SYSTEMATICS OF *LEPTOMORPHUS* AND PHYLOGENY OF THE SCIOPHILINI (DIPTERA: MYCETOPHILIDAE)

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ABSTRACT

A taxonomic revision and phylogenetic analysis of the world fauna of *Leptomorphus* Curtis (Diptera: Mycetophilidae) were undertaken. Forty-five valid species of *Leptomorphus* are recognized, including 12 new species and three new synonyms. Species descriptions, diagnoses and illustrations are provided for 37 species, along with a key to adults. Eight recently described Oriental and Australasian species for which material was unavailable are excluded from the key. The phylogenetic analysis used 73 adult morphological characters and supported the monophyly of *Leptomorphus*. Four major clades were found within the genus, but no support was found for previously recognized subgenera. A phylogenetic analysis was also conducted at the generic level for the tribe Sciophilini, to which *Leptomorphus* belongs. The analysis included 81 exemplar species, representing all but one of the genera currently or previously placed in the Sciophilini, scored for 96 adult morphological characters. The resulting phylogeny showed a monophyletic Sciophilini supported by four synapomorphies and containing 34 monophyletic genera: *Acnemia* Winnertz, *Acomoptera* Vockeroth, *Adicroneura* Vockeroth, *Afrocnemia* Matile, *Allocotocera* Mik, *Anaclileia* Meunier, *Aneura* Marshall, *Austrosciophila* Tonnoir, *Azana* Walker, *Baeopterogyna* Vockeroth, *Cluzobra* Edwards, *Drepanocercus* Vockeroth, *Duretophragma* Borkent **gen. n.**, *Eudicrana* Loew, *Leptomorphus* Curtis, *Loicia* Vockeroth, *Megalopelma* Enderlein, *Monoclona* Mik, *Morganiella* Tonnoir & Edwards, *Neoallocotocera* Tonnoir, *Neoaphelomera* Miller, *Neotrizygia* Tonnoir & Edwards, *Neuratelia* Rondani, *Paramorganiella* Tonnoir, *Paratinia* Mik, *Paratrizygia* Tonnoir, *Parvicellula* Marshall, *Phthinia* Winnertz, *Polylepta* Winnertz, *Sciophila* Meigen, *Stenophragma* Skuse, *Tasmanina* Tonnoir, *Taxicnemis* Tonnoir & Edwards, and *Trizygia* Skuse. Four genera which had been placed in the Sciophilini by some previous authors (*Coelophthinia* Edwards, *Impleta* Plassmann, *Speolepta* Edwards, and *Syntemna* Winnertz) were excluded from the tribe and placed in the Gnoristini. New generic diagnoses were given for

all genera in the tribe. The new genus *Duretophragma*, formerly constituting part of the paraphyletic genus *Stenophragma*, is described and illustrated and 10 new generic combinations resulted from recognition of the new genus.

RÉSUMÉ

Une révision taxonomique et une analyse phylogénétique de la faune mondiale du genre *Leptomorphus* Curtis (Diptera: Mycetophilidae) ont été effectuée. Quarante-cinq espèces valides sont reconnues, incluant 12 nouvelles espèces et trois nouveaux synonymes. Des descriptions, caractères diagnostiques et illustrations sont présentés pour 37 espèces, de même qu'une clef d'identification des adultes. Huit espèces orientales et australasiennes sont exclues de la clef parce que des spécimens représentant ces espèces n'étaient pas disponibles. L'analyse phylogénétique, basée sur 73 caractères morphologiques des adultes, supporte la monophylie de *Leptomorphus* et met en évidence quatre clades, mais ne soutient pas les sous-genres reconnus antérieurement. Une analyse phylogénétique de la tribu à laquelle appartient le genre *Leptomorphus,* Sciophilini, a également été effectuée, basée sur 96 caractères morphologiques des adultes provenant de 81 espèces exemplaires représentant tous les genres compris antérieurement ou présentement dans la tribu, sauf un. Quatre synapomorphies corroborent la monophylie de Sciophilini qui contient 34 genres également monophylétiques: *Acnemia* Winnertz, *Acomoptera* Vockeroth, *Adicroneura* Vockeroth, *Afrocnemia* Matile, *Allocotocera* Mik, *Anaclileia* Meunier, *Aneura* Marshall, *Austrosciophila* Tonnoir, *Azana* Walker, *Baeopterogyna* Vockeroth, *Cluzobra* Edwards, *Drepanocercus* Vockeroth, *Duretophragma* Borkent **gen. n.**, *Eudicrana* Loew, *Leptomorphus* Curtis, *Loicia* Vockeroth, *Megalopelma* Enderlein, *Monoclona* Mik, *Morganiella* Tonnoir et Edwards, *Neoallocotocera* Tonnoir, *Neoaphelomera* Miller, *Neotrizygia* Tonnoir et Edwards, *Neuratelia* Rondani, *Paramorganiella* Tonnoir, *Paratinia* Mik, *Paratrizygia* Tonnoir, *Parvicellula* Marshall, *Phthinia* Winnertz, *Polylepta* Winnertz, *Sciophila* Meigen, *Stenophragma* Skuse, *Tasmanina* Tonnoir, *Taxicnemis* Tonnoir et Edwards, et *Trizygia* Skuse. Quatre genres classés par certains auteurs dans Sciophilini sont ici exclus de la tribu et placés dans Gnoristini: *Coelophthinia* Edwards, *Impleta* Plassmann, *Speolepta* Edwards, et *Syntemna* Winnertz. Des nouveaux caractères diagnostiques sont

présentés pour tous les genres inclus dans la tribu. L'auteur propose un nouveau genre, *Duretophragma*, une fraction du genre paraphylétique *Stenophragma,* établissant ainsi 10 nouvelles combinaisons au niveau générique. Une description et illustrations du genre sont présentées.

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PREFACE

The thesis is composed of four chapters, two of which are original manuscripts that have been submitted for publication in refereed journals.

Chapter 1.

This chapter constitutes a general introduction and literature review of Mycetophilidae systematics focused on the tribe Sciophilini and genus *Leptomorphus*.

Chapter 2.

This chapter consists of a manuscript that is in press at the journal *Zootaxa*:

Borkent, C.J. and Wheeler, T.A. Systematics and phylogeny of *Leptomorphus* Curtis (Diptera: Mycetophilidae).

Chapter 3.

This chapter is a manuscript submitted to the journal *Systematic Entomology*:

Borkent, C.J. and Wheeler, T.A. Phylogeny of the tribe Sciophilini (Diptera: Mycetophilidae).

Chapter 4.

This chapter is a general discussion and conclusion.

Note: Any nomenclatural changes or new taxa proposed in this thesis should not be considered valid until published in primary journals as defined by the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature 1999)

CONTRIBUTION OF AUTHORS

Christopher James Borkent designed and executed the research in both data chapters and conducted all specimen-based work, field work, data collection and writing. Terry A. Wheeler was responsible for the supervision of the thesis research, providing lab facilities, equipment and research funding, and the editing of the manuscripts.

CLAIM TO ORIGINALITY

The work presented in this thesis is considered to be an original contribution to knowledge in the following respects:

1. The cosmopolitan genus *Leptomorphus* is revised for the first time, providing diagnoses, descriptions, figures and a key for all species, twelve of which are newly described.

2. The first phylogenetic analysis of relationships within *Leptomorphus* is presented, confirming the monophyly of the genus, but rejecting previous subgeneric hypotheses.

3. The tribe Sciophilini, which contains *Leptomorphus*, is subjected to a comprehensive phylogenetic analysis for the first time, including all available genera from the tribe.

4. Limits of the Sciophilini are redefined as a result of the phylogenetic analysis and revised diagnoses of all Sciophilini genera are given. Four genera are excluded from the tribe: *Coelophthinia* Edwards, *Impleta* Plassmann, *Speolepta* Edwards, and *Syntemna* Winnertz, and three genera are added: *Acomoptera* Vockeroth, *Adicroneura* Vockeroth, *Drepanocercus* Vockeroth.

5. The new genus *Duretophragma* is described and illustrated and 10 species are transferred to the genus.

CHAPTER 1. GENERAL INTRODUCTION AND LITERATURE REVIEW

Systematics and diversity of Diptera

The true flies (Diptera) form an estimated 10% of described multi-cellular species on the planet, with more than 150 000 extant species, though it is clear from numerous surveys that many species await description (Brown 2005, Pape *et al.* 2011). Although we know much about the biology of economically, medically or forensically important species, little or nothing is known about the immature stages, ecological roles, or evolutionary relationships of the majority of described Diptera species (Brown 2005, Yeates & Wiegmann 2005, Pape *et al.* 2009).

Several recent projects have significantly advanced our knowledge of Diptera diversity and phylogeny. The Manual of Central American Diptera (Brown *et al.* 2009, 2010) has provided identification tools for all families of Diptera in this region, along with current information on the phylogeny and ecology of the Diptera in general and specifically for each family. It provided the first comprehensive overview of Diptera of any tropical region. The FLYTREE project (http://www.inhs.uiuc.edu/research/FLYTREE/) attempted to interpret the phylogenetic relationships between all families of Diptera using both molecular and morphological information. The project led to a number of publications on both the higher level phylogeny of Diptera (Moulton & Wiegmann 2003, 2007, Blagoderov *et al.* 2007, Yeates *et al.* 2007, Bertone *et al.* 2008, Kutty *et al.* 2008, Wiegmann *et al.* 2011), and relationships within families or genera (Beckenbach & Borkent 2003, Holston *et al.* 2007, Lim *et al.* 2009). The project also facilitated comprehensive generic revisions and phylogenies (e.g., Holston & Irwin 2005, Brake & Mathis 2006, Winterton 2007), and an online atlas of Diptera morphology (www.ces.csiro.au/biology/fly/flyGlossary.html). The cumulative

work by Wiegmann *et al.* (2011) brought together all available genetic analyses (using a subset of 14 genes and complete mitochondrial genomes for each exemplar) with 371 morphological character states. Though they initially claim to do a a combined analysis they actually only analyze the sequence data. Many of the resulting phylogenetic patterns differed from previous hypotheses, and from analyses based solely on morphology.

Two recently published books deal with the diversity and evolution of the Diptera. Yeates & Wiegmann (2005) provide a multi-authored overview of the evolutionary biology of Diptera, focusing on their phylogeny, importance in the development of phylogenetic theory, genomics and developmental biology, and evolutionary ecology and biogeography. Many of the chapters speak to the utility of molecular data in addressing questions within these areas. Pape *et al.* (2009) provide detailed discussion of the diversity of Diptera in each biogeographic region, the problems with, and approaches to, estimating Diptera diversity, and the role of bioinformatics in Diptera diversity studies.

Online resources providing overviews of diversity have also been developed for Diptera, the largest of these being Systema Dipterorum (www.diptera.org, Pape & Thompson 2010) a central repository for nomenclatural and reference information on the order. There are also several family or family group specific web resources available or in development (e.g. Sciaroidea.info, Milichiidae.info and see: www.diptera.info/weblinks.php), which range from world catalogs to databases with literature (in pdf format), images and distribution maps, as well as keys.

Even with these large projects there is still a lack of phylogenetic consensus over much of the order. The recent higher level molecular or 'total evidence' work has principally been associated with the FLYTREE project, in which the topology of the phylogenetic tree has varied from publication to publication, and has not converged on a consistent arrangement of clades as new exemplars and genes were added (e.g., compare Yeates *et al.* 2007, Bertone *et al.* 2008 and

Wiegmann *et al.* 2011).

Higher level phylogenetics of the Diptera

The most recent higher level phylogeny from Wiegmann *et al.*(2011), based on both morphological and molecular data, has a number of clades that do not agree with any previous phylogeny. There are several problems with the analysis. First, using a "total evidence" approach combining molecular and morphological data would mean that the data from the many thousands of base-pairs swamped the 371 morphological character states. However, the morphological data were not actually analyzed or presented as initially claimed, so the readers cannot determine how or if morphological characters influenced the results in the paper. Some of the results conflicted with well-established phylogenetic hypotheses based on earlier morphological data and interpretation. The authors, however, did not comment on the significance of their new conclusions. As such, further research is needed to better interpret the phylogenetic relationships between the families of Diptera, especially in areas of the tree in which their results differ significantly from the prevailing views. Even with these flaws this study was used as the basis for the revised classification presented by Pape *et al.* (2011). Though the results of Wiegmann *et al.* (2011) are less than conclusive, they did explore and develop primers for a large number of genes (12 nuclear genes (CAD, TPI, PGD, AATS1, AATS2, G6PD, PEPCK, PER, pug, SIA, SNF, stx, GART), 28S and 18S ribosomal DNA and complete mitochondrial sequences). Many of these (the latter eight nuclear genes) were previously unused in Diptera. These will be useful in future phylogenetic work, along with other recently developed primers for these and other genes such as 12S, Cytb, COI, EF-1a, *white* and *wingless* (Gibson *et al.* 2011) in Diptera.

Recent higher level phylogenies of the Diptera based solely on new morphological character sets are less common than those based on sequence data. Sinclair *et al.* (2007) found several new synapomorphies in the internal anatomy

of the male genitalia suggesting relationships between the suborders of nematocerous Diptera, as did Starý's (2008) detailed investigation of the dipteran wing stalk. Blagoderov *et al.* (2007) produced a phylogeny based on morphological characters of late Triassic fossil nematocerous Diptera. Woodley *et al.* (2009) provided a current review of the phylogeny of the Diptera with discussion of morphological synapomorphies and molecular evidence supporting the various clades.

Morphological studies within the Diptera

Many recent studies on phylogenetic relationships of or within families have had great success using morphological characters to find strongly supported hypotheses of relationship within their groups. These studies often focused on previously underused or unexamined body regions, or other life stages. For example, Brooks (2005) undertook the first detailed study of the male and female genitalia of the Dolichopodinae (Dolichopodidae) finding a number of previously unnoticed characters. Giroux *et al.* (2010) undertook a detailed scanning electron microscope study of the male genitalia of the Sarcophaginae (Sarcophagidae). Their morphological study redefined or clarified some genitalic homologies and their phylogeny resolved the placement of a number of problematic taxa and found male genitalic character support for many of the clades. In a revision of the genus *Neotelmatoscopus* Tonnoir (Psychodidae) Curler & Courtney (2009) used characters from all life stages to examine the monophyly of the genus and species relationships within the group. Most of the support for both the genus and the clades within it were from synapomorphies based on characters of immature stages. Brammer & von Dohlen (2010) found 78 new morphological characters in Stratiomyiidae and showed that two of the subfamilies were paraphyletic, confirming many of the results found in a previous molecular analysis based on two genes (EF-1a and 28s rRNA, Brammer & von Dohlen 2007). These examples and many others, indicate that there is still much undocumented morphological

data including characters of phylogenetic utility, still available in hyper-diverse groups such as the Diptera. There are many examples of essentially unexplored character sets across the order: much of the adult thorax; numerous larval features including especially first instars (which can retain plesiomorphic conditions; Borkent & McKeever 1990), anterior segments, the hypopharynx and the epipharynx; pupal characters remain virtually uninterpreted; and internal anatomy, particularly of the male genitalia and the sclerites and musculature (Michelsen 1996) need intensive study (as done for the Hymenoptera, see Mikó *et al.* 2007). Other examples of morphological character sets with potential include: sperm ultrastructure (Dallai *et al.* 2007, 2008), wing interference patterns (Shevtsova *et al.* 2011) and eye structure (Buschbeck & Hoy 1998). The use of new microscopy techniques also holds promise for exploring these character sets and finding new ones (Jenner 2006).

Morphological character states also need to be carefully mapped across taxa and extensive outgroup comparisons made. Many morphological studies have been conducted without a phylogenetic context, usually because phylogeny is not the goal of the study and/or the number of exemplar taxa is inadequate to make clear phylogenetic statements. For example, the female genitalia have been described for each of the families of nematocerous Diptera but have never been interpreted phylogenetically across the families. Many of these morphological studies reveal methods for exploring these characters and should be expanded by systematists to include a greater number of relevant exemplar taxa.

Molecular studies within the Diptera

It is clear that molecular data vary in their usefulness in interpreting phylogenetic information at different levels of diversification. However, this is no different than morphology, where different character sets are informative at different levels. Some molecular data are better at delineating diversification between ancient families, suborders or orders (usually nuclear genes or whole

mitochondrial genomes (Danforth *et al.* 2005, Cameron *et al.* 2007)), and others for interpreting relationships between species and relatively young genera (typically mitochondrial genes (Petersen *et al.* 2007)). This is due to their observed rate of mutation, with slower mutating nuclear genes supposedly providing clearer data for older groups, but not being variable enough for younger groups such as genera, where quickly mutating mitochondrial genes are assumed to be more useful. However, this is not always the case (see examples below).

Wiegmann *et al.* (2011) used five nuclear genes to interpret all families of Diptera (CAD, TPI, PGD and AATS1, and 28S ribosomal DNA) and an additional nine nuclear genes (AATS2, G6PD, PEPCK, PER, pug, SIA, SNF, stx, and GART, 18S ribosomal DNA) and the complete mitochondrial genome for select families (their "Tier 1"). It was unclear from their analysis which of the genes may have been better at discerning older relationships than others. It was also unclear which of the genes gave differing results. Even so, the genes selected by Wiegmann *et al.* (2011) have generally been recognized as useful in interpreting older groups.

There have been many molecular phylogenetic studies at the superfamily or family level within the Diptera. In a phylogenetic investigation of the superfamily Tephritoidea, Han & Ro (2005) used three mitochondrial genes (12S, 16S and COII). Their analysis resulted in two monophyletic groups that corresponded to Pallopteroidea and Otitoidea sensu Hennig (1958). However, they do not resurrect these groups pending further study. Using a well-resolved Sepsidae phylogeny resulting from an analysis of 10 genes (nuclear genes 18S, 28S, AATS, EF1a, and Histone 3, and mitochondrial genes 12S, 16S, COI, COII and CYB) Puniamoorthy *et al.* (2010) studied the female genitalia of recently diverged sepsid sister taxa, in order to test the species specificity of the genitalia. They found that female genitalia are highly diverse and diagnostic for species and are evolving at a faster rate than generally assumed, probably due to post-copulatory female choice. Cranston *et al.* (2012) analyzed four genes (18S, 28S, CAD and

COI) and showed the Chironomidae, as well as most of the subfamilies and tribes, to be monophyletic. Kutty *et al.* (2007) used data from seven genes (12S, 16S, Cytb, COI, 28S, Ef1-alfa, Pol II) to test the monophyly of the Scathophagidae and determine the relationships between the included genera. They found good support for a monophyletic family, two subfamilies and most of the genera, and then used their phylogeny to explore the evolution of larval feeding within the family, showing the utility of phylogeny for understanding patterns of natural history evolution. Conversely, in an investigation of the phylogeny of bat flies (Strebliidae and Nycteribiidae), a group with a relatively simplified morphology, Dittmar *et al.* (2006) were unable to find consensus between four genes (18S rDNA, 16S rDNA, COII, and cytB) and did not retrieve a monophyletic Strebliidae; a monophyletic Nycteribiidae and relationships between the Hippoboscoidea were weakly supported.

Within genera, molecular data has also been useful for studying species groups and relationships, and confirming or refuting morphologically-based species limits. With a combination of nuclear (28S) and mitochondrial (12S, ND1 and CO1) genes Smith & Brown (2010) explored the phylogeny of the genus *Anevrina* (Phoridae). They obtained a monophyletic genus and strongly supported, fully resolved species relationships, falling into two monophyletic clades. Kopp & True (2002) used four nuclear genes (28S rRNA, Amy, GPDH and kl3) and two mitochondrial genes (COI and ND1) to obtain a phylogeny of the oriental *Drosophila melanogaster* group. In their preferred tree, they found that morphological characters previously used for phylogenetic work in the group were unreliable, particularly the male genitalia, which showed multiple instances of convergence. Morales-Hojas *et al.* (2011) resolved the relationships of the *Drosophila virilis* group using six nuclear genes (Adh, fused, Gpdh, NonA, CG9631 and CG7219) and two rRNA genes (12S and 16S). These trees were then used to analyze and discuss biogeographic patterns. Petersen *et al.* (2007) used data from COI to confirm that the subtle morphological differences used to

distinguish two parapatric species of *Ornithomya* Latreille (Hippoboscidae) were supported by differences at the genetic level.

As shown in the examples above there is a tendency for higher level relationships to be better resolved by nuclear genes, and lower levels by mitochondrial genes. However, between the two extremes of species and order levels there is a range of use of both types of genes.

The study of new genes, and development of specific primers, such as the work done by Wiegmann *et al.* (2011) and Gibson *et al.* (2011), must continue. These genes will increase researcher's ability to determine which genes are most appropriate for their group, and provide more consistent phylogenetic conclusions. It is clear that the way forward for taxonomy and systematics will involve both molecular and morphological data sources, as either data set alone may provide weak support to parts of the tree. The inclusion of a second data source can often help resolve these grey areas, providing a more clearly resolved phylogeny and classification (e.g. Kutty *et al.* 2007, Petersen *et al.* 2007).

Combined potential of molecules and morphology

There are also a number of ways in which molecular and morphological tools can be used in concert to maximize the retrieval and relevance of new characters for phylogenetic analysis. Many of these remain little used in Diptera and should be considered when planning future projects. Much morphological data remains to be gathered from immature stages of Diptera (Woodley *et al.* 2009). The extraction of these data can be done through careful rearing, when immatures can be found and reared without damage (as for *Leptomorphus*, where hanging pupae can be collected with a minimum of handling, see below). However, in groups where rearing is difficult, due to the habitat or food requirements of the immatures, the acquisition of these data can be greatly facilitated by DNA barcoding techniques (Hebert *et al*. 2003, Meier 2008, Meier & Lim 2009). The

use of DNA-barcoding allows the linking of separate specimens of immature stages with adults (Stur & Ekrem 2010), or females with males (Kurina *et al.* 2011), within a species. This allows immature and female characters to be associated with the proper species, especially if non-destructive DNA extraction methods are used, (Rowley *et al.* 2007, Hunter *et al.* 2008, Thomsen *et al.* 2009), and increases the number of available morphological characters (Meier 2008, Meier and Lim 2009). DNA-barcoding may also help to expose cryptic species within species that were initially thought to be variable for a particular morphological character, thereby helping delimit character states (Meier 2008).

Studies that attempt to determine the pathway from gene to structure will also be very useful in linking these two data types. This is the goal of evo-devo studies (Brakefield 2011), where there are already some promising results in other organisms; for example, linking a bacterial genome to its metabolic function (Francke *et al.* 2005), or associating variation in two lepidopteran genes that results in differences in wing pattern (Martin & Reed 2010). Though these types of studies are in their infancy in phylogenetic work (Minelli 2009), they will potentially allow workers to confirm or refute morphological homologies based on the genes and developmental pathways that produce those homologies, thereby reducing the effect of convergence on phylogeny estimation.

In molecular studies, insertions or deletions of a large number of nucleotides (longer than 1-2 nucleotides long) are typically assumed to be uninformative, and therefore are removed from the analysis (Swofford *et al.* 1996, Brammer & von Dohlen 2007, Bertone *et al.* 2008). However, these insertions and deletions, along with other rare genomic changes, such as recognition of ancestral horizontal gene transfers conserved within lineages (Huang and Gogarten 2006, Fournier *et al.* 2009), or the presence/absence of introns (Moulton & Wiegmann 2003), can be considered as synapomorphies of groups and can be particularly useful at higher taxonomic levels (Rokas and Holland 2000, Rokas *et al.* 2003). As more genes

and genomes are sequenced, an increasing number of rare genomic changes will be discovered, such as the recent discovery of carotenoid biosynthetic genes from fungi horizontally transferred to the genome of Cecidomyiidae (J. Stireman Pers. Comm.), and should be very useful in determining higher level relationships (Rokas and Holland 2000, Rokas *et al.* 2003, Fournier *et al.* 2009).

Phylogeny and classification of nematocerous Diptera

Traditionally the Diptera have been split into two major suborders, the Nematocera (midges, gnats and mosquitoes) and the Brachycera (higher flies). The Brachycera are clearly a monophyletic group in all studies, but they arise from within the Nematocera with either Anisopodidae (Blagoderov *et al.* 2007, Woodley *et al.* 2009) or the clade containing Anisopodidae as their sister group, (Bertone *et al.* 2008, Wiegmann *et al.* 2011) making the latter suborder paraphyletic. The paraphyly of the Nematocera has led to the preferential use of the term 'nematocerous Diptera' rather than Nematocera. Though there has been a recent suggestion that the infraorders of nematocerous Diptera be considered suborders (Amorim & Yeates 2006) and referred to collectively as the 'lower Diptera', most authors continue to refer to either nematocerous Diptera or Nematocera and retain the infraorder classification (Woodley *et al.* 2009, Pape *et al.* 2011).

Following the phylogeny of Woodley *et al.* (2009), and largely based on the analysis of Wood and Borkent (1989), the nematocerous Diptera is composed of seven suborders: Axymyiomorpha (1 family), Bibionomorpha (11 families), Blephariceromorpha (3 families), Culicomorpha (8 families), Psychodomorpha (6 families), Ptychopteromorpha (2 families), and Tipulomorpha (1 family). The Tipulomorpha are placed as the sister group to the remaining Diptera and the relationships between the remaining suborders remains uncertain (Woodley *et al.* 2009). Other studies have rearranged the families contained in the nematocerous suborders or united two or more suborders (e.g. Starý 2008, Bertone *et al.* 2008,

Wiegmann *et al.* 2011).

The Bibionomorpha contains the largest number of nematocerous families principally due to the elevation of many of the Mycetophilidae *s.l.* subfamilies to family rank (i.e. Keroplatidae, Bolitophilidae etc.). Within this suborder the Sciaroidea is consistently placed as a well supported, monophyletic, apical clade irrespective of the types of characters used (Woodley *et al.* 2009, Wiegmann *et al.* 2011)

The Sciaroidea *sensu* Wood & Borkent (1989) [= Mycetophiliformia (Amorim & Rindal 2007)] contains nine families (Bolitophilidae, Cecidomyiidae, Diadocidiidae, Ditomyiidae, Keroplatidae, Lygistorrhinidae, Mycetophilidae, Rangomaramidae (Jaschhof & Didham 2002), and Sciaridae) as well as 20 unplaced genera sometimes referred to as the *Heterotricha* group (Chandler 2002, Jaschhof 2011, though Amorim & Rindal (2007) include these in the Rangomaramidae). Unfortunately the relationships between the families within this group are not well resolved, even though there have been a number of phylogenetic analyses of the group in recent years (Chandler 2002, Jaschhof & Didham 2002, Hippa & Vilkamaa 2005, 2006, Amorim & Rindal 2007). Most of these studies were undertaken in an attempt to place the newly described Rangomaramidae and the various unplaced genera and did not use many exemplars from the other families of the Sciaroidea.

Amorim & Rindal's (2007) phylogenetic results are unique among recent analyses of the Sciaroidea, as they place the Cecidomyiidae and Sciaridae basal to the remaining Sciaroidea. All other studies placed either the Sciaridae or both families at the apex of the group (Chandler 2002, Jaschhof & Didham 2002, Hippa & Vilkamaa 2005, 2006). Given the range of topologies found within the Sciaroidea in these recent studies, caution must be taken in making statements about relationships within the group and further detailed collaborative study is clearly needed in future analyses in order to choose proper exemplars and

characters (see comments by Jaschhof (2011)).

Biology of the Mycetophilidae

The Mycetophilidae, small- to medium-sized (2-20 mm) nematocerous flies, are a ubiquitous component of forest ecosystems. They occur in humid habitats on all continents except Antarctica, and are particularly prevalent in woodlands with large amounts of leaf litter, humus, dead wood, and accompanying fungal hyphae (Hutson *et al.* 1980, Hovemeyer 1992, Irmler *et al.* 1996, Blagoderov & Grimaldi 2004). Mycetophilidae also seem to be particularly diverse and abundant in virgin forests (Økland 1996, Økland *et al.* 2005).

Little is known about the habits of Mycetophilidae adults or larvae. Some adults can be important pollinators (Okuyama *et al.* 2004) including of some sexually deceptive orchids (Gaskett 2011). Most adults are probably a food source for vertebrate and invertebrate predators (Mahaulpatha 2002, Russo *et al.* 2011, Williams *et al.* 2011). Some species also appear to act as vectors of fungal spores to new growth sites on dead or dying wood (Bouchard & Bouchard-Madrelle 2005). The immature stages of most Mycetophilidae are undescribed. The majority of larvae studied are those found feeding in fungal fruiting bodies (Buxton 1960, Ševčík 2010, Jakovlev 2011), where they are primary prey items for other invertebrates. Larvae found in other habitats (i.e. dead wood, bird's nests) presumably feed on fungal hyphae found there (Hutson *et al.* 1980, Irmler *et al.* 1996, Jakovlev 2011). It is thought that the actions of larval feeding may be an important part of wood-decay succession, contributing to soil build-up on forest floors (Alexander 2002). Unfortunately, little study has gone into the role of Mycetophilidae in wood-decay succession, probably due to the lack of comprehensive species level taxonomic revisions, and associated keys to species, for many genera. Much taxonomic work remains to be done, particularly outside of the Palaearctic region, to fill this gap and reduce the taxonomic impediment to undertaking biodiversity and ecological studies on Mycetophilidae.

Review of Mycetophilidae classification

The Mycetophilidae can be easily distinguished from other nematocerous Diptera families by the following characteristics: eyes separated dorsally, wing without discal cell, wing veins M and CuA joining at wing base (if at all), coxa large and hardly mobile, tibia with large apical spurs (Vockeroth 2009).

The family is placed phylogenetically within the Sciaroidea (=Mycetophiliformia, Amorim & Rindal 2007) in the suborder Bibionomorpha (*sensu* Amorim & Yeates 2006). Over the last few years there have been a number of phylogenetic studies of the relationships between the families of the Sciaroidea (see above). In the majority of these the sister group to the Mycetophilidae is the family Lygistorrhinidae (Chandler 2002, Hippa & Vilkamaa 2006, Amorim & Rindal 2007). These two families together form the Mycetophiloidea, whose sister group is in turn the Keroplatoidea, a group of four families (Amorim & Rindal 2007). The family Mycetophilidae is thought to have arisen in the early Cretaceous, as this is the earliest record of individuals attributable to this family in the fossil record (Blagoderov & Grimaldi 2004).

The Mycetophilidae currently consists of approximately 4100 described extant species in 180 genera (Pape *et al.* 2011). They are traditionally divided into three subfamilies: the Sciophilinae, Manotinae, and Mycetophilinae; though only the latter two are thought to be monophyletic (Söli 1997b, Hippa *et al.* 2004, Rindal & Söli 2006). Within these subfamilies, a number of tribes have been delimited following Edwards (1925), Tuomikoski (1966) and Matile (1971). The observed paraphyly of the Sciophilinae led to the suggestion that no subfamilies be recognized within the Mycetophilidae, retaining only a modified tribal classification (Söli 1997b). However, many workers have raised the tribes of the Sciophilinae to subfamily level in their discussions of phylogeny (see Gammelmo 2004).

Subsequent work on the subfamily Mycetophilinae and its two tribes has further clarified the limits of each tribe, and supports the monophyly of each tribe and the subfamily (Rindal & Söli 2006, Rindal *et al.* 2007, 2009a, b). The five tribes within the Sciophilinae are not as well defined, with only the tribes Sciophilini and Mycomyini appearing monophyletic (Söli 1997b). Further clarification of the tribes and subfamilies of the Mycetophilidae will become apparent when more morphological and molecular characters are explored, and more information on immatures is collected (Matile 1997a, Söli 1997b, Rindal & Söli 2006, Rindal *et al.* 2007, 2009a, b).

The incomplete and unpublished thesis of Tozoni (1998) has been cited by a number of authors, as she presents a phylogeny of the Mycetophilidae showing monophyletic clades for the four main tribes (raised in her work to subfamilies) of the Sciophilinae. The conclusions of this study should be treated with caution as it is incomplete, and contains much missing data and some errors in coding, probably due to a reliance on published descriptions rather than specimen study. The study does serve as source for potential characters to explore in addition to those presented by Söli (1997b).

