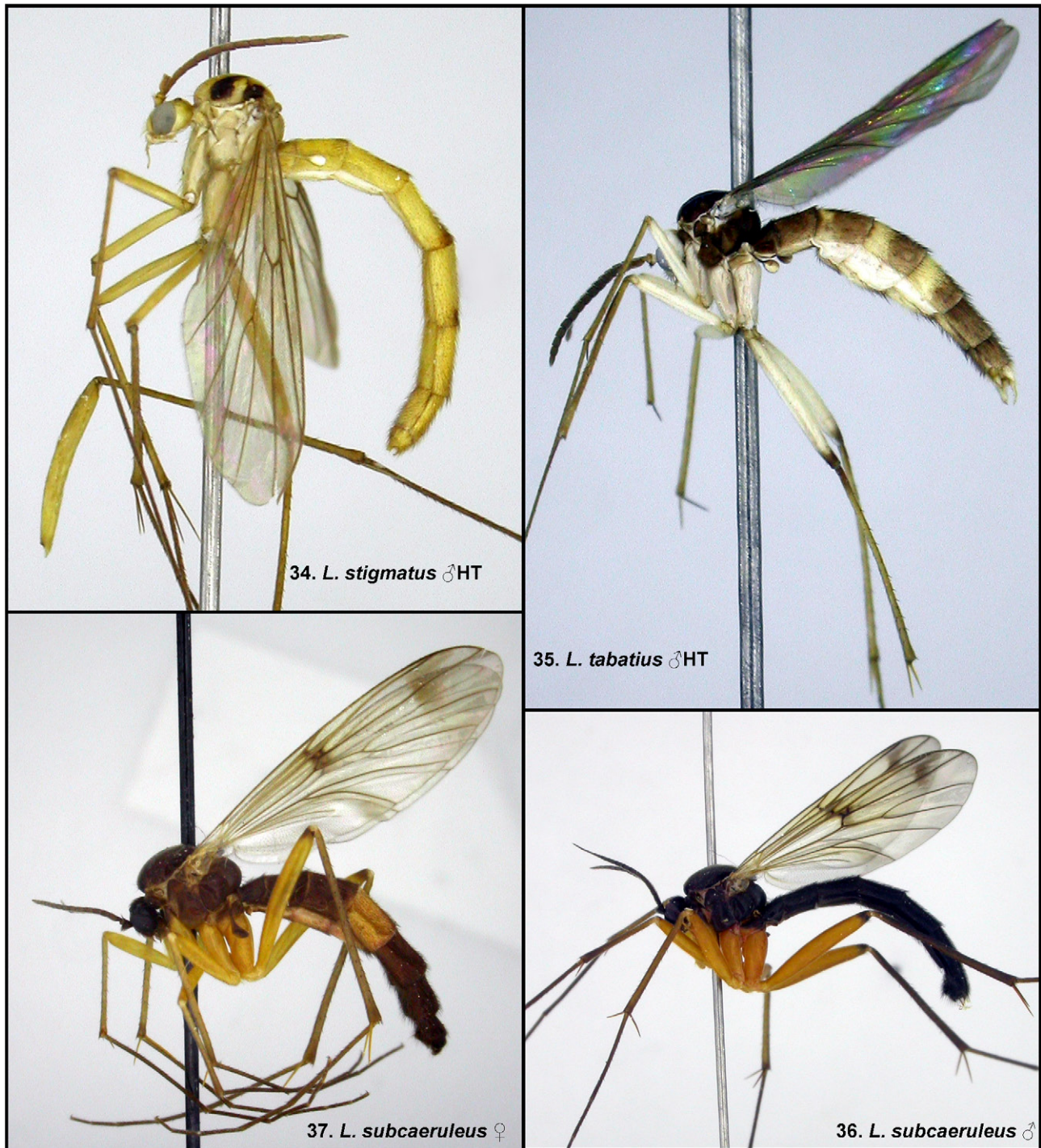
FIGURES 24–29. *Leptomorphus habitus*. 24. *L. nebulosus*, female, dark form. 25. *L. nebulosus*, male, dark form. 26. *L. nebulosus*, female, common colour. 27. *L. nebulosus*, male, light form. 28. *L. obscurus*, male. 29. *L. neivai*, male.





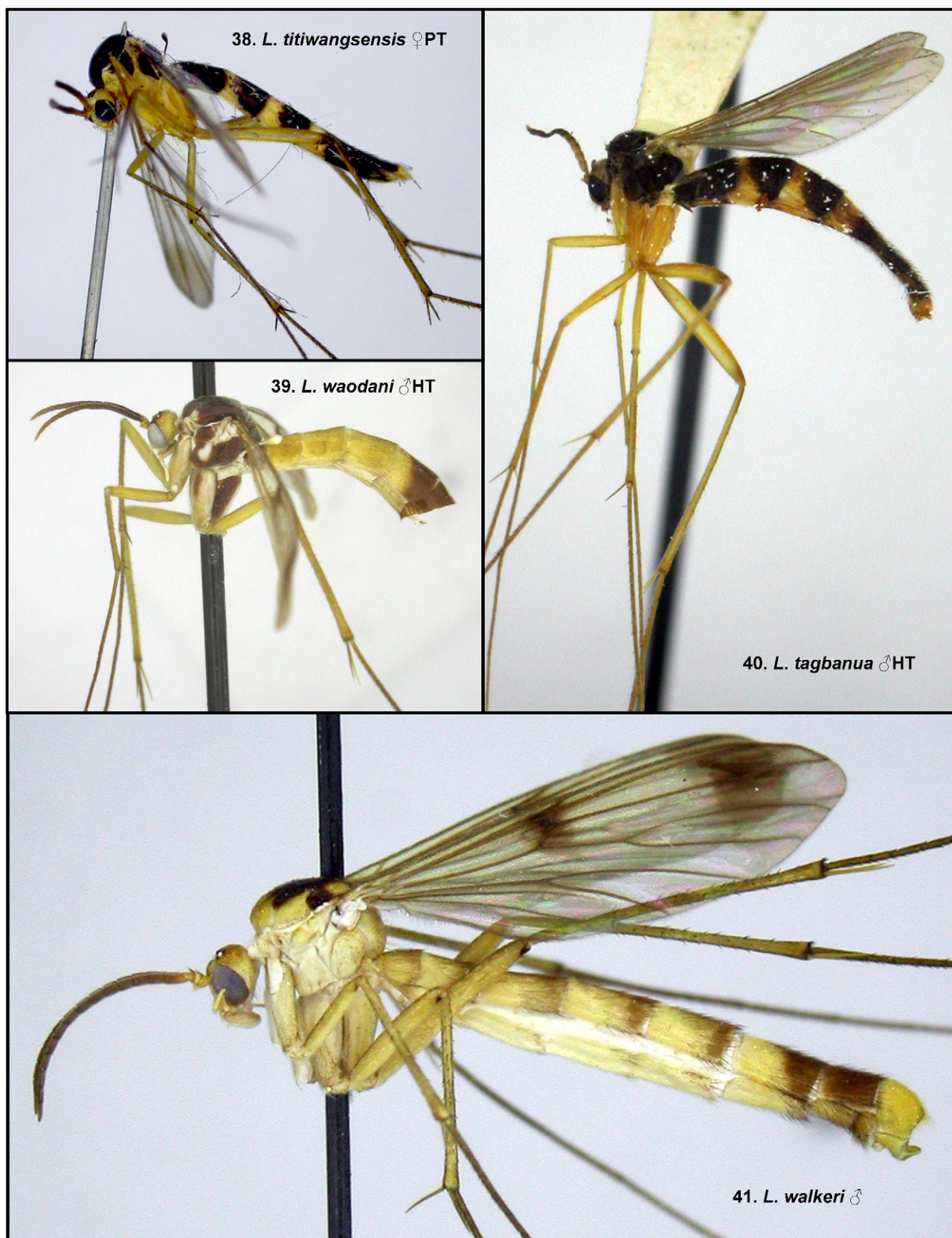
**FIGURES 30–33. *Leptomorphus habitus*. 30. *L. ornatus*, female. 31. *L. panorpiformis*, male. 32. *L. perplexus*, paratype female. 33. *L. quadrimaculatus*, male.**





**FIGURES 34–37.** *Leptomorphus habitus*. 34. *L. stigmatus*, holotype male. 35. *L. tabatius*, holotype male. 36. *L. subcaeruleus*, male. 37. *L. subcaeruleus*, female.



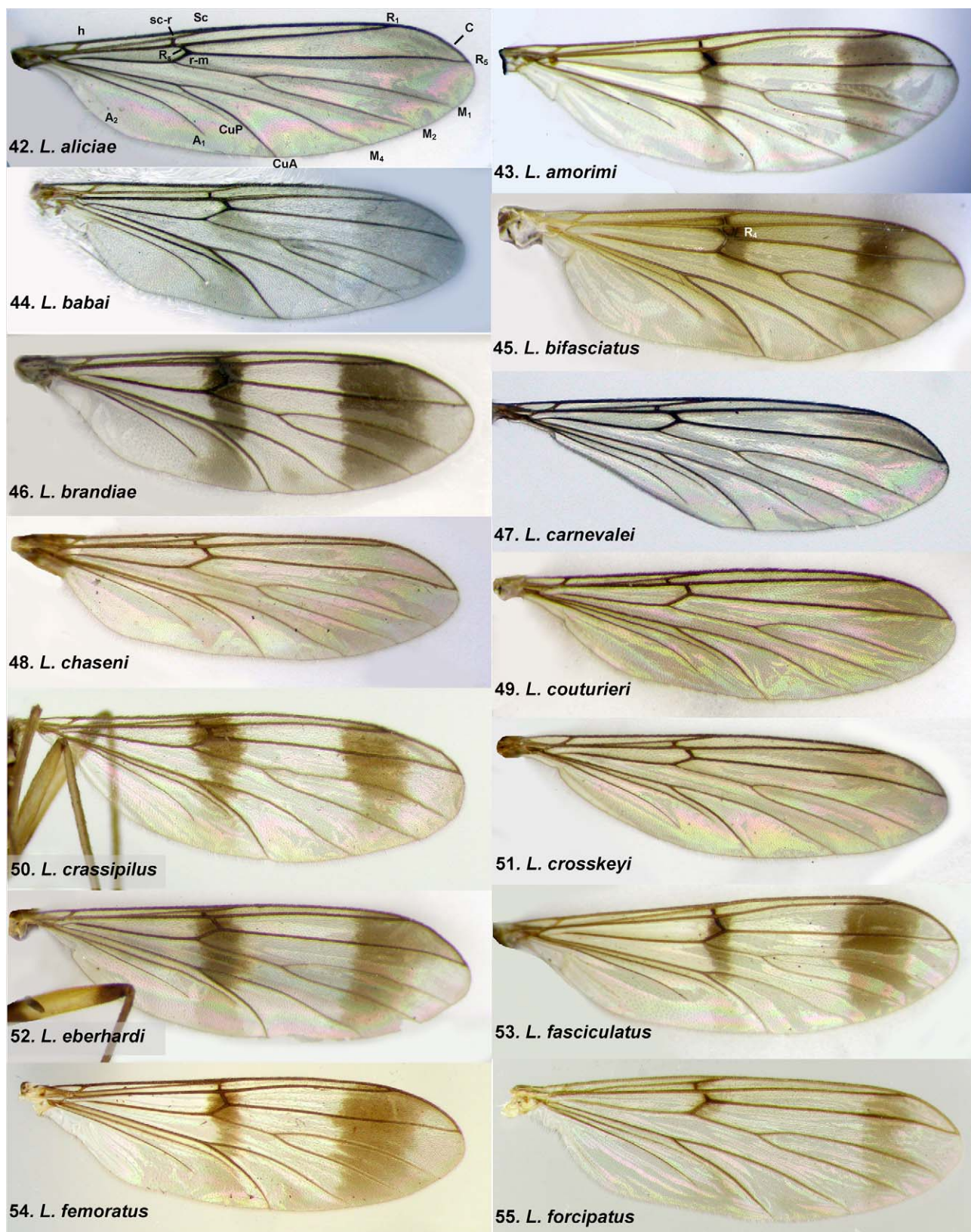


FIGURES 38–41. *Leptomorphus habitus*. 38. *L. titiwangensis*, paratype female. 39. *L. woadani*, holotype male. 40. *L. tagbanua*, holotype male. 41. *L. walkeri*, male.



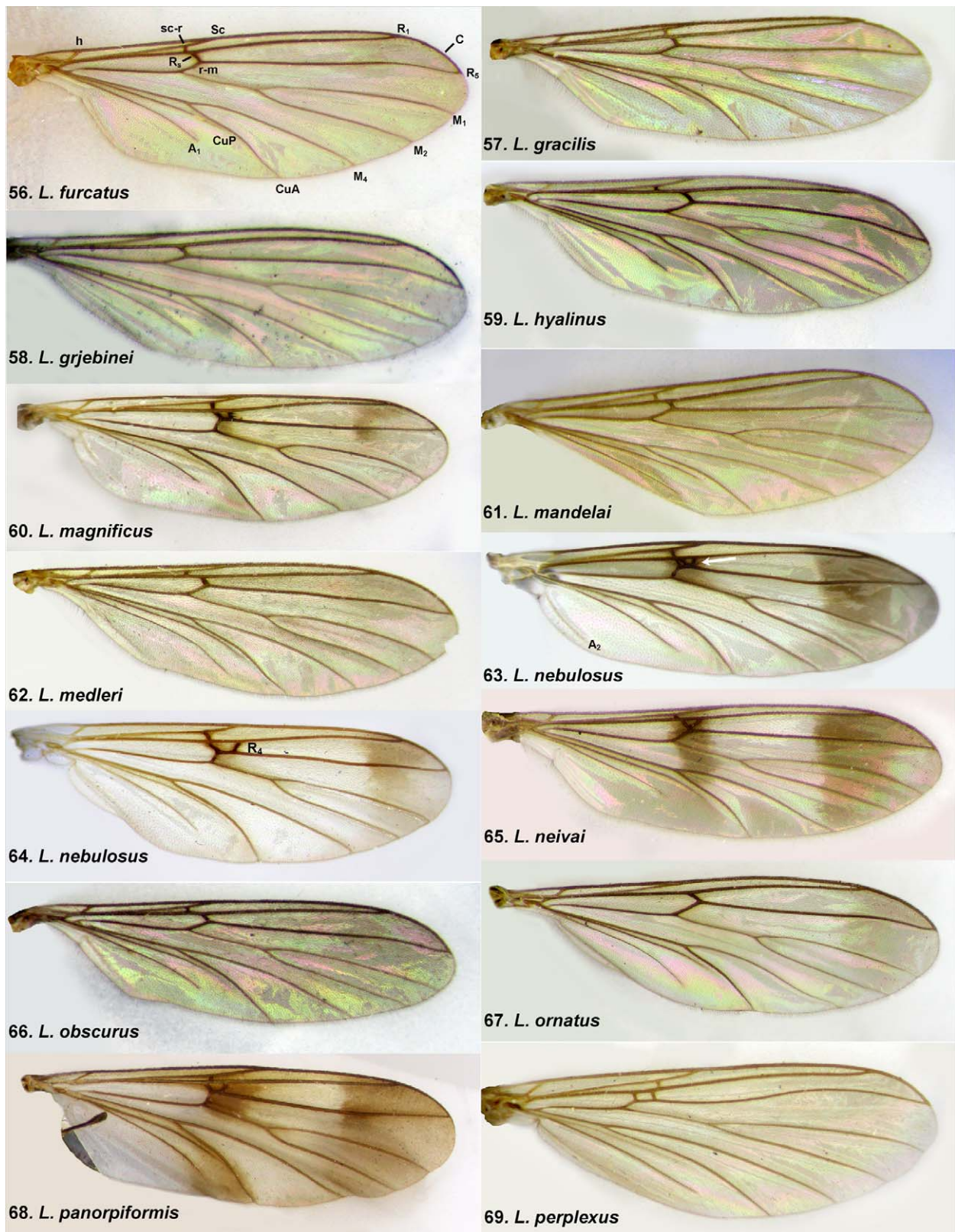
**TERMS OF USE**

This pdf is provided by Magnolia Press for private/research use.  
Commercial sale or deposition in a public library or website is prohibited.