Within the Mycetophilidae, there have been few systematic monographs revising all species in a genus, and even fewer providing species-level phylogenies (but see Vaisanen 1984, Matile 1996, Söli 1997a, 1997c, Kjærandsen 2006). These types of publications are vital for researchers investigating both phylogeny and insect biodiversity and ecology, as they provide detailed studies of morphology, a means of identifying specimens beyond the level of genus, and a phylogenetic framework to test hypotheses of evolutionary history. Understanding the phylogenetic relationships in a selected taxon will allow for interpretation of the ecological and behavioural features of these Mycetophilidae.

The tribe Sciophilini

The Sciophilini contains more than 520 species in 38 genera. It is one of the four tribes originally described by Edwards (1925) within Sciophilinae and contained those genera with macrotrichia on the wing membrane and bristles on the mediotergite. Söli (1997b) suggested that Sciophilini was monophyletic based on a 'tentative phylogeny' of the Sciophilinae that included a subset of genera assigned to this tribe. He retrieved a monophyletic clade supported by 12 unambiguous character state changes. However, the genera included in the analysis only represented a third of the genera placed in this tribe and all were Palaearctic.

The Australasian/Oceanian region contains seven endemic Sciophilini genera. This may reflect divergence due to the long isolation of the Australasian fauna from other regions, or it may be a reflection of the taxonomic approach of Tonnoir (1929). The six new genera he described from Australia were not compared with the types of genera previously described from the region by Skuse (1888, 1890). His unfulfilled expectation was that future workers would compare this work to previous types and synonymise where needed.

Other than Söli (1997b), most systematic studies on this tribe have been in the context of regional revisions, with no phylogenetic study of the relationships. Notable exceptions include a preliminary study of Sciophilini genera in the *Azana* Walker group by Matile (1998) who suggested that these ten genera formed a monophyletic group, though no phylogenetic analysis was undertaken, and phylogenetic studies of *Cluzobra* Edwards (Matile 1996), *Leptomorphus* Curtis (Borkent & Wheeler in press) and the Afrotropical species of *Sciophila* Meigen (Söli 1997a).

The genus *Leptomorphus* Curtis

The genus *Leptomorphus* is found worldwide, with the exception of Antarctica, and contains more than 35 species. As with most Mycetophilidae they inhabit moist and humid woodlands. The larvae are found on live polypore and wood encrusting fungi, where they collect and eat the falling spores using silk sheets they produce (Eberhard 1970, Santini 1985). Pupation takes place while hanging from a silk line under the host fungus (Eberhard 1970, Plachter 1980, Santini 1985). On emergence, adult males of some species search out and defend female pupae in preparation for mating when the female emerges (Eberhard 1970). Feeding habits of the adults are unknown. 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. In cold climates the species overwinter as eggs laid singly on dead wood (Brocher 1931, Santini 1985).

Members of *Leptomorphus* are some of the largest, most robust and colourful mycetophilids, ranging in body length from 6-14 mm, and in 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 the following combination of characters: 3 ocelli; interommatidial bristles absent or very sparse and short; wing surface with macrotrichia but no microtrichia (i.e. all trichia equal in length); 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 preepisternum II bare; antepronotum and proepisternum setose; and abdominal sternites with two mediolateral fold lines.

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. He noted that the wings of *Diomonus* were identical to *Leptomorphus*

except that R_{2+3} was present. Over the following ~80 years several more species were assigned to these two genera. Though there was some further discussion of the similarity between these genera, they were kept separate, and were even placed in different subfamilies of Mycetophilidae by Johannsen (1910, 1912).

Edwards (1925) synonymized these two genera as he felt that the only difference between them was the presence of R_{2+3} in *Diomonus*, a characteristic known to vary within genera of the Mycetophilidae. Edwards (1925) also placed *Leptomorphus* in the tribe Sciophilini where it has remained since. Most authors have followed this synonymization, though Matile (1977) gave *Diomonus* subgeneric status and questioned the validity of the synonymization.

Matile (1977, 1997b) described ten new species, the first from the Afrotropical region. Matile (1977) also divided the genus into four subgenera. *Leptomorphus* (*s.s.*), *Diomonus*, *Gymnoscutum* Matile, and *Austroleptomorphus* Matile. The limits of the subgenera were based principally on the presence or absence of two wing veins and the number of setae on the scutum or scutellum. No phylogenetic hypothesis has been proposed for the genus or subgenera, as a larger revision was thought necessary before any phylogeny could be considered reliable (Matile 1997b).

Most species of *Leptomorphus* 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 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, 1997b) and a recent paper naming eight new species from the Oriental and northwestern Australasian realms (Papp & Ševčík 2011).

Objectives

The purpose of this thesis work was two-fold: to revise the genus *Leptomorphus* including a phylogeny of the species relationships, and to explore the phylogenetic relationships between the genera of the Sciophilini.

In the first study (Chapter 2) the world fauna of the genus *Leptomorphus* is revised and the monophyly of the genus and previously described subgenera are phylogenetically tested. All species known prior to 2011 (due to the timing of this research, eight recently described (December 2011) species are not included) and new species discovered here are described, and the habitus, wings, male genitalia and distributions figured. A hypothesis of the phylogenetic relationships between species is presented and the monophyly of each of the subgenera rejected. The distribution of morphological characters across the phylogenetic tree is discussed in relation to their support for the monophyletic clades within the tree.

The second study (Chapter 3) explores the limits, monophyly and classification of the tribe Sciophilini using morphological characters. Exemplar taxa of all currently and previously included genera are included, with representative species from multiple biogeographic regions used for genera that are widely distributed. The patterns of relationships within the tribe were discussed and generic diagnoses provided for all included genera.

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CONNECTING STATEMENT

Taxonomic revisions of genera are essential to providing an understanding of the diversity of both the species and morphology of a given genus. When this information is accompanied by a phylogenetic hypothesis of species relationships these revisions give the reader a complete picture of both the evolutionary history and current status of the genus. This type of revisionary work is critical to studies of biodiversity and biogeography as it provides, respectively, a comprehensive source for identification of specimens and a phylogeny for testing biogeographic and ecological patterns. There have been very few comprehensive revisions of mycetophilid genera and even fewer have included a species-level phylogeny. The widespread and species-rich genus *Leptomorphus* Curtis was selected for revision as a first step toward unraveling the systematics of the tribe Sciophilini. A worldwide revision of *Leptomorphus* will provide a foundation for future ecological and biodiversity workers requiring biological information and identification tools for this genus. The phylogeny of the genus was explored in order to evaluate previous, untested, assumptions of relationships between the species of the genus, as well as to test the monophyly of the genus.

CHAPTER 2. SYSTEMATICS AND PHYLOGENY OF *LEPTOMORPHUS* CURTIS (DIPTERA: MYCETOPHILIDAE)

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, 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*, was 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.

Table of Contents

Introduction

The genus *Leptomorphus* Curtis, 1831 (Diptera: Mycetophilidae *s.s.*) 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 Palaearctic (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_{2+3} was present. Over the following ~80 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_{2+3} 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_{2+3}) 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 (Söli 1997, Rindal *et al.* 2009). In these studies, the genus is consistently placed within the subfamily Sciophilinae and tribe Sciophilini. Söli (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 (C. Borkent, unpub. data) as shown in the current study.

This paper provides the first world revision of the genus *Leptomorphus* and 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 Simplemappr (Shorthouse 2010).

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 ± 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 Söli (1997) for some genitalic interpretation. The only exception is in the case of the posterior wing veins CuA_1 and CuA_2 of Cumming & Wood (2009), which are interpreted here as veins M_4 and CuA respectively (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 (Söli 1997, C. Borkent, unpub. data), 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 of the 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

Species of *Leptomorphus* are distinguished from other Sciophilini genera (those genera unique in having two fold lines on at least sternites 3-6 (Söli 1997) and bristles present on the mediotergite and laterotergite) by the following combination of characteristics: 3 ocelli; interommatidial 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 katepisternum 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.

Generic description

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

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; interommatidial 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, in all species but *L. perplexus*, close together at vertex on a dark background, 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 hairs on remainder. Laterotergite with several bristles and setae, sometimes with covering of appressed hairs. 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 ½ 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 Rs. R_{2+3} absent or present near base of Rs, 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. False CuP present as a darkened crease running just behind posterior fork but not reaching to wing margin. CuP not reaching wing margin. A_1 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 CuP 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 ~½ 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° to either side.

Male genitalia: Sternite 9 ranging from bare, membranous, or small rounded sclerite (<½ 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 fused with aedeagus, erroneously considered the ejaculatory apodeme in 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 not strikingly modified. 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 Figs. 138-139). These species would likely run to *L. tagbanua* with the exception of *L. alienus*, which would run to *L. tabatius*. Papp & Ševčík (2011) provided a key to these eight species.

1. Vein R_{2+3} present (i.e. Figs. 64, 65) … 2

   - Vein R_{2+3} 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 (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_{2+3} 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_{2+3} joining R_5 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 hairs (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 hairs (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 hairs and without bristles; Neotropical or Afrotropical…10
    - Scutellum without covering of fine hairs, 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 bare except for a few 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 ¾ towards apex, fore- and midtibia with apical ½ 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 Amazonian basin, 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 ¼ of length of tergite 9 towards apex, gonocoxite with scalloped edge apicomedially and hook-like process laterally (Fig. 92) (southern Brazil, Fig. 142) …*L. amorimi* 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 ½ the length of medial, thin and rod-like (Fig. 98); female unknown (northern Argentina, 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 ¼ 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 ¾ 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 genitalia unique, 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)

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 2Xas long as face. Face yellow; 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 5 segments, 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 interommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Three ocelli; 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 ± 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; disc 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 5.19 ± 0.61 mm (4.76 - 5.66 mm,

n = 8). Hyaline, with 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_{2+3} 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 just apical of origin of r-m. A_1 faintly present. **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, ventral lobe prominent 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. T**horax**: Length 1.46mm (max: 1.72mm, min: 1.23mm, n = 4). **Wing** : Length 6.44mm (max: 7.46mm, min: 5.25mm, n = 4). **Abdomen**: Cercus yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus aliciae* is known from Ivory Coast,

Ghana, Nigeria, Cameroon, Central African Republic, and Uganda (Fig. 135), at elevations from 45-725 m.

TAXONOMIC 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 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. m#ht/ L. Matile det. 1974; HOLOTYPE m#/ Leptomorphus aliciae/ Matile/ Det. C.J. Borkent, 2011" [MNHN].

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

Other material: GHANA, Western Region, Ankasa game prod. Reserve, 6-12.xii.1993, J. Kjærendsen, T.Andersen. (1m#, ZMUN); Boti Falls, 28.x-4.xi.1994. (2m#, ZMUN); Kakum N.P., 31.x-8.xi.1994. (3m#, ZMUN); IVORY COAST, Taï, 9.v.1980, G. Couturier. (1m#, MNHN); NIGERIA, Ibadan, 25.viii.1962, D.C. Eidt. (1f#, CNC); Illaro Forest, 3.iii.1974, M.A. Cornes. (1f#, MNHN); Sapoba, 11.ix.1962, D.C. Eidt. (1m#, 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 hairs; male foretibia with a dense row (comb) of short anteroventral bristles;

palp segment 5 with thick covering of fine, white, setulae; male genitalia unique, gonocoxite arising ¼ of length of tergite 9 towards apex, gonocoxite with scalloped edge apicomedially, hook-like process laterally and short basomedial gonocoxal lobe bearing several long setae (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; 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 5 segments, 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 interommatidial 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; disc of scutum covered with hairs; 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 hairs; bristles absent. Prescutum brown. Mediotergite dark brown with 4 bristles on posterolateral corners, and covering of appressed hairs. Laterotergite brown, with covering of appressed hairs; anterior margin of laterotergite abutting katepisternum. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum brown with posterodorsal corner yellow. Antepronotum 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 7.54 mm (n = 1). Hyaline, with 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 before origin of Rs. R_{2+3} 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_1 faintly present. **Abdomen**: Tergites principally brown to dark brown, T2-5 with parellel 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 isoceles 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 apicomedially, 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. T**horax** : Length 2.01 mm (n = 1). Metepisternum brown. **Wing**: Length 8.28 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: *Leptomorphus amorimi* is known from southern Brazil (Fig. 142).

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 useful 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 m#/ *Leptomorphus amorimi*/ Borkent, new species / C.J. Borkent 2011" [MCZ]

Paratype: BRAZIL, Santa Catarina, Nova Teutonia, v.1964, F. Plaumann. (1f#, 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 unique, gonostylus a single blunt taper (Fig. 93).

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; 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 with 5 segments, all 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 interommatidial setulae scattered on surface. Occiput brown on anterior 1/2-2/3, remainder yellow with appressed, anteriorly directed setae. Three ocelli; 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 1.23 mm (1.19 - 1.27 mm, n = 2). Mostly brown, with anterolateral area yellow. Scutum dark brown with blue-green specks; disc 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 5.25 mm (5.08 - 5.41 mm, n = 2). Hyaline, with apical macula light, reaching wing tip, extending faintly along posterior wing margin into apex of cell cua1, 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 Rs. R_{2+3} 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_1 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: *Leptomorphus babai* is known from Japan (Fig. 141)

TAXONOMIC 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 m#/ KPU 0163/ Leptomorphus/ babai/ SASAKAWA" [OMNH].

Paratype: labelled as for holotype except 7.VI.1955 (1m#, 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_{2+3} present and forming a quadrilateral cell; male genitalia unique (Fig. 94).

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 1.5Xas long as face. Face yellow to light brown; 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 5 segments, 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 interommatidial setulae scattered on posterior half. Occiput light-dark brown with appressed, anteriorly directed setae. Three ocelli; 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 ± 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; disc 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 2. Anepimeron light brown to brown. Anepisternum light brown to brown. Katepisternum brown. Antepronotum 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 8.09 ±1.42 mm (7.13 - 9.59 mm, n = 10). Hyaline, with 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 Rs. R_{2+3} 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_1 faintly present. **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 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. T**horax**: Length 1.89 ± 0.39 mm (1.48 - 2.13 mm, n = 10). **Wing**: Length 7.36 ± 1.12 mm (6.23 - 8.12 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: *Leptomorphus bifasciatus* is known from British

Columbia east to Maine and south to North Carolina (Fig. 147), at elevations from 25-1800 m.

TAXONOMIC 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. 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: xxx). 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 was 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 m#/ *Leptomorphus bifasciatus* / (Say) / Det. C.J. Borkent, 2011" [LEM].

Other material: CANADA, BC, Kinbasket Reservoir, Bush Arm, 10-11.viii.2009, Cooper, Beauchesne and Associates Ltd. (1m#, RBCM); ON, Coniston, 27.vii, E.S. Parish. (1m#, USNM); Foresters Falls, 14.viii.1991, J.R. Vockeroth. (1m#,

CNC); Lake Abitibi, 4.viii.1925, N.K. Bigelow. (1m#, CNC); 7.viii.1925. (1m#, CNC); Tobermory, Dunk's Bay, 26.viii.1996, S.A. Marshall. (1m#, DEBU); Bruce Co., William Henry Marsh, 31.viii.1999, S.A. Marshall. (1f#, DEBU); Carleton Co., 8km S Richmond, 30.viii.2008, D.M. Wood. (1m#, LEM); QC, 2.3km SSW Rapide-Danseur, 29.vi-28.vii.2007, A. Hibbert. (1m#, LEM); 30.vi-29.vii.2007. (2m#, 1f#, LEM); Lake Duparquet Res. and Train. For., 12.vii-1.viii.2006, A. Hibbert. (1f#, LEM); Mont St-Bruno, 24.vi-1.vii.2008, V. Levesque. (1m#, LEM); Mont St-Hilaire, 18-24.ix.2001, E. Fast. (1m#, LEM); 3.viii.2007, C.J. Borkent. (1m#, LEM); 1-8.vii.2008, V. Levesque. (1m#, LEM); 23-30.vi.2008. (1m#, LEM); Old Chelsea, 13.ix.1956, J.R. Vockeroth. (1m#, CNC); Rougemont, 14-21.vii.2008, V. Levesque. (1m#, LEM); 21-28.vii.2008. (2m#, 1f#, LEM); 23-30.vi.2008. (1m#, LEM); 30.vi-7.vii.2008. (1m#, LEM); SK, Belanger, Osten Sacken. (1m#, MCZ); USA, MA, Chester, 5.viii.1911. (1m#, MCZ); ME, York Co., West Lebanon, 28.viii-3.ix.1990, D.W. Barry. (1m#, UNHC); NC, Mason Co., Highlands, 20.vi.1957, J.R. Vockeroth. (1m#, CNC); 21.vi.1957, J.R. Vockeroth. (1m#, CNC); 24.vi.1958, J.L. Laffoon. (1m#, ISUI); NH, Dolly Copp, White Mtns., 13.vii.1931, A.L. Melander. (1f#, USNM); Mt. Washington, A.T. Slosson. (1m#, CUIC, 1m#, USNM); Carr. Co, 1mi. N Wonalancet, E Fk. Spring Brk., 18-23.vii.1985, D.S. Chandler. (1m#, UNHC); 24-30.vii.1985. (1m#, UNHC); 18.ix-1.x.1985. (1m#, UNHC); The Bowl, 2.5mi. NW Wonalancet, 2-10.viii.1984, D.S. Chandler. (1f#, UNHC); 20-26.vii.1984. (2m#, UNHC); 28.vi-4.vii.1984. (1m#, UNHC); 31.vii-6.viii.1985. (1m#, UNHC); Coos Co., 1mi. NE East Inlet Dam, 22.viii-12.ix.1986, D.S. Chandler. (1m#, UNHC); 10-24.vii.1986. (2m#, UNHC); 25.vi-9.vii.1986. (2m#, UNHC); 13-26.ix.1986. (1f#, UNHC); Norton Pool, 3mi. NE East Inlet Dam, 8-21.viii.1986, D.S. Chandler. (1m#, UNHC); 27.ix-17.x.1986. (1f#, UNHC); Straf Co., 1mi. SW Durham, 13.vii.1991, W.J. Morse. (1f#, UNHC); 4mi. W Durham, 23-26.viii.1982, R.M. Reeves. (2m#, UNHC); 13-15.vii.1982. (1m#, UNHC); Spruce Hole, 3mi. SW Durham, 7-20.viii.1987, D.S. Chandler. (1m#, UNHC);

NY, Adirondacks, Avalanche Trl, 30.vii.1929, A.L. Melander. (1f#, ANSP); Albany Co., Huyck Preserve, Rensselaerville, 4.vii.1968, W.G., M.J. Eberhard. (1m#, 1f#, MCZ); Greene Co., viii, (1m#, CMNH); Hamilton Co., vic. Jockeybush Outlet, 5.viii.1961, J.L. Laffoon. (1f#, ISUI); PA, Centre Co., Bear Meadows, 6.ix.1979, P.H. Adler. (1f#, USNM); McKean Co, 4.9km S Ludlow, Pigeon Run, 4.viii.1994, M.J. Ricke. (1m#, CMNH); TN, Burrville, 14.vii.1953, Benesh. (1m#, MNHN); VA, Giles Co., Clover Hollow, 9.viii.1967, Ento. Class. (1m#, SEMC); Mt. Lake Biol. Sta., 26.vi.1975, G.W. Byers. (1f#, SEMC); VT, Brattleboro, 1909, H. Kahl. (1m#, CMNH); Morrison, White Mtns. (3m#, 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 hairs; male foretibia with a dense row (comb) of short anteroventral bristles; palp segment 5 with thick covering of fine, white, setulae; male genitalia unique, tergite 9 rounded basally, tapering to a single, long, point posteriorly that extends beyond cerci, gonocoxite without gonocoxal lobe (Fig. 95).

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; 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 5 segments, 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 interommatidial setulae scattered on surface. Occiput brown 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 1.31 mm (n = 1). Dark brown with yellow lateral spots. Scutum dark brown/black with blue-green specks, pair of small yellow anterolateral spots; disc of scutum covered with hairs; 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 hairs; bristles absent. Prescutum yellow. Mediotergite dark brown with 6 bristles on posterolateral corners, and covering of appressed hairs. Laterotergite brown, with covering of appressed hairs; anterior margin of laterotergite abutting katepisternum 2. Anepimeron brown with posterodorsal corner yellow. Anepisternum dark brown. Katepisternum 2 brown with dorsal third yellow. 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 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, with 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 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 it's own length prior to origin of Rs. R_{2+3} 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_1 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: *Leptomorphus brandiae* is known from Costa Rica (Fig. 143), at elevations from 300-560 m.

ETYMOLOGY: This species is named for my wife Brandi Borkent, as it is a particularly beautiful species, as well as in thanks for her support and encouragement in all matters relating to life during my doctoral program and 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 m#/ *Leptomorphus brandiae* /Borkent, new species / C.J. Borkent 2011" [LEM].

Paratypes: COSTA RICA: Alajeula, 4.3km SSE La Fortuna, 15.viii.2010, C.J. Borkent [with cast off pupal skin] (2m#, 1f#, 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 genitalia unique, 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).

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; 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 5 segments, 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 interommatidial 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 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; disc 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 katepisternum 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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, with 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_{2+3} 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_1 faintly present. **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: *Leptomorphus carnevalei* is known from the Republic of the Congo and Democratic Republic of the Congo (Fig. 135), at elevations

from 315-475 m.

TAXONOMIC 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./ m#ht/ L. Matile det. 1974" [MNHN].

Paratypes: DEMOCRATIC REPUBLIC OF THE CONGO, Luebo, II.[19]59, F.J. François. (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.

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 1.5Xas long as face. Face yellow; 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 5 segments, 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 interommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Three ocelli; 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; disc 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 thicknessalong 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 5.33 mm (n = 1). Hyaline, with 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_{2+3} 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 at same level as r-m. A_1 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: *Leptomorphus chaseni* is known from northern Borneo [Kenokok, Mt Kinabalu] (Fig. 137), at an elevation of 1000 m.

TAXONOMIC 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 female, pinned on double mount, labelled "[Circular label with red edge] HOLO-/ TYPE; B.N. BORNEO/ Mt. Kinabalu,/ Kenok,/ 3,300 ft./ 26th.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 genitalia unique, 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)

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; 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 5 segments, 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 interommatidial 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 with electric blue green specks. **Thorax**: Length 1.33 ± 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; disc 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 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 5.78 ± 0.42 mm (5.49 - 6.15 mm, n = 7). Hyaline, with 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 Rs. R_{2+3} 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_1 faintly present. **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: *Leptomorphus couturieri* is known from Ivory Coast

and Ghana, (Fig. 135), at elevations from 120-200 m.

TAXONOMIC 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./ m# holotype/ L. Matile det. 1995" [MNHN].

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

Other material: GHANA, Western Region, Ankasa game prod. Reserve, 9.xii.1993, J. Kjaerendsen; T. Andersen. (1m#, ZMUN); same except 8-15.xi.1994. (2m#, ZMUN); 31.x-8.xi.1994. (3m#, ZMUN); IVORY COAST, Taï, 6.v.1980, G. Couturier. (1m#, 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 hairs; male foretibia with a dense row (comb) of short anteroventral bristles; palp segment 5 with thick covering of fine, white, setulae; male genitalia unique, 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 ½ the length of medial, thin and rod-like (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; 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 with 5 segments, all 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 interommatidial 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; disc of scutum covered with hairs; 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 hairs. Prescutum yellow. Mediotergite brown with 4 bristles on posterolateral corners, and covering of appressed hairs. Laterotergite brown, with covering of appressed hairs; anterior margin of laterotergite abutting katepisternum 2. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum 2 brown with dorsal third 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 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 5.99 mm (n = 1). Hyaline, with 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 Rs. R_{2+3} 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_1 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 ~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: *Leptomorphus crassipilus* is known from Argentina (Fig. 142).

ETYMOLOGY:: The species name is in reference to the multiple rows of thick (*crassi-*) setae (*-pilus*) on the apex of tergite 9, which is currently 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 m#/ *Leptomorphus crassipilus*/ Borkent, new species / C.J. Borkent 2011" [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*).

Leptomorphus (Gymnoscutum) crosskeyi Matile, 1997: 148. (given again as new replacement name for *africanus*) (junior synonym, junior homonym)

References: Crosskey 1980: 1221 (catalogue appendix as *L. africanus*); Matile 1997: 143, 147-150 (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 brown; male genitalia unique, 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).

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; 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 5 segments, 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. 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. **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; disc 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 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 5.51 mm (5.25 - 5.74 mm, n = 4). Hyaline, with 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_{2+3} absent. R_5 straight, slight posterior turn near tip. M_1 reaching apex before R_5, apices of M veins thinning towards margin. M_4-CuA fork arising just apically of origin of r-m. A_1 faintly present. **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 6.52 mm (6.4 - 6.64 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: *Leptomorphus crosskeyi* is known from Ghana, Central African Republic, and Uganda (Fig. 136), at elevations from 180-1250 m.

TAXONOMIC 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. m#ht/ L. Matile det. 1974; HOLOTYPE m#/ *Leptomorphus crosskeyi*/ Matile/ Det. C.J. Borkent, 2011" [MNHN].

Paratypes: Labelled as for holotype (1f#, labelled as Allotype, MNHN); except 2.x.1970 (1f#, MNHN); 20.viii.1967 (1m#, 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. (1m#, MNHN); same, except 2.x.1970. (1f#, MNHN); GHANA, Kakum N.P., 8-15.x.1994. (1m#, ZMUN); UGANDA, Kibale Forest, 12.xii.1971-9.i.1972, R.L. Masou. (1m#, 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 hairs; male foretibia with a dense row (comb) of short anteroventral bristles; palp segment 5 with thick covering of fine, white, setulae 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).

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; 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 5 segments, 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 interommatidial 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 1.48 mm (n = 1). Dark brown with yellow lateral spots. Scutum dark brown with blue-green specks; disc of scutum covered with hairs; 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 hairs; bristles absent. Prescutum yellow. Mediotergite dark brown with 4 bristles on posterolateral corners, and covering of appressed hairs. Laterotergite brown, with covering of appressed hairs; anterior margin of laterotergite abutting katepisternum 2. Anepimeron brown with posterodorsal corner yellow.

Anepisternum dark brown. Katepisternum 2 brown with dorsal third yellow. Antepronotum 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 6.40 mm (n = 1). Hyaline, with 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 Rs. R_{2+3} 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_1 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 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 6.48 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: *Leptomorphus eberhardi* is known from Costa Rica (Fig. 143), at elevations from 615-1325 m.

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 m#/ *Leptomorphus eberhardi*/ Borkent, new species / C.J. Borkent 2011" [ZMUN].

Paratypes: COSTA RICA: La Suiza, x.1923, P. Schild (1f#, 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 hairs; 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).

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; 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 with 5 segments, all 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 interommatidial 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 2.5X their own diameter from eye margin, ocellar triangle dark brown. **Thorax**: Length 1.73 ± 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; disc of scutum covered with hairs (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 hairs; bristles absent. Prescutum anterior half yellow, posterior half brown. Mediotergite dark brown with 6 bristles on posterolateral corners, and covering of appressed hairs. Laterotergite brown, with covering of appressed hairs; anterior margin of laterotergite abutting katepisternum 2. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum 2 brown with posterodorsal corner yellow. Antepronotum 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 6.60 ± 0.93 mm (5.82 - 7.54 mm, n = 10). Hyaline, with 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 Rs. R_{2+3} 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_1 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 gonoocoxal lobe as long as gonocoxite, arising mediobasally and armed with 4 long laterlally pointing apical bristles, bearing gonostylus at apex. Gonostylus with two lobes, dorsal lobe short and broad with a number of setae, 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 6.40 mm (6.07 - 6.72 mm, n = 2). **Legs**: Foretibia without comb of short setae on anteroventral surface. **Abdomen**: Cercus yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus fasciculatus* is known from Panama, Ecuador, Peru, Bolivia, Brazil (Sao Paulo, Mato Grosso, Rio de Janeiro) (Fig. 142), at elevations from 55-700 m.

TAXONOMIC 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/ 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 m#/ *Leptomorphus fasciculatus* /Edwards / Det. C.J. Borkent, 2011" [MTD].

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

Other material: BRAZIL, MT, Maracaju, vi.1937, Serviço Febre Amarela. (1m#, 1, MZSP); RJ, Nova Iguaçu, Reserva Biologica do Tinguá, 5-8.iii.2002, S.T.P. Amarante. (1m#, MZSP); SP, R. Parana, Porto Cabral, 1-25.vi.1944, Trav. Fo., Carrera, E. Dente. (1m#, MZSP); ECUADOR, Orellana, 1km S Onkone Gare Camp, 22.vi.1996, T.L. Erwin. (1m#, LEM); 5.ii.1996. (1m#, LEM); Tiputini Biodiversity Stn., 24.x.1998, T.L. Erwin. (1m#, LEM); PANAMA, Cabima, 23.v.1911, A. Busck. (2f#, USNM); Chilibre, 1.i.1940, G. Fairchild. (1m#, MCZ); Canal Zone, Barro Colorado Isle., 26.vii.1982, R.B. & L.S. Kimsey. (2m#, CNC); Barro Colorado Isle., Dodge. (1f#, USNM); PERU, Pichis River, Puerto de Yessup, 1903. (1m#, 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 hairs; male foretibia with a dense row (comb) of short anteroventral bristles; palp segment 5 with thick covering of fine, white, setulae; male genitalia unique, 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)

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; 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 with 5 segments, all 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 interommatidial 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 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; disc of scutum covered with hairs; 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 hairs; bristles absent. Prescutum anterior half yellow, posterior half brown. Mediotergite dark brown with 4-6 bristles on posterolateral corners, and covering of appressed hairs. Laterotergite brown, with covering of appressed hairs; anterior margin of laterotergite abutting katepisternum 2. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum 2 brown with posterodorsal corner yellow. Antepronotum 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 6.27 mm (6.0 - 6.56 mm, n = 2). Hyaline, with 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 Rs. R_{2+3} 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_1 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 woth 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 6.81 mm. **Legs**: Foretibia without comb of short setae on anteroventral surface. **Abdomen**: Cercus yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus femoratus* is known from Peru and Bolivia (Fig. 143), at elevations from 650-1230 m.

TAXONOMIC 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 m#/ *Leptomorphus femoratus* /Edwards / Det. C.J. Borkent, 2011" [MTD]

Other material: PERU, Monson Valley, Tingo Maria, 11.xii.1954, E.I Schlinger, E.S. Ross. (1m#, MZSPMZUSP); Huanuco, Rio Monzan, 13.x.1960, J. Schunke. (1f#, 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); Zaitzev and Ševčík, 2002: 204 (removed from synonymy with *L. quadrimaculatus*); Ševčík & Papp 2003: 288 (Hungary); Gammelmo & Söli 2006: 60, (Norway); Ševčík 2006: 14 (biology, photo of adults en copula), 2010: 17 (fungal association); Kjaerendsen *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 unique, gonocoxite smoothly curved along entire length, not swollen at apex (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; 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 with 5 segments, all 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 interommatidial setulae in ~1/4 of the ommatidial junctions, scattered on all but medial margin. Occiput brown with appressed, anteriorly directed setae. Three ocelli; 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; disc 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 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 7.19 mm (6.56 - 7.54 mm, n = 3). Hyaline, with

apical macula not reaching wing tip, extending faintly along posterior wing margin into apex of cell cua1 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_{2+3} 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_1 faintly present. **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 ~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. See Zaitzev & Ševčík (2002) for description of female.

Immatures: Undescribed.

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

copulation lasts several hours (Ševčík 2006).

DISTRIBUTION: *Leptomorphus forcipatus* is known from Finland, Czech Republic, Slovakia, Sweden, Norway, Hungary, Germany and Switzerland (Fig. 140), at elevations from 35-780 m.

TAXONOMIC 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. 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" [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. (1m#, LEM); GERMANY, Saxony, Sachsische Schweiz N.P., 22-23.vi.1989, U. Kallweit. (1m#, MTD); NORWAY, AK, As; Arungen, Syverud, 15.viii-3.ix.2003, E. Rindal, L. Aarvik. (1m#, ZMUN); SLOVAKIA, Polana Biosphere Reserve, 24.v-11.vii.2007, J. Roháček, J. Ševčík. (1m#, 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 r1; medial spot absent (Fig. 56); male genitalia unique, sternite 9 bearing a medial invagination for posterior 2/3 and with 2 dark, apical points (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; 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 with 5 segments, 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 interommatidial 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 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; disc 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 katepisternum 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 5.15 ± 1.24 mm (4.02 - 6.15 mm, n = 10). Hyaline, with apical macula 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 a few short setae. Vein sc-r present, apical end joining R within its own length prior to origin of Rs. R_{2+3} absent. R_5 straight, slight posterior turn near tip. M_1 reaching apex at same level as R_5, apices of M veins reaching wing margin. M_4-CuA fork arising apically of origin of r-m. A_1 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 5.86 mm (5.41 - 6.31mm, n = 2). **Legs**: Foretibia without comb of short setae on anteroventral surface. **Abdomen**: Cercus yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus furcatus* is known from New Mexico and Arizona south to Northern Mexico (Fig. 148), at elevations from 915-2255 m.

ETYMOLOGY: The species name refers to the strongly forked nature of sternite 9, particularly the strongly sclerotized apicolateral points, a condition currently 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.2077, el 7400'/ (32°54.8'N 108°13.6'W)/ Malaise trap, J.E. O'Hara; HOLOTYPE m#/ *Leptomorphus furcatus* / Borkent, new species / C.J. Borkent 2011" [LEM]

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

CAS); 14.viii.1985. (1m#, 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 unique, posterolateral projection (tergal evagination) of tergite 9 either square or with slightly acute angle on medial corner, gonostylus with shortest lobe rounded (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; 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 5 segments, 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 interommatidial setulae absent. Occiput yellow with dorsolateral brown spots, 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 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; disc 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 katepisternum 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 5.08 mm (4.76 – 5.41 mm, n = 1). Hyaline, with 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_{2+3} absent. R_5 straight, slight posterior turn near tip. M_1 reaching apex before R_5, apices of M veins fading near margin but reaching wing margin. M_4-CuA fork arising apically of origin of r-m. A_1 faintly present. **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: *Leptomorphus gracilis* is known from the Central African Republic and Gabon (Fig. 135), at elevations from 200-520 m.

TAXONOMIC 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. m#ht/ L. Matile det. 1974; HOLOTYPE m#/ *Leptomorphus gracilis*/ Matile/ Det. C.J. Borkent, 2011" [MNHN].

Other material: GABON, Makokou M'Passa, Bale Affl., 7-16.v.1979, J. Legrand (1m#, MNHN, HT of *L. elegans*); same except 21-28.v.1979, (1m#, 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 unique, gonostylus with only a single lobe, apical tergal evaginations present (Fig. 105). This is also the only species currently known from Madagascar.

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; 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 5 segments, 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 interommatidial setulae absent. Occiput yellow with appressed, anteriorly directed setae. Three ocelli; 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; disc 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 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 yellow with small brown spot anterodorsally. Antepronotum 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 5.17 mm (n = 1). Hyaline, with 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_{2+3} absent. R_5 straight, slight posterior turn near tip. M_1 reaching apex just before R_5, apices of M veins reaching wing margin. M_4-CuA fork arising after apex of r-m. A_1 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 indentaiton. 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 5.04 mm (4.59 - 5.49mm, n = 2). **Abdomen**: Sternites white/yellow. Cercus yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus grjebinei* is known from the eastern rainforests of Madagascar (Fig. 134), at elevations from 1000-1100 m.

TAXONOMIC 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. m#ht/ L. Matile det. 1974" [MNHN].

Paratypes: Same data as holotype (1f#, labelled as Allotype, MNHN).

Other material: MADAGASCAR, Prov. Fianarantsoa, 7km W Ranomafana, 1100m, 1-7.XI.1988, W.E. Steiner (1f#, 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; male genitalia unique, gonostylus with single large, hook-tipped lobe (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; 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 with 5 segments, 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 interommatidial setulae scattered on surface. Occiput brown with appressed, anteriorly directed setae. Three ocelli; 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 anterio- medio- and posterolateral yellow spots, to yellow with spot at wing base and thick Y-shape originating posteriorly both dark brown; disc 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 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 5.34 ± 0.89 mm (4.67 - 6.07 mm, n = 10). Hyaline, with 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_{2+3} 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 well before origin of r-m. A_1 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 base3 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 ± 0.22 mm (1.07 - 1.48 mm, n = 10). **Wing**: Length 6.07 ± 1.54 mm (4.26 - 6.89 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 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: *Leptomorphus hyalinus* is known from Alaska and BC east to Maine and Florida (Fig. 149), at elevations from 5-915 m.

TAXONOMIC DISCUSSION: The color 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. 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 m#/ *Leptomorphus hyalinus*/ Coquillett / Det. C.J. Borkent, 2011" [USNM].

Other material: CANADA, BC, Hixon, 10.viii.1966, E.D.A. Dyer. (1m#, CNC); MB, Aweme, 18.viii.1912, E. Criddle. (1f#, ANSP); ON, 7.5km W Carleton Place, 14.x.2000, L. Masner. (2f#, CNC); Lancaster, 1.vii.2003, R. Zeran. (1f#, LEM); Ottawa, 1.ix.1968, J.R. Vockeroth. (1m#, CNC); 1.ix.1993. (1m#, CNC); 23.ix.1993. (1m#, CNC); Tobermory, Dunk's Bay, 12.viii.1996, S.A. Marshall. (1m#, DEBU); Bruce Co., Dunk's Bay, 25.viii-1.ix.2005, S.A. Marshall. (1f#, DEBU); QC, 2.3km SSW Rapide-Danseur, 29.vi-28.vii.2007, A. Hibbert. (3m#, 1f#, LEM); 30.vi-29.vii.2007. (3m#, 1f#, LEM); 27.v-29.vi.2007. (1m#, LEM); Lake Duparquet Res. and Train. For., 11-31.vii.2006, A. Hibbert. (1m#, 2f#, LEM); 19.vi-11.vii.2006. (1f#, LEM); Old Chelsea, 2.vii.1959, J.R. Vockeroth. (1f#, CNC); Ste-Anne-de-Bellevue, Morgan Abrtm., 12.vii.2007, C.J. Borkent. (1m#, LEM); 17.vii.2007. (9m#, 4, LEM); 18.vii.2007. (5m#, 7, LEM); 21.ix.2007. (1f#, LEM); 20.viii.2008. (1f#, LEM); Terrasse-Vaudreuil, Molson Reserve, 15-18.vii.1999, S.E. Brooks. (1m#, LEM); USA, AK, 11mi. S Anderson Jct., Rte 3mi. 270, 23.vi-11.viii.1984, S. & J. Peck. (1f#, CNC); FL, Flamingo, 4.vi.1963, G.R. Sutter. (1m#, ISUI); Gainesville, 8-22.xii.1986, W. Mason. (2m#, 1f#, CNC); IA, Ames, 1.xi.1946, D.E. Hardy. (1m#, ISUI); Sioux City, 5.ix.1949, J.L. Laffoon. (1f#, ISUI); 8.ix.1951. (2m#, 1, ISUI); Boone Co., Ledges State Park, 13.x.1950, J.L. Laffoon. (1m#, ISUI); 18.ix.1951. (1m#, ISUI); 3.vii.1961. (1m#, ISUI); Polk Co., Alleman, 27.viii.1952, J.L. Laffoon. (1m#, ISUI); Van Buren Co., Lacey-Keosauqua St. Pk., 9.ix.1949, J. Laffoon, J. Slater. (1m#, ISUI); 10.ix.1949. (1m#, ISUI); IN, La Fayette, 18.viii.1916, J.M. Aldrich. (1f#, USNM); KS, Riley Co., Manhattan, 14.vi.1968, G.F. Hevel. (1m#, USNM); MA, Barre, 16.ix.2008, C. Eiseman. (1f#, LEM); MD, Laurel, 25.vi.1965. (1m#, CNC); Plummers Island, 21.vii.1971, K.V. Krombein. (1m#, USNM); ME, York Co., West Lebanon, 31.vii-6.viii.1990, D.W. Barry. (1m#, UNHC); 11-17.ix.1990. (1f#, UNHC); MN, Clearwater Co., Lake Itasca, 3.ix.1950, J.L. Laffoon. (1f#, ISUI); MO, Wayne Co., Williamsville, x.1987, J. Becker. (3f#, CNC); NC, Looking Glass Rock Nr. Pisgah Forest, 19.vii.1957, J.G. Chilcott.

(1m#, CNC); Rainbow Falls, Gr. Sm. Mtns N.P., 28.v.1999, L. Quate. (1m#, CNC); NH, Jefferson Notch, 20.vii.1961, W.W. Wirth. (1f#, USNM); Rock. Co., Seabrook, Backdunes, 7-12.vii.1989, D.S. Chandler. (1m#, UNHC); NJ, Trenton, 23.viii.1909. (1f#, USNM); NY, Ft. Montgomery, 16.ix.1923, F.M. Schott. (1m#, MCZ); Ithaca, (1m#, 1f#, types of *L. ypsilon*, CUIC); Poughkeepsie, 23.viii.1936, H.K. Townes. (1m#, ANSP); OH, Summit Co., 28.viii.1937, L.J. Lipovsky. (1f#, SEMC); SC, Anderson Co., Pendleton, Tanglewood Sprg., x.1987, J. Morse. (2m#, 1f#, CNC); 30.viii.1987. (1m#, CUAC); TN, Sevier Co., Twin Creeks, 14-29.viii.2006, J. Gulbransen. (3m#, 1f#, LEM); 31.vii-15.viii.2006. (2f#, 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_{2+3} 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.

DESCRIPTION: *Male*. (Fig. 21) **Head**: dark brown-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; slightly wider than tall triangle, covered with many strong bistles. 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 with 5 segments, 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 interommatidial setulae scattered on posterior half. Occiput dark brown with appressed, anteriorly directed setae. Three ocelli; 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 ± 0.48 mm (1.64 - 2.46 mm, n = 10). Scutum yellow; disc 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 katepisternum 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 7.65 ± 1.5 mm (6.56 - 9.1mm, n = 10). Hyaline, with 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 Rs. R_{2+3} 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_1 faintly present. **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. T**horax**: Length 2.13 ± 0.62 mm (1.39 - 2.46mm, n = 10). **Wing**: Length 8.00 ± 1.10 mm (7.22 - 8.69 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: *Leptomorphus magnificus* is known from mid-western Quebec and Ontario south to Georgia, and from Maine east to Indiana (Fig. 145), at elevations from 5-1160 m.

TAXONOMIC DISCUSSION: None of the unknown number of specimens 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] m# HOLOTYPE/ *Diomonus/ magnificus*/ Johannsen; [red label] HOLOTYPE/ Cornell U./ No. 1969; LECTOTYPE m#/ *Leptomorphus magnificus*/ (Johannsen)/ Det. C.J. Borkent,

2011" [CUIC]

Paralectotypes: [all with paralectotype labels by C.J. Borkent] labelled as for holotype except 1.vii, (1f#, labelled as allotype, CUIC); OH, Salineville (1f#, labelled as paratype, CUIC); MA, Mt. Greylock , 8.viii.[19]07, O. Bryant (1m#, 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. (1m#, DEBU); 15-31.vii.1994. (1m#, DEBU); Bala, 19.vii.1932, A.S. Walley. (1f#, CNC); Rondeau Park, 18.vii.1962, S.M. Clark. (1f#, CNC); Bruce Co., Little Cove, 4.ix.2004, S.A. Marshall. (1m#, DEBU); Elgin Co., Fingal Wildlife Management Area, 21.vi.1992, I. Carmichael. (1m#, CNC); QC, 2.3km SSW Rapide-Danseur, 28.v-30.vi.2007, A. Hibbert. (1m#, LEM); Mont St-Hilaire, 2-8.vii.2001, E. Fast. (1m#, LEM); 18-24.ix.2001. (3m#, LEM); 1-8.vii.2008, V. Levesque. (2m#, LEM); 14-21.vii.2008. (1m#, LEM); 21-28.vii.2008. (1m#, LEM); 22-29.vii.2008. (1m#, LEM); 24.vi-1.vii.2008. (1m#, LEM); 30.vi-7.vii.2008. (1m#, 1f#, LEM); Old Chelsea, 18.vii.1987, L. Masner. (1f#, CNC); Rougemont, 7-14.vii.2008, V. Levesque. (1m#, 1f#, LEM); 14-21.vii.2008. (1m#, LEM); 30.vi-7.vii.2008. (3m#, 2f#, LEM); Masham Twp., Duncan Lake, ix.1977, D.M. Wood. (1f#, CNC); 24-30.viii.2000. (1m#, LEM); USA, CT, Redding, 9.viii.1938, A.L. Melander. (1f#, USNM); GA, Union Co., Neels Gap, 21.vi.1967, G.W. Byers. (1m#, SEMC); IN, LaPorte Co., Michigan City (E. edge), 3.vii.1968, G.W. Byers. (1m#, SEMC); Owen Co., McCormick's Cr., 26.vi.1950, G.W. Byers. (2m#, SEMC); Parke Co., Turkey Run St. Pk., 10.vi.1951, G.W. Byers. (1f#, SEMC); MA, Montgomery, 24.viii.1896. (1f#, USNM); Petersham, vi.1941. (1f#, MCZ); ME, York Co., West Lebanon, 28.viii-3.ix.1990, D.W. Barry. (1m#, UNHC); NC, Highlands, 21.vi.1957, J.R. Vockeroth. (1f#, CNC); NH, Glen House, 19.vii.1915. (1f#, MCZ); Carr. Co., 1mi. N Wonalancet, E Fk., Spring Brk., 18-31.x.1985, D.S. Chandler. (1m#,

UNHC); 14-21.viii.1985. (2m#, UNHC); 22-28.viii.1985. (1m#, 1f#, UNHC); 18.ix-1.x.1985. (1m#, UNHC); 2.5mi. NW Wonalancet, 21-27.vi.1984, D.S. Chandler. (1m#, UNHC); 12-19.vii.1984. (4m#, 1f#, UNHC); 27.vii-1.viii.1984. (1m#, UNHC); 2-10.viii.1984. (1m#, UNHC); 11-16.viii.1984. (2m#, UNHC); 17-22.viii.1984. (2m#, UNHC); 23.viii-1.ix.1984. (3m#, UNHC); 2-17.ix.1984. (2m#, UNHC); 14-21.vi.1985. (1m#, UNHC); 11-17.vii.1985. (1m#, UNHC); 18-23.vii.1985. (1m#, UNHC); 24-30.vii.1985. (3m#, UNHC); 31.vii-6.viii.1985. (2m#, UNHC); Grafton Co., Bridgewater, Newfound Lk., Whitemore Pt., 23-25.vii.1994, S.D. Gaimari. (1m#, CSCA); Rock. Co., 1mi. W Odiorne Pt., 22-24.vi.1983, D.S. Chandler. (1m#, UNHC); Odiorne Pt, 16-20.ix.1983, D.S. Chandler. (1m#, UNHC); Straf Co., 1mi. SW Durham, 24.vii-6.viii.1987, D.S. Chandler. (1m#, UNHC); 30.ix.1987. (1m#, UNHC); 8.x.1990, W.J. Morse. (1m#, UNHC); 4mi. W Durham, 2-5.viii.1982, R.M. Reeves. (1m#, UNHC); Durham, 29.viii.1978, W.J. Morse. (1m#, UNHC); Spruce Hole, 3mi. SW Durham, 24.vii-6.viii.1987, D.S. Chandler. (1m#, UNHC); 15.x-4.xi.1987, D.S. Chandler. (1m#, UNHC); NY, Accord, viii.1959, F. Hough. (1m#, USNM); Beaver Creek, McLean Res., 30.viii.1924. (1f#, CUIC); Hamburg, 8.ivi.1908, M.C. VanDuzee. (1m#, CAS); Irving, 30.vi.1918, M.C. VanDuzee. (1m#, CAS); Ithaca, 16.viii.1898. (1f#, CUIC); 2.vii.1915. (1f#, CUIC); 15.viii.1928, A.L. Melander. (1f#, ANSP); 17.ix.1936, H.K. Townes. (1m#, ANSP); O.A. Johannsen. (1f#, CUIC); S. Wales, 9.vii.1911, M.C. VanDuzee. (1f#, CAS); West Point, 4.ix.1927, W. Robinson. (1m#, 1f#, USNM); Albany Co., Huyck Preserve, Rensselaerville, 3.vii.1968, W.G., M.J. Eberhard. (3m#, MCZ); 9.vii.1968, W.G., M.J. Eberhard. (1f#, MCZ); Greene Co., Onteora Mt., 26.vii.1929, L.O. Howard. (1m#, USNM); Greene Co., viii.1910. (1f#, CMNH); PA, Hazleton, 12.ix.1917, Dietz. (1f#, ANSP); Allegheny Co., Pittsburgh, Mt Troy, 18.vi.1970, J. Bauer. (1m#, CMNH); Centre Co., Bear Meadows, 11.ix.1979, P.H. Adler. (1m#, USNM); Forest Co., 5km SE Marienville, 22.ix.1993, J. Rawlins, W. Zanol. (2m#, SEMC); Warren Co., 2.2km NW Truemans, 12.vii.1994, M. Ricke. (3m#,

CMNH); 12.vii.1994, M. Ricke. (1m#, SEMC); 4.6km ESE Donaldson, Tionesta Scenic Area, 27.ix.1994, W. Metheny. (2m#, CMNH); Westmor. Co. (1m#, CMNH); SC, Oconee Co., Coley Cr., 15-16.vi.1987, Hamilton; Hoffman. (1m#, CUAC); TN, Sevier Co., Twin Creeks, 31.vii-15.viii.2006, J. Gulbransen. (1f#, LEM); VT, Dorset, vii.1962, C. Parsons. (1?, MCZ); WV, Cheat River. (1m#, 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 unique, tergal evagination bearing ventrally-directed fold along most of posterior margin and small point on apicomedial corner (Fig. 109).

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; 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 with 5

segments, all 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 interommatidial 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 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; disc 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 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 6.48 mm (n = 1). Hyaline, with 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_{2+3} 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 before origin of r-m. A_1 faintly present. **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: *Leptomorphus mandelai* is known from South Africa (Fig. 134).

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 m#/ *Leptomorphus mandelai* /Borkent, new species / C.J. Borkent 2011" [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 unique, lateral lobes of tergal evagination gradually tapering to a medial point; sternite 9 a posteriorly directed triangle (Fig. 110).

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; 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 with 5 segments, all 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 interommatidial 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 with electric blue green specks. **Thorax**: Length 1.01 ± 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); disc 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 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 4.85 ± 0.8 mm (4.18 - 5.41 mm, n = 10). Hyaline, with apical macula absent or, if present, very light, restricted to apical 1/4 of cell r1; 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_{2+3} 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 well before origin of r-m. A_1 faintly present. **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. T**horax**: Length 1.22 ± 0.17 mm (1.11 - 1.34 mm, n = 5). **Wing**: Length 5.71 ± 0.7 mm (5.25 - 6.07 mm, n = 5). **Abdomen**: Cercus yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus medleri* is known from Guinea and Nigeria (Fig. 136), at elevations from 215-750 m.

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 m#/ Leptomorphus medleri/ Matile/ Det. C.J. Borkent, 2011" [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. (6m#, 1f#, MNHN); Ibadan, 3.vii.1922 (1f#, BMNH).

Other material: GUINEA, Mt. Nimba, 18-19.vi.1991, Girard et Legrand. (1f#, MNHN); NIGERIA, Ibadan, 23.vii.1962, D.C. Eidt. (2f#, CNC); same except 31.viii.1962 (1m#, CNC); 3.ix.1962 (1m#, CNC); 18.ix.1962 (1m#, CNC); 1962 (1m#, 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 nebulescens. 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); Söli *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_{2+3} present; male genitalia with two long sickle-like structures (aedeagus) curving dorsally (Fig. 111).

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-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; 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 with 5 segments, 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 interommatidial setulae scattered on posterior half. Occiput dark brown with appressed, anteriorly directed setae. Three ocelli; 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 ± 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; disc 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 2. Anepimeron brown. Anepisternum dark brown. Katepisternum 2 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 8.18mm (±1.45, max: 9.59mm, min: 7.54.mm, n = 10). Hyaline, with 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_{2+3} 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_1 faintly present. **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 ± 0.70 mm (1.85 - 2.95mm, n = 10). **Wing**: Length 8.03mm (±2.08, max: 9.84mm, min: 6.48mm, 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: *Leptomorphus nebulosus* is known from much of the Nearctic, particularly Canada and the eastern USA (Fig. 144), at elevations from 20-1800 m.

TAXONOMIC DISCUSSION: Specimens of the subspecies *L. s. gurneyi* (previously synonymized with *L. subcaeruleus*; Poole & Gentili (1996)) are actually a lighter form of *L. nebulosus*. This species' colour ranges from lighter (yellowish with some dark spots) in the south-west part of the range to completely black in the north. As no discrete boundaries can be seen at this time between the lighter and darker forms I 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 m#/ *Leptomorphus nebulosus* /(Walker) / C.J. Borkent 2011" [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. (1m#, CNC); 23km NE Nelson, 10.vii.2008, A. Borkent. (1m#, LEM); 2km W Little Slocan Lk. Cmpgnd., 1.vii.2008, A. Borkent. (3m#, 1f#, LEM); 3.8mi. S Steamboat, 22.vi.1989, P.H. Arnaud, Jr. (1m#, CAS); 6km E Salmon Arm, 13.vi.2009, A. Borkent. (1m#, LEM); Kaslo, 18.vii, A.N. Caudell. (1f#, USNM); Likely, 6.vii.1938, G.S. Walley. (1m#, CNC); Robson, 14.vi.1948, H.R. Foxlee. (1m#, CNC); Rosebery, 11.vii.2008, A. Borkent. (1m#, 1f#, LEM); Quesnel, 26.vi.1948, G.J. Spencer, (1m#, UBCZ); Salmon Arm, 1.vi.2006, A. Borkent. (1f#, LEM); 10.vi.2006. (1f#, LEM); 12.vi.2006. (1f#, LEM); 26.vi.2006. (1f#, LEM); 7.vii.2007. (1f#, LEM); 9.vii.2007. (1m#, LEM); 14.ix.2008. (1m#, LEM); 12.vi.2008, C.J. Borkent. (1m#, 2f#, LEM); Trinity Valley, 13.vii.1937, K. Graham. (1m#, CNC); ON, Algonquin Park (South of Shirley Lake), 21-28.vii.1984, K. Pendreigh. (1m#, CNC, 1m#, DEBU); 16-24.vi.1984. (1m#, DEBU); 18-26.v.1984. (2m#, CNC); 18-26.v.1984. (3m#, DEBU); Fathom 5 N.P., N Cove Isl., 25.vi.1995, S.A. Marshall. (1m#, DEBU); Finland, 8.vii.1960, S.M. Clark. (1m#, CNC); Macdiarmid, 6.vii.1922, Bigelow. (1m#, CNC); Orwell, 14.vi.1978, W.A. Attwater. (1f#, DEBU); Kent Co., Rondeau Prov.Pk., Spicebush Trail, Carolinian Forest, 15.viii-7.ix.2003, Marshall *et al.* (1f#, DEBU); Rondeau Park, 14.viii-7.ix.2003, Buck & Marshall. (1f#, DEBU); 15.viii-7.ix.2003, Marshall *et al.* (1f#, DEBU); QC, 2.3km SSW Rapide-Danseur, 27.v-29.vi.2007, A. Hibbert. (1m#, LEM); Laniel, 12.vi.1944, A.R. Brooks. (1m#, CNC); Masham

Twp., Duncan Lake, 13.ix.1975, D.M. Wood. (2m#, 1f#, CNC); 17.ix.1975. (1f#, CNC); 1.ix.1985. (1m#, 3f#, CNC); 8.ix.1985. (1m#, CNC); 11.ix.1985. (1m#, 2f#, CNC); 16.ix.1985. (1f#, CNC); 16.ix.1985. (1m#, 1f#, CNC); 10-12.ix.1986. (1m#, CNC); 12.ix.1986. (1m#, CNC); 7.x.1985. (4m#, CNC); 10.x.1985. (3m#, 1f#, CNC); USA, IA, Boone Co., Ledges State Park, 13.x.1950, J.L. Laffoon. (1m#, ISUI); 18.ix.1951. (1f#, ISUI); Winneshiek Co., Kendallville, 14.vii-4.viii.2008, M.J. Hatfield. (1m#, LEM); KS, Douglas Co., U. Kansas Nat. Hist. Res., 13.vi.1974, C.W. Young. (1m#, CMNH); 10-20.vi.2005, Z.H. Falin. (1f#, SEMC); 20.vi.2005. (1m#, SEMC); 19-24.vii.2005. (1m#, SEMC); 7-16.ix.2005. (1f#, SEMC); 16.ix-1.x.2005. (2m#, SEMC); MD, Cabin John, R.M. Fouts. (1m#, USNM); Patuxent Refuge, Bowie, 4.vii.1945. (1f#, USNM); Plummer's Island, 1906, D.H. Clemons, H.S. Barber. (1f#, USNM); 27.vi.1909, W.L. McAtee. (1f#, USNM); 8.viii.1917, Schwarz & Barber. (1m#, USNM); Calvert Co., Port Republic, 12-15.x.1996, D.M. Wood. (1f#, CNC); Prince George Co., Camp Springs, 20.ix.1979, G.F. Hevel. (1f#, USNM); Wash. Co., 5km NE Boonsboro, Greenbrier St. Pk., 12-14.viii.1989, M.E. Steiner *et al.* (1m#, USNM); ME, Houlton, 5.vii. (1f#, USNM); MI, Isle Royale, 3-7.viii.1936, C.W. Sabrosky. (1m#, USNM); MO, Camp Crowder, 7.x.1942, A.B. Gurney. (2m#, 1f#, USNM, Type specimens of *L. s. gurneyi*); MS, Oxford, 20.vi.1966, F.M. Hull. (1f#, CNC); NH, Carriage Road, Mt. Washington, G. Dimmock. (1f#, USNM); Carr. Co., 1mi. N Wonalancet, E Fk., Spring Brk., 18-23.vii.1985, D.S. Chandler. (1m#, UNHC); The Bowl (2.5mi. NW Wonalancet), 8-14.vi.1984, D.S. Chandler. (2m#, UNHC); The Bowl (2.5mi. NW Wonalancet), 15-20.vi.1984. (3m#, UNHC); The Bowl (2.5mi. NW Wonalancet), 28.vi-4.vii.1984. (1m#, UNHC); The Bowl (2.5mi. NW Wonalancet), 20-26.vii.1984. (2m#, UNHC); The Bowl (2.5mi. NW Wonalancet), 2-10.viii.1984. (1m#, UNHC); The Bowl (2.5mi. NW Wonalancet), 11-16.viii.1984. (3m#, 2f#, UNHC); The Bowl (2.5mi. NW Wonalancet), 18.ix-3.x.1984. (2m#, UNHC); The Bowl (2.5mi. NW Wonalancet), 20.x-7.xi.1984. (1m#, UNHC); NJ, Stockton, 1-15.vii.1906. (1f#, USNM); NY, 7mi. south town

of Long Lake, 26.viii.1956, J.L. Laffoon. (1m#, 1f#, ISUI); Essex Co., foot Cliff Mtn, 26.vii.1920, J. Bequaert. (1m#, MCZ); PA, North Mt., 1.ix.1917. (1f#, USNM); Warren Co., 2.2km NW Truemans, 4.viii.1994, M.J. Ricke. (1m#, CMNH); SC, Anderson Co., Pendleton, Tanglewood Sprg., x.1987, J. Morse. (1f#, CNC); 22.vii.1987. (1m#, CUAC); 30.ix.1987. (1f#, CUAC); VA, Fairfax Co., Dead Run, 22.vi.1915, R.C. Shannon. (1f#, USNM); Turkey Run, mouth, 24.vi.2006, W.N. Mathis, T. Zatwarnicki. (1f#, USNM); WA, Pierce Co., 6.5km W Ashford, 8.vii.2008, C.J. Borkent. (1m#, LEM); 9.vii.2008. (1m#, LEM); 10.vii.2008. (3f#, LEM); WV, Hampshire Co., 8km NW Capon Bridge (Buffalo Gap Camp), 12-14.ix.1986, W.E. Steiner; J.M. Swearingen. (1f#, 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_{2+3} present and forming a triangular cell (rather than rectangular), and with lateral lobes of parameres longer than tergite 9 and bending sharply dorsally (Fig. 112).

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; 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 5 segments, 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 interommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Three ocelli; 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 ± 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; disc of scutum covered with hairs; 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 hairs; bristles absent. Prescutum light brown. Mediotergite brown with 8-12 bristles on posterior third, and covering of appressed hairs. Laterotergite brown, with covering of appressed hairs; anterior margin of laterotergite abutting katepisternum 2. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum 2 brown with dorsal third white. Antepronotum 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 5.94 ± 0.78 mm (5.33 - 6.48 mm, n = 10). Hyaline, with apical macula reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell cua1, cup, not joining with medial macula; medial macula extending from R_1 to fork of CuA and M_4. 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_{2+3} present, forming a triangular cell by originating at, or close to, the junction of Rs and r-m. 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 just apical of origin of r-m. A_1 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 aedeadgus; basal bridge between apodeme lobes with dorsally directed pair of hooks; joined basally with aedeagus.

Female adult. As for male, except as follows. **Head**: T**horax**: Length 1.49mm (±0.28, max: 1.72mm, min: 1.27mm, n = 10). **Wing**: Length 6.18 ± 0.82 mm (5.49 - 6.81 mm, n = 10). **Legs**: Foretibia without comb of short setae on anteroventral surface. **Abdomen**: Sternites yellow. Cercus yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus neivai* is known from the Brazilian states of Sao Paulo, Parana, and Santa Catarina, as well as adjacent areas of north-eastern Argentina (Lane 1958) and south-eastern Paraguay (Fig. 142), at elevations from 150-925 m.

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/ C.J. Borkent 2011" [BMNH]. This specimen was chosen as it was in the best condition of the five syntypes available.

Paralectotypes labelled as for lectotype except without F.W. Edwards determination label and:

21-IX-1938. (sex ? (broken abdomen)); 26.VIII.1937 (1f#); 16.VI.1937 (sex ? (broken abdomen)); 8.VI.1937 (1f#), All paralectotypes in BMNH. In the original dedscription Edwards (1940) lists seven type specimens. We are only aware of

these five specimens, with the remaing two considered lost.

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

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; 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 5 segments, 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 interommatidial setulae scattered on surface. Occiput yellow with some adventitious brown spotting anteriorly, 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 with electric blue green specks. **Thorax**: Length 1.08 ± 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; disc 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 katepisternum

2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 5.14 ± 0.71 mm (4.51 - 5.74 mm, n = 10). Hyaline, with apical macula absent or very light at R_5 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_{2+3} 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 before origin of r-m. A_1 faintly present. **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. T**horax**: Length 1.32 ± 0.20 mm (1.19 - , 1.48 mm, n = 9). **Wing**: Length 6.07 ± 0.93 mm (5.33 – 6.81 mm, n = 9). **Abdomen**: Cercus yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus obscurus* is known from Guinea, Ivory Coast, Ghana, Gabon, the Central African Republic and the Republic of the Congo (Fig. 136), at elevations from 120-750 m.

TAXONOMIC 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. m#ht/ L. Matile det. 1974; HOLOTYPE m#/ *Leptomorphus obscurus*/ Matile/ Det. C.J. Borkent, 2011" [MNHN].

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

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

25. *Leptomorphus ornatus* Brunnetti

(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).

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; 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 with 5 segments, all 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 interommatidial 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 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; disc 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 katepisternum 2. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum 2 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 5.47 mm (5.00 - 5.74 mm, n = 3). Hyaline, with apical macula light, beginning at apex of R_1 and M_4 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_{2+3} 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 apically of origin of r-m. A_1 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: *Leptomorphus ornatus* is known from Bangladesh, India (Assam) and Nepal (Fig. 137), at elevations from 30-2070 m.

TAXONOMIC 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. (1f#, BMNH); NEPAL, Kathmandu, Godavaril [= Godawari?], 21.vii.1967, Can. Exp. (1f#, CNC); Pulchauki, 14.vii.1967, Can. Exp. (1f#, 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).

Mycomya 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_{2+3} present and with apical 4-5 flagellomeres white (remainder dark brown). Males without an apical spine-like process. Male genitalia unique, aedeagal lobes bifurcate (Fig. 114).