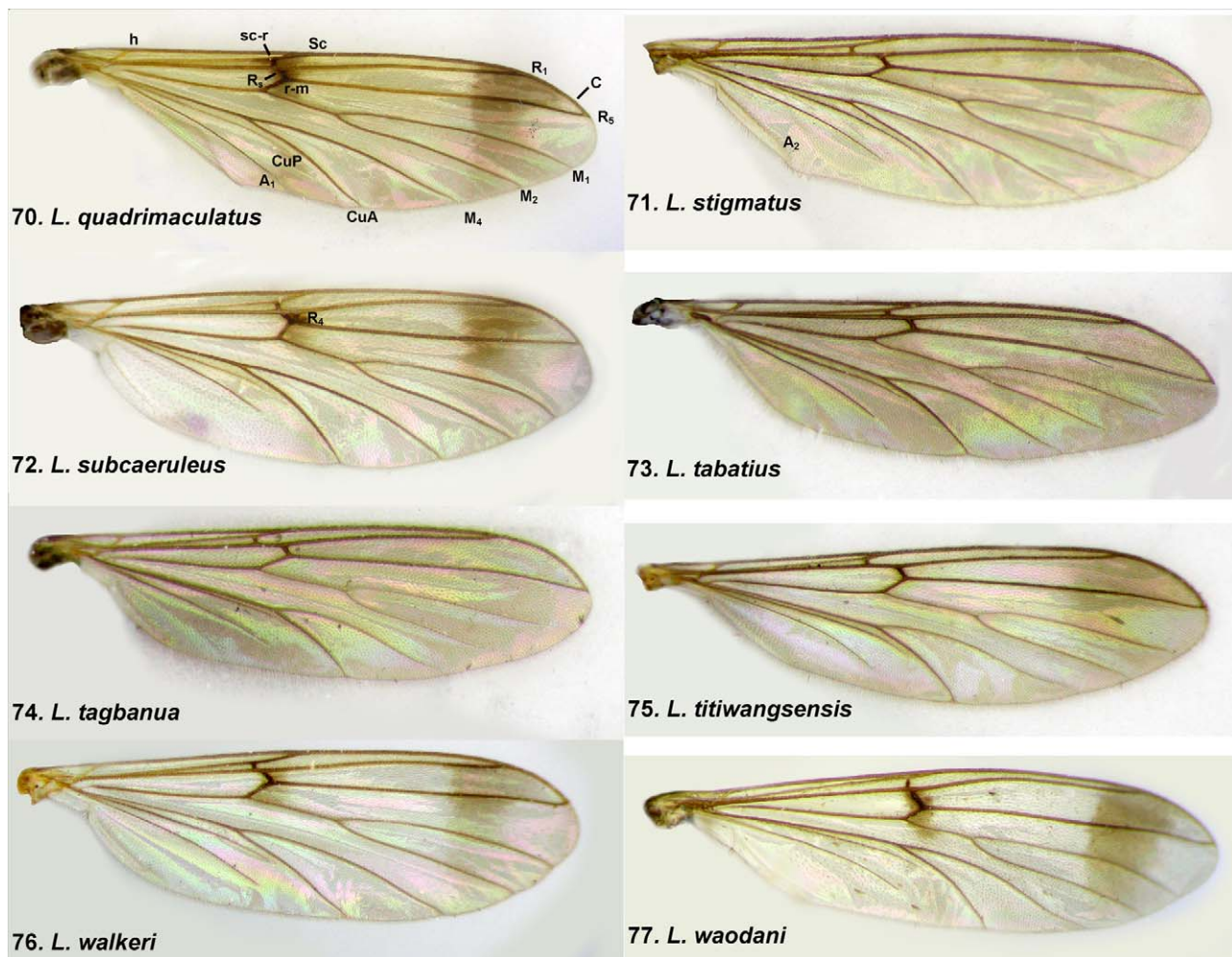


**FIGURES 42–55. *Leptomorphus* wings.** 42. *L. aliciae*, dorsal. 43. *L. amorimi* paratype female, dorsal. 44. *L. babai* holotype male, ventral. 45. *L. bifasciatus* lectotype, ventral. 46. *L. brandiae* paratype female, dorsal. 47. *L. carnevalei* allotype, dorsal. 48. *L. chaseni* holotype female, dorsal. 49. *L. couturieri*, ventral. 50. *L. crassipilus* holotype male, ventral. 51. *L. crosskeyi*, ventral. 52. *L. eberhardi* paratype female, ventral. 53. *L. fasciculatus* paratype male, dorsal. 54. *L. femoratus* holotype male, ventral. 55. *L. forcipatus* dorsal. **Abbreviations:** A<sub>1</sub>, A<sub>2</sub> = Anal veins; C = costa; CuA = anterior branch of cubitus; CuP = posterior branch of cubitus; h = humeral crossvein; M<sub>1</sub>, M<sub>2</sub>, M<sub>4</sub> = branches of the media; r-m = radial-medial crossvein; R<sub>s</sub> = radial sector vein; R<sub>1</sub>, R<sub>4</sub>, R<sub>5</sub> = branches of the radius; Sc = subcosta; sc-r = subcostal-radial crossvein.



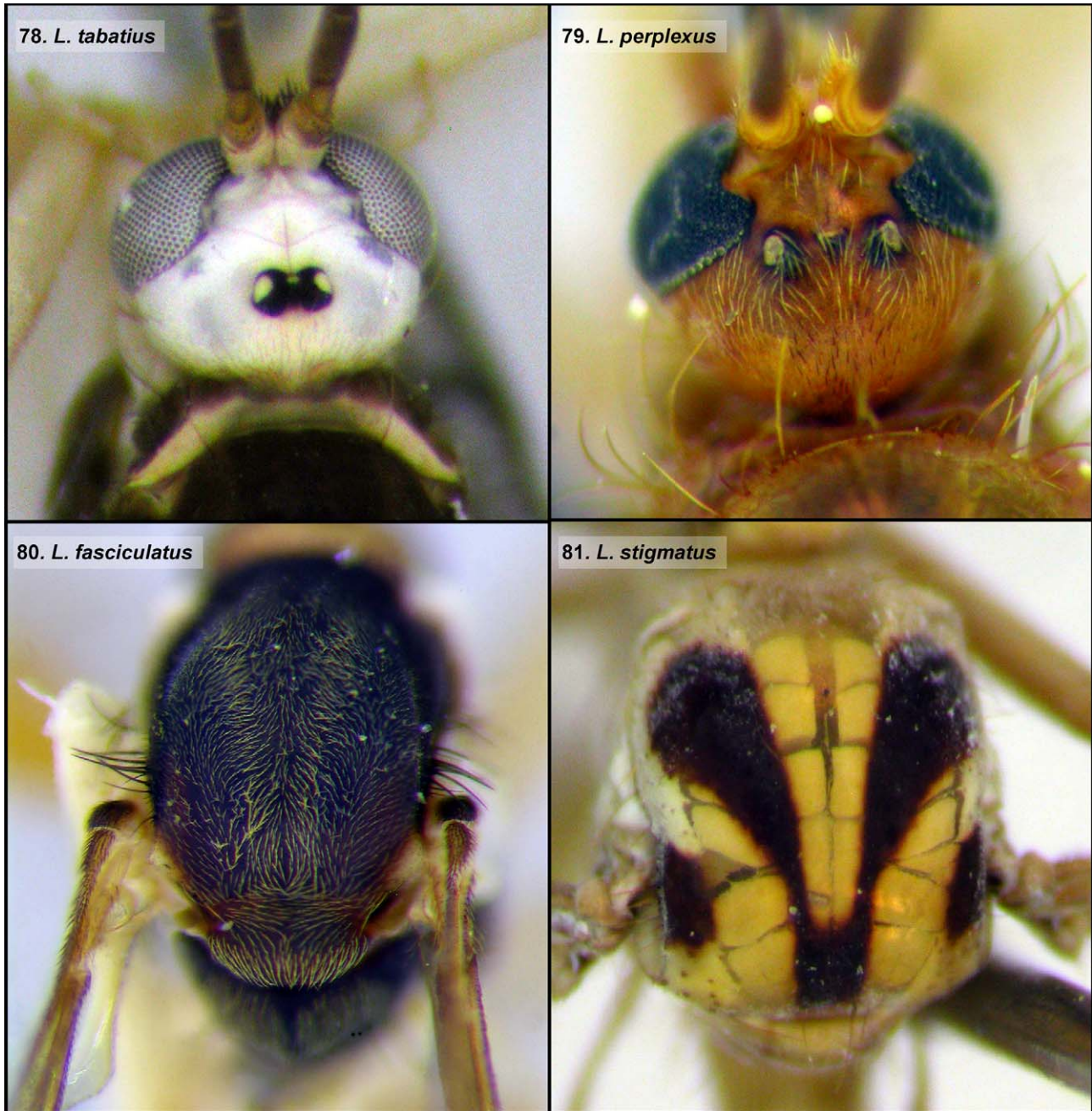


**FIGURES 56–69. *Leptomorphus* wings.** 56. *L. furcatus* paratype male, dorsal. 57. *L. gracilis*, ventral. 58. *L. grjebinei*, ventral. 59. *L. hyalinus*, ventral. 60. *L. magnificus*, ventral. 61. *L. mandelai* holotype male, ventral. 62. *L. medleri*, ventral. 63. *L. nebulosus* dark form, dorsal. Arrow indicates cell  $r_4$  (contains an extra vein in this specimen). 64. *L. nebulosus* light form, dorsal. 65. *L. neivai* ventral. 66. *L. obscurus* ventral. 67. *L. ornatus* ventral. 68. *L. panorpiformis* ventral. 69. *L. perplexus* paratype female, dorsal. **Abbreviations:**  $A_1$ ,  $A_2$  = Anal veins; C = costa; CuA = anterior branch of cubitus; CuP = posterior branch of cubitus; h = humeral crossvein;  $M_1$ ,  $M_2$ ,  $M_3$ ,  $M_4$  = branches of the media; r-m = radial-medial crossvein;  $R_s$  = radial sector vein;  $R_1$ ,  $R_2$ ,  $R_3$  = branches of the radius; Sc = subcosta; sc-r = subcostal-radial crossvein.

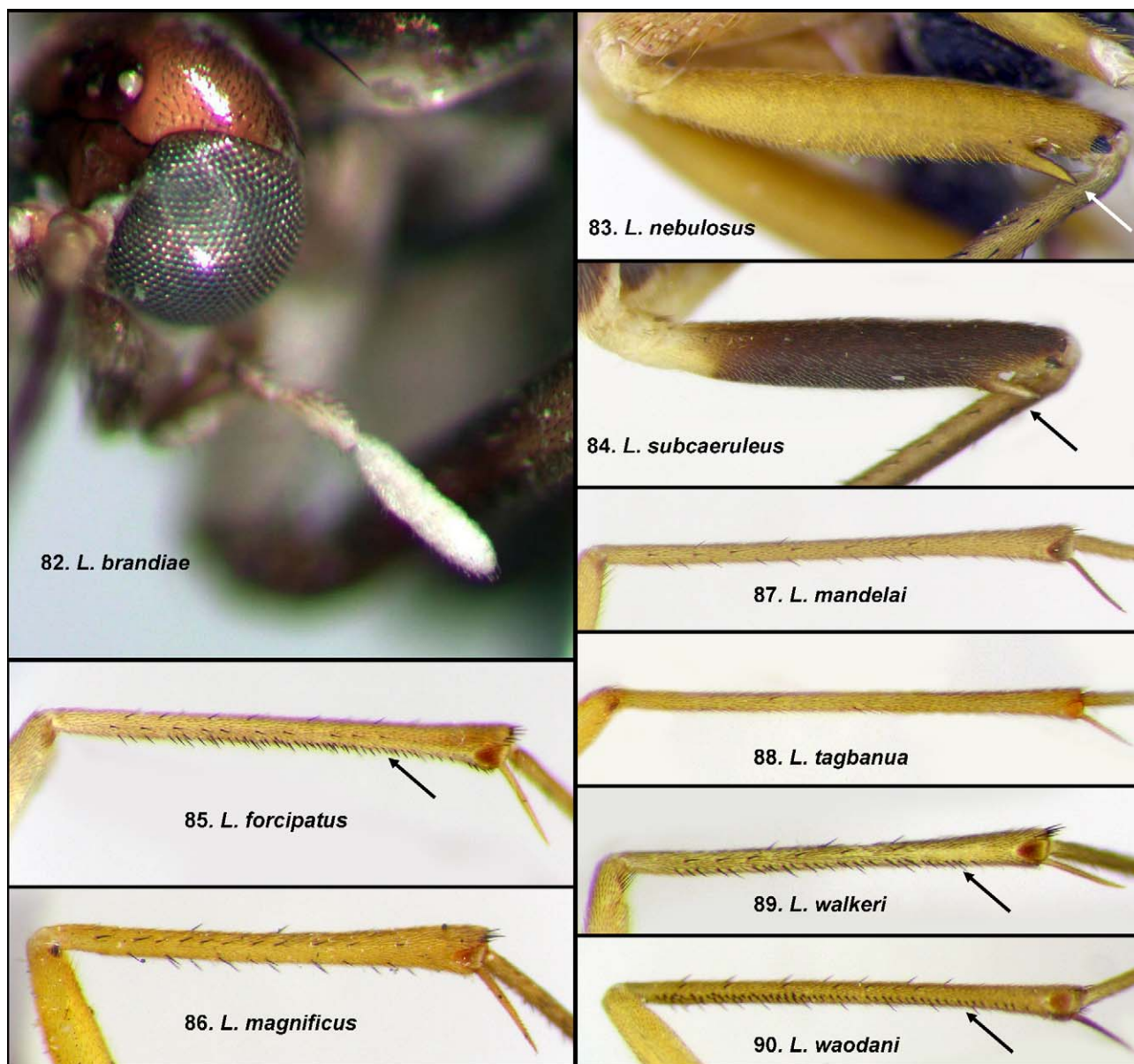


**FIGURES 70–77. *Leptomorphus* wings.** 70. *L. quadrimaculatus*, ventral. 71. *L. stigmatus* holotype male, dorsal. 72. *L. subcaeruleus*, ventral. 73. *L. tabatius* holotype male, dorsal. 74. *L. tagbanua* holotype male, ventral. 75. *L. titiwangsensis* paratype female, dorsal. 76. *L. walkeri*, ventral. 77. *L. waodani* holotype male, dorsal. **Abbreviations:** A<sub>1</sub>, A<sub>2</sub> = Anal veins; C = costa; CuA = anterior branch of cubitus; CuP = posterior branch of cubitus; h = humeral crossvein; M<sub>1</sub>, M<sub>2</sub>, M<sub>4</sub> = branches of the media; r-m = radial-medial crossvein; Rs = radial sector vein; R<sub>1</sub>, R<sub>4</sub>, R<sub>5</sub> = branches of the radius; Sc = subcosta; sc-r = subcostal-radial crossvein.



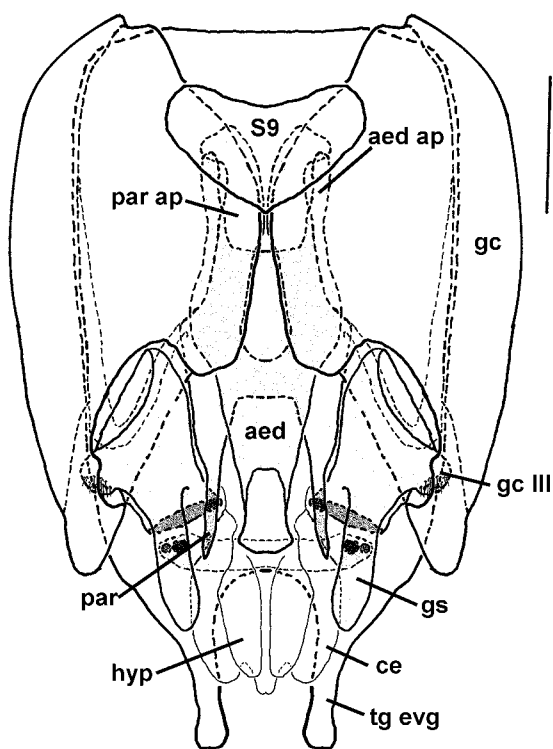
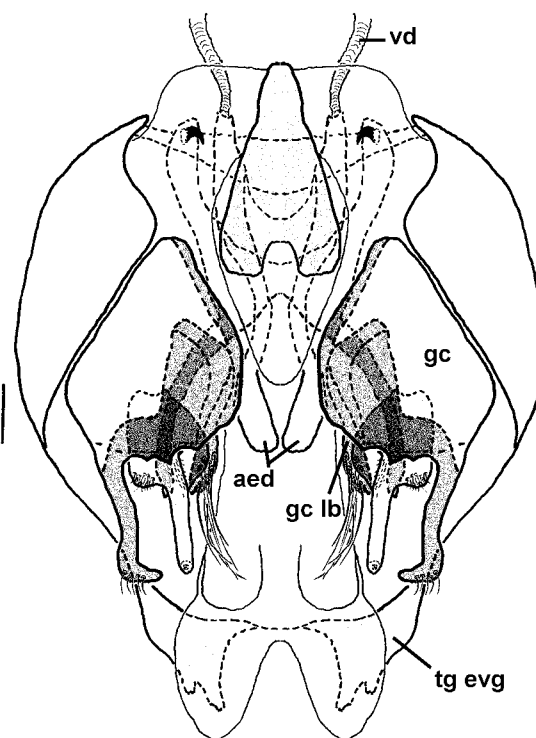
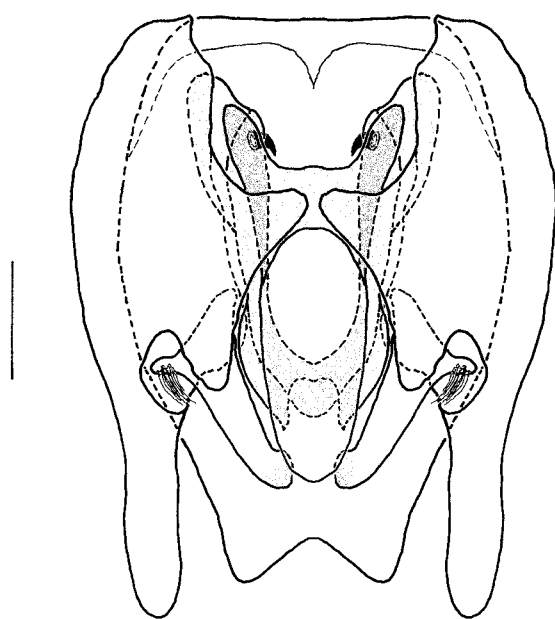
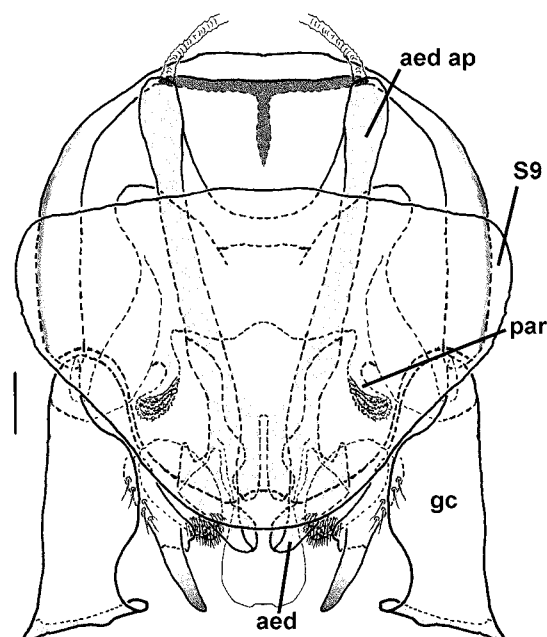


**FIGURES 78–81. *Leptomorphus* morphology.** 78–79. Dorsal view of head showing ocelli placement and arrangement. 78. *L. tabatius*. 79. *L. perplexus*. 80–81. Dorsal view of scutum. 80. *L. fasciculatus* showing covering of fine trichia. 81. *L. stigmatus* showing pattern and lack of setae or trichia.



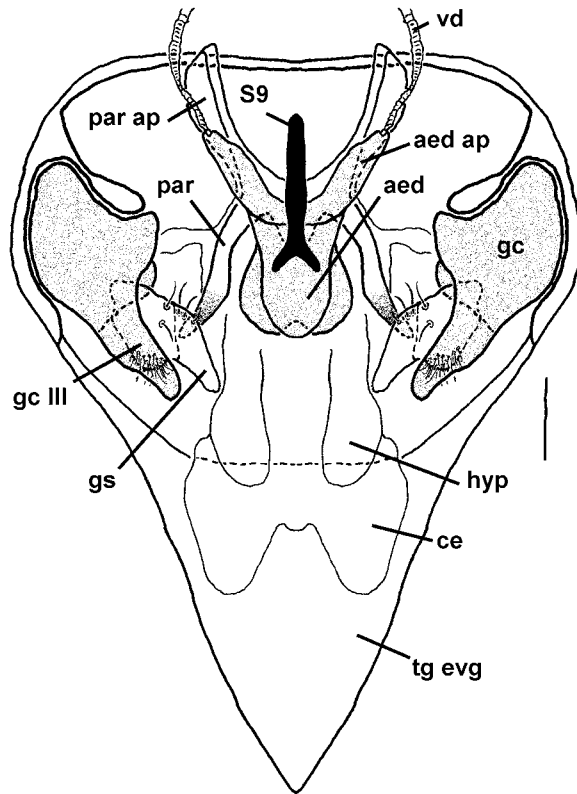
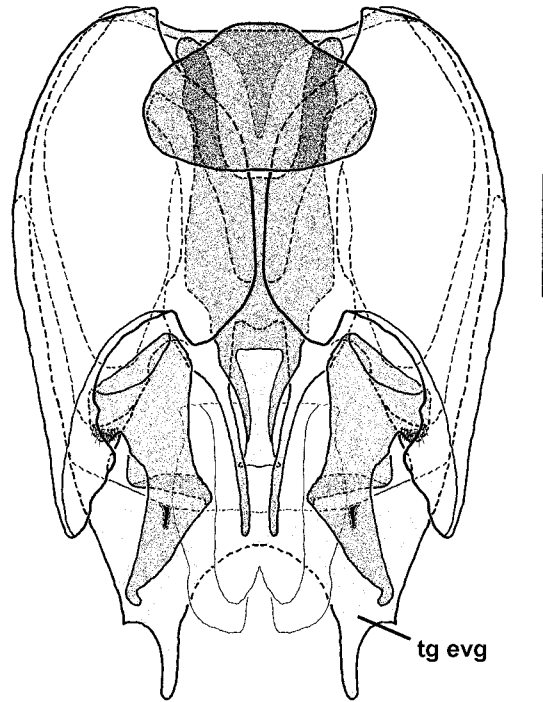
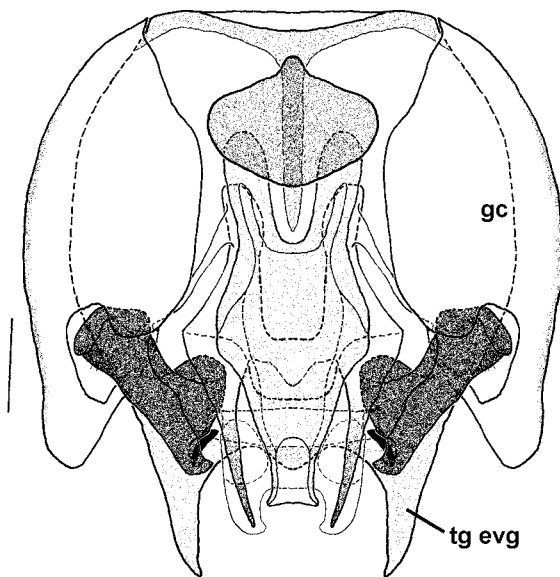
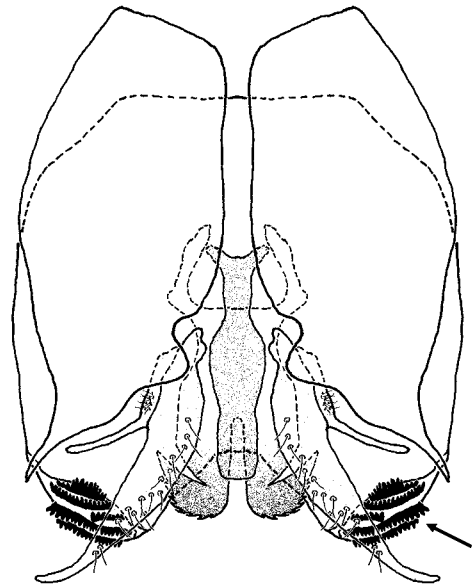
**FIGURES 82–90. *Leptomorphus* morphology.** 82. Head of *L. brandiae*, anterolateral, showing swollen palpus segment 5 covered in fine white trichia. 83–84. Male midfemur, anterior, showing apicoventral process (arrow). 83. *L. nebulosus*. 84. *L. subcaeruleus*. 85–90. Male foretibia, posterior, showing presence (arrow) or absence of dense comb of ventral bristles. 85. *L. forcipatus*. 86. *L. magnificus*. 87. *L. mandelai*. 88. *L. tagbanua*. 89. *L. walkeri*. 90. *L. waodani*.



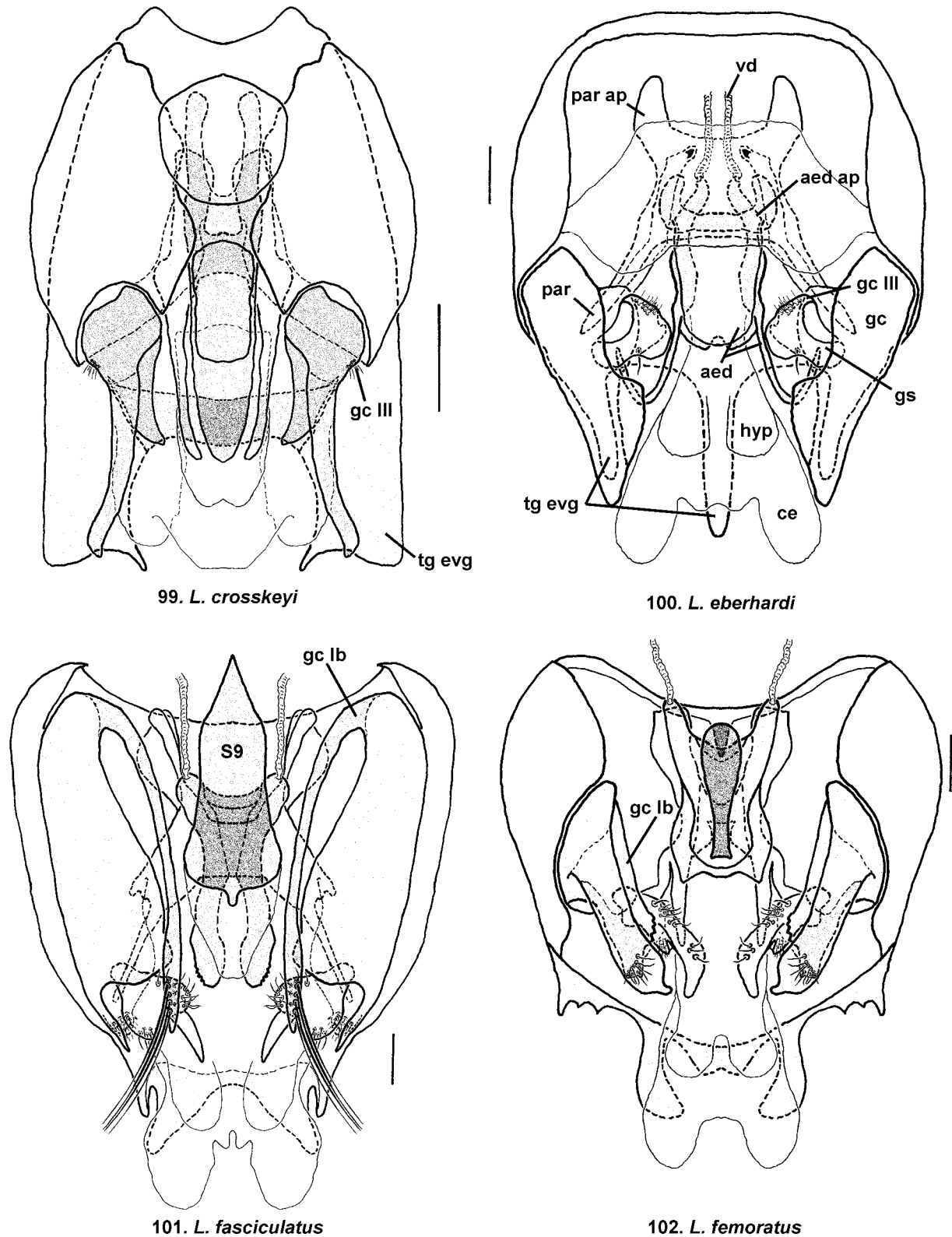
91. *L. aliciae*92. *L. amorimi*93. *L. babai*94. *L. bifasciatus*

**FIGURES 91–94. *Leptomorphus* male genitalia, ventral. 91. *L. aliciae*. 92. *L. amorimi*. 93. *L. babai*. 94. *L. bifasciatus*. Abbreviations:** aed = aedeagus; aed ap = aedeagal apodeme; ce = cercus; gc = gonocoxite, III = section 3; gc lb = gonocoxal lobe; gs = gonostylus; hyp = hypoproct; par = paramere; par ap = parameral apodeme; S9 = sternite 9; tg evg = apical evagination of tergite 9; vd = *vas deferens*. Scale bar = 0.1mm.