DESCRIPTION: *Male*. (Fig. 31) **Head**: dark brown-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; 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 with 5 segments, 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 interommatidial setulae scattered on posterior half. Occiput dark brown with appressed, anteriorly directed setae. Three ocelli; 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; disc 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 katepisternum 2. Anepimeron brown. Anepisternum dark brown. Katepisternum 2 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 9.72 mm (8.28 - 10.58 mm, n = 4). Hyaline, with apical macula very dark, reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell cua1,

cup, a1, 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, fv, and CuP. 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_{2+3} 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_1 faintly present. **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 survace, 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 toptal length. Parameres as broad lobes with rounded apex, apodemes ~1/2 length of parameres.

Female. As for male, except as follows. **Thorax**: 2.56 ± 0.57 mm (2.13 - 3.03 mm, n = 8). **Wing**: Length 8.90 ± 1.91 mm (7.22 - 10.17 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: *Leptomorphus panorpiformis* is known from Japan (Hokkaido, Honshu (Okada 1938)) and far eastern Russia (Fig. 141), at elevations from 30-1400 m.

TAXONOMIC 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] Mycomya/ [line of Japanese text]/ panorpiformis/ Mats.; HOLOTYPE m#/ *Leptomorphus/ panorpiformis* (Matsumura) / C.J. Borkent 2011" [EIHU].

Other material: JAPAN, 12.viii (1f#, OMNH); Hokkaido, Karibu, 22.viii.1966, P. Savolainen. (1f#, MZHF); Honshu, Hyogo Pref., Haga, 4.vi.2003, R. Matsumoto. (1m#, OMNH); Nagano Pref., Matsumoto, 15.vii.1997, R. Matsumoto. (1f#, OMNH); Shinano Noziji, 10.vii.1941, T. Nakatane. (1 specimen of unknown sex (damaged), OMNH); Okayama Pref., Niimi: Nishio, 19.viii.1998, R. Matsumoto. (1f#, LEM); Yamanashi Pref., Hirogawara: Fuefuki, 19.vii.1997, R. Matsumoto.

(1f#, OMNH); Kyushu, Fukuoka, Hiko-san Biol. Lab., 10-11.viii.1980, K. Mikkola. (1f#, MZHF); Kumamoto Pref., Kikuchisuigen, 2.vii.1976, Y. Yoshiyasu. (1m#, LEM); Miyazaki Pref, Takakuma, 14.vii.1960, A. Nagatomi. (1 specimen of unknown sex (damaged), OMNH); Oita Pref., Yufu, 21.vi.1997, R. Matsumoto. (1f#, OMNH); Shikoku, Ehime Pref., Ishizuchi Mt N. P., 11-18.viii.1980, S. Peck. (1m#, 1f#, CNC).

27. *Leptomorphus perplexus* Borkent, new species

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

DIAGNOSIS: The only extant species of *Leptomorphus* with R_{2+3} 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).

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; 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 with 5 segments, all 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 interommatidial setulae (in most interommatidial junctions) on all but medial margin. Occiput yellow with appressed, anteriorly directed setae. Three ocelli; 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; disc 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 katepisternum 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 yellow. Antepronotum 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 6.58 mm (5.99 - 6.89 mm, n = 4). Hyaline, with 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_{2+3} 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_1 present. **Abdomen**: Tergites principally yellow, T1

light brown. Cercus yellow.

Male. Unknown.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus perplexus* is known from USA, CA (Tuolumne Co., Amador Co.) (Fig. 148), at elevations ~750 m.

TAXONOMIC DISCUSSION: Even though this species exhibits a number of plesiomorphic characteristics (see phylogeny section), I have placed it in *Leptomorphus* as 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_{2+3} 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 placing this species in *Leptomorphus.*

MATERIAL EXAMINED: *Holotype:* here designated, adult female, pinned, labelled "CAL.: Tuolumne Co./ Basin Creek Cmpgd./ 31.v.1963/ P.H. Arnaud, Jr.; HOLOTYPE f#/ *Leptomorphus perplexus* / Borkent, new species / C.J. Borkent 2011" [USNM]

Paratypes: labelled as for holotype (3f#). All paratypes in USNM.

Other material: I have also seen a photo (P. Kerr, CSCA) of a female specimen from Indian Grinding Rock State Park, Amador County, CA, that agrees with this species.

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 taxonomic discussion under *L. subforcipatus* for more information.

DESCRIPTION: *Male*. (Fig. 33) **Head**: brown-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; 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 with 5 segments, all 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 interommatidial setulae scattered on all but medial margin. Occiput brown with appressed, anteriorly directed setae. Three ocelli; 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 ± 0.41 mm (1.64 – 2.13 mm, n = 5). Dark brown. Scutum dark brown/black with blue-green specks; disc 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 katepisternum 2. Anepimeron brown. Anepisternum brown. Katepisternum 2 brown. Antepronotum 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 7.87 mm (6.89 - 8.77 mm, n = 4). Hyaline, with apical macula dark, reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell cua1, cup, a1, 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 Rs. R_{2+3} 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_1 faintly present. **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 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 veryu 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 ± 0.37 mm (1.68 - 2.17 mm, n = 6). **Wing**: Length 7.38 ± 1.12 mm (6.72 - 8.12 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: *Leptomorphus quadrimaculatus* is known from Far Eastern Russia and Japan (Fig. 141) at elevations from 30-1050 m. Records from Western Europe are probably *L. forcipatus,* which was previously synonymized with *L. quadrimaculatus*.

TAXONOMIC 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 f#/ *Leptomorphus/ quadrimaculatus* (Mats.)/ Det. C.J. Borkent, 2011" [EIHU].

Other material: JAPAN, Hokkaido, Tokachi, Ashoromura, 5.viii.1949, R. Matsuda. (1m#, OMNH); Honshu, Kyoto, Ashiu, 7.vi.1964, M. Sasakawa. (1f#,

OMNH); Yamanashi Pref., Hirogawara, Ashiyasu, 19.vii.1997, R. Matsumoto. (1m#, OMNH); 20.vii.1997, R. Matsumoto. (1m#, OMNH); 13.vii.1996, T. Saigusa. (1m#, OMNH); Kitazawa, Senjodake, 25.vii.1961, T. Saigusa. (1f#, LEM); RUSSIA, Far East, Primorskiy, Lazo, 11.vii.1979, A. Zaitzev. (1m#, 2f#, CNC); Lazo, Sokolchi, 12.viii.1979, A. Zaitzev. (1f#, 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 unique, tergite 9 ending in square lobe (tergal evagination) bearing small medial point; sternite 9 more or less oval shaped (Fig. 115).

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; 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 with 5 segments, all 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 interommatidial 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 1.8 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); disc 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 katepisternum 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 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 6.23 mm (n = 1). Hyaline, with 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_{2+3} absent. R_5 straight, slight posterior turn near tip. M_1 reaching apex just before R_5, apices of M veins reaching wing margin. M_4-CuA fork arising before origin of r-m. A_1 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 smnall medial bump, apodemes 3/4 length of parameres.

Female. As for male, except as follows. **Thorax**: Length 1.8 mm. **Wing**: Length 7.22 mm. **Abdomen**: Cercus dark yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus stigmatus* is known from Tanzania (Fig. 134).

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 stigmatus* / Borkent, new species / C.J. Borkent 2011" [ZMUN].

Paratypes: Labelled as for holotype (1f#, 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_{2+3} present; male genitalia with two long sickle-like structures (aedeagus) curving dorsally (Fig. 117).

DESCRIPTION: *Male*. (Fig. 36) **Head**: dark brown-black, somewhat dorsoventrally compressed in anterior view. Antenna dark brown; scape medium to dark brown, with brown-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; slightly wider than tall triangle, covered with many strong bistles. 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 5 segments, 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 interommatidial setulae scattered on posterior half. Occiput dark brown with appressed, anteriorly directed setae. Three ocelli; 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 ± 0.56 mm (1.72 - 2.54 mm, n = 10). Dark brown. Scutum dark brown/black with blue-green specks; disc 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 katepisternum 2. Anepimeron brown. Anepisternum dark brown. Katepisternum 2 dark brown. Antepronotum 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 7.97 ± 1.72 mm (6.89 - 9.43 mm, n = 10). Hyaline, with 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 Rs. R_{2+3} 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_1 faintly present. **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. T**horax**: Length 2.03 ± 0.34 mm (1.8 - 2.3 mm, n = 10). **Wing**: Length 7.76 ± 1.16 mm (6.81 - 8.61 mm, n = 10). **Legs**: Midfemur without apical spine-like process. **Abdomen**: 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: *Leptomorphus subcaeruleus* is known from South Dakota east to New Brunswick, and from Ontario south to North Carolina (Fig. 146), at elevations from 5-1830 m.

TAXONOMIC DISCUSSION: *Leptomorphus subcaeruleus gurneyi* is actually a pale form of *L. nebulosus* (see discussion under *L. nebulosus*). 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 m#/ *Leptomorphus/ subcaeruleus* (Coquillett) /Det. C.J. Borkent, 2011" [USNM].

Other material: CANADA, NB, Newcastle, 6.vii.1971, B.V. Petersen. (1f#, CNC); ON, 6mi. W Richmond, 6.vii.1971, J.E.H. Martin. (1f#, CNC); Algonquin Park, Swann Lake, 1-10.vii.1994, E.R. Barr. (1m#, DEBU); Bouck's Hill, 18.vi.2003, R. Zeran. (3m#, LEM); Greenbush, 10.vii.1999, R. Hainault. (1m#, CNC); Hall's Lake, 19.vii.1961, G.K. Morris. (1m#, DEBU); Innisville, 5.vii.1963, W.R.M. Mason. (1f#, CNC); 16.vii.1963. (1m#, CNC); Lancaster, 1.vii.2003, R. Zeran. (4m#, LEM); Morrisburg, 18.vi.2003, R. Zeran. (1m#, LEM); Niagara Falls, 10.ix.1910, M.C. VanDuzee. (1f#, CAS); One sided Lake,

12.vii.1960, S.M. Clark. (1m#, CNC); Ottawa. (1m#, USNM); Bruce Co., Little Cove, 4.ix.2004, S.A. Marshall. (1m#, DEBU); Dunks Bay, 22.viii.2003, S.A. Marshall. (1m#, DEBU); Carleton Co., 8km S Richmond, 30.viii.2008, D.M. Wood. (1m#, LEM); Dufferin Co., nr. Mansfield, 19-20.ix.1992, J Skevington, A Goering. (1f#, CNC); Lanark Co., N. Burgess Twp., 1.viii.1970, D.M. Wood. (2f#, CNC); 24.viii.1972. (1f#, CNC); QC, 2.3km SSW Rapide-Danseur, 30.vi-29.vii.2007, A. Hibbert. (1m#, 1f#, LEM); 28.v-30.vi.2007. (1m#, LEM); Aylmer, 15.vii.1924, C.H. Curran. (1m#, CNC); Kirk's Ferry, 22.viii.1924, E.P. Ide. (1f#, CNC); Lake Duparquet Res. and Train. For., 12.vii-1.viii.2006, A. Hibbert. (3m#, 1f#, LEM); Mont St-Bruno, 1-8.vii.2008, V. Levesque. (2m#, LEM); 24.vi-1.vii.2008. (3m#, LEM); Mont St-Hilaire, 11-18.ix.2001, E. Fast. (1m#, LEM); 18-24.ix.2001. (2m#, LEM); 15-22.vii.2008, V. Levesque. (1m#, LEM); 17-23.vi.2008. (2m#, LEM); 30.vi-7.vii.2008. (2m#, LEM); 23-30.vi.2009. (1m#, LEM); Norway Bay, 30.viii.1938, G.E. Shewell. (1f#, CNC); Rougemont, 16-23.vii.2008, V. Levesque. (1m#, LEM); Ste-Anne-de-Bellevue, Morgan Abrtm., 31.vii.2007, C.J. Borkent. (1m#, LEM); 3.vii.2010. (4m#, 5f#, LEM); 30.vi.2010. (4m#, 2f#, LEM); USA, CT, Redding, 17.vii.1931, A.L. Melander. (1f#, USNM); Stamford, 3.vii.1944. (1m#, USNM); MA, Holliston, 2.vii, N. Banks. (1m#, MCZ); Petersham, vii.1926, A.L. Melander. (1m#, ANSP); Petersham, vi.1941. (1f#, MCZ); MD, Garrett Co., New Germany St. Pk., 7.vi.1977, Byers, May, Young. (1m#, SEMC); ME, York Co., West Lebanon, 5-9.vii.1990, D.W. Barry. (1m#, UNHC); MI, Isle Royale, 3-7.viii.1936, C.W. Sabrosky. (1f#, USNM); Berrien Co., St Joseph, 15.vi.1975, D.D. Wilder. (1m#, CAS); NC, Highlands, 26.vi.1957, W.R.M. Mason. (1m#, 1f#, CNC); Sunburst, 6.v.1912. (1m#, NCSU); NH, Dover, 30.vi.1974, A.H. Mason. (1f#, UNHC); Hampton, 25.vii.1903, S.A. Shaw. (1f#, CUIC); Carr. Co., 1mi. N Wonalancet, E Fk., Spring Brk., 29.viii-5.ix.1985, D.S. Chandler. (1f#, UNHC); 2.5mi. NW Wonalancet, 28.vi-4.vii.1984, D.S. Chandler. (1m#, UNHC); Rock. Co., 1mi. W Odiorne Pt., 22-24.vi.1983, D.S. Chandler. (1m#, UNHC); Straf Co., 1mi. SW Durham, 24.vii-6.viii.1987,

D.S. Chandler. (1m#, UNHC); 4mi. W Durham, 14-20.ix.1982, R.M. Reeves. (1m#, UNHC); Durham, 14.viii.1957, W.J. Morse. (1m#, 1f#, UNHC); 22.vii.1984. (1m#, UNHC); 10.vii.1989. (1m#, UNHC); NY, Axton, 12-22.vi.1901, A.D. MacG, C.O.H. (1f#, CUIC); Beaver Creek, McLean Res., 30.viii.1924. (1f#, CUIC); 1.ix.1925. (1m#, CUIC); East Aurora, 30.vii.1922, M.C. Van Duzee. (1m#, CAS); Erie Co., Protection, 18.vii.1915, M.C. Van Duzee. (1f#, CAS); PA, Ohiopyle, viii.1907, H. Kahl. (1m#, CMNH); State College, 6.viii.1949, C.W. Sabrosky. (1m#, USNM); Clarion Co., Cook Forest St Pk., 11.viii.1961, J.L. Laffoon. (1m#, ISUI); Forest Co., nr. Marienville, 27.ix.1994, W. Metheny. (1f#, CMNH); Huntingdon Co., Cornpropstsmills, 28.vi.1973, D.J. Shetlar. (1m#, CAS); Moreland Co., Powdermill Nature Reserve, 20.vii.1956, H.K. Clench, N. Richmond. (1m#, CMNH); SD, Harney Peak, Harney Nat. For., 24.vii.1951, G.W. Byers. (1m#, SEMC); Lawrence Co., 6.2mi. SW Lead, 10.vii.1959, G.W. Byers. (1m#, SEMC).

31. *Leptomorphus subforcipatus* Zaitzev & Ševčík

(Figures 118, 140)

Leptomorphus subforcipatus Zaitzev & Ševčík, 2002: 208.

DIAGNOSIS: This species is very similar to *L. quadrimaculatus*, differing only in the lighter colour of the thorax. The perceived difference in the genitalia (Zaitzev & Ševčík 2002) is very slight (slightly more bulbous apex of gonocoxite in *L. subforcipatus*) and likely due to the membranous nature of the gonocoxite.

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 with 5 segments, yellow. Three ocelli; 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, with apical macula reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell cua1, 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** (Fig. 118A, B, see originals in 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: *Leptomorphus subforcipatus* is known from NW Russia and SE Finland (Fig. 140), at elevations from 125-200 m.

TAXONOMIC 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*, being only lighter in colour. Because colour can vary within a species of *Leptomorphus,* I suspect that *L. subforcipatus* is a synonym of *L. quadrimaculatus*. However, until types can be compared I 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 m# and 1f# from type locality, 4 m# from other locations in northwestern Russia and 1m# 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 unique, tergite 9 bearing two long lateral processes posteriorly, so that tergite 9 is ~2X as long as wide (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; 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 with 5 segments, all 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 interommatidial setulae absent. 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 black. **Thorax** : Length 1.19 mm (n = 1). Dark brown. Scutum dark brown with a pair of small yellow posterolateral spots; disc 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 2. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum 2 brown. Antepronotum 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 mm (n = 1). Hyaline, with 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_{2+3} 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_1 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: *Leptomorphus tabatius* is known from Sulawesi, Indonesia (Fig. 137).

TAXONOMIC 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 m#/ *Leptomorphus tabatius* / Borkent, new species / C.J. Borkent 2011" [UCDC]. The holotype was collected as part of an International Cooperative Biodiversity Group study of this biodiversity hotspot.

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 unique, wider than long (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; 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 with 5 segments, all yellow; segments increasing in length, segment 3 appears spherical (difficult to tell in specimen). Labellum yellow. Eye with interommatidial setulae absent. 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 1.03 mm (n = 1). Dark brown. Scutum dark brown with blue-green specks; disc 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 katepisternum 2. Anepimeron brown. Anepisternum dark brown. Katepisternum 2 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 4.02 mm (n = 1). Hyaline, with 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_{2+3} absent. R_5 straight, slight posterior turn near tip. M_1 reaching apex just before R_5, apices of M veins fading before wing margin. M_4-CuA fork arising apically of origin of r-m. A_1 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: *Leptomorphus tagbanua* is known from Coron Island in the Philippines (Fig. 137).

TAXONOMIC 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 m#/ *Leptomorphus tagbanua* / Borkent, new species / C.J. Borkent 2011" [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 unique, outer margin of the gonocoxite straight, and with the gonocoxite longer than, and placed apically on, tergite 9 (Fig. 121).

DESCRIPTION: *Male*. **Head**: yellow. Antenna; flagellomere 6 2X as long as broad. Clypeus yellow. Palpus with 5 segments, yellow. Three ocelli; 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, with apical macula reaching wing tip though fainter towards tip, extending faintly along posterior wing margin into apex of cell cua1, cup, not joining with medial macula; medial macula present from Sc to M fork. M_4-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** (Fig. 121A, B, see originals in 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: *Leptomorphus talyshensis* is known from Azerbaijan (Fig. 140).

TAXONOMIC 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 (1m#, 1f#, IEE).

35. *Leptomorphus titiwangsensis* 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; vein sc-r present (though faint in one specimen); male genitalia unique, gonocoxite as long as tergite 9 with margins distinguishable, apex of gonostylus bifurcated, aedeagal apodemes present (Fig. 122).

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; 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 with 5 segments, all 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 interommatidial setulae scattered on surface. Occiput yellow with appressed, anteriorly directed setae. Three ocelli; 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; disc 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 2. Anepimeron brown. Anepisternum brown. Katepisternum 2 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 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 4.46 mm (4.35 - 4.51 mm, n = 3). Hyaline, with 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_{2+3} 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 just apically of origin of r-m. A_1 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 5.58 mm (5.41 - 5.74 mm, n = 2). **Abdomen**: Cercus yellow.

Immatures. Unknown.

BIOLOGY: Unknown.

DISTRIBUTION: *Leptomorphus titiwangsensis* is known from Peninsular Malaysia (Fig. 137), at elevations from 1220-1280 m.

TAXONOMIC 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 20th 1932/ [underside of label] H.M. Pendlebury/ F.M.S./ Museums.; HOLOTYPE m# / *Leptomorphus / titiwangsensis* Borkent / C.J. Borkent 2011" [BMNH]

Paratypes: labelled as for holotype except 29.i.1929 (1m#, 1f#); 29.v.1932 (1f#); viii.1926, B. Gater (1m#). 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); Poole and Gentili, 1996: 194 (catalogue); Söli 1997: 6, 9, 10, 14, 32, 34, 46-47 (figure of head, palp, and genitalia, phylogenetic matrix exemplar); Söli *et al.* 2000: 52 (figure of palp); Kurina 2003: 61 (Germany); Kurina *et al.* 2005: 483 (Sweden); Gammelmo & Söli 2006: 60, 65 (Norway); Kjaerendsen *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 unique, gonocoxite shorter than tergite 9, sternite 9 not reaching lateral margins of tergite 9 (Fig. 123).

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; 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 with 5 segments, all 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 interommatidial setulae scattered on posterior margin. Occiput yellow with appressed, anteriorly directed setae. Three ocelli; 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; disc 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 katepisternum 2. Anepimeron yellow. Anepisternum yellow. Katepisternum 2 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 7.13 ± 2.18 mm (4.84 - 8.2 mm, n = 10). Hyaline, with 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 Rs. R_{2+3} 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_1 faintly present. **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 ± 0.26 mm (1.48 - 1.89 mm, n = 10). **Wing**: Length 7.04 ± 1.19 mm (6.15 - 8.04 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 which 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). Pupation occurs underneath 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: *Leptomorphus walkeri* is known from Europe (Fig. 140), at elevations from 35-1400 m. Previous records of *L. walkeri* from the Nearctic were due to misidentification of *L. hyalinus*.

TAXONOMIC 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 in the original description): "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. (1f#, ZSM); Tirol, Igls, 8.vii.1953, J.R. Vockeroth. (2m#, CNC); CZECH REPUBLIC, Lanzhot, Ranspurk, 7-9.viii.1991, L. Masner. (1m#, CNC); BOHEMIA, Josefuv Dul, Jedlový dul, 1-22.ix.2005, J. Preisler & P. Vonička. (1m#, LEM); BOHEMIA, viii.1900. (1m#, MTD); FRANCE, 15.xi.1966. (1m#, MNHN); 30.x.1966. (1m#, MNHN); Centre, Indre-et-Loire, Richelieu, 24.viii.1963. (1m#, MNHN); 25.viii.1963. (1m#, MNHN); Île-de-France, Seine-et-Marne, Fontainebleau, 14.vii.1992, G. Hodebert. (1f#, MNHN); Saint-Augustin, vii.1969, L. Matile. (1m#, MNHN); Poitou-Charentes, Deux-Sèvres, Saint-Martin-de-Sanzay, 14 1971, G. Couturier. (1m#, MNHN); Provence-Alpes-Côte d'Azur, Bouches-du-Rhône, St-Braume, 1919, A. de Perrin. (1f#, MNHN); Hautes-Alpes, Saint-Bonnet-en-Champsaur, vii.1975, C. Girard. (1f#, MNHN); Seine et Marne, Bois-le-Roi, 25.viii.1984, P.H. Arnaud, Jr. (1m#, CAS); GERMANY, Jungfernhardt, Siebengebirge, 27.ix.1957, E. Schmidt. (1m#, CNC); Markgröningen, 21.ix.1970. (1f#, SMNS); Baden-Württemberg, 23km NW Freiburg, 26.x.1984, FVA-Abt.

Ws Freiburg. (1f#, ZSM); Bavaria, Eltmann, Naturpark Steigerwald, 12.viii.1995, A. Floren. (1m#, ZSM); Schöngeising, 12.vii.1986. (1m#, ZSM); North Rhine-Wesphalia, Cologne, 2.v-15.xi.1995, A.G.W. Topp. (1m#, MTD); Saxony, Sächsische Schweiz, (1f#, MTD); Württemberg. (1m#, SMNS); NORWAY, AK, Nesodden, Skoklefall, 27.vi-9.vii.2005, O. Lønnue. (1m#, LEM); SLOVAKIA, Polana Biosphere Reserve, 24.v-11.vii.2007, J. Roháček, J. Ševčík. (1m#, LEM); SWITZERLAND, Cheserex, 28.viii.1931, E. Roman. (1f#, MNHN); Lugano, vi.1906, W. Schnuse. (1m#, MTD); UK, Anderson Co., Northwood, 4.x.1924, E.E. Austen. (1m#, BMNH); Hampshire, Minstead, 30.vii.1963, L.W. Siggs. (1f#, BMNH); New Forest, 2.x.1901, F.C. Adams. (1f#, BMNH); 25.viii.1901. (1m#, MNHN); 13.ix.1905. (1f#, MNHN); 29.viii.1910, B. Sharp. (1m#, BMNH); New Forest, Gorley, 12.viii.1972, Cranston, Dear. (1m#, BMNH); Hertfordshire, Hitch Wood, 22.ix.1918, F.W. Edwards. (2f#, BMNH); 22.ix.1918. (1m#, CNC); ix.1918. (1f#, BMNH); Monmouthshire, Monnow Valley, 8.vii.1912, J.H. Wood. (1m#, BMNH); Surrey, Old Coulsdon, 19.ix.1934. (1m#, 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 hairs; 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 unique, 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).

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; 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 with 5 segments, all 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 interommatidial 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; disc of scutum covered with hairs; 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 hairs; bristles absent. Prescutum anterior half yellow, posterior half brown. Mediotergite dark brown with 6 bristles on posterolateral corners, and covering of appressed hairs. Laterotergite brown, with covering of appressed hairs; anterior margin of laterotergite abutting katepisternum 2. Anepimeron brown with posterodorsal corner yellow. Anepisternum brown. Katepisternum brown with posterodorsal corner yellow. Antepronotum 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 6.72 mm (n = 1). Hyaline, with 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_{2+3} 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_1 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: *Leptomorphus waodani* is known from Ecuador (Fig. 143).

ETYMOLOGY: This species is named in honour of the Waodani 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 m#/ *Leptomorphus waodani* / Borkent, new species / C.J. Borkent 2011" [USNM].

Specimens 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_{2+3} absent] (2f#, 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_{2+3} present] (1f#, 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] (1f#, 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 MZSP (Lane & Sturm 1958). The male genitalia are similar to *L. amorimi* and *L. waodani* but appear unique] (1m#, 1f#, MZSP).

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.

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. Interommatidial 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 (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 (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. Disc of scutum with covering of setae: present (0), absent (1) (C.I. = 0.25, R.I. = 0.77).
20. Disc of scutum with covering of fine hairs: 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 hairs: 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 hairs: absent (0), present (1) (C.I. = 1.00, R.I. = 1.00).
28. Laterotergite with covering of appressed fine hairs: absent (0), present (1) (C.I. = 1.00, R.I. = 1.00).
29. Laterotergite meeting katepisternum2 ventrally (anepimeron obscured ventrally by 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 (*sensu* Saigusa 2006): present (0), absent (1) (C.I. = 0.25, R.I. = 0.79).
36. Macrotrichia in basal third of wing: densely and evenly distributed (0), sparsely distributed near wing veins (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): alternating long and short (0), single length (1) (C.I. = 0.50, R.I. = 0.90).
39. Calypter 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_{2+3}: 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. Length of gonocoxite relative to medial length of tergite 9: >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. Ventral gonostylar lobe relative to length of dorsal (smaller) lobe: absent (0), <2X(1), > 2X (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 (2:1), and wing vein C ending at R_5 (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). The genus also has several other synapomorphies supporting the monophyly of *Leptomorphus* (see generic diagnosis.

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): interommatidial 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_{2+3} 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).

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, north-eastern Australasian, eastern Palaearctic, 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 s*pecies 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* are a monophyletic group 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): interommatidial 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_{2+3} 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 hairs (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), disc of scutum covered with hairs (Fig. 80, 20:1), scutellum with covering of fine hairs (24:1), mediotergite with covering of appressed hairs (27:1), and ten homoplasious character states: face without bristles (9:2), frons brown (10:1), no inter-antennal bristles on frons (11:2), disc of scutum without covering of setae (19:1), dorsocentral setae present as a single, anterior, large seta (22:2), laterotergite abutting katepisternum (29:1), median wing spot present (34:1), no macrotrichia in cell a (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 an unfinished, 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 pseudotracheae 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.