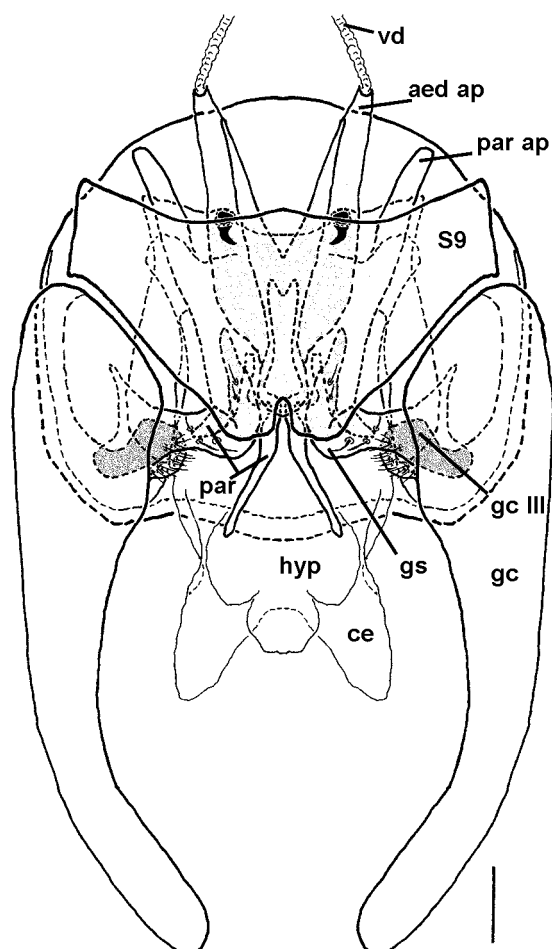


95. *L. brandiae*96. *L. carnevalei*97. *L. couturieri*98. *L. crassipilus*

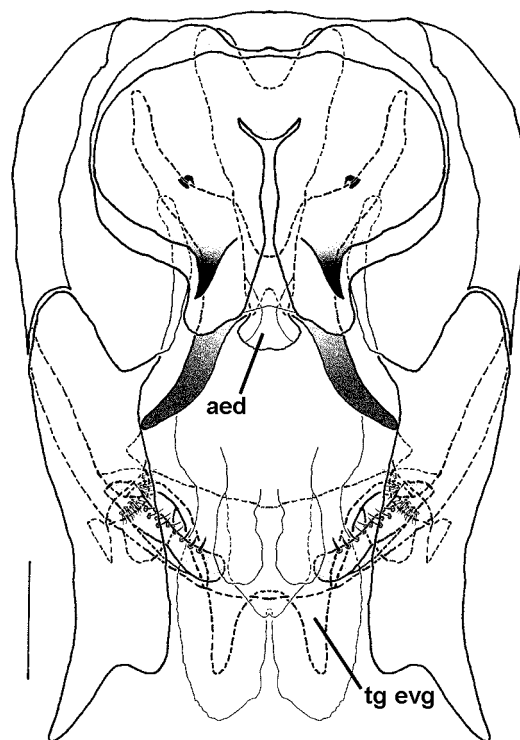
**FIGURES 95–98. *Leptomorphus* male genitalia, ventral.** 95. *L. brandiae*. 96. *L. carnevalei*. 97. *L. couturieri*. 98. *L. crassipilus*, arrow indicates dense rows of thick blunt bristles, arrangement of components reconstituted from crushed genitalia of holotype. **Abbreviations:** aed = aedeagus; aed ap = aedeagal apodeme; ce = cercus; gc = gonocoxite, III = section 3; gs = gonostylus; hyp = hypoproct; par = paramere; par ap = parameral apodeme; S9 = sternite 9; tg evg = apical evagination of tergite 9; vd = *vas deferens*. Scale bar = 0.1mm.

99. *L. crosskeyi*100. *L. eberhardi*101. *L. fasciculatus*102. *L. femoratus*

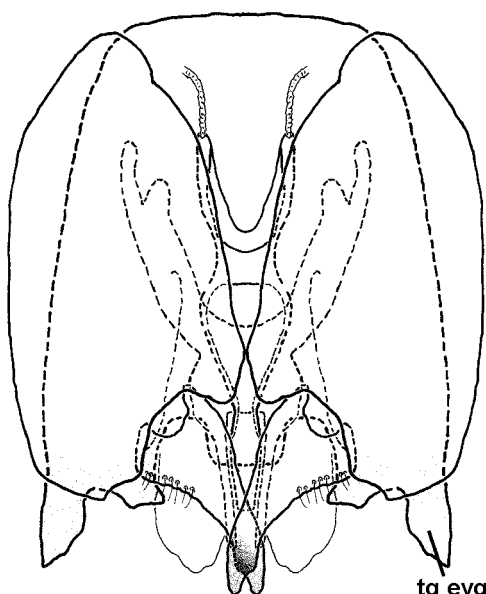
**FIGURES 99–102. *Leptomorphus* male genitalia, ventral. 99. *L. crosskeyi*. 100. *L. eberhardi*. 101. *L. fasciculatus*. 102. *L. femoratus*. Abbreviations:** aed = aedeagus; aed ap = aedeagal apodeme; ce = cercus; gc = gonocoxite, III = section 3; gc lb = gonocoxal lobe; gs = gonostylus; hyp = hypoproct; par = paramere; par ap = parameral apodeme; S9 = sternite 9; tg evg = apical evagination of tergite 9; vd = *vas deferens*. Scale bar = 0.1mm.



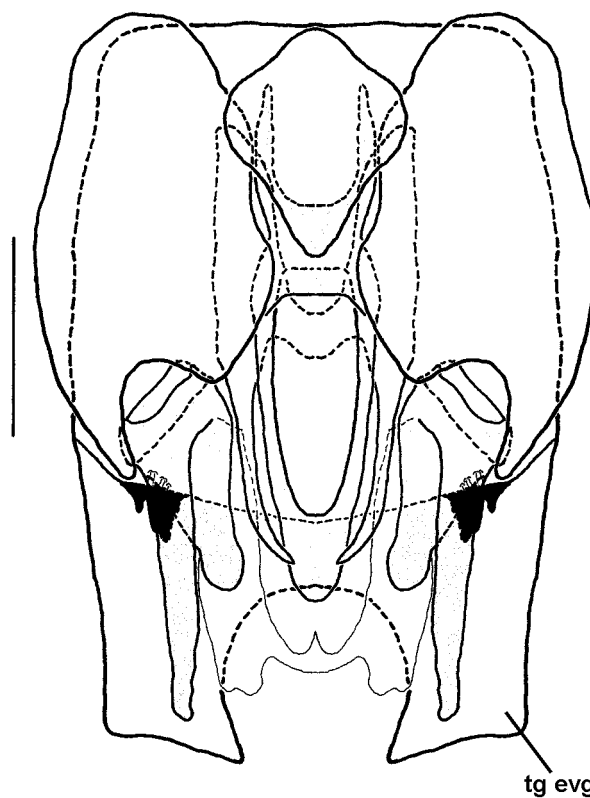
103. *L. forcipatus*



104. *L. furcatus*



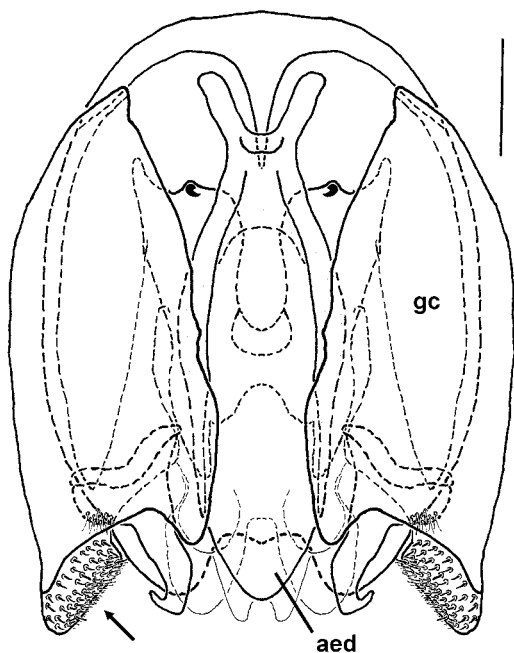
105. *L. grjebinei*



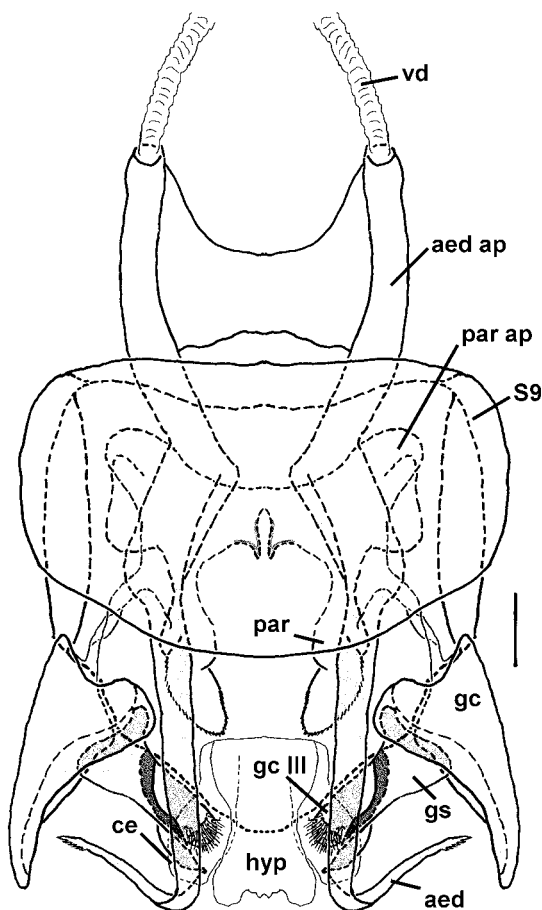
106. *L. gracilis*

**FIGURES 103–106. *Leptomorphus* male genitalia, ventral. 103. *L. forcipatus*. 104. *L. furcatus*. 105. *L. grjebinei*. 106. *L. gracilis*. Abbreviations: aed = aedeagus; aed ap = aedeagal apodeme; ce = cercus; gc = gonocoxite, III = section 3; gs = gonostylus; hyp = hypoproct; par = paramere; par ap = parameral apodeme; S9 = sternite 9; tg evg = apical evagination of tergite 9; vd = vas deferens. Scale bar = 0.1mm.**

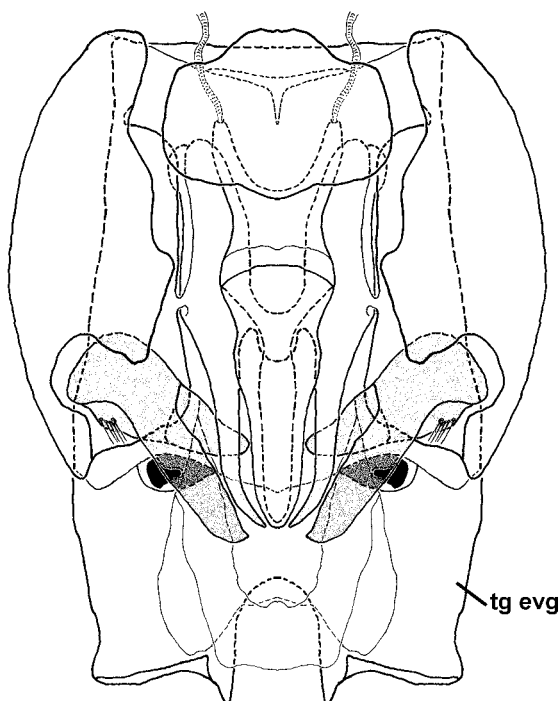




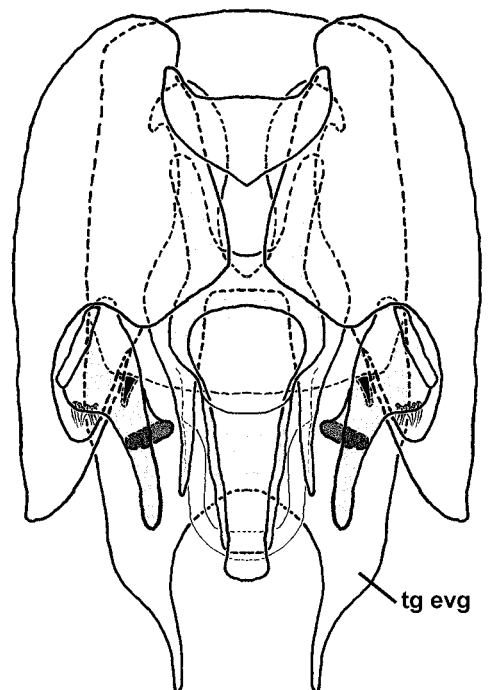
107. *L. hyalinus*



108. *L. magnificus*

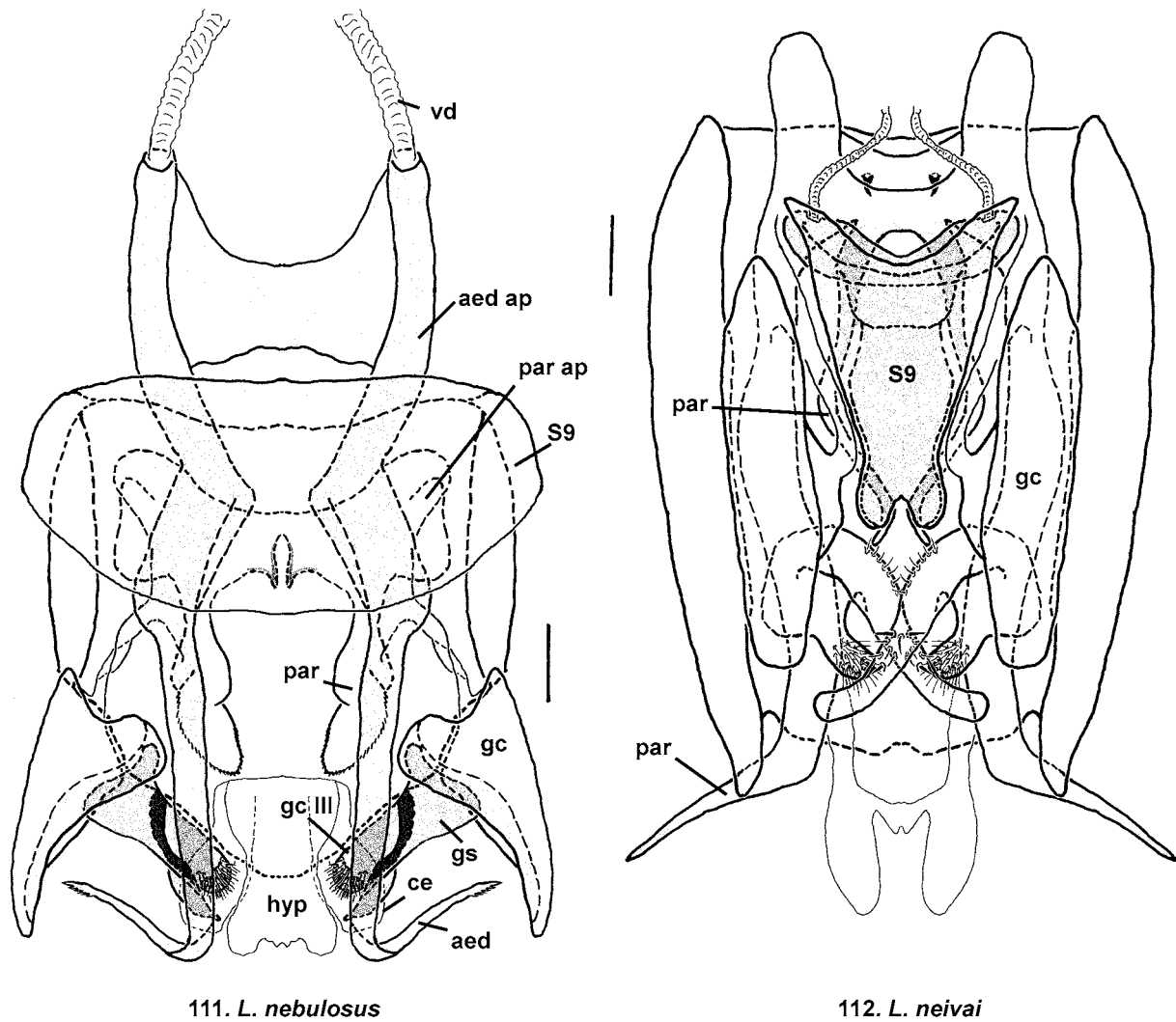


109. *L. mandelai*

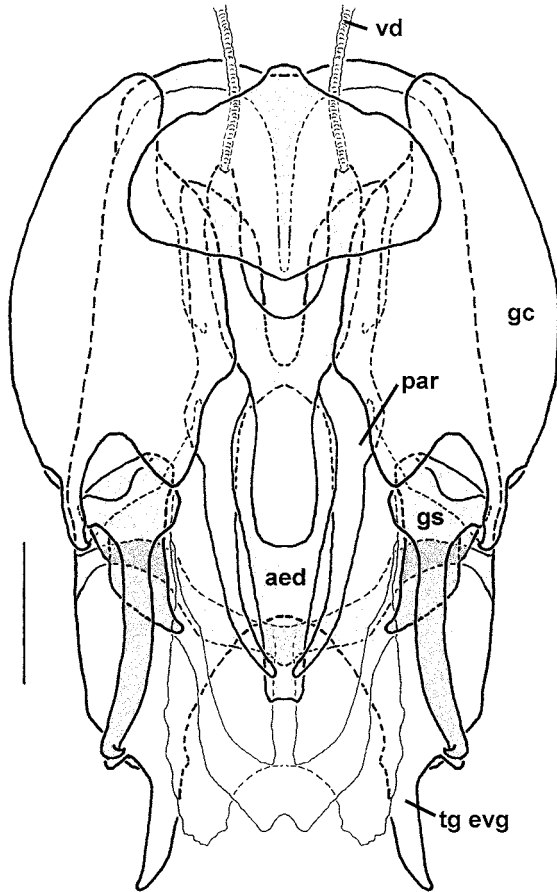


110. *L. medleri*

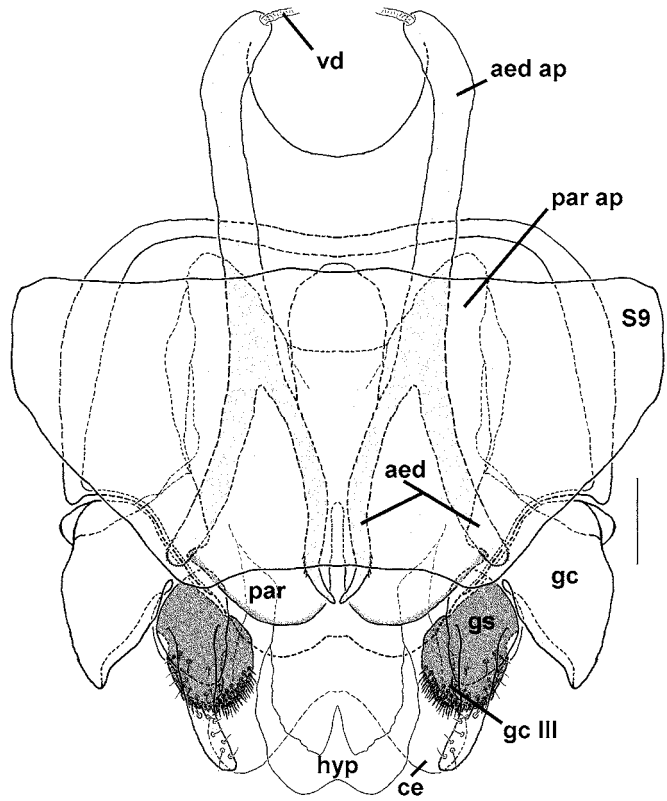
**FIGURES 107–110. *Leptomorphus* male genitalia, ventral.** 107. *L. hyalinus*. Arrow indicates patch of short, thick bristles on apex of gonocoxite. 108. *L. magnificus*. 109. *L. mandelai*. 110. *L. medleri*. **Abbreviations:** aed = aedeagus; aed ap = aedeagal apodeme; ce = cercus; gc = gonocoxite, III = section 3; gs = gonostylus; hyp = hypoproct; par = paramere; par ap = parameral apodeme; S9 = sternite 9; tg evg = apical evagination of tergite 9; vd = *vas deferens*. Scale bar = 0.1mm.



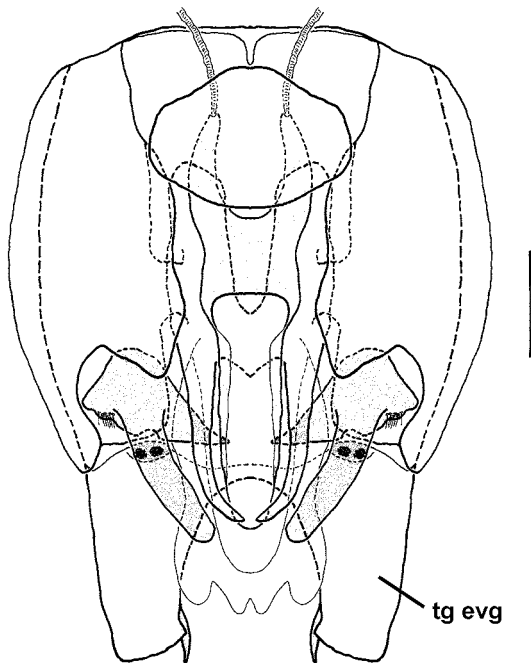
**FIGURES 111–112. *Leptomorphus* male genitalia, ventral. 111. *L. nebulosus*. 112. *L. neivai*. Abbreviations:** aed = aedeagus; aed ap = aedeagal apodeme; ce = cercus; gc = gonocoxite, III = section 3; gs = gonostylus; hyp = hypoproct; par = paramere; par ap = parameral apodeme; S9 = sternite 9; tg evg = apical evagination of tergite 9; vd = *vas deferens*. Scale bar = 0.1mm.



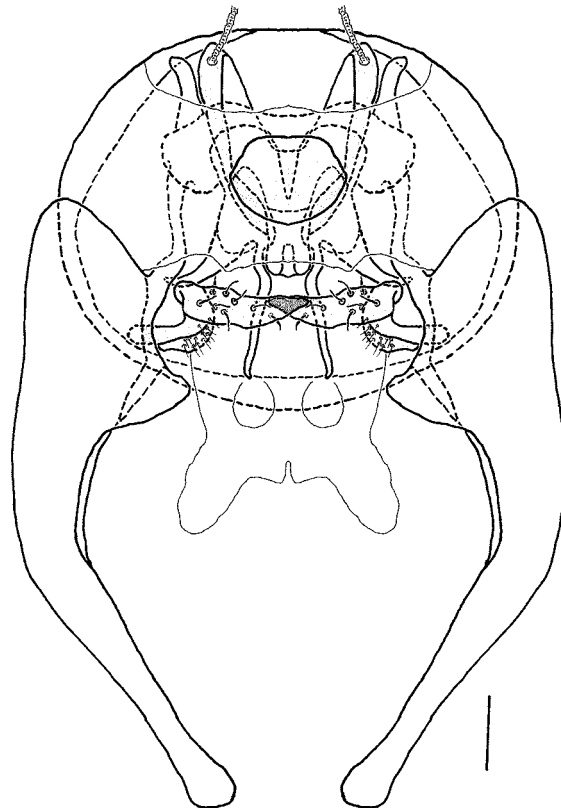
113. *L. obscurus*



114. *L. panorpiformis*



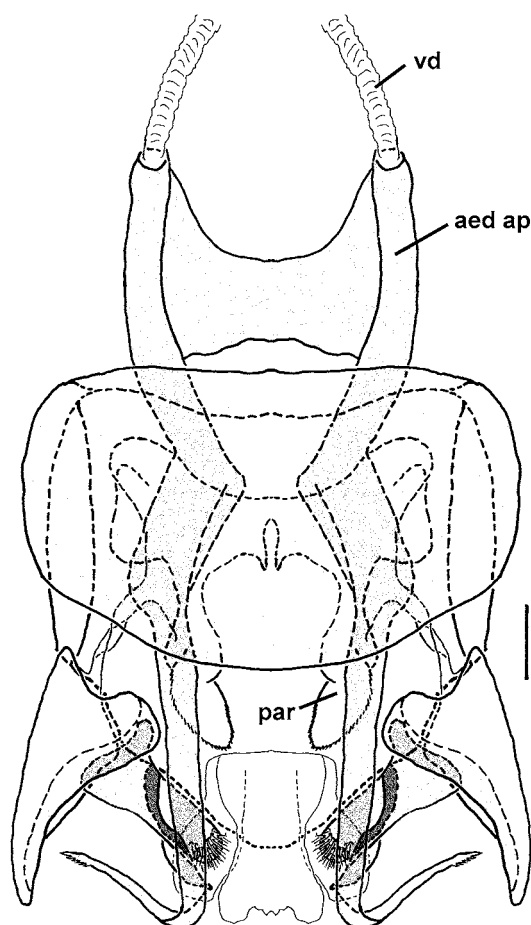
115. *L. stigmatus*



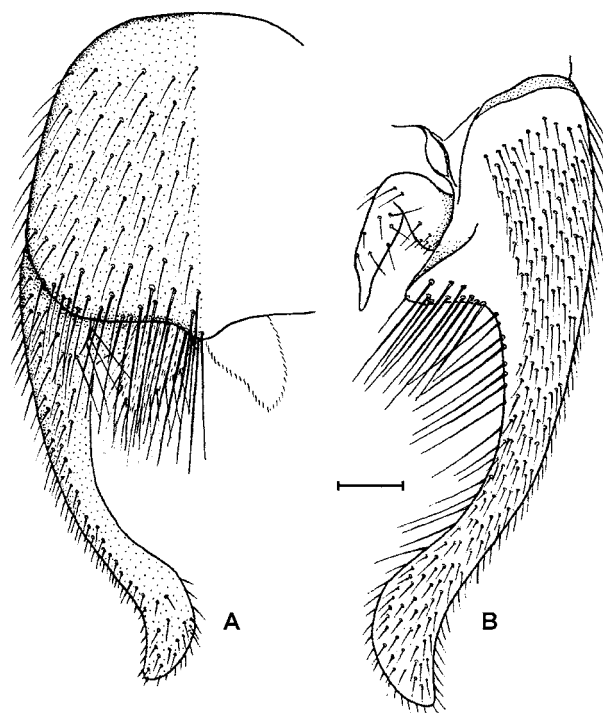
116. *L. quadrimaculatus*

**FIGURES 113–116. *Leptomorphus* male genitalia, ventral. 113. *L. obscurus*. 114. *L. panorpiformis*. 115. *L. stigmatus*. 116. *L. quadrimaculatus*. Abbreviations:** aed = aedeagus; aed ap = aedeagal apodeme; ce = cercus; gc = gonocoxite, III = section 3; gs = gonostylus; hyp = hypoproct; par = paramere; par ap = parameral apodeme; S9 = sternite 9; tg evg = apical evagination of tergite 9; vd = vas deferens. Scale bar = 0.1mm.

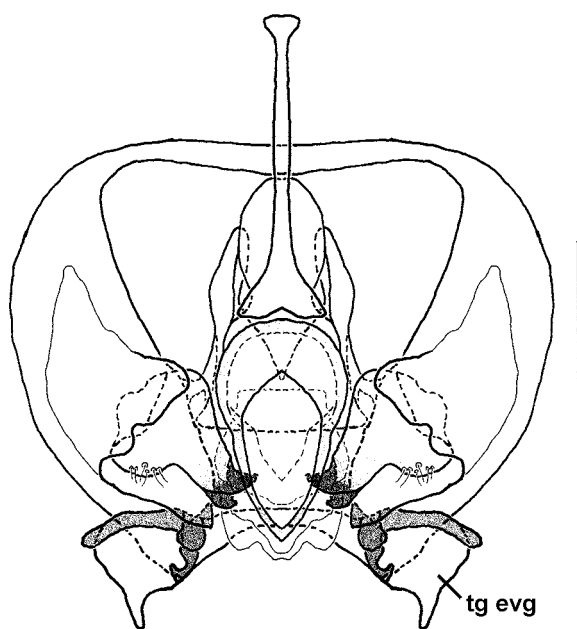




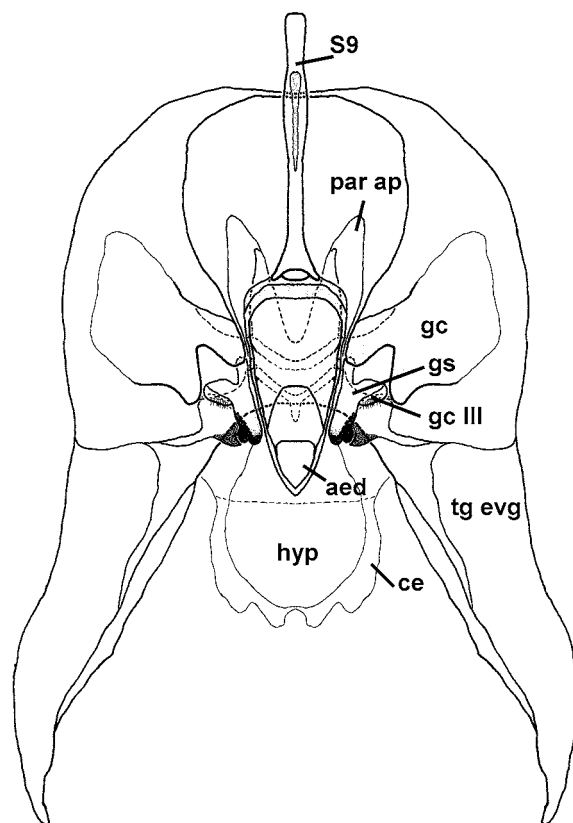
117. *L. subcaeruleus*



118. *L. subforcipatus*

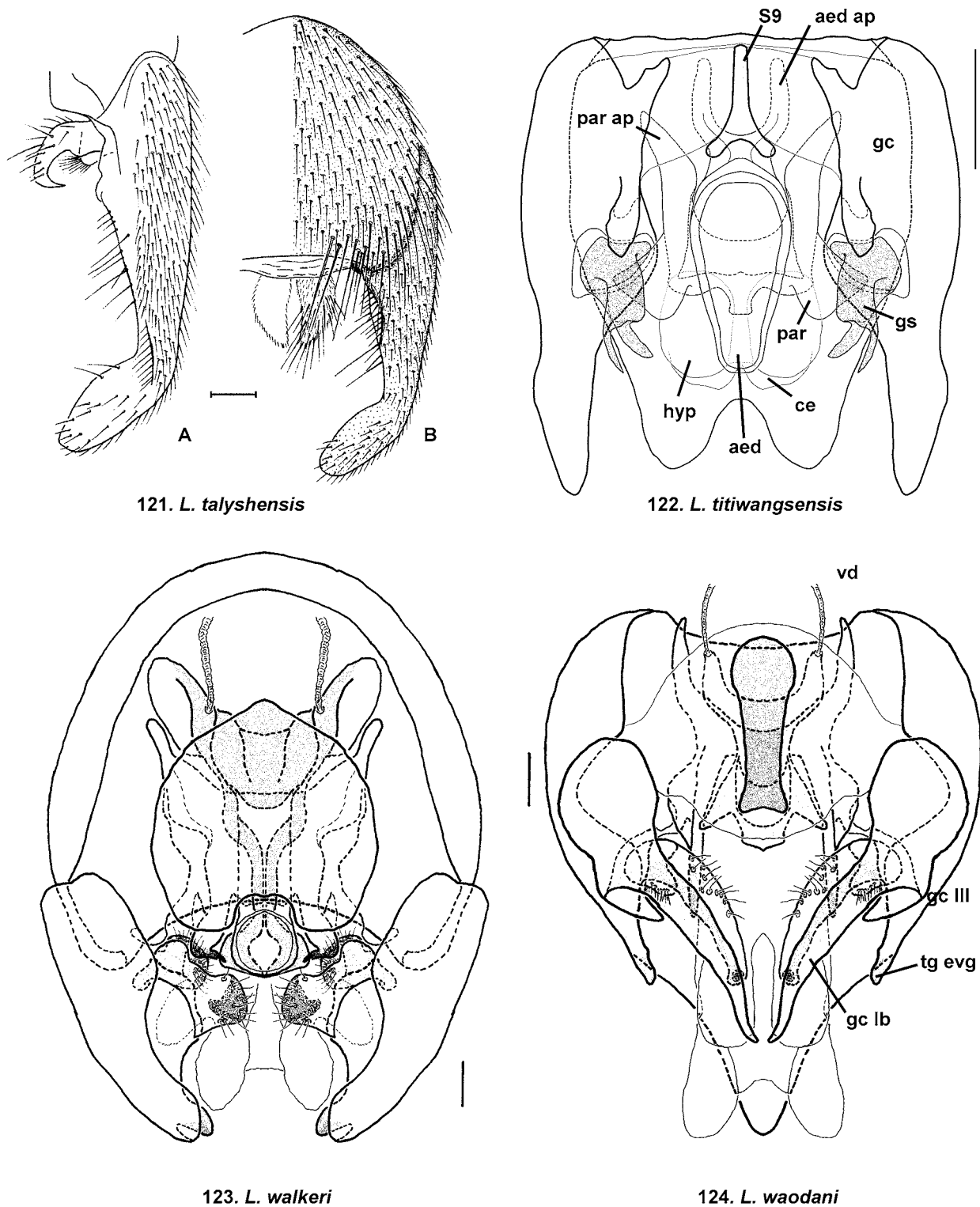


119. *L. tagbanua*



120. *L. tabatius*

**FIGURES 117–120. *Leptomorphus* male genitalia.** 117. *L. subcaeruleus*, ventral. 118. *L. subforcipatus* (reprinted with permission from Zaitzev & Ševčík 2002), **A.** dorsal. **B.** gonocoxite and gonostylus, ventral. 119. *L. tagbanua*, ventral. 120. *L. tabatius*, ventral. **Abbreviations:** aed = aedeagus; aed ap = aedeagal apodeme; ce = cercus; gc = gonocoxite, III = section 3; gs = gonostylus; hyp = hypoproct; par = paramere; par ap = parameral apodeme; S9 = sternite 9; tg evg = apical evagination of tergite 9; vd = vas deferens. Scale bar = 0.1mm.