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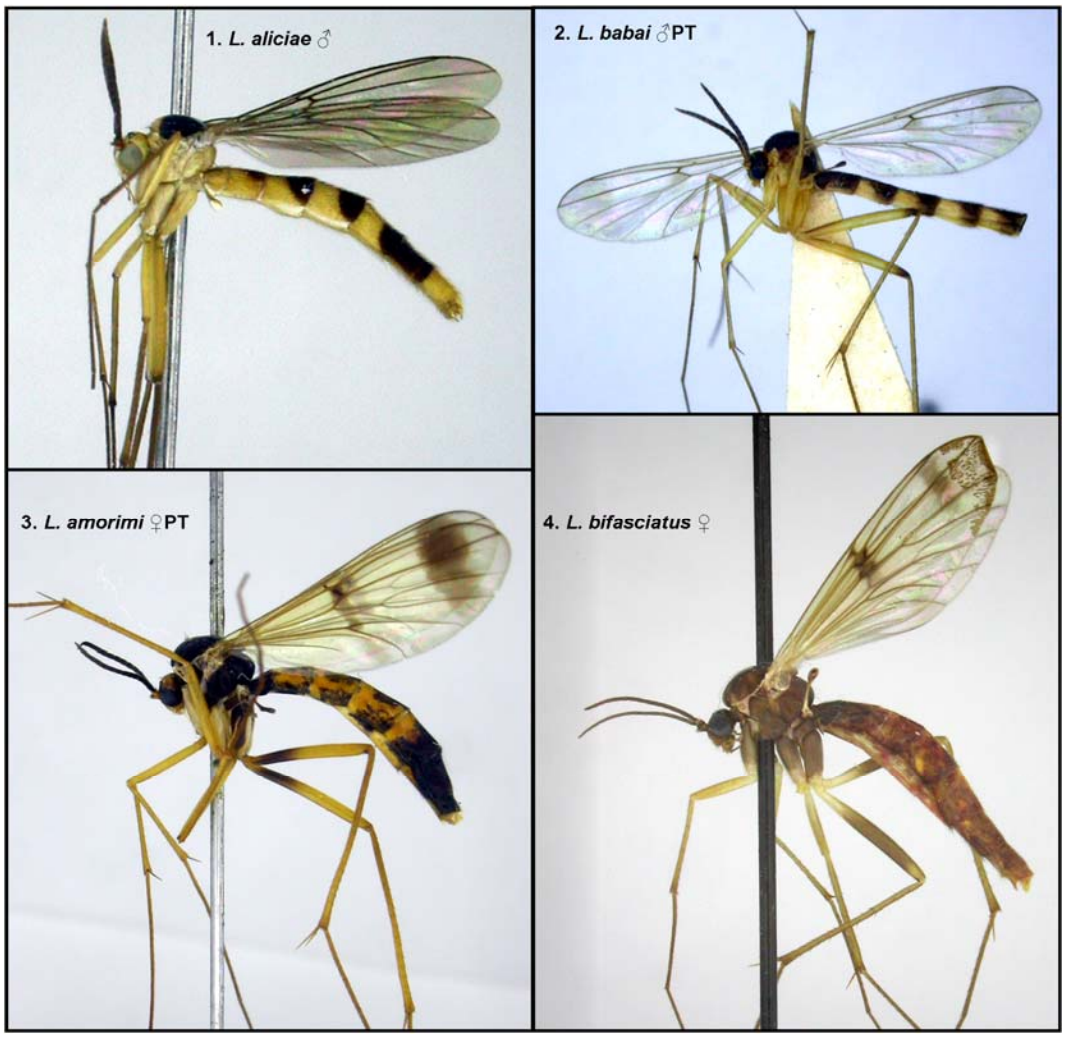
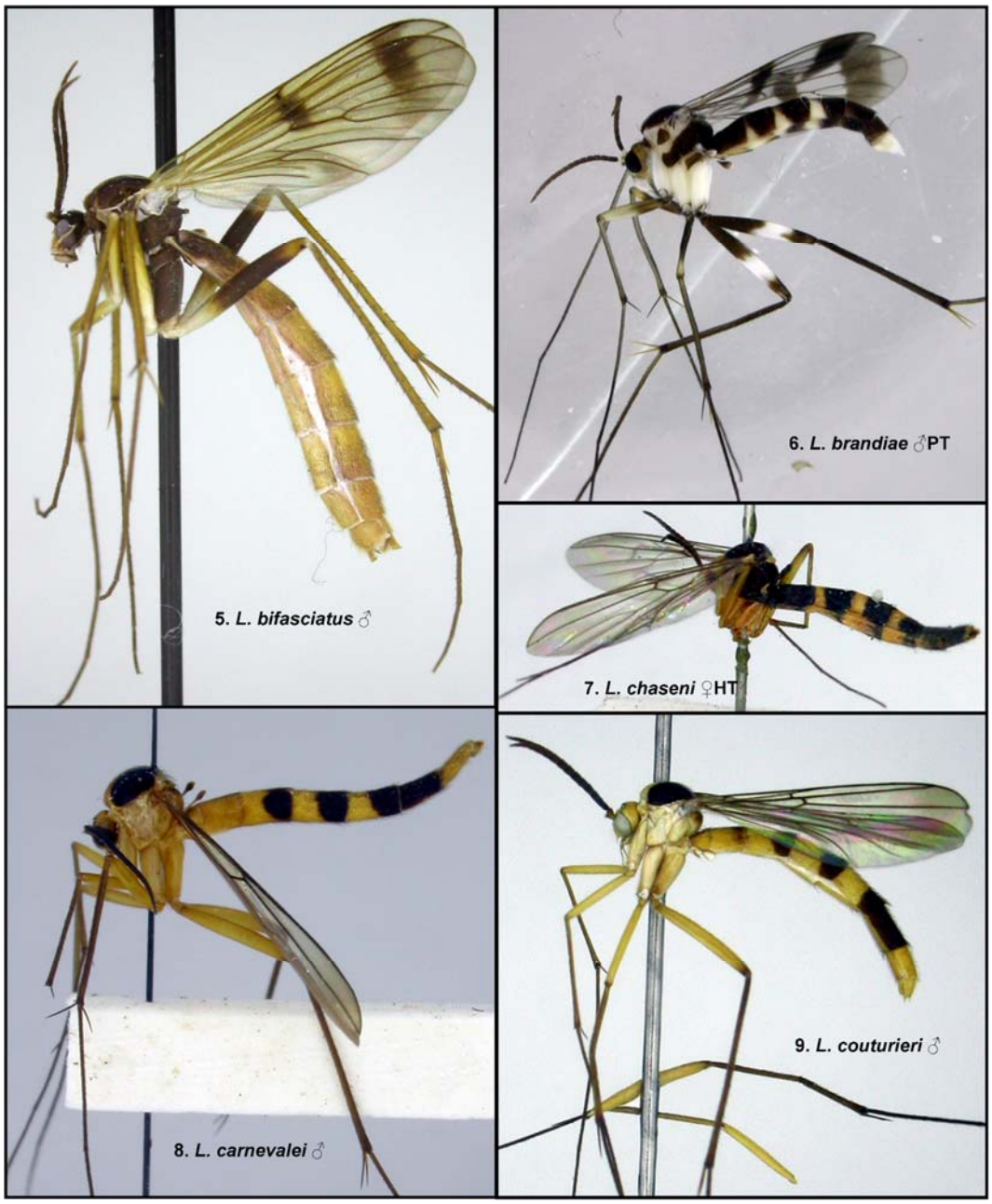
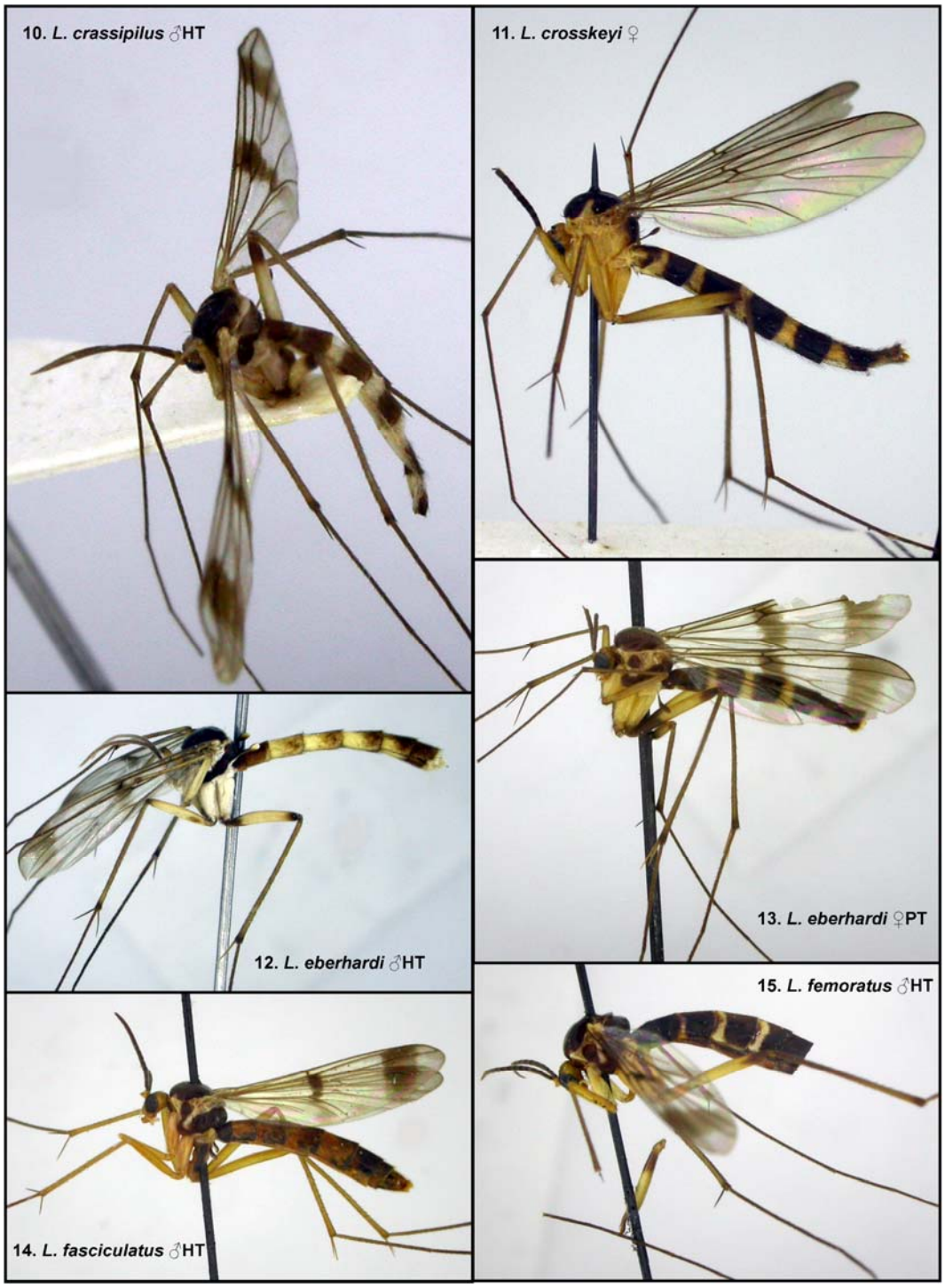


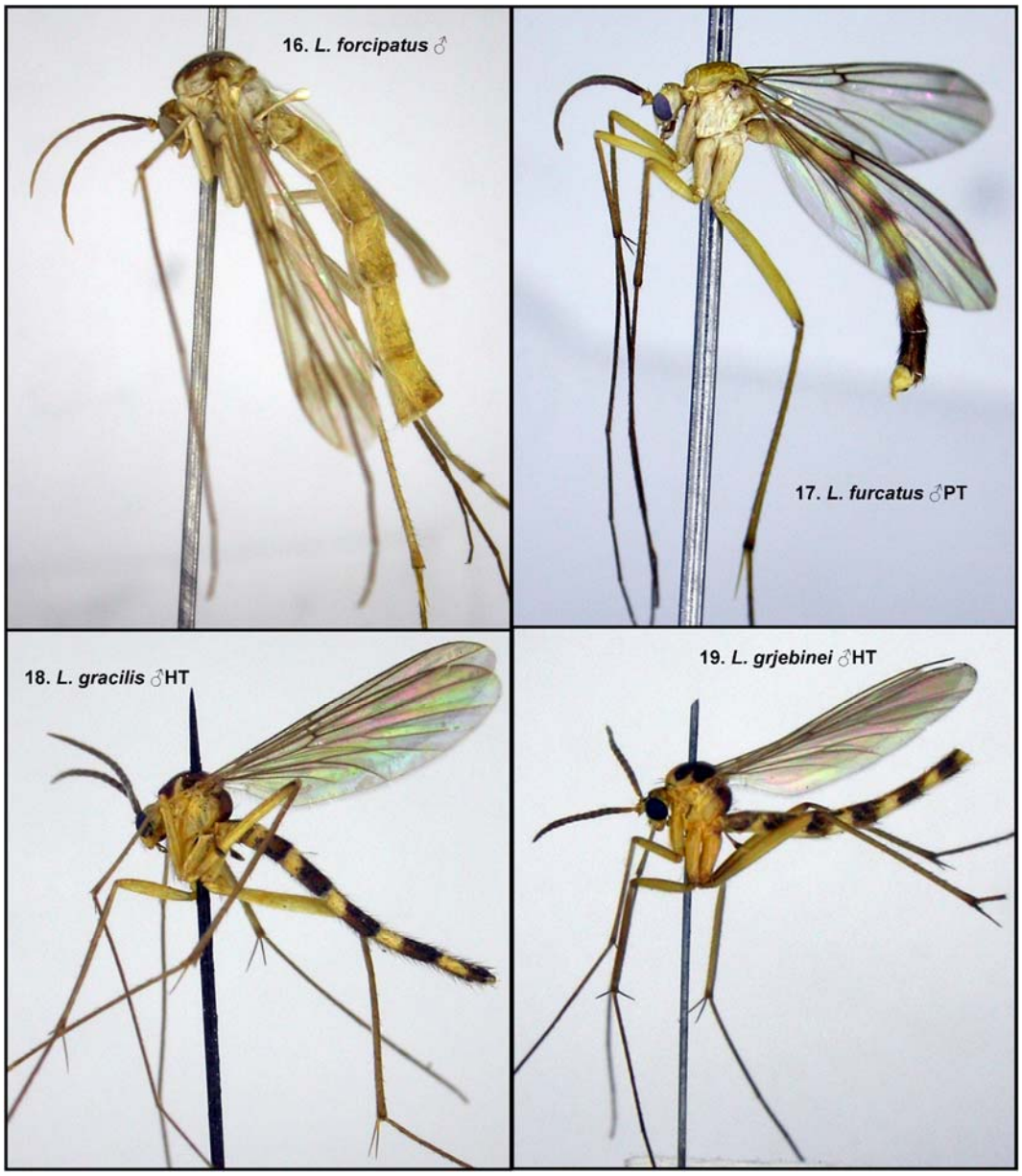
Figures 1-4. *Leptomorphus* habitus. 1. *L. aliciae*, male. **2.** *L. babai*, paratype male. **3.** *L. amorimi*, paratype female. **4.** *L. bifasciatus*, female.



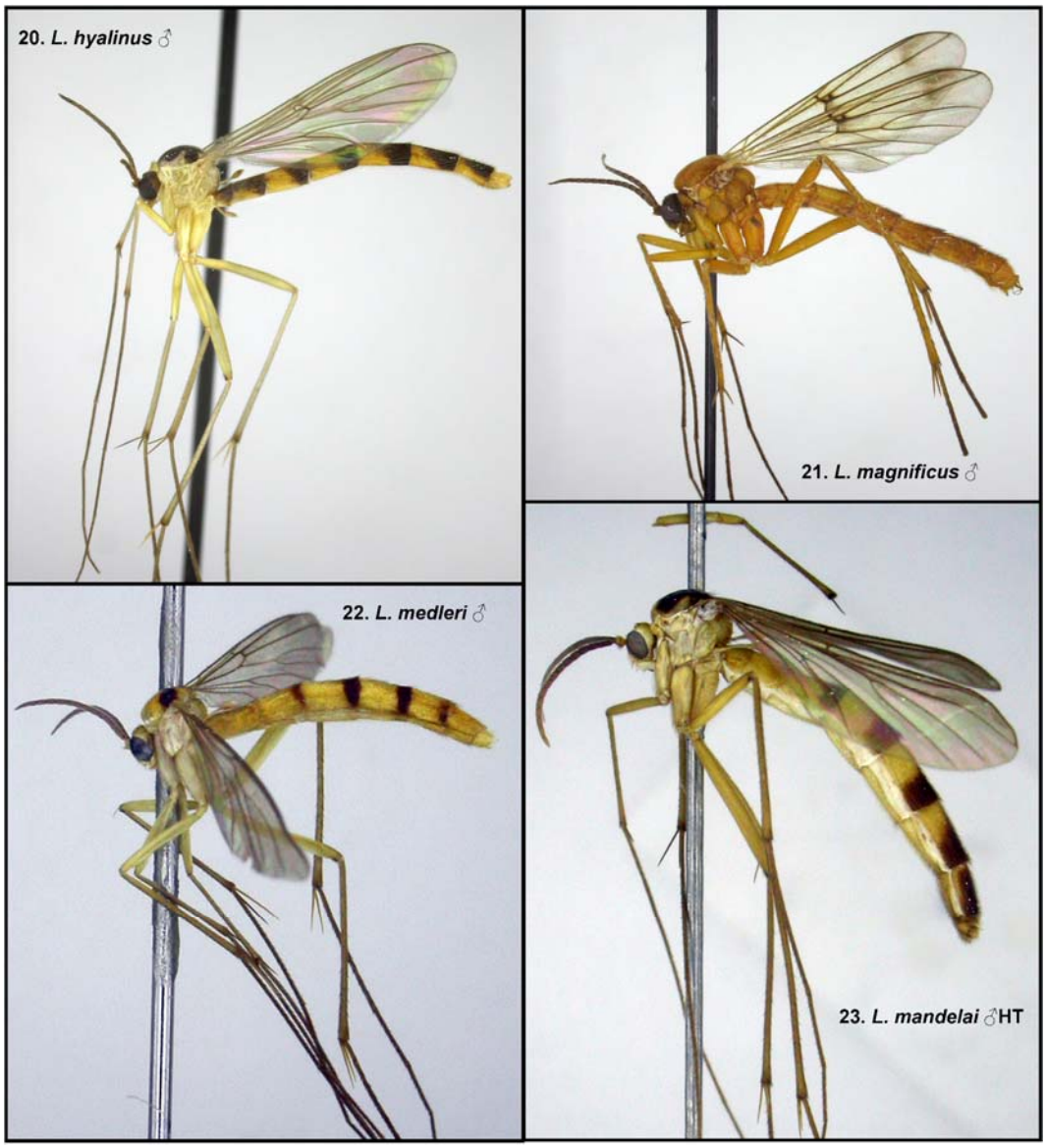
Figures 5-9. *Leptomorphus* habitus. 5. *L. bifasciatus*, neotype male. **6.** *L. brandiae*, paratype male. **7.** *L. chaseni*, holotype female. **8.** *L. carnevalei*, male. **9.** *L. couturieri*, male.



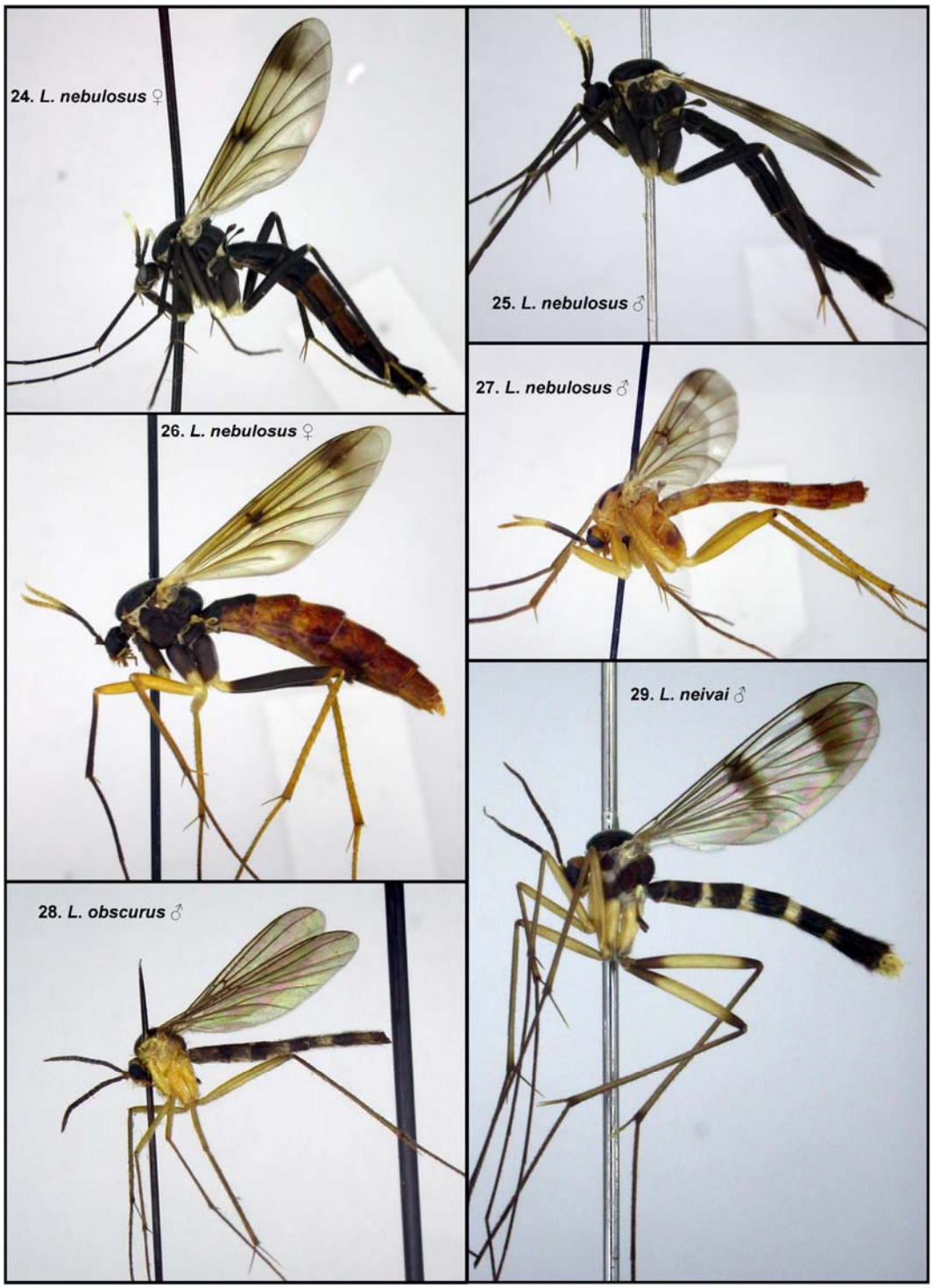
Figures 10-15. *Leptomorphus* habitus. 10. *L. crassipilus*, holotype male. **11.** *L. crosskeyi*, female. **12.** *L. eberhardi*, holotype male. **13.** *L. eberhardi*, paratype female. **14.** *L. fasciculatus*, holotype male. **15.** *L. femoratus*, holotype male.



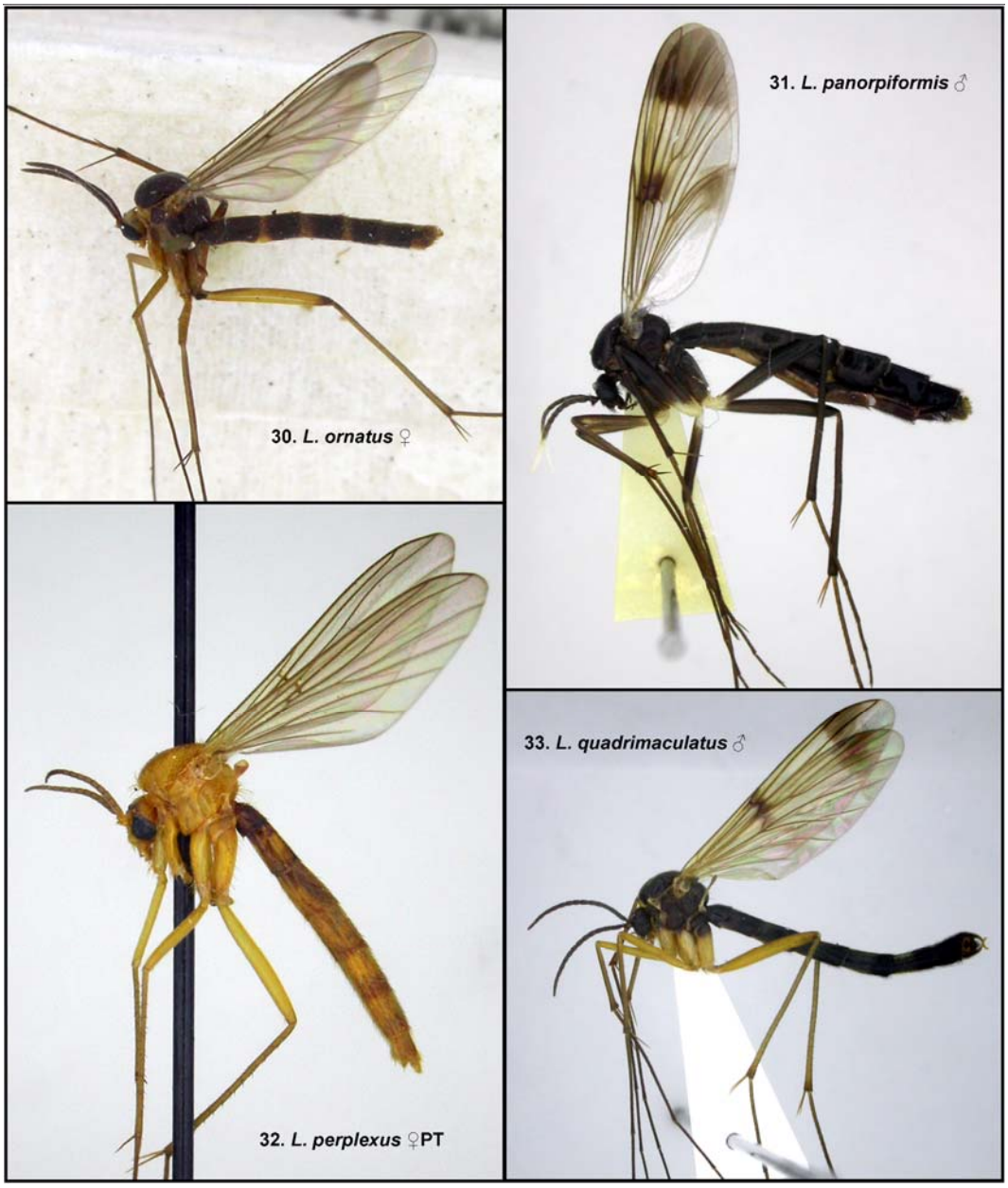
Figures 16-19. *Leptomorphus* habitus.16. *L. forcipatus*, male. **17.** *L. furcatus,* paratype male. **18.** *L. gracilis,* holotype male. **19.** *L. grjebinei*, holotype male.



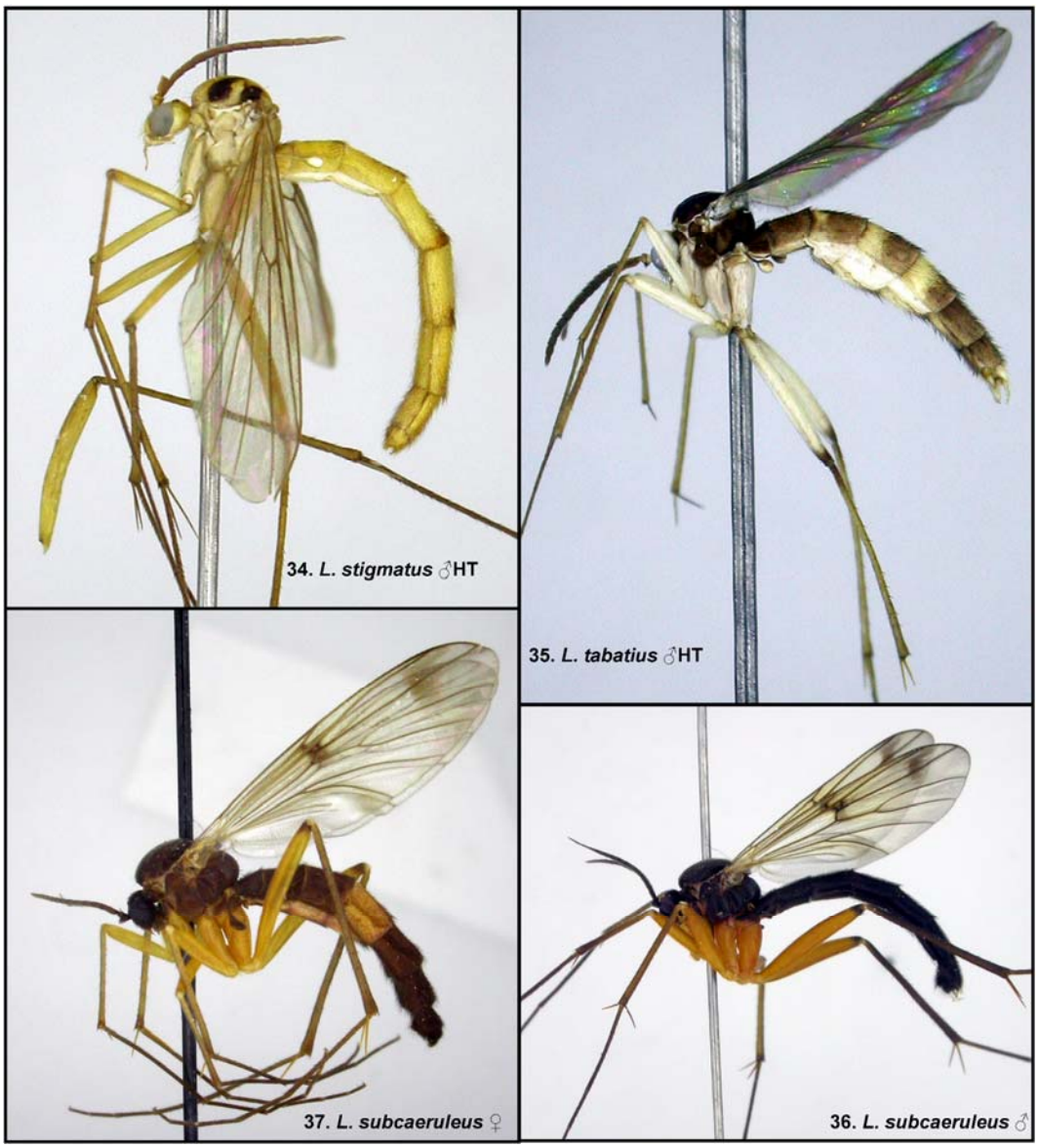
Figures 20-23. *Leptomorphus* habitus. 20. *L. hyalinus*, male. **21.** *L. magnificus*, male. **22.** *L. medleri*, male. **23.** *L. mandelai,* holotype male.



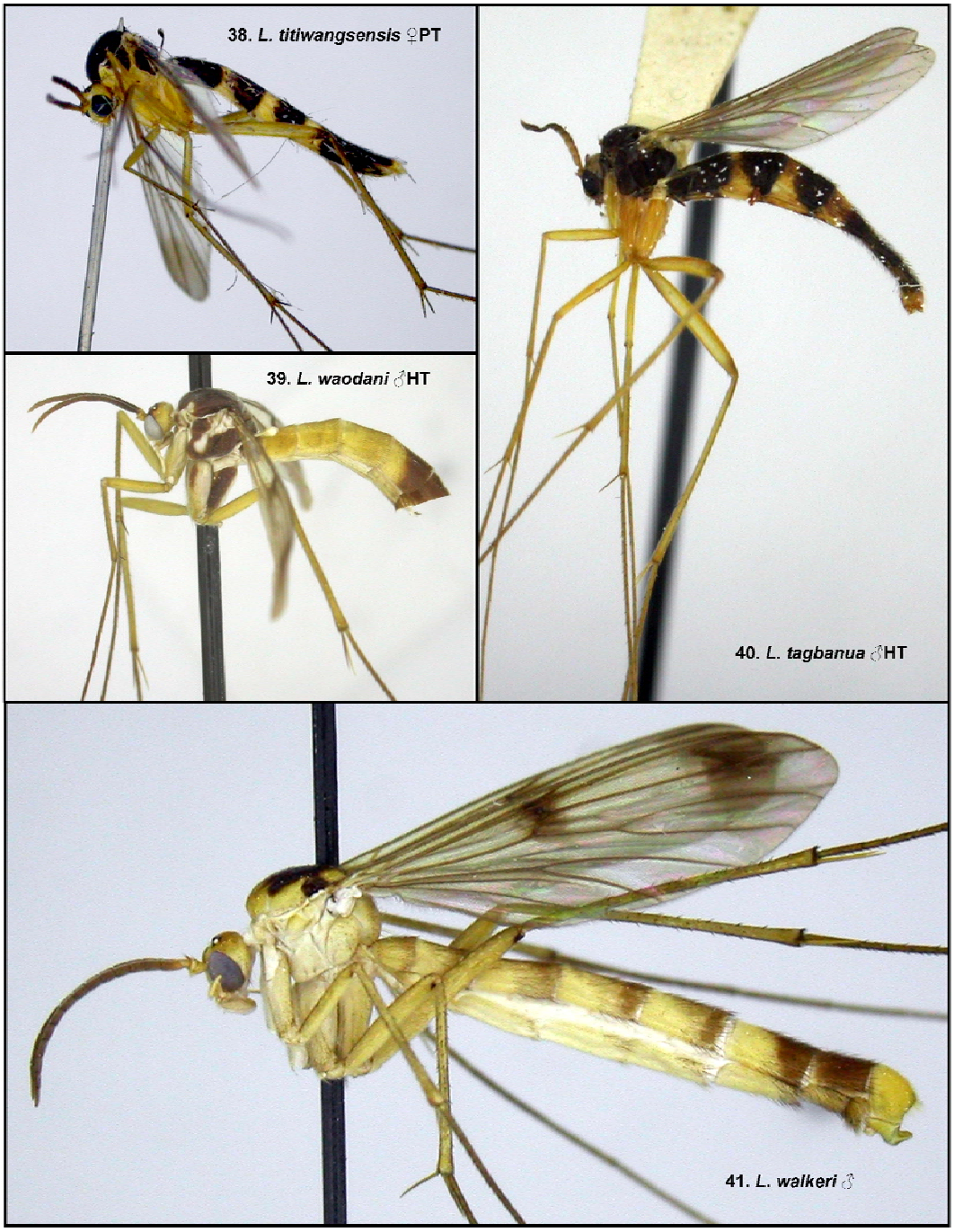
Figures 24-29. *Leptomorphus* habitus. 24. *L. nebulosus,* female, dark form. **25.** *L. nebulosus,* male, dark form. **26.** *L. nebulosus,* female, common colour. **27.** *L. nebulosus,* male, light form. **28.** *L. obscurus*, male. **29.** *L. neivai*, male.



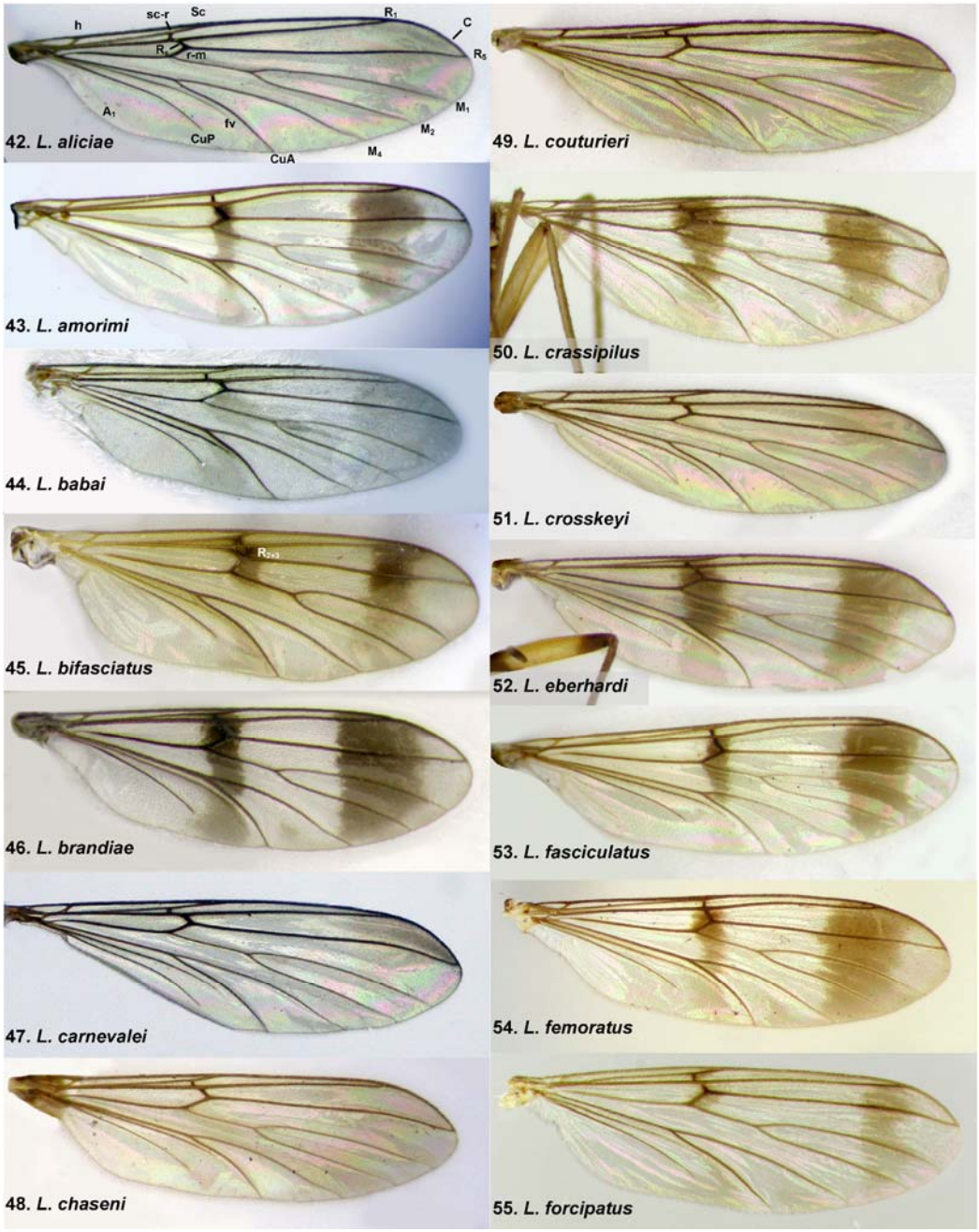
Figures 30-33. *Leptomorphus* habitus. 30. *L. ornatus*, female. **31.** *L. panorpiformis*, male. **32.** *L. perplexus*, paratype female. **33.** *L. quadrimaculatus*, male.



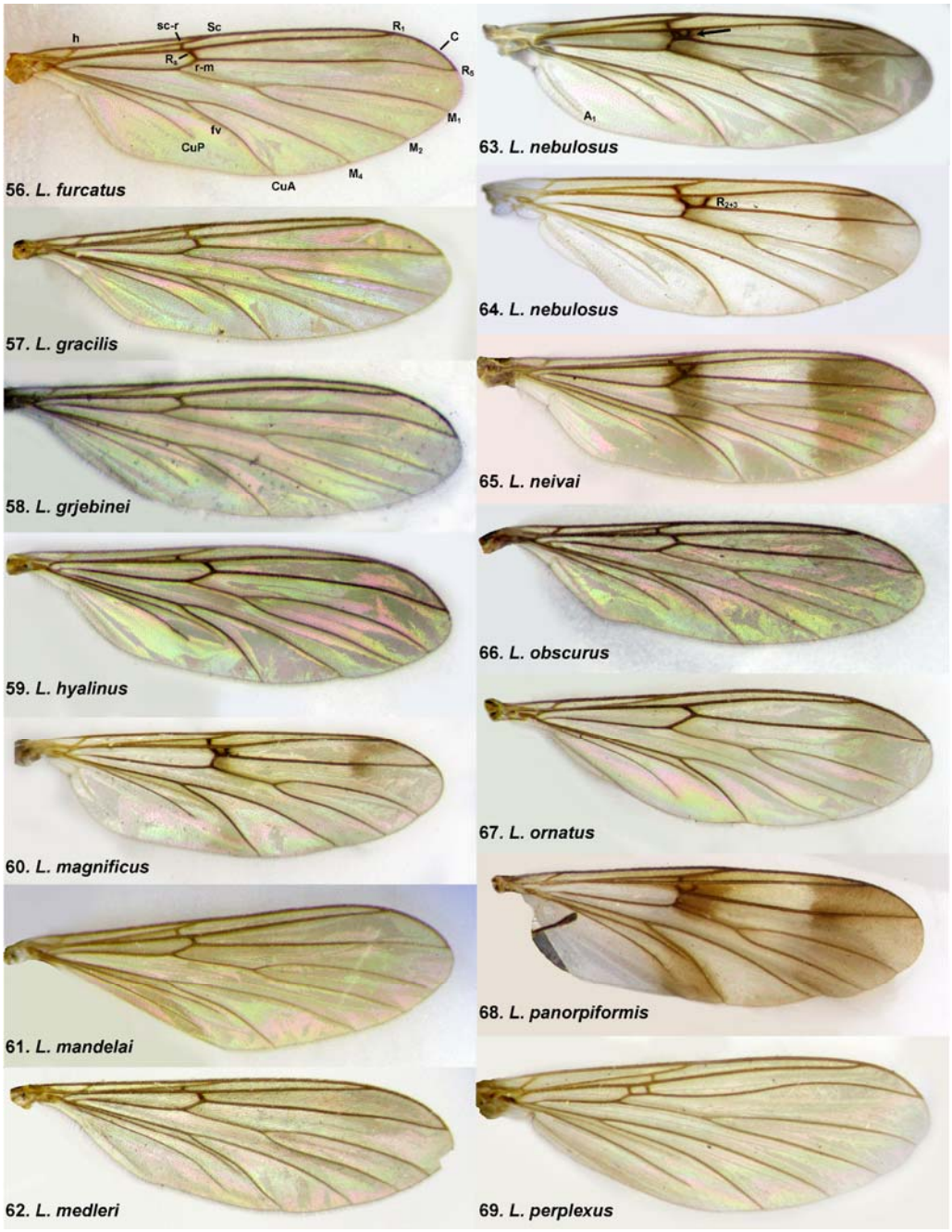
Figures 34-37. *Leptomorphus* habitus. 34. *L. stigmatus*, holotype male. **35.** *L. tabatius,* holotype male. **36.** *L. subcaeruleus*, male. **37.** *L. subcaeruleus*, female.



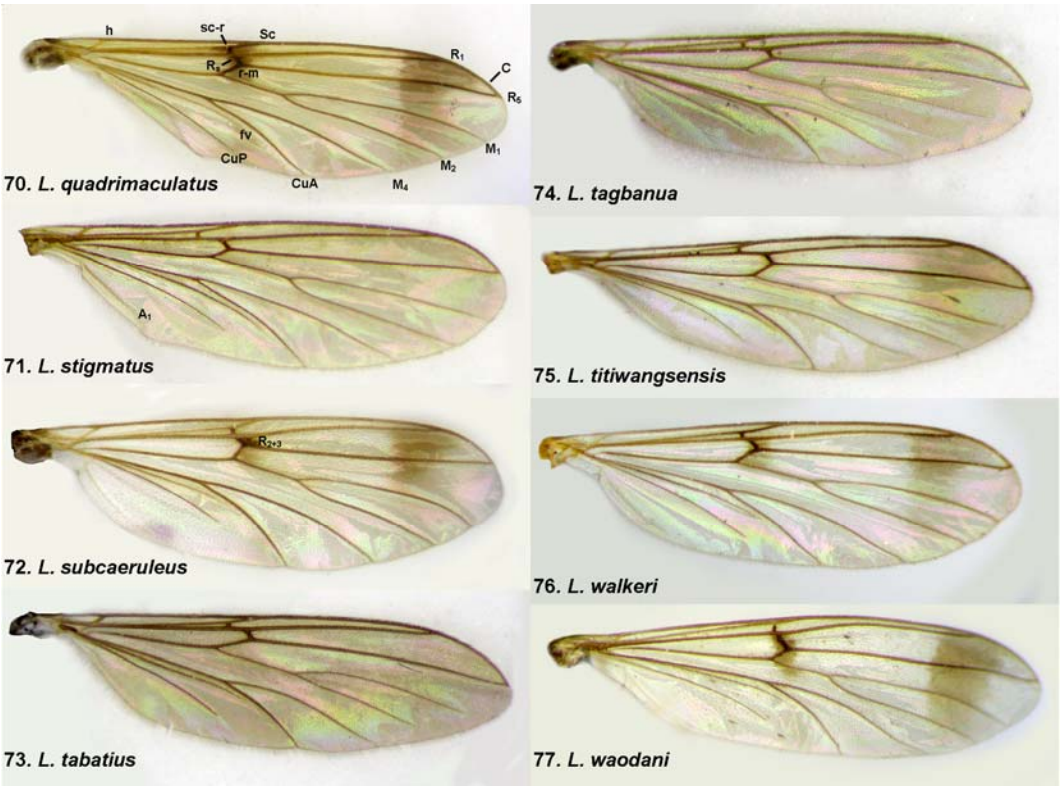
Figures 38-41. *Leptomorphus* habitus. 38. *L. titiwangsensis,* paratype female. **39.** *L. waodani,* holotype male. **40.** *L. tagbanua,* holotype male. **41.** *L. walkeri*, male.



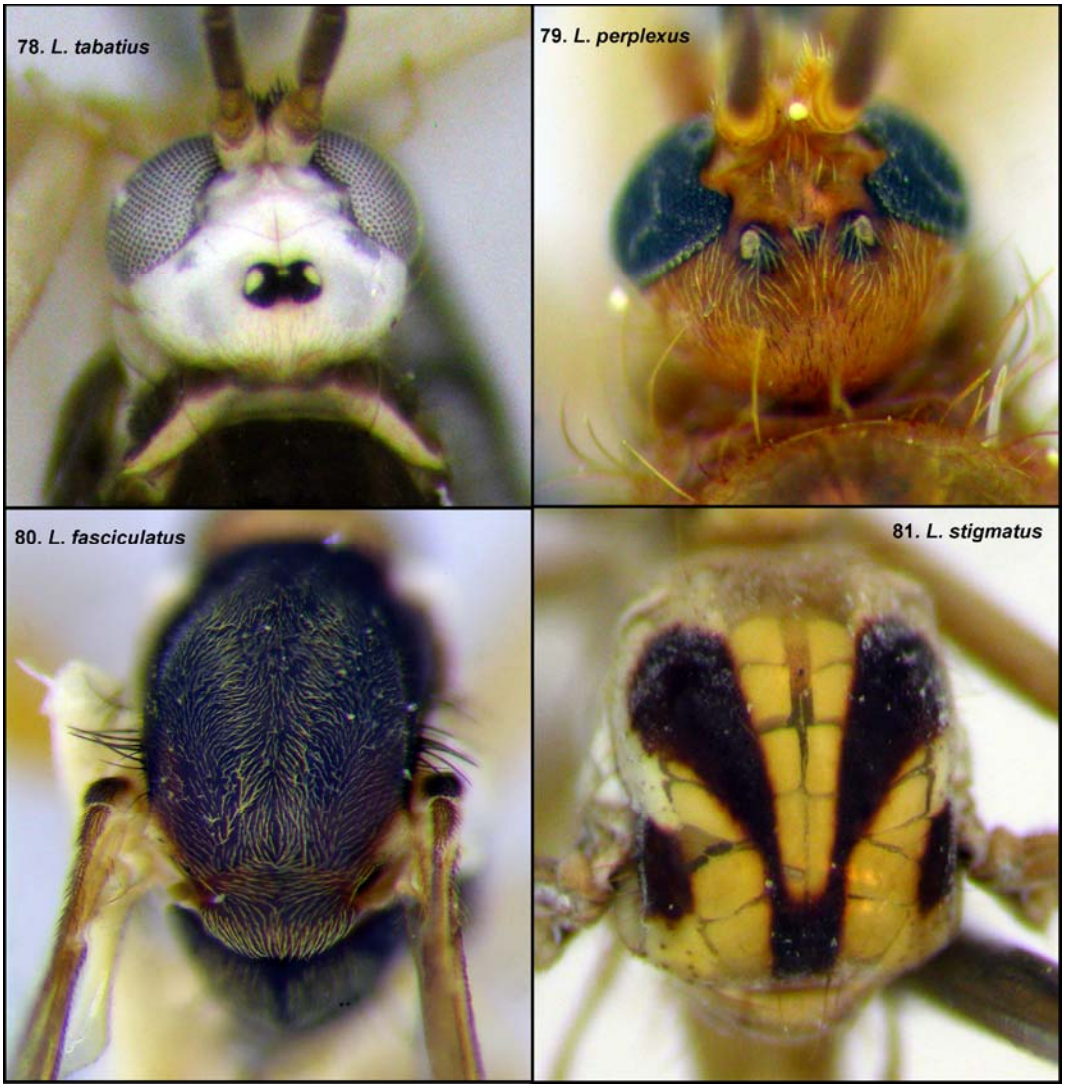
Figures 42-55. *Leptomorphus* wings. 42. *L. aliciae*, dorsal. **43.** *L. amorimi* paratype female, dorsal. **44.** *L. babai* holotype male, ventral. **45.** *L. bifasciatus* lectotype, ventral. **46.** *L. brandiae* paratype female, dorsal. **47.** *L. carnevalei* allotype, dorsal. **48.** *L. chaseni* 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_1- Anal vein; C- costa; CuA- anterior branch of cubitus; CuP- posterior branch of cubitus; fv – false vein; h- humeral crossvein; M_1, M_2, M_4,- branches of the media; r-m- radial-medial crossvein; Rs- radial sector vein; R_1, R_{2+3}, R_5- branches of the radius; Sc- subcosta; sc-r- subcostal-radial crossvein.



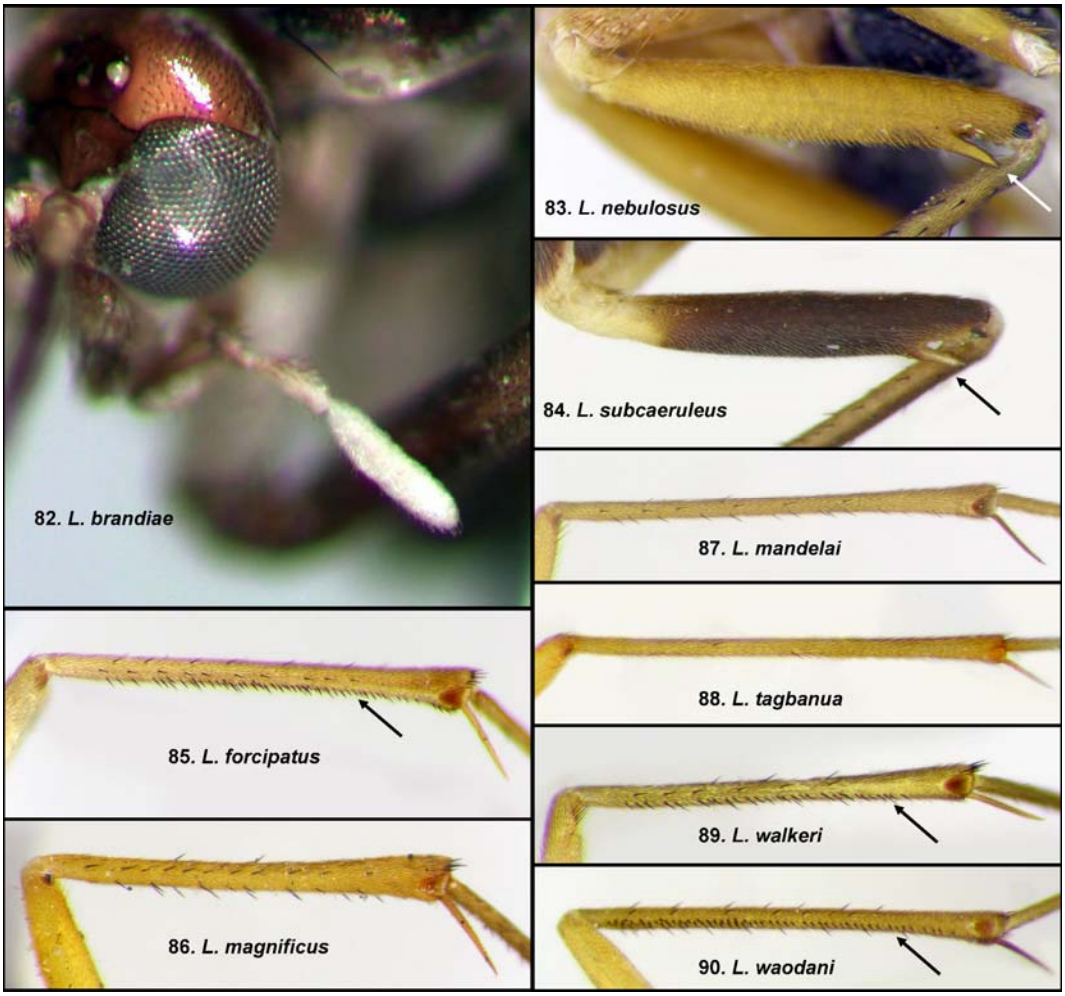
Figures 56-69. *Leptomorphus* wings. 56. *L. furcatus* paratype male, dorsal. **57.** *L. gracilis*, ventral. **58.** *L. grjebinei*, ventral. **59.** *L. hyalinus*, ventral. **60.** *L. magnificus*, ventral. **61.** *L. mandelai* holotype male, ventral. **62.** *L. medleri*, ventral. **63.** *L. nebulosus* dark form, dorsal. Arrow - cell r_{2+3} (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- Anal vein; C- costa; CuA- anterior branch of cubitus; CuP- posterior branch of cubitus; fv – false vein; h- humeral crossvein; M_1, M_2, M_4,- branches of the media; r-m- radial-medial crossvein; Rs- radial sector vein; R_1, R_{2+3}, R_5- branches of the radius; Sc- subcosta; sc-r- subcostal-radial crossvein.



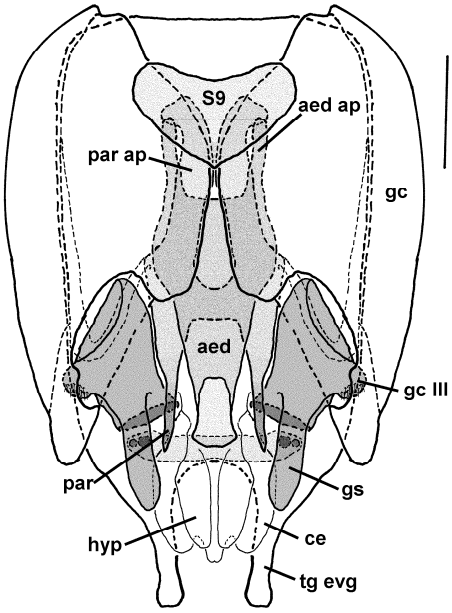
Figures 70-77. *Leptomorphus* wings. 70. *L. quadrimaculatus*, ventral. **71.** *L. stigmatus* holotype male, dorsal. **72.** *L. subcaeruleus*, ventral. **73.** *L. tabatius* holotype male, dorsal. **74.** *L. tagbanua* holotype male, ventral. **75.** *L. titiwangsensis* paratype female, dorsal. **76.** *L. walkeri*, ventral. **77.** *L. waodani* holotype male, dorsal. **Abbreviations**: A_1- Anal vein; C- costa; CuA- anterior branch of cubitus; CuP- posterior branch of cubitus; fv – false vein; h- humeral crossvein; M_1, M_2, M_4,- branches of the media; r-m- radial-medial crossvein; Rs- radial sector vein; R_1, R_{2+3}, R_5- branches of the radius; Sc- subcosta; sc-r- subcostal-radial crossvein.



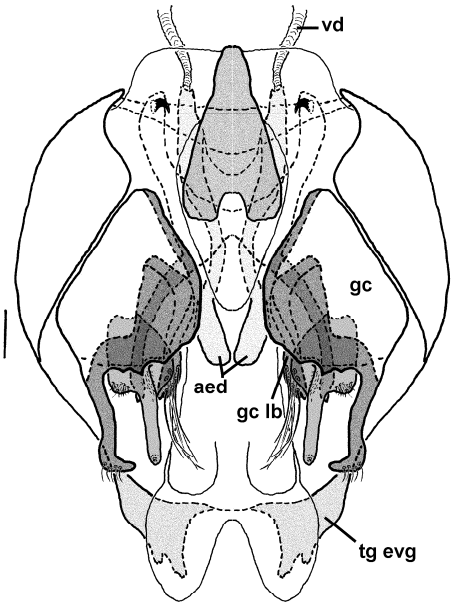
Figures 78-81. *Leptomorphus* morphology. 78-79. Dorsal view of head showing ocelli placement and arrangement. **78.** *L. tabatius.* **79.** *L. perplexus.* **80-81.** Dorsal view of scutum. **80.** *L. fasciculatus* showing covering of fine hairs. **81.** *L. stigmatus* showing pattern and lack of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



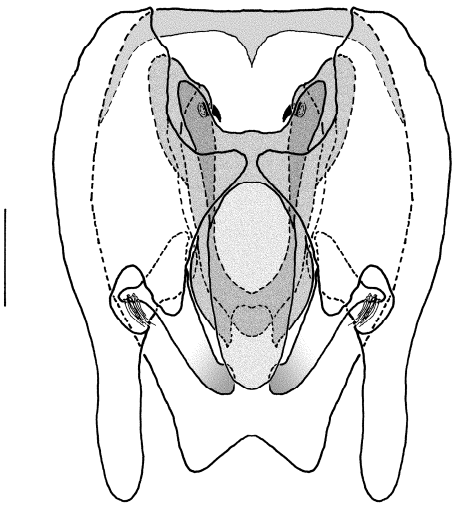
Figures 82-90. *Leptomorphus* morphology. 82. Head of *L. brandiae*, anterolateral, showing swollen palpus segment 5 covered in fine white hairs. **83-84.** Male midfemur, anterior, showing apicoventral process (arrow). **83.** *L. nebulosus.* **84.** *L. subcaeruleus.* **85-90.** Male foretibia, posterior, 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.*



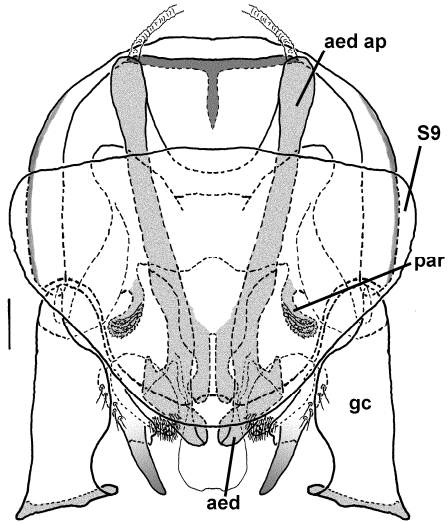
91. *L. aliciae*



92. *L. amorimi*

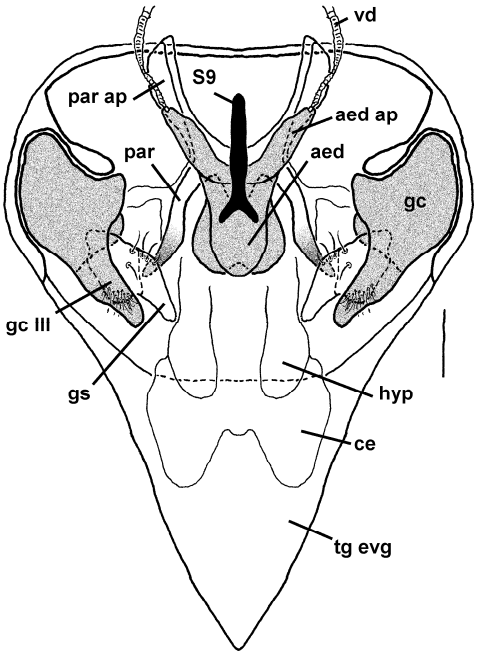


93. *L. babai*

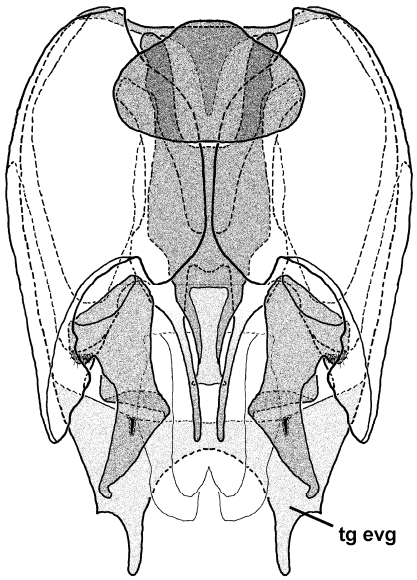


94. *L. bifasciatus*

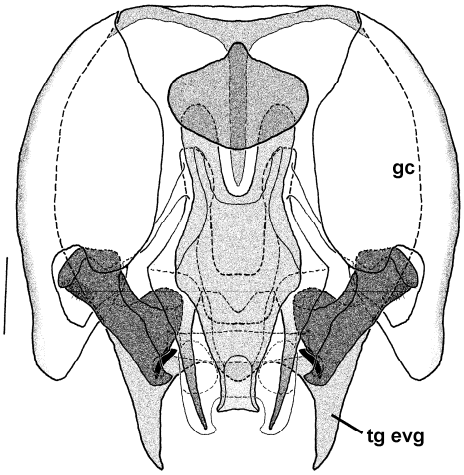
Figures 91-94. *Leptomorphus* male genitalia, ventral. 91. *L. aliciae*. **92.** *L. amorimi.* **93.** *L. babai.* **94.** *L. bifasciatus.* **Abbreviations**: aed- aedeagus; aed ap- aedeagal apodeme; ce- cercus; gc- gonocoxite, III- section 3; gc lb- gonocoxal lobe; gs- gonostylus; hyp- hypoproct; par-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



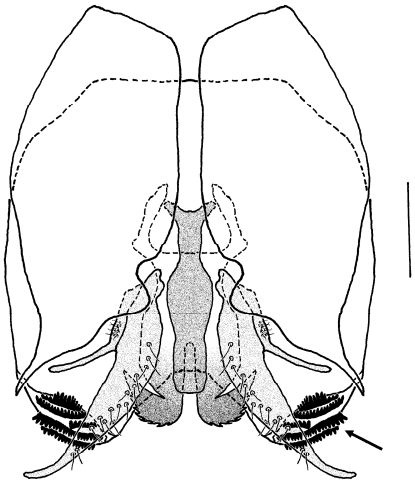
95. *L. brandiae*



96. *L. carnevalei*

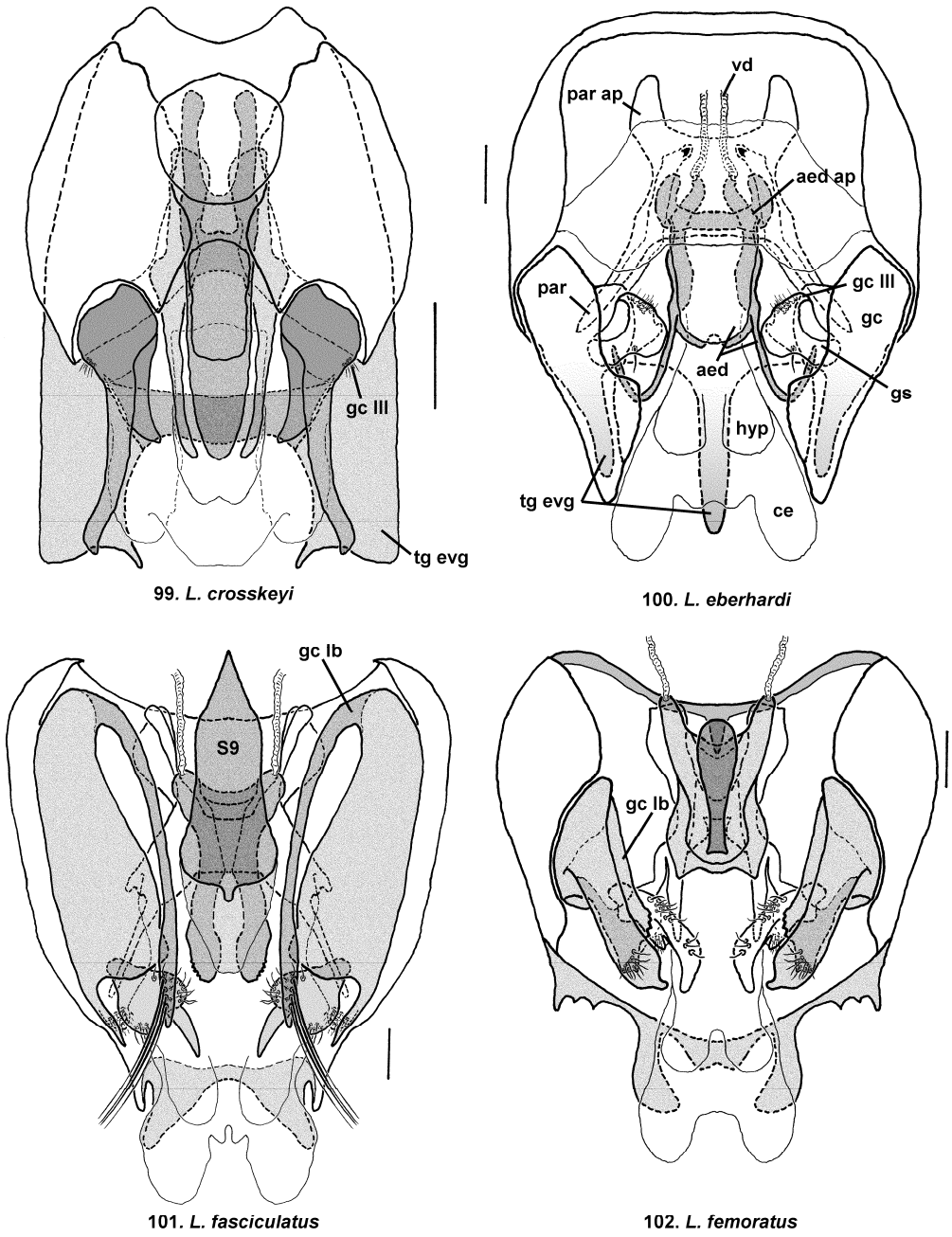


97. *L. couturieri*

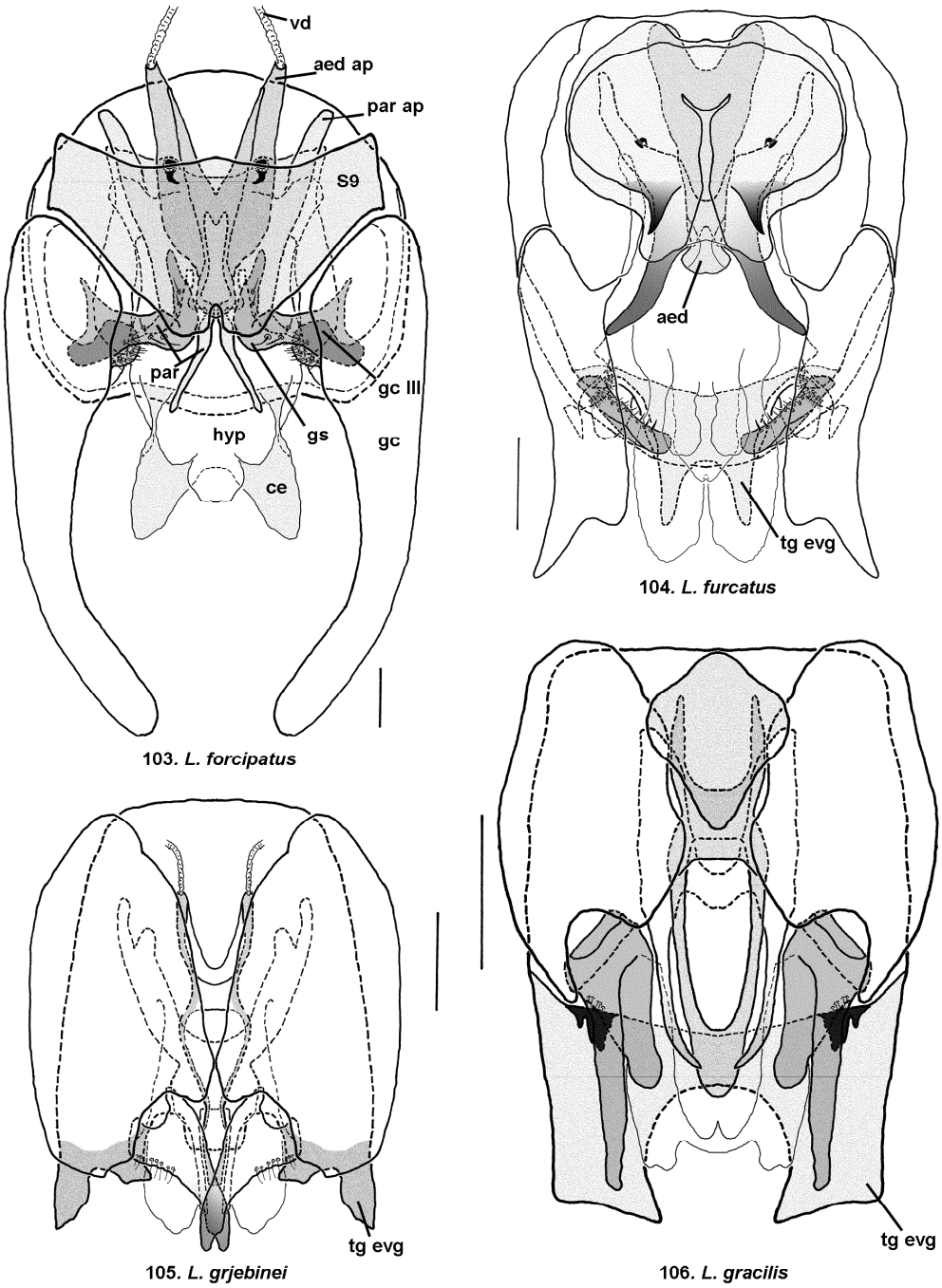


98. *L. crassipilus*

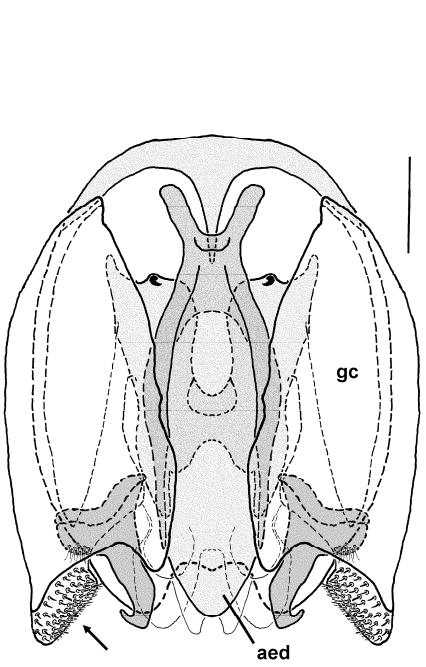
Figures 95-98. *Leptomorphus* male genitalia, ventral. 95. *L. brandiae.* **96.** *L. carnevalei.* **97.** *L. couturieri.***98.** *L. crassipilus*, arrow indicates dense rows of thick blunt bristles, arrangement of components reconstituted from crushed genitalia of holotype. **Abbreviations**: aed- 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.