121. *L. talyshensis*

122. *L. titiwangsensis*

123. *L. walkeri*

124. *L. waodani*

**FIGURES 121–124. *Leptomorphus* male genitalia.** 121. *L. talyshensis* (reprinted with permission from Zaitzev & Ševčík 2002), **A.** gonocoxite and gonostylus, ventral. **B.** dorsal. 122. *L. titiwangsensis*, ventral. 123. *L. walkeri*, ventral. 124. *L. waodani*, ventral. **Abbreviations:** aed = aedeagus; aed ap = aedeagal apodeme; ce = cercus; gc = gonocoxite, III = section 3; gc lb = gonocoxal lobe; gs = gonostylus; hyp = hypoproct; par = paramere; par ap = parameral apodeme; S9 = sternite 9; tg evg = apical evagination of tergite 9; vd = *vas deferens*. Scale bar = 0.1mm.



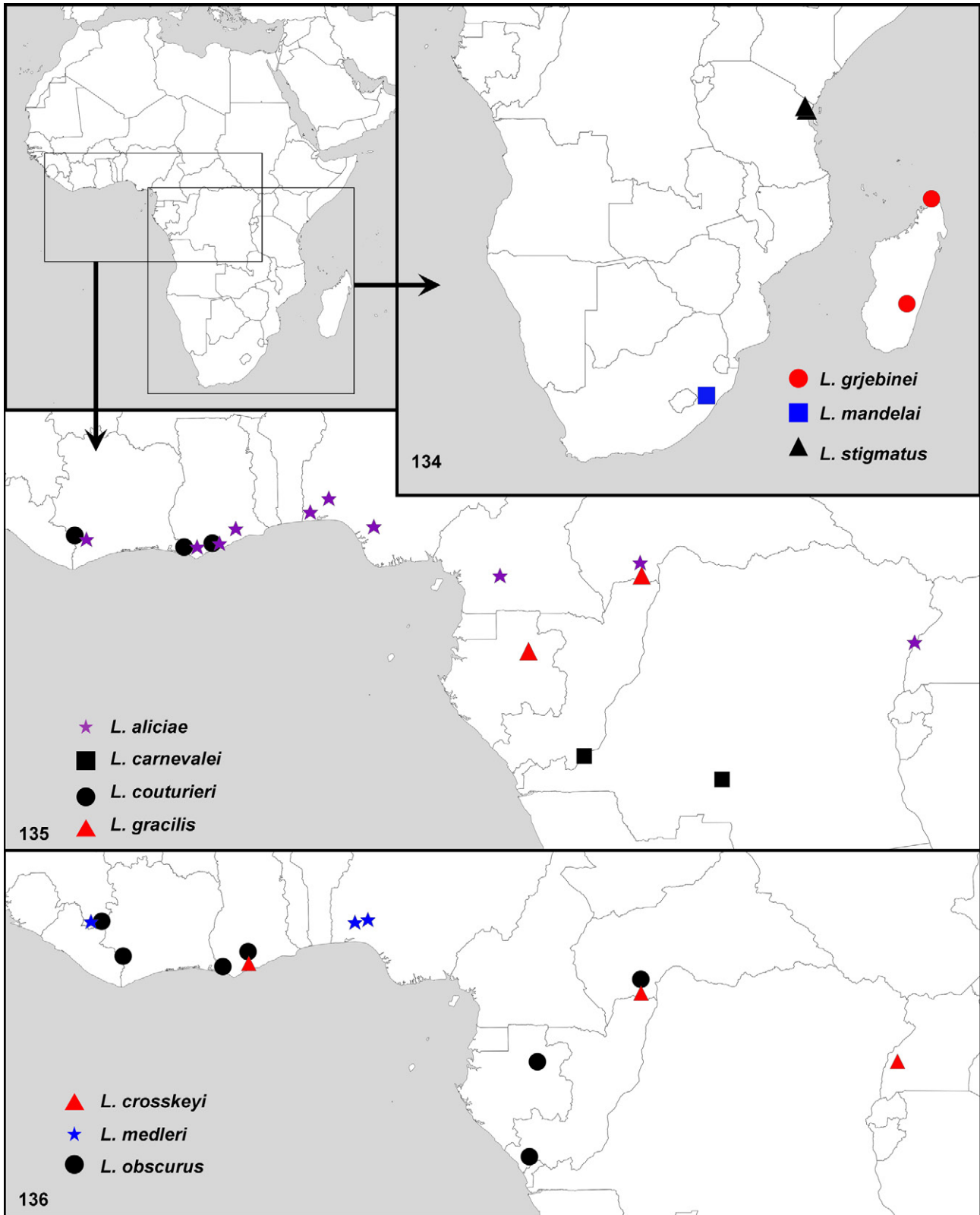
**TERMS OF USE**

This pdf is provided by Magnolia Press for private/research use.  
Commercial sale or deposition in a public library or website is prohibited.

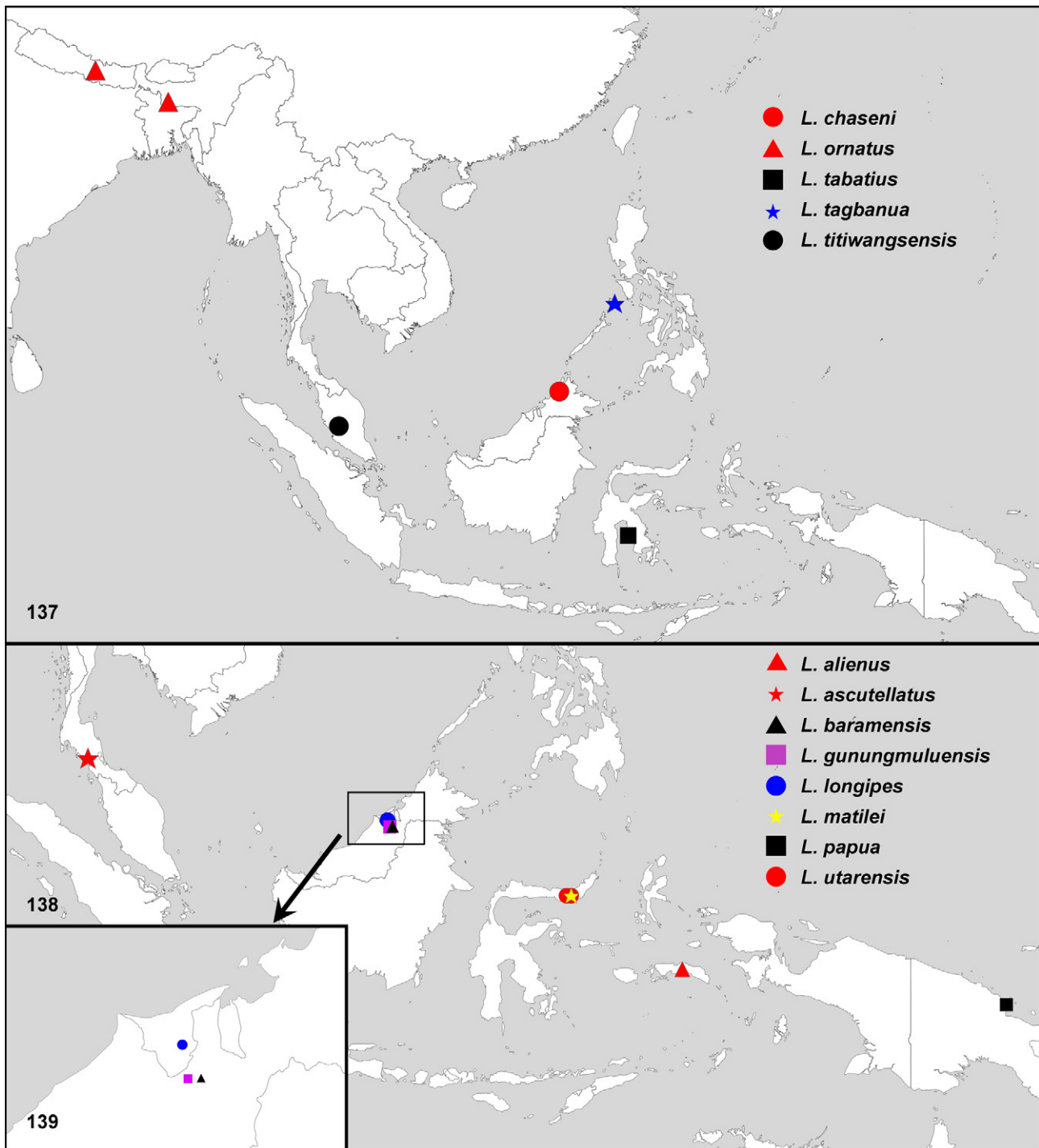


**FIGURES 125–133. *Leptomorphus* immatures and host fungi. 125. *Fomitopsis pinicola*, host fungus to larvae of *L. nebulosus*. 126. *Cerrena unicolor*, host fungus to *L. hyalinus*. 127–131. *Leptomorphus* larvae. 127. *L. brandiae*. 128. *L. nebulosus* in situ on *F. pinicola*. 129. *L. nebulosus* (photograph: A. Borkent). 130. *L. subcaeruleus*. 131. Fully mature larva of *L. nebulosus* beginning to pupate. 132–133. *Leptomorphus* pupae. 132. *L. hyalinus*. 133. *L. nebulosus*. Arrow indicates final larval skin left behind on anchor line (photograph: A. Borkent).**

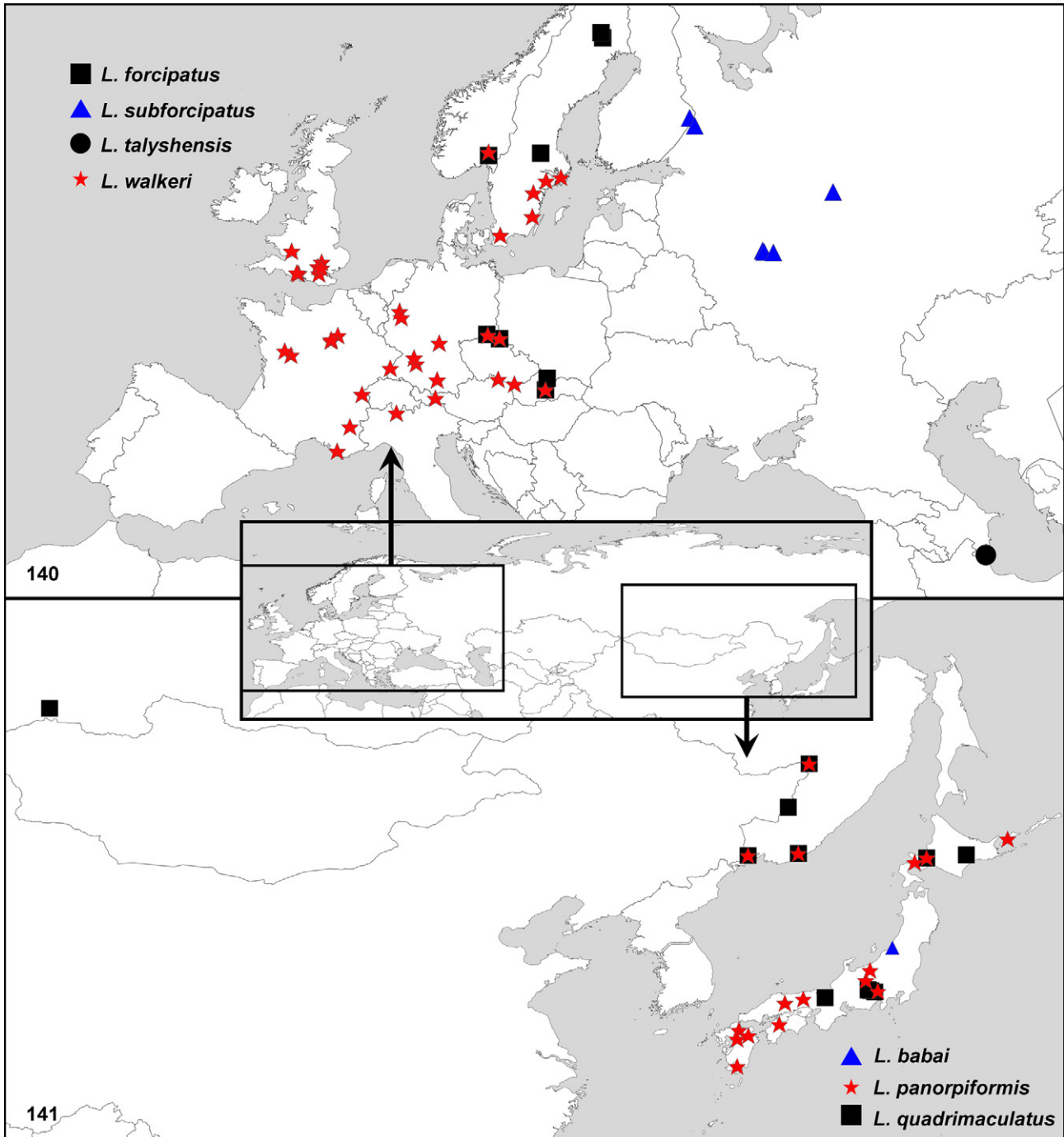




**FIGURE 134–136. Distribution of Afrotropical *Leptomorphus*.** 134. *L. grjebinei* (red circle), *L. mandelai* (blue square), *L. stigmatus* (black triangle). 135. *L. aliciae* (purple star), *L. carnevalei* (black square), *L. couturieri* (black circle), *L. gracilis* (red triangle). 136. *L. crosskeyi* (red triangle), *L. medleri* (blue star), *L. obscurus* (black circle).