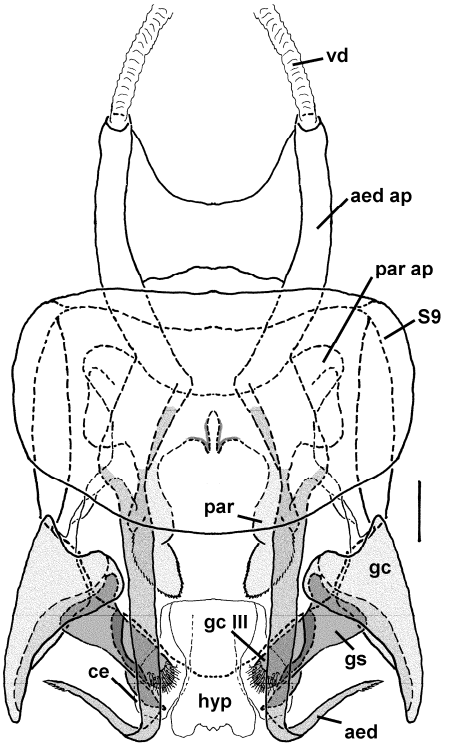
Figures 99-102. *Leptomorphus* male genitalia, ventral. 99. *L. crosskeyi.* **100.** *L. eberhardi.* **101.** *L. fasciculatus.* **102.** *L. femoratus.* **Abbreviations**: aed- aedeagus; aed ap- aedeagal apodeme; ce- cercus; gc- gonocoxite, III- section 3; gc lb- gonocoxal lobe; gs- gonostylus; hyp-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



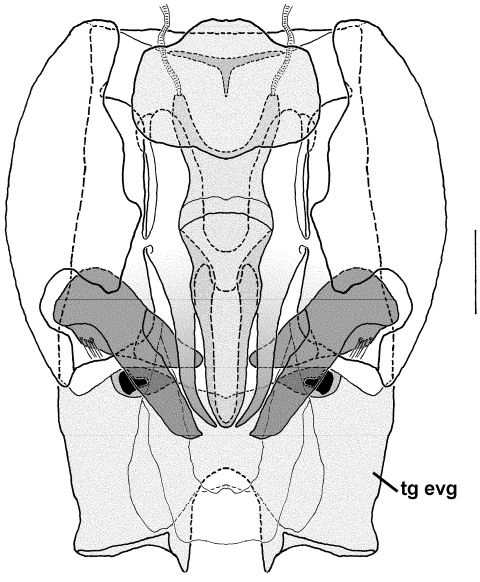
Figures 103-106. *Leptomorphus* male genitalia, ventral. 103. *L. forcipatus.* **104.** *L. furcatus.* **105.** *L. grjebinei.* **106.** *L. gracilis.* **Abbreviations**: aed- aedeagus; aed ap- aedeagal apodeme; ce- cercus; gc- gonocoxite, III- section 3; gs- gonostylus; hyp- hypoproct; par- paramere;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



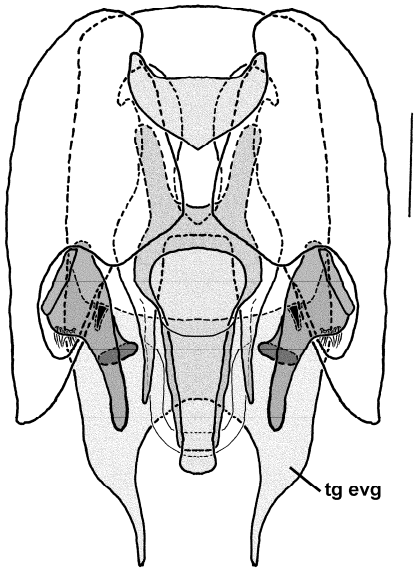
107. *L. hyalinus*



108. *L. magnificus*

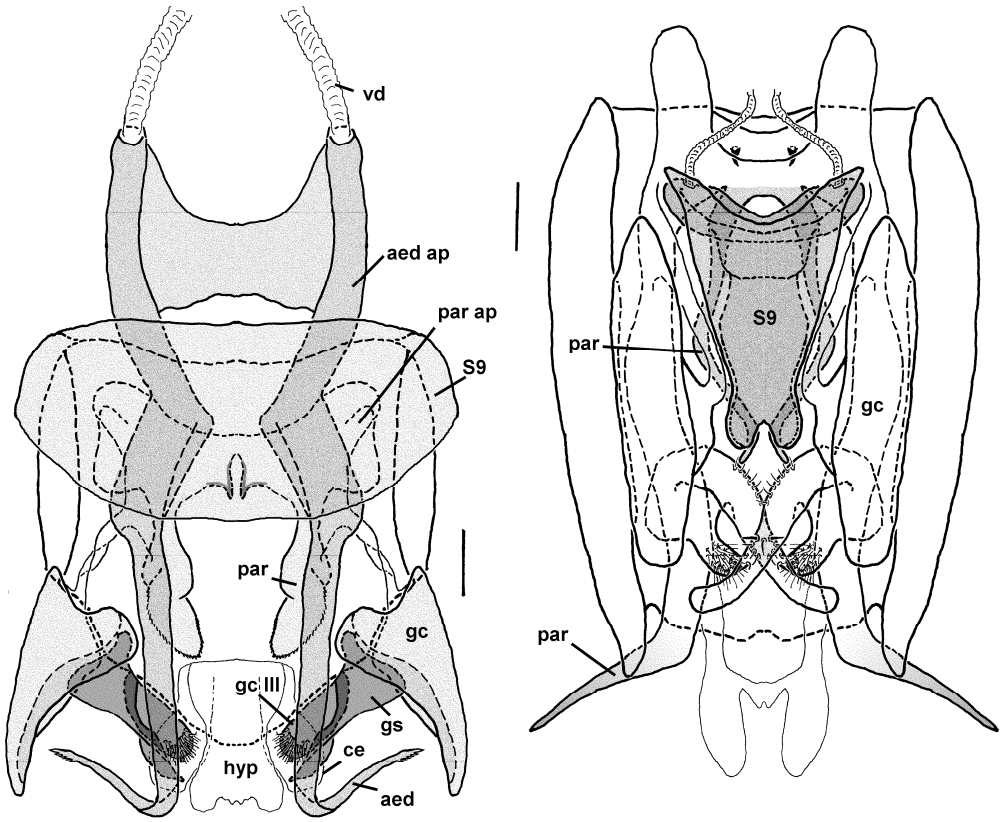


109. *L. mandelai*

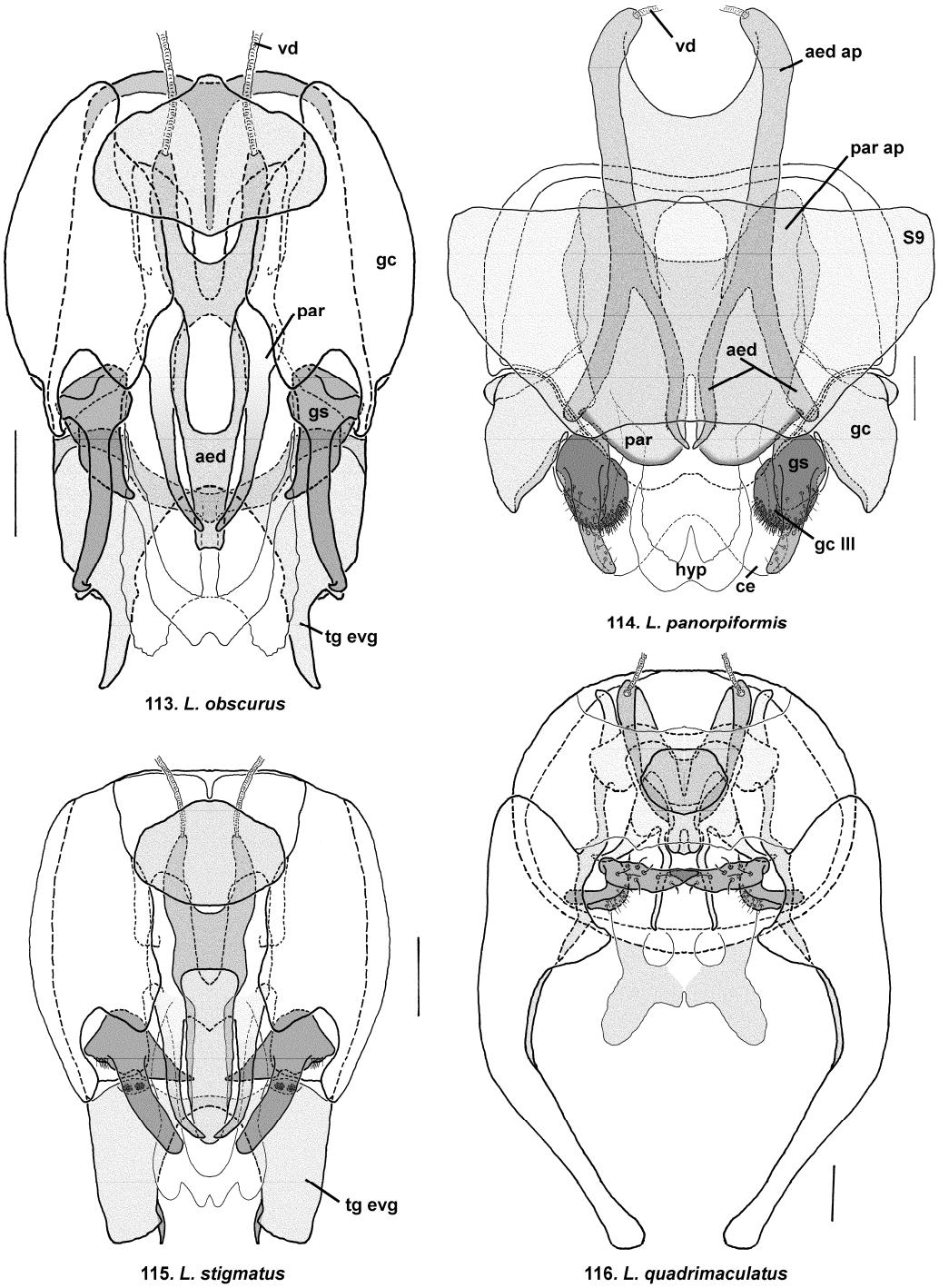


110. *L. medleri*

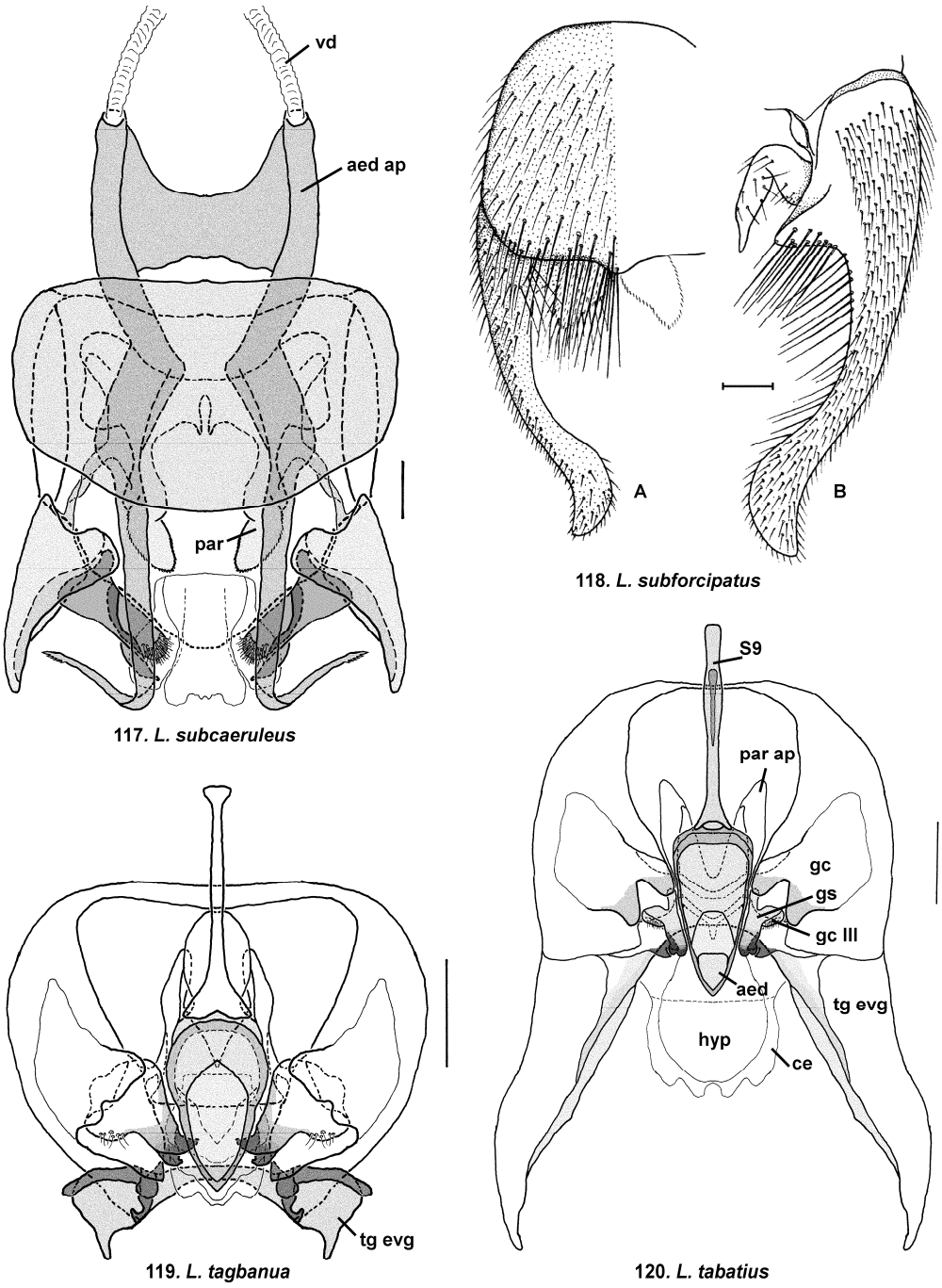
Figures 107-110. *Leptomorphus* male genitalia, ventral. 107. *L. hyalinus.* Arrow indicates patch of short, thick bristles on apex of gonocoxite. **108.** *L. magnificus.* **109.** *L. mandelai.* **110.** *L. medleri.* **Abbreviations**: aed- aedeagus; aed ap- aedeagal apodeme; ce- cercus; gc- gonocoxite, 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.



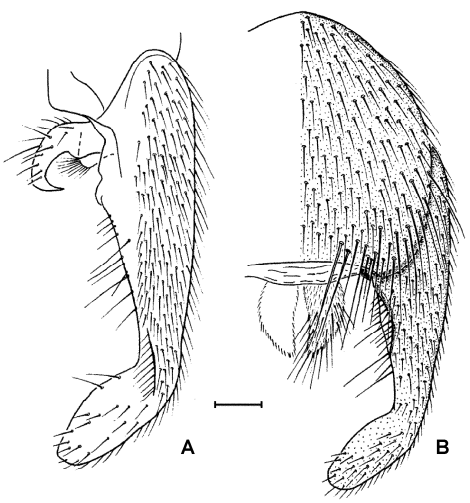
Figures 111-112. *Leptomorphus* male genitalia, ventral. 111. *L. nebulosus.* **112.** *L. neivai.* **Abbreviations**: aed- aedeagus; aed ap- aedeagal apodeme; ce- cercus; gc- gonocoxite, III- section 3; gs- gonostylus; hyp- hypoproct; par- paramere; par ap- parameral apodeme; S9- sternite 9; tg evg-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



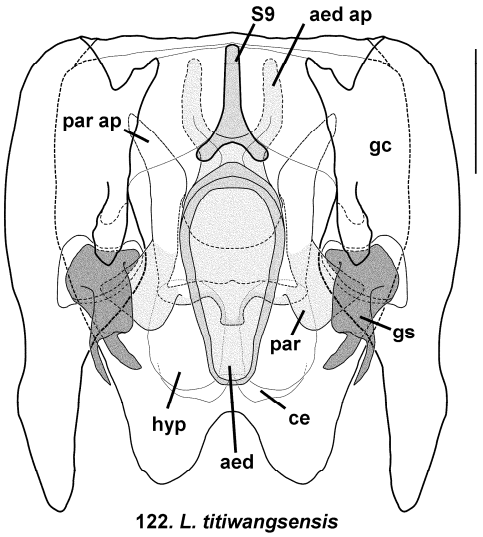
Figures 113-116. *Leptomorphus* male genitalia, ventral. 113. *L. obscurus.* **114.** *L. panorpiformis.* **115.** *L. stigmatus.* **116.** *L. quadrimaculatus*. **Abbreviations**: aed- aedeagus; aed ap- aedeagal apodeme; ce- cercus; gc- gonocoxite, III- section 3; gs- gonostylus; hyp- hypoproct; par-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



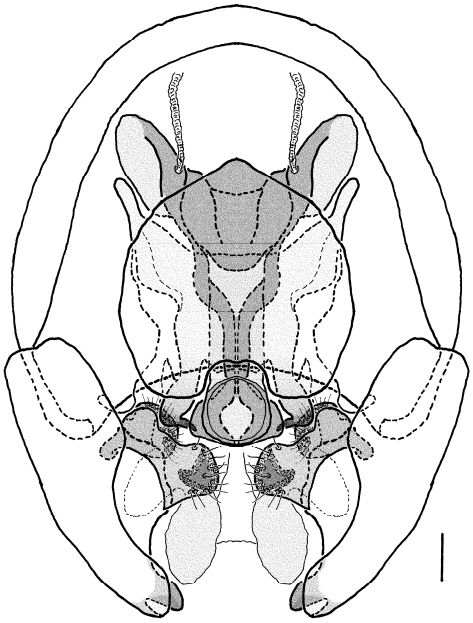
Figures 117-120. *Leptomorphus* male genitalia. 117. *L. subcaeruleus*, ventral. **118.** *L. subforcipatus* (after Zaitzev & Ševčík 2002), **A.** dorsal. **B.** gonocoxite and gonostylus, ventral. **119.** *L. tagbanua,* ventral. **120.** *L. tabatius*, ventral. **Abbreviations**: aed- aedeagus; aed 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.



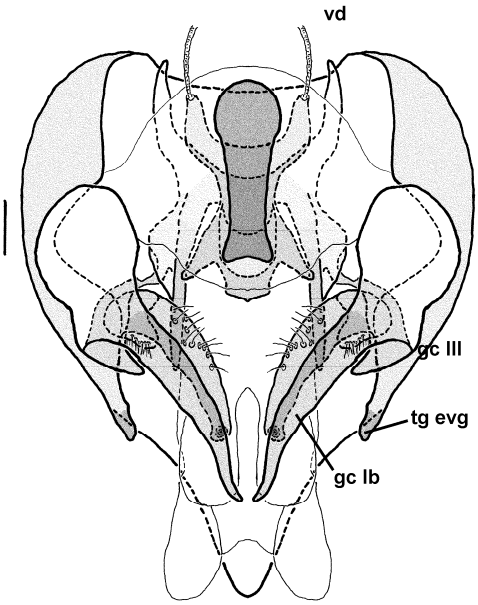
121. *L. talyshensis*



122. *L. titiwangsensis*

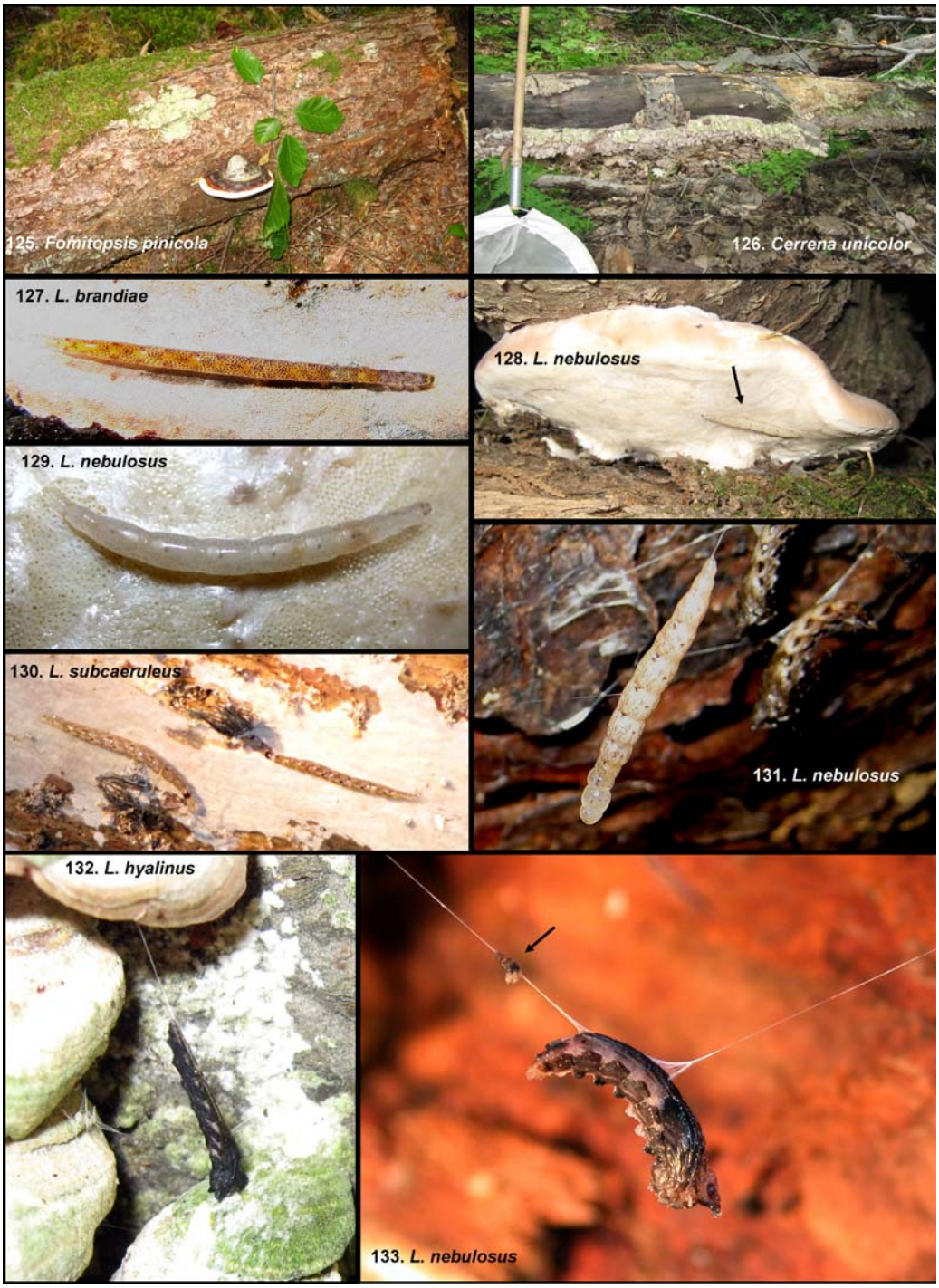


123. *L. walkeri*



124. *L. waodani*

Figures 121-124. *Leptomorphus* male genitalia. 121. *L. talyshensis* (after 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.



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).

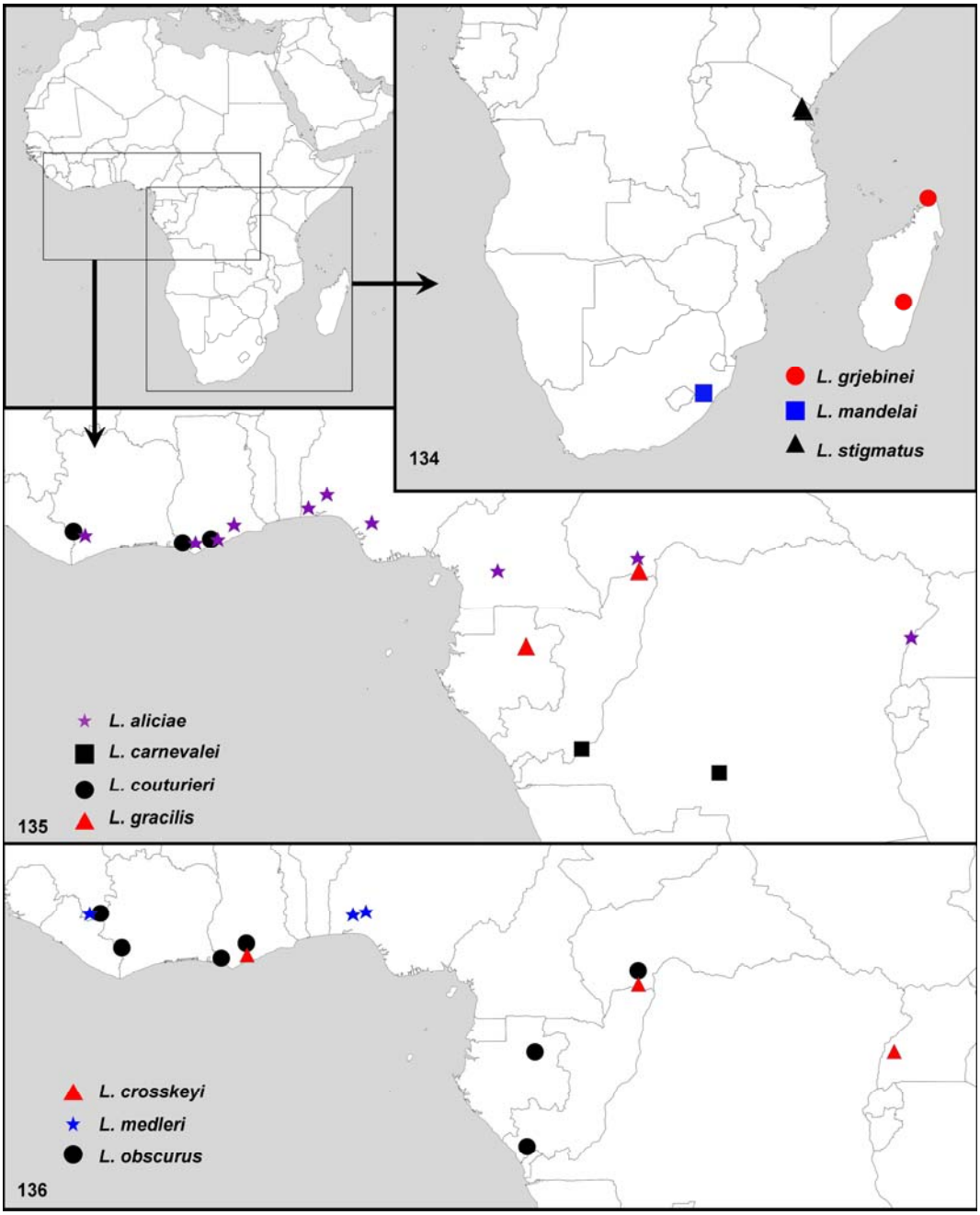


Figure 134-136. Distribution of Afrotropical *Leptomorphus*. 134. *L. grjebinei* (red circle), *L. mandelai* (blue square), *L. stigmatus* (black triangle). **135.** *L. aliciae* (purple star), *L. carnevalei* (black square), *L. couturieri* (black circle), *L. gracilis* (red triangle). **136.** *L.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

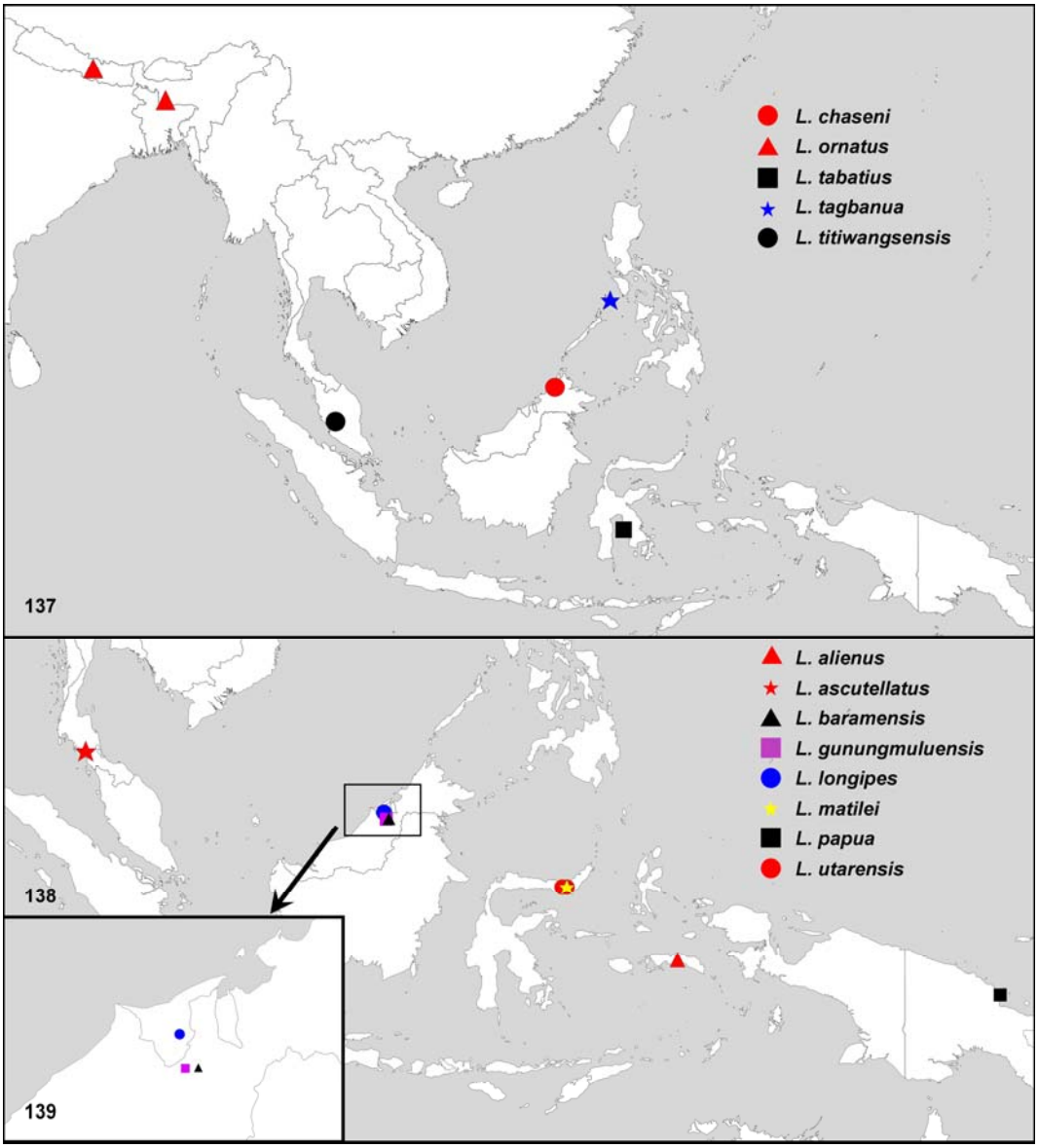


Figure 137-139. Distribution of Oriental and Australasian *Leptomorphus.* 137. *L. chaseni* (red circle), *L. ornatus* (red triangle), *L. tabatius* (black square), *L. tagbanua* (blue star), *L. titiwangsensis* (black circle). **138.** Species described by Papp & Ševčík 2011. *L. alienus* (red triangle), *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.*