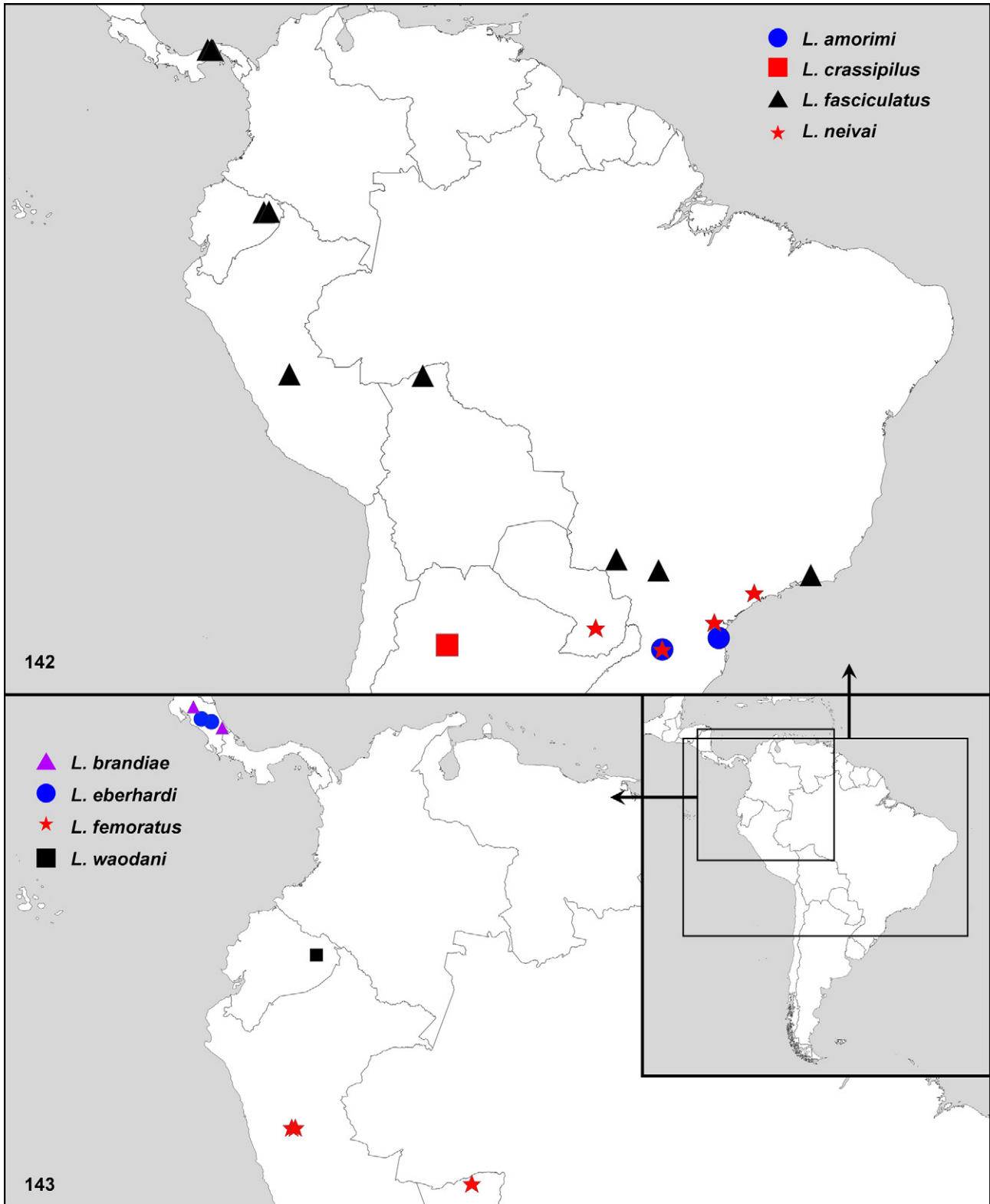


**FIGURE 137–139. Distribution of Oriental and Australasian *Leptomorphus*.** 137. *L. chaseni* (red circle), *L. ornatus* (red triangle), *L. tabatius* (black square), *L. tagbanua* (blue star), *L. titiwangsensis* (black circle). 138. Species described by Papp & Ševčík 2011. *L. alienus* (red triangle), *L. ascutellatus* (red star), *L. baramensis* (black triangle), *L. gunungmuluensis* (purple square), *L. longipes* (blue circle), *L. matilei* (yellow star), *L. papua* (black square), *L. utarensis* (red circle). 139. Expanded view of northern Borneo showing distribution of *L. baramensis*, *L. gunungmuluensis*, and *L. longipes*.



**FIGURE 140–141. Distribution of Palearctic *Leptomorphus*.** 140. *L. forcipatus* (black square), *L. subforcipatus* (blue triangle), *L. talyshensis* (black circle), *L. walkeri* (red star). 141. *L. babai* (blue triangle), *L. panorpiformis* (red star), *L. quadrimaculatus* (black square).





**FIGURE 142–143. Distribution of Neotropical *Leptomorphus*.** 142. *L. amorimi* (blue circle), *L. crassipilus* (red square), *L. fasciculatus* (black triangle), *L. neivai* (red star). 143. *L. brandiae* (purple triangle), *L. eberhardi* (blue circle), *L. femoratus* (red star), *L. waodani* (black square).

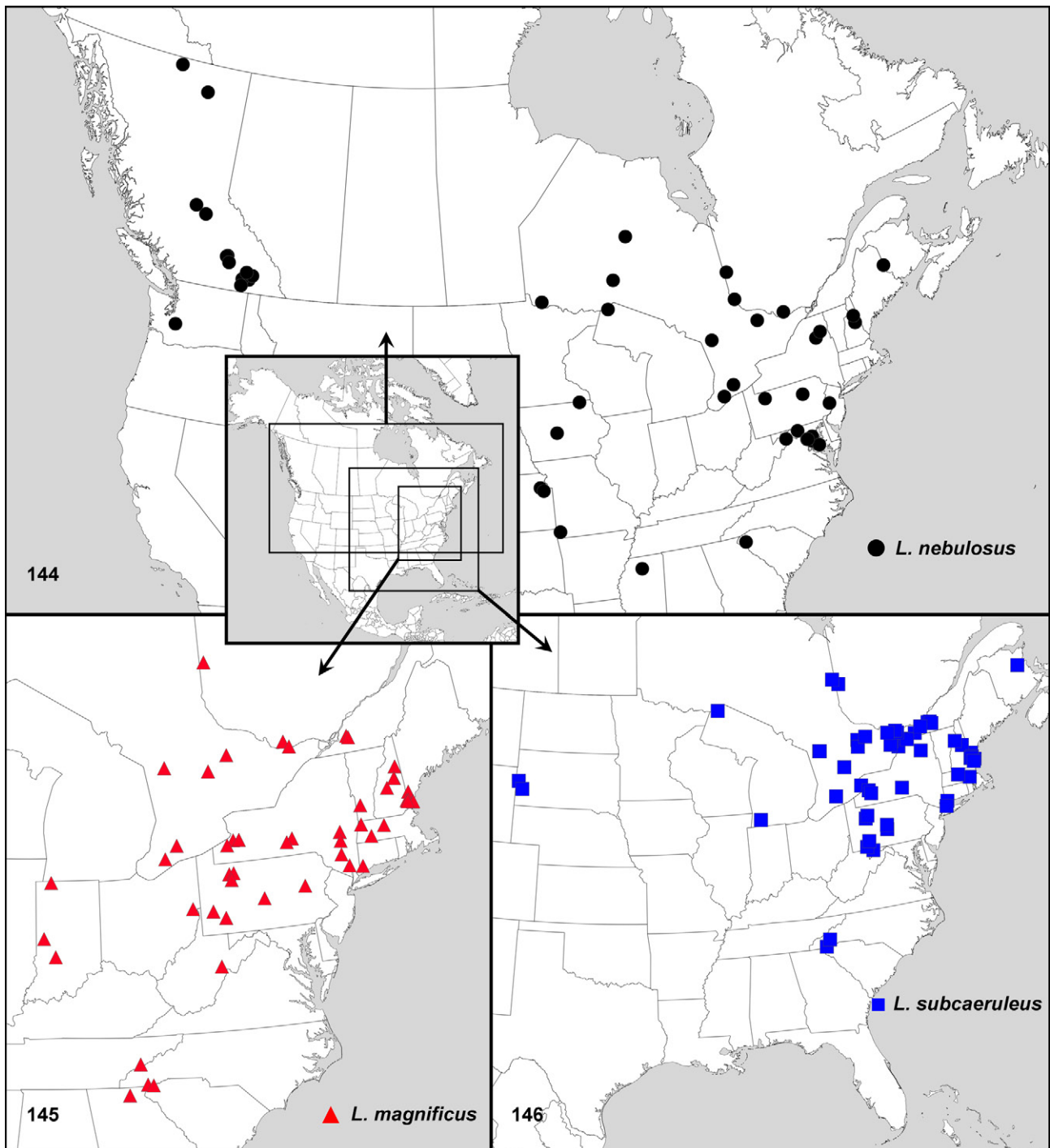


FIGURE 144–146. Distribution of Nearctic *Leptomorphus*. 144. *L. nebulosus* (black circle). 145. *L. magnificus* (red triangle). 146. *L. subcaeruleus* (blue square).

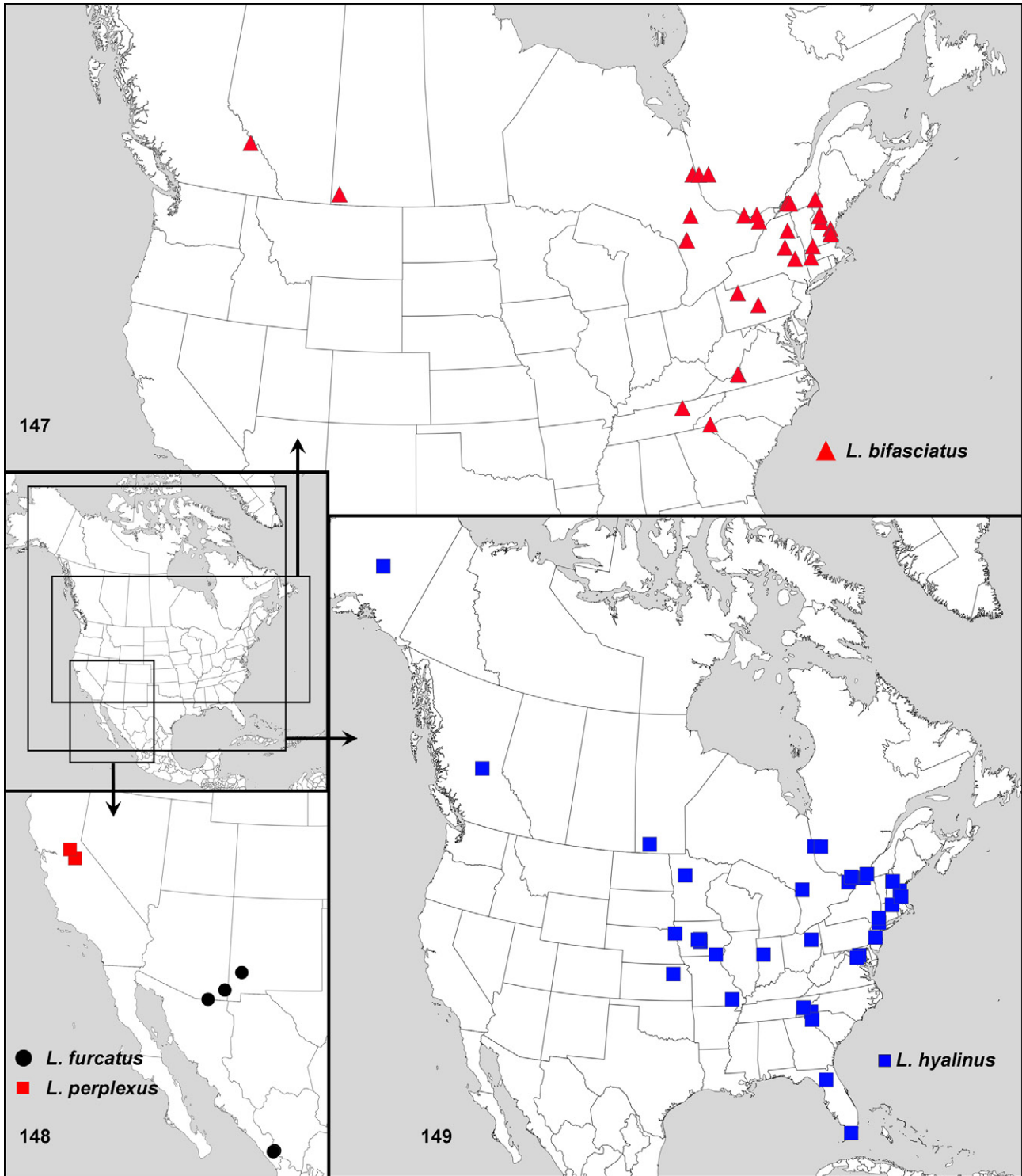


FIGURE 147–149. Distribution of Nearctic *Leptomorphus*. 147. *L. bifasciatus* (red triangle). 148. *L. furcatus* (black circle), *L. perplexus* (red square). 149. *L. hyalinus* (blue square).



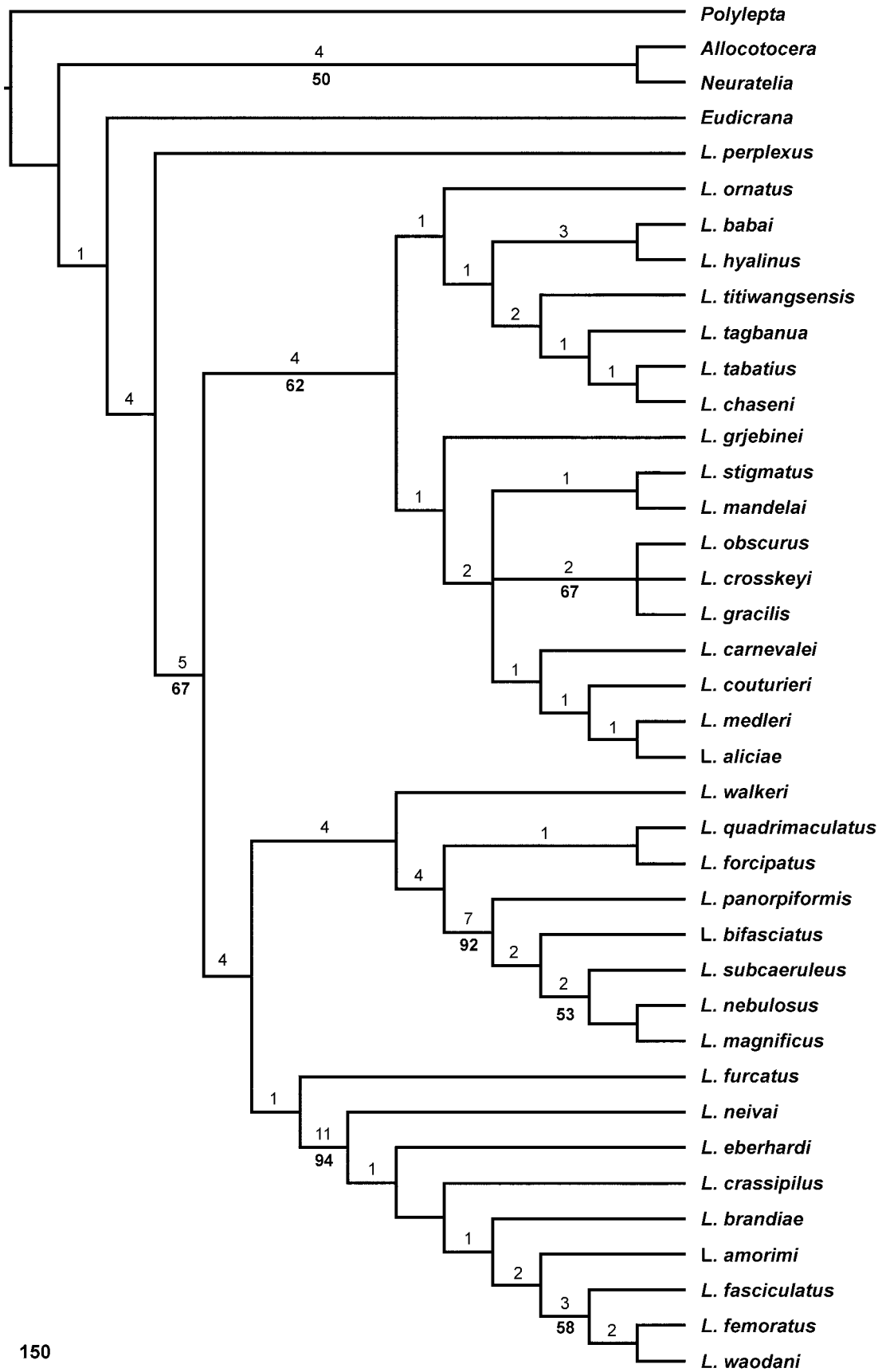
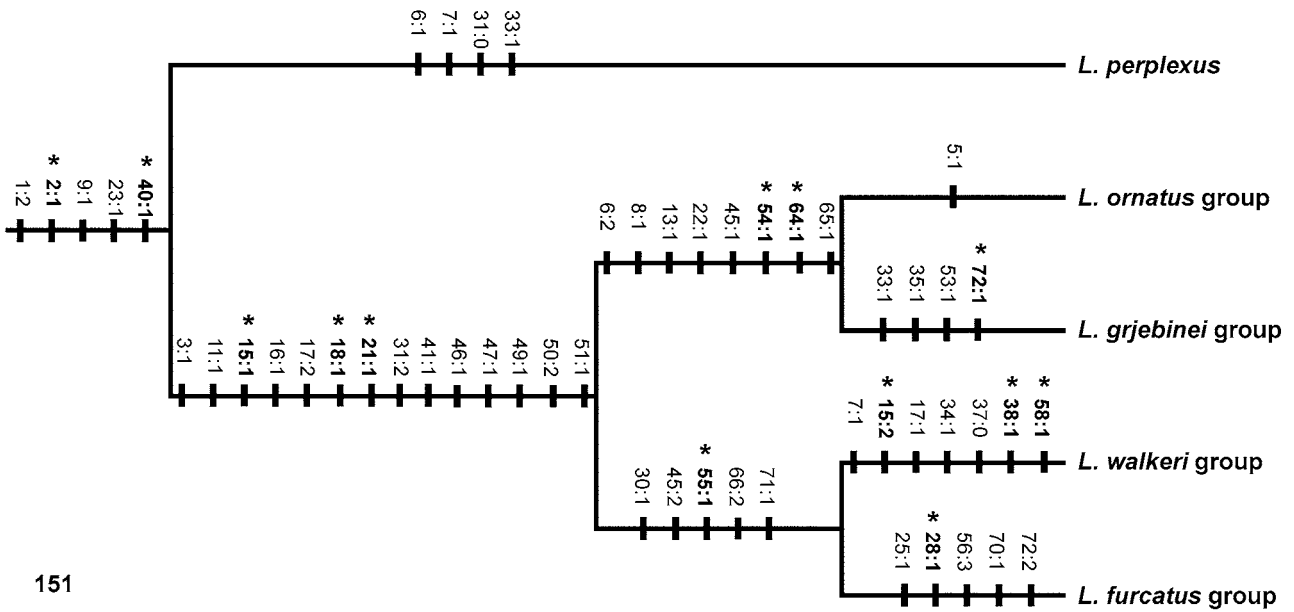
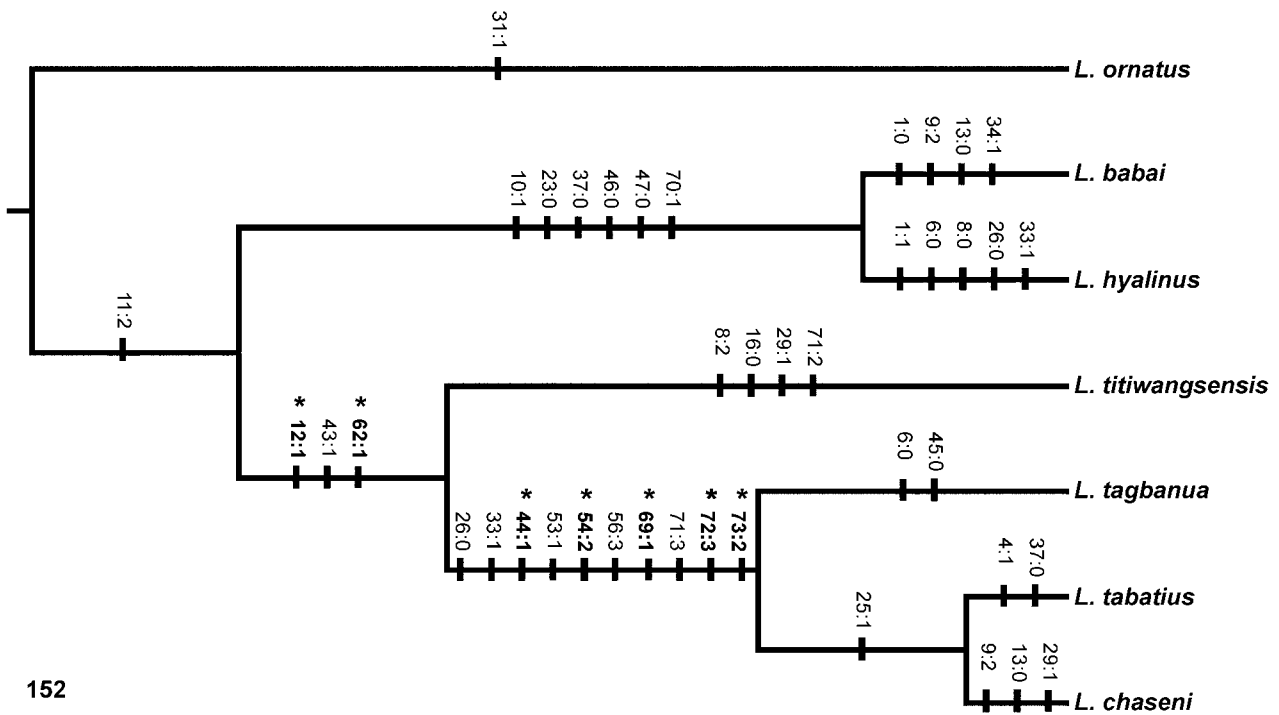


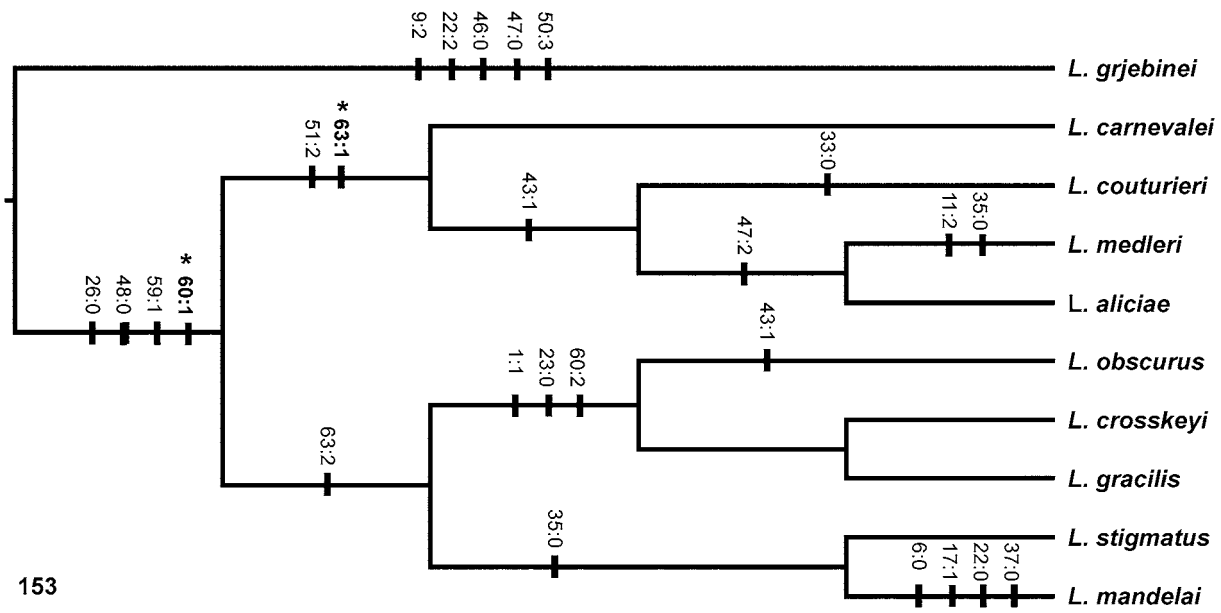
FIGURE 150. Strict consensus tree of three equally parsimonious trees found in the phylogenetic analysis. Bremer support values are shown above the branches and bootstrap values >50% are shown in bold below the branches.



**FIGURE 151.** One of three equally parsimonious trees showing the relationships at the base of the tree between *L. perplexus* and the four major species groups. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.

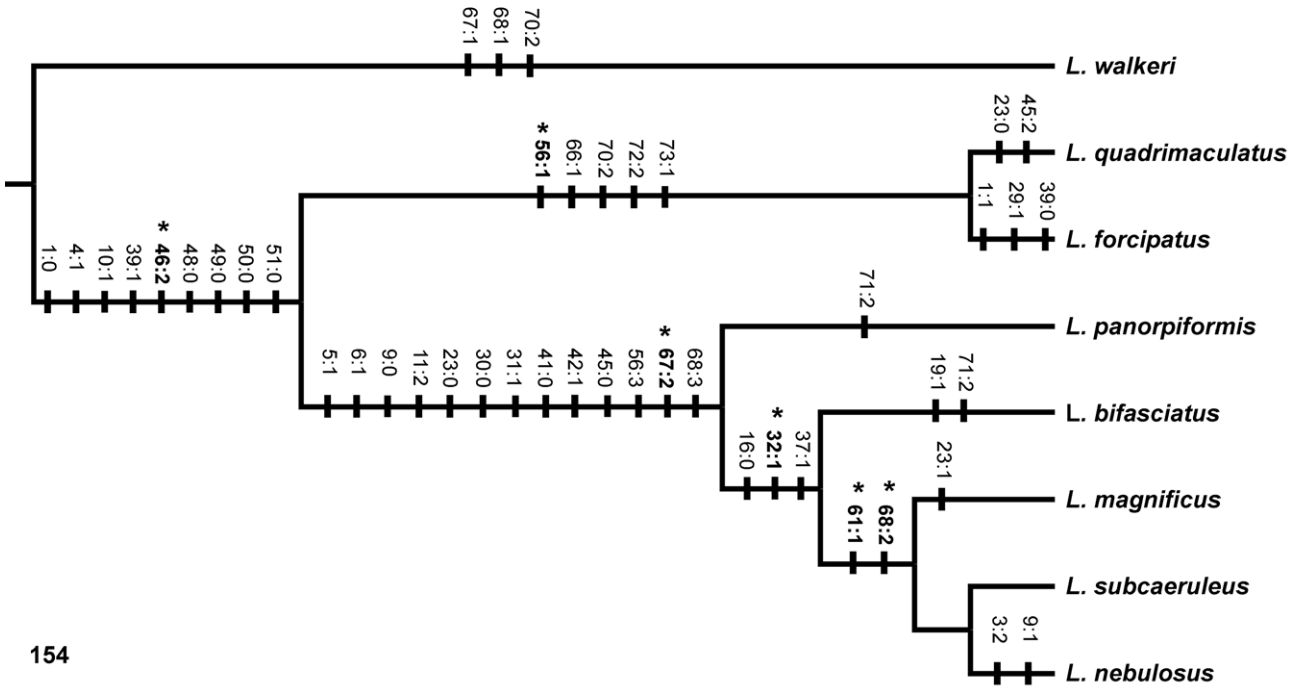


**FIGURE 152.** One of three equally parsimonious trees showing the relationships between species in the *L. ornatus* species group. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.



153

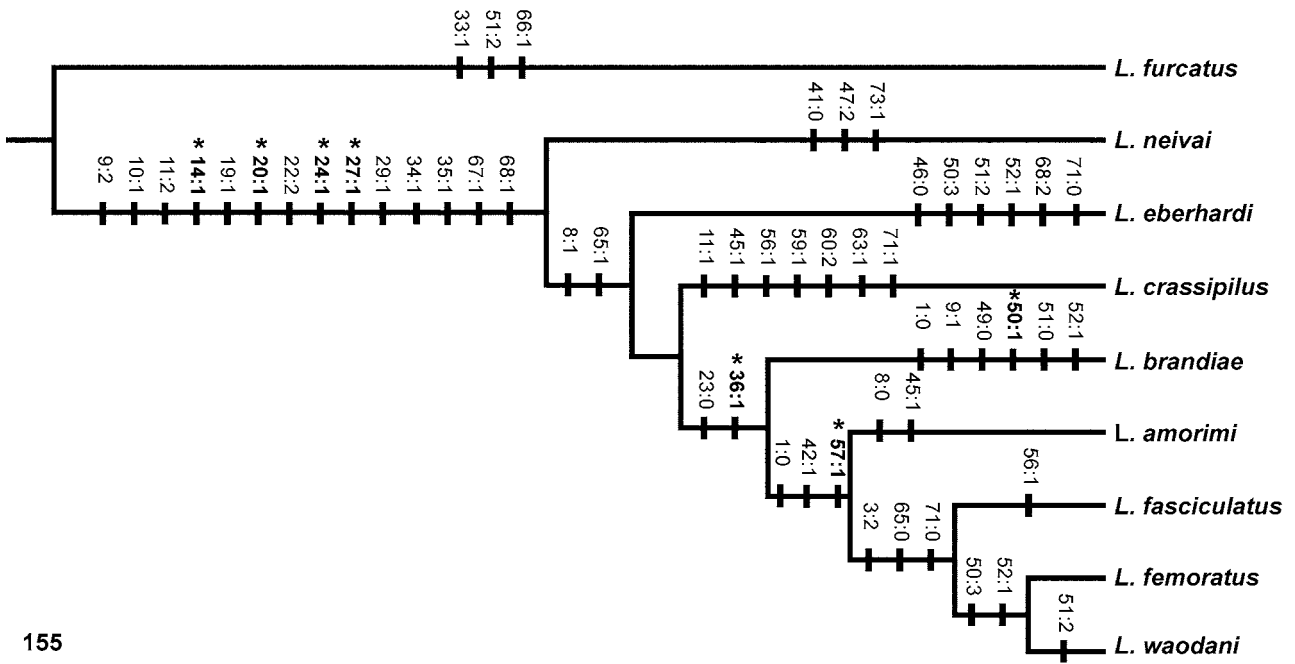
FIGURE 153. One of three equally parsimonious trees showing the relationships between species in the *L. grjebinei* species group. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.



154

FIGURE 154. One of three equally parsimonious trees showing the relationships between species in the *L. walkeri* species group. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.





155

**FIGURE 155.** One of three equally parsimonious trees showing the relationships between species in the *L. furcatus* species group. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.