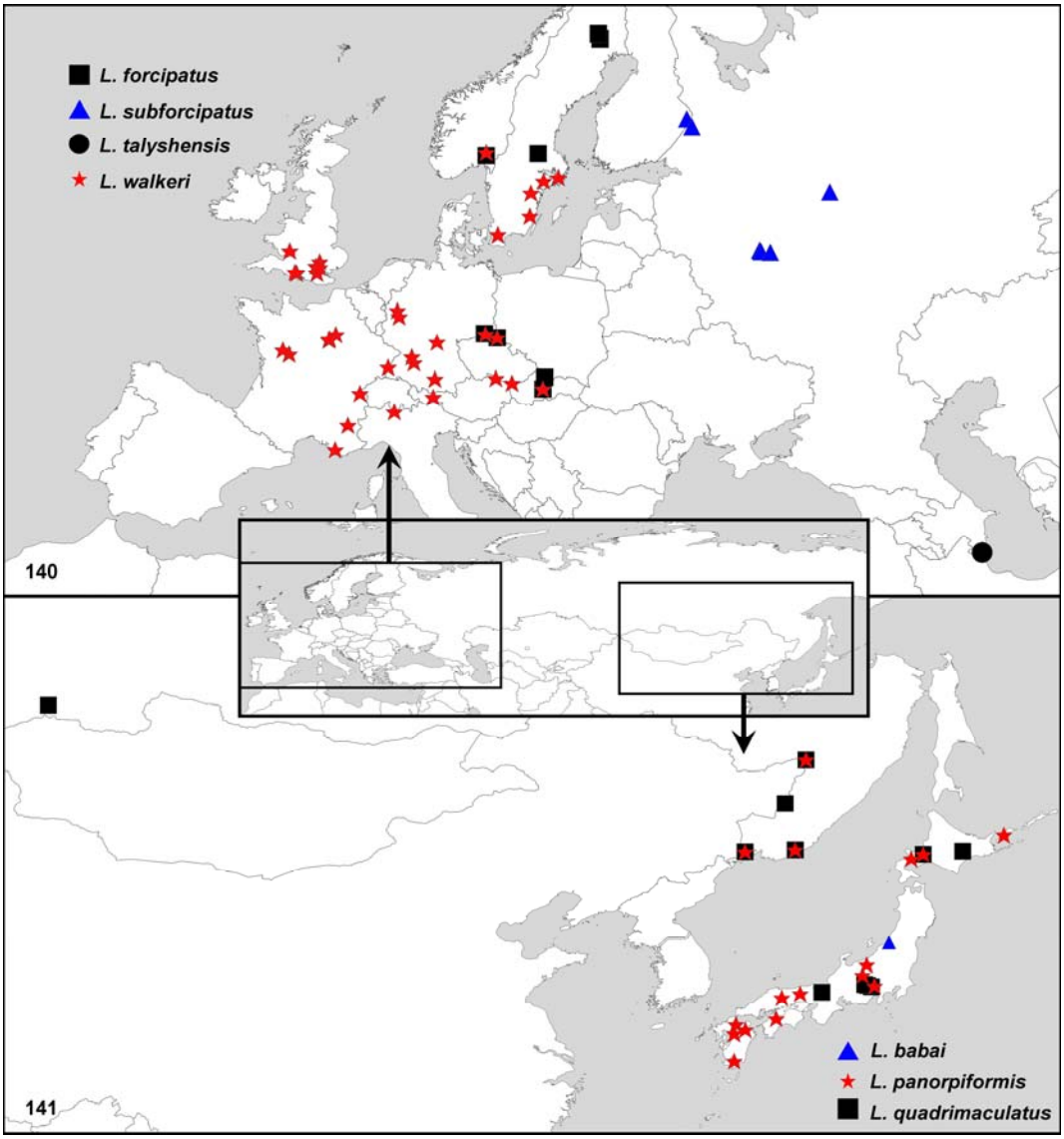


Figure 140-141. Distribution of Palaearctic *Leptomorphus.* 140. *L. forcipatus* (black square), *L. subforcipatus* (blue triangle), *L. talyshensis* (black circle), *L. walkeri* (red star). **141.** *L. babai* (blue triangle), *L. panorpiformis* (red star), *L. quadrimaculatus* (black square).

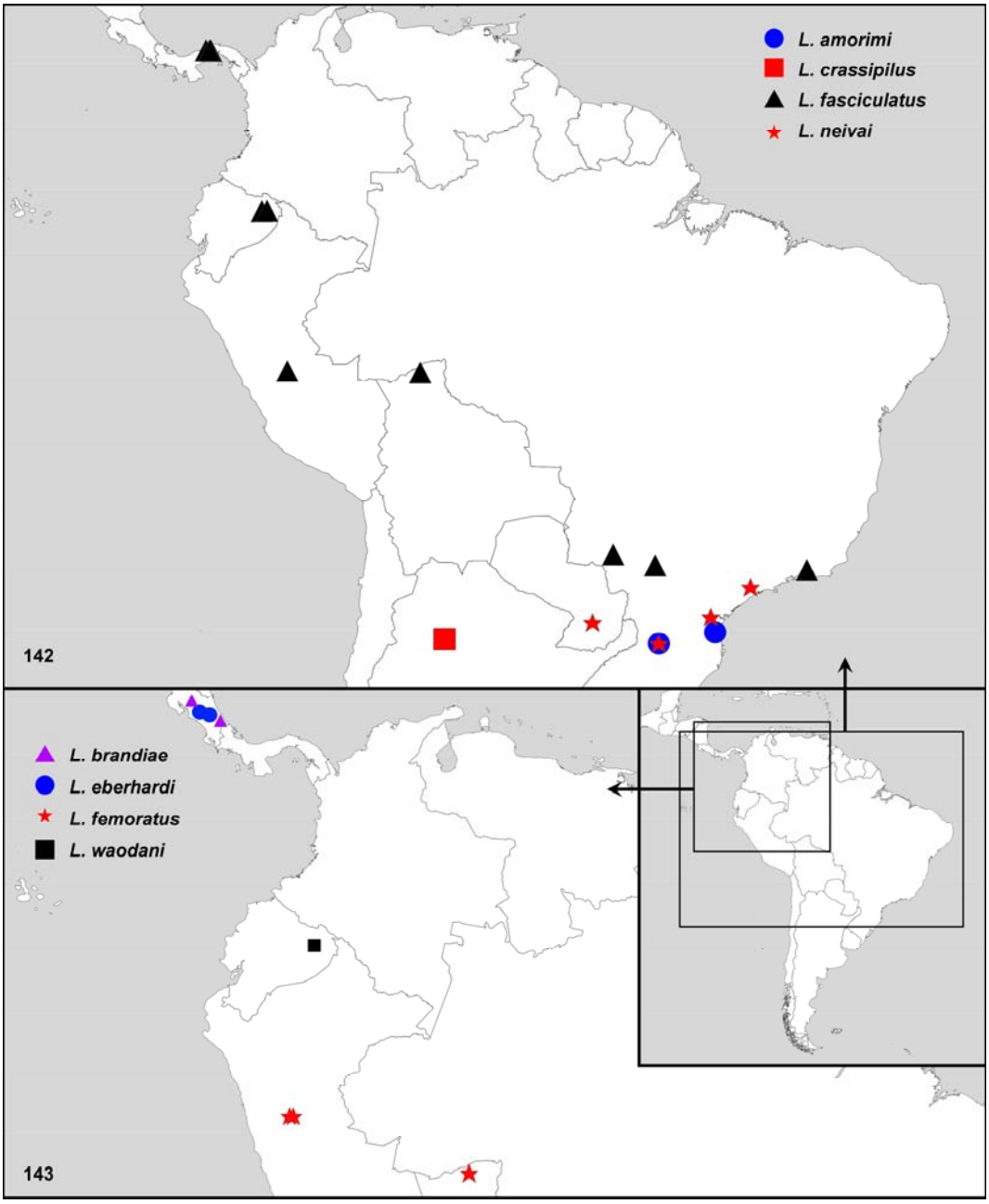


Figure 142-143. Distribution of Neotropical *Leptomorphus*. 142. *L. amorimi* (blue circle), *L. crassipilus* (red square), *L. fasciculatus* (black triangle), *L. neivai* (red star). **143.** *L. brandiae* (purple triangle), *L. eberhardi* (blue circle), *L. femoratus* (red star), *L. waodani* (black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

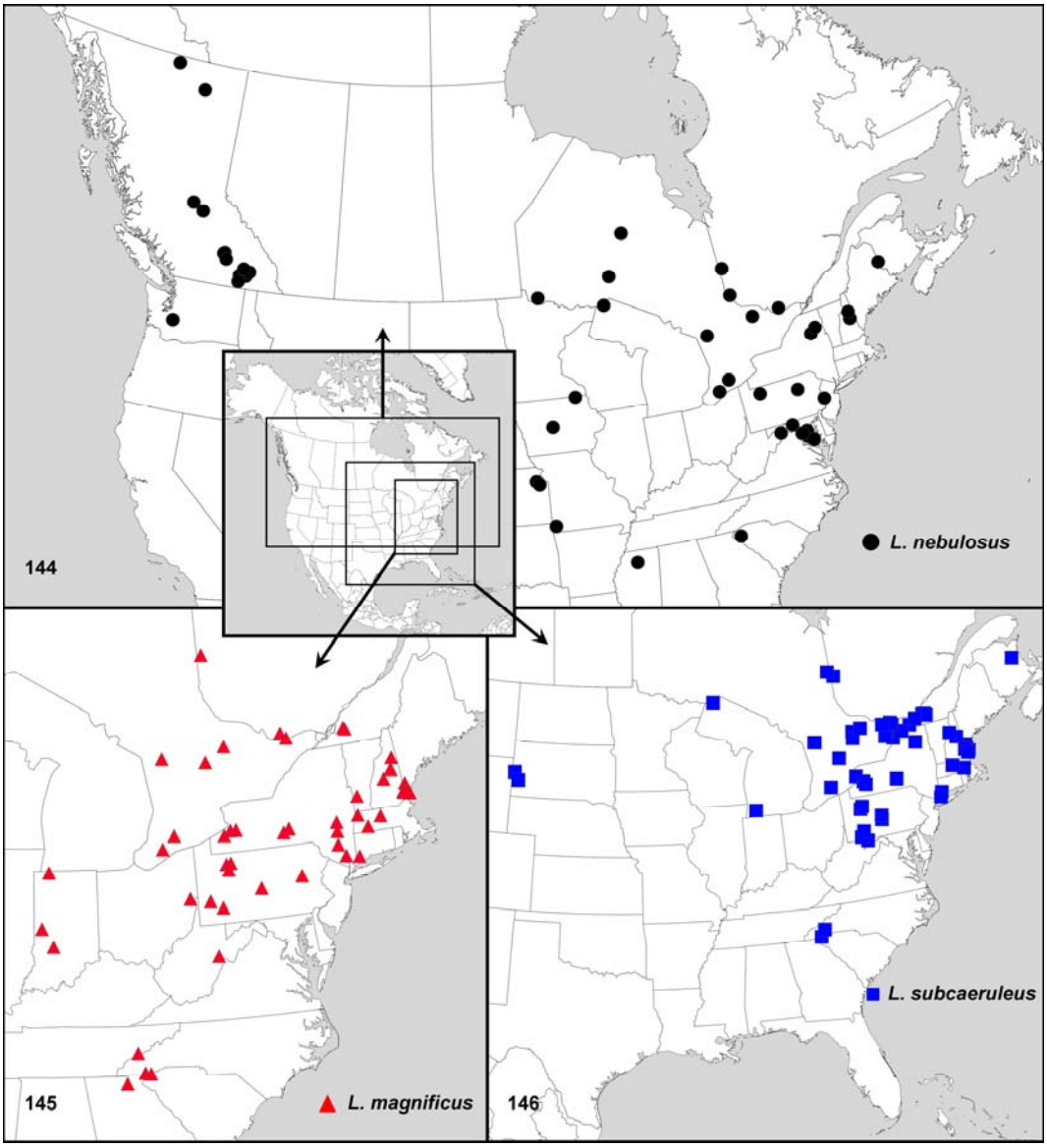


Figure 144-146. Distribution of Nearctic *Leptomorphus.* 144. *L. nebulosus* (black circle). **145.** *L. magnificus* (red triangle). **146.** *L. subcaeruleus* (blue square).

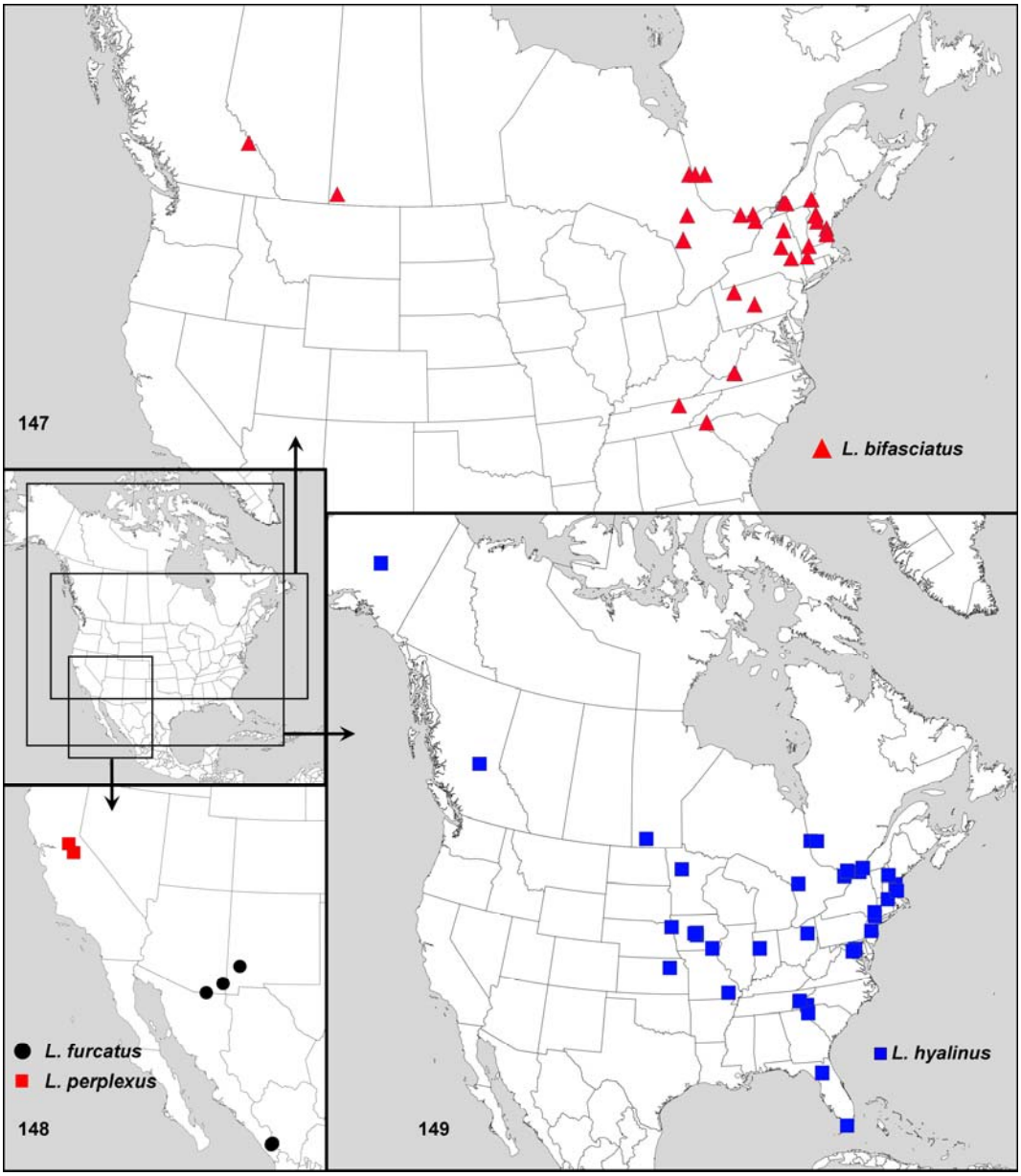


Figure 147-149. Distribution of Nearctic *Leptomorphus*. 147. *L. bifasciatus* (red triangle). **148.** *L. furcatus* (black circle), *L. perplexus* (red square). **149.** *L. hyalinus* (blue square).

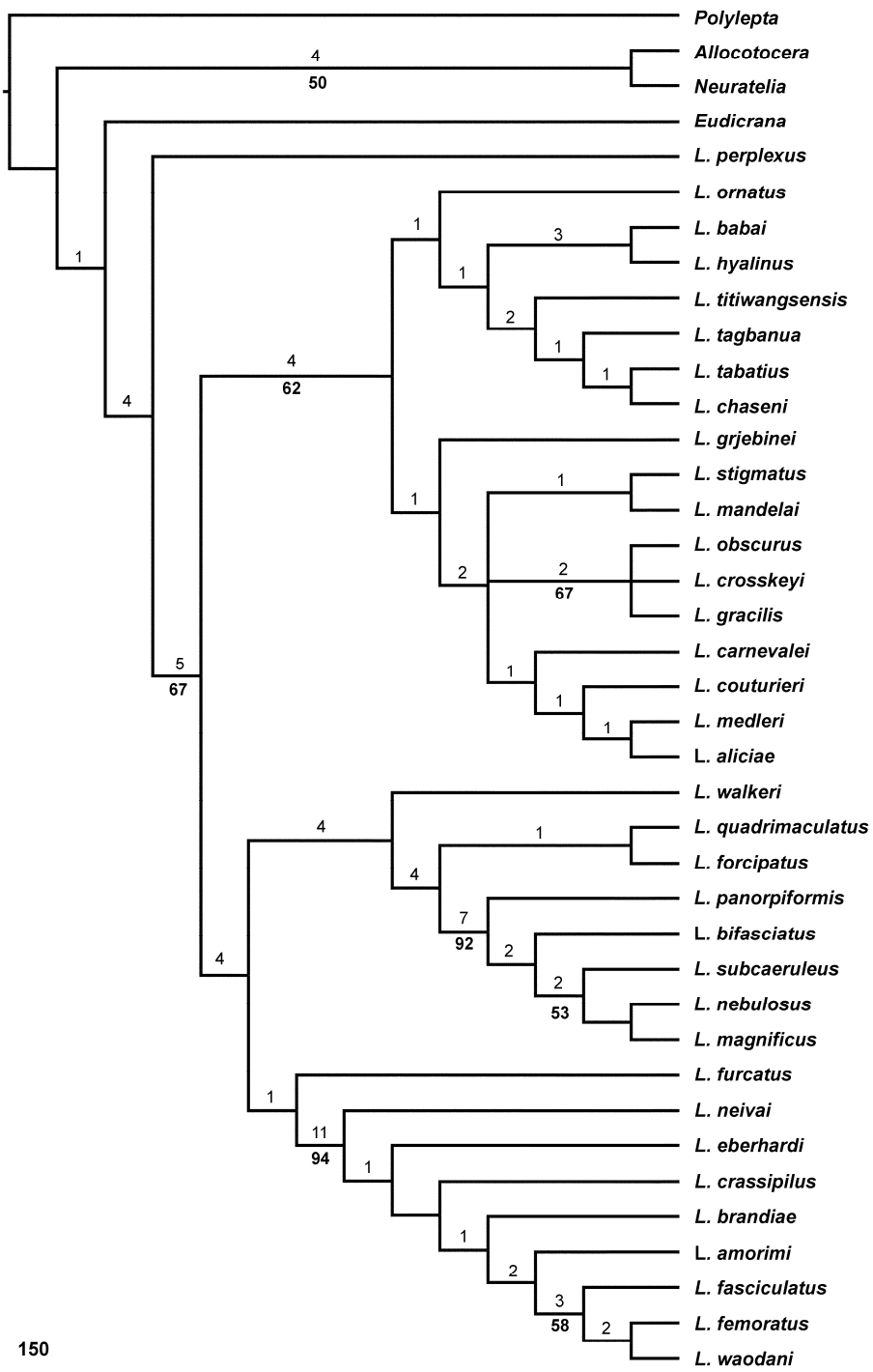


Figure 150. Strict consensus tree of three equally parsimonious trees found in the phylogenetic analysis. Bremer support values are shown above the branches and bootstrap values >50% are shown in bold below the branches.

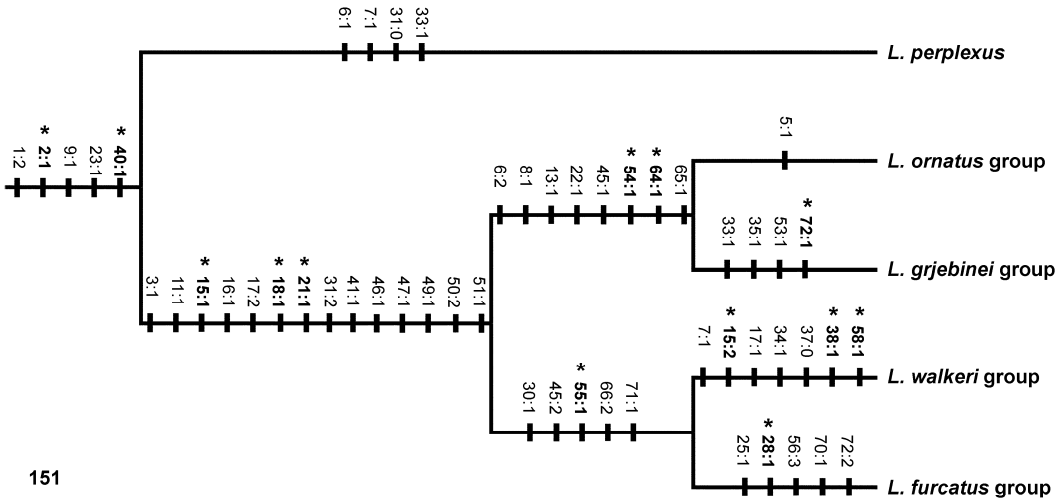


Figure 151. One of three equally parsimonious trees showing the relationships at the base of the tree between *L. perplexus* and the four major species groups. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.

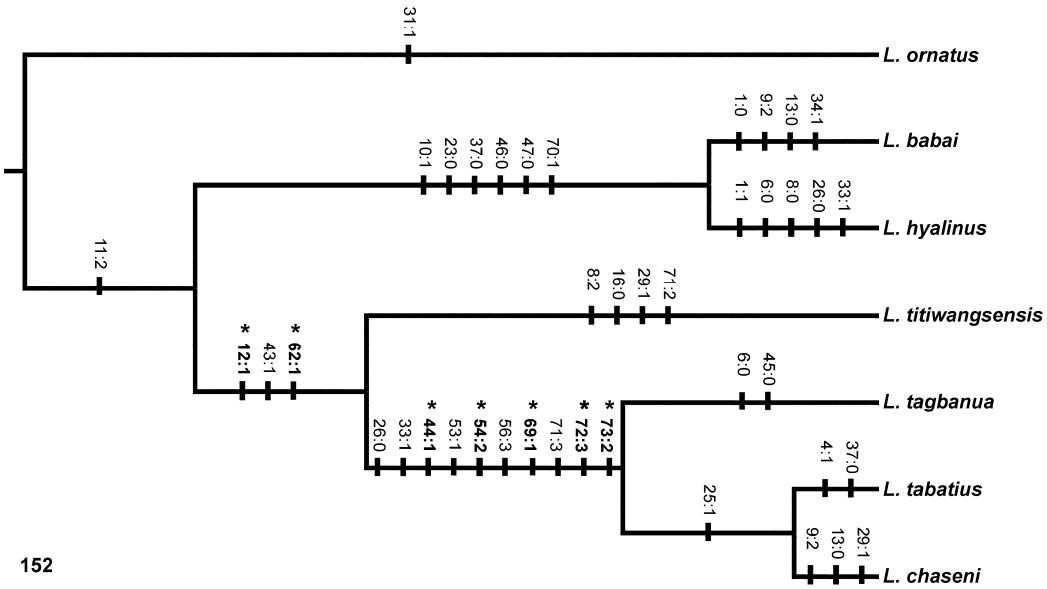


Figure 152. One of three equally parsimonious trees showing the relationships between species in the *L. ornatus* species group. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.

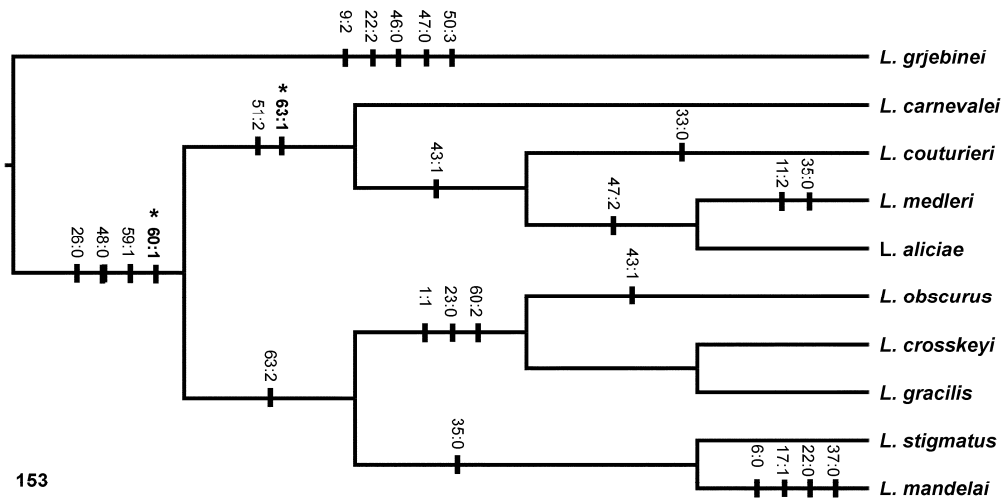


Figure 153. One of three equally parsimonious trees showing the relationships between species in the *L. grjebinei* species group. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.

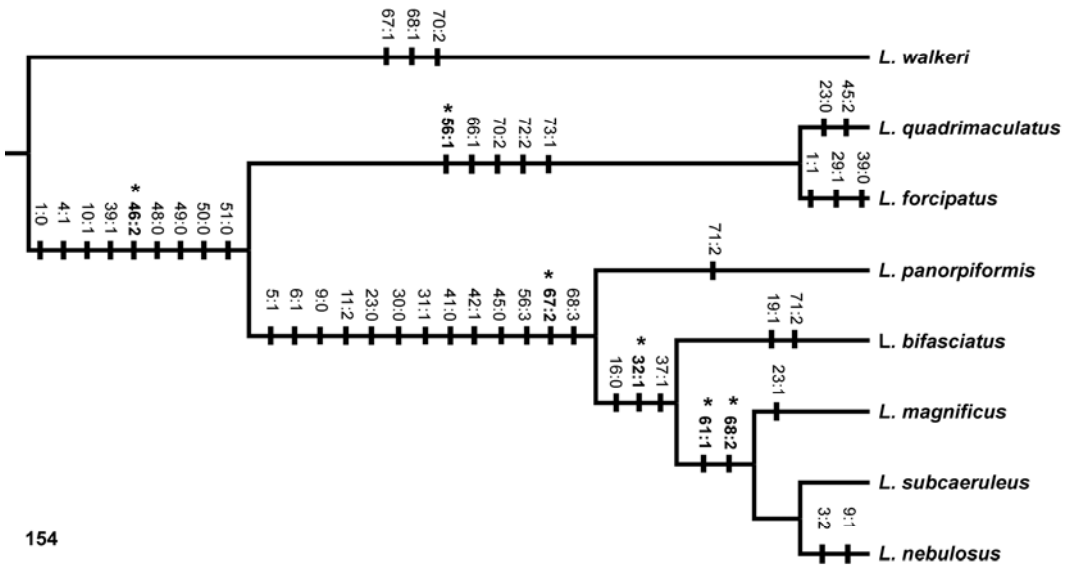


Figure 154. One of three equally parsimonious trees showing the relationships between species in the *L. walkeri* species group. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.

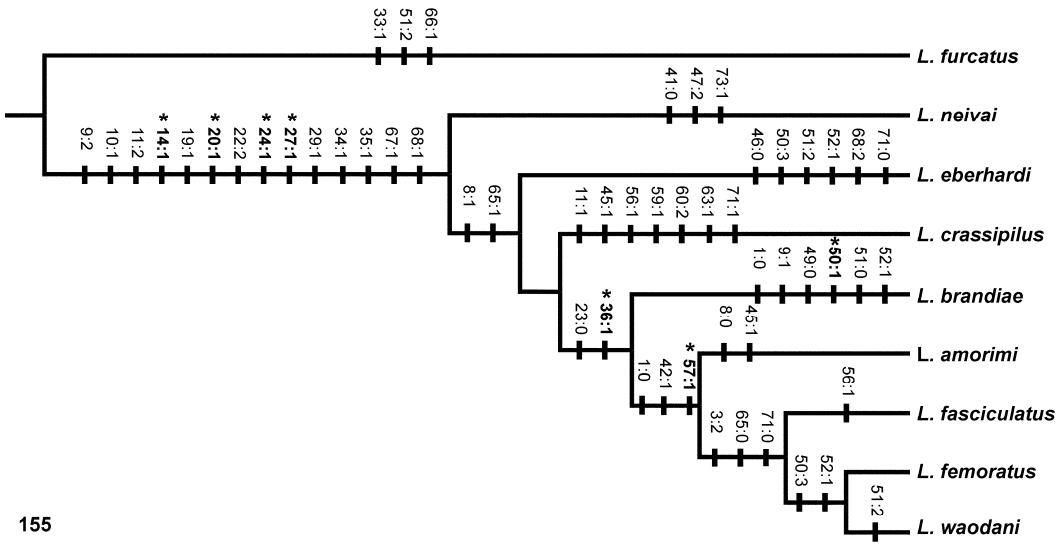


Figure 155. One of three equally parsimonious trees showing the relationships between species in the *L. furcatus* species group. Character state changes are indicated on each branch by a black bar. Uniquely derived synapomorphies are indicated in bold and with an asterisk.

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

Abbreviation	Institution or Collection
ANSP	Academy of Natural Sciences, Philadelphia, Pennsylvania, USA.
BMNH	Natural History Museum, London, UK.
CAS	California Academy of Sciences, San Francisco, California, USA.
CMNH	Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA.
CNC	Canadian National Collection, Ottawa, Ontario, 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.
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.
MZHF	Finnish Museum of Natural History, University of Helsinki, Helsinki, Finland.
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.

Table 1. Continued.

Abbreviation	Institution or Collection
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.
UBCZ	University of British Columbia, Beaty Biodiversity Museum, Spencer Entomological Museum, Vancouver, BC, Canada.
UCDC	R.M. Bohart Museum of Entomology, University of California, Davis, CA, USA.
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.

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 "?".

	123456789	1111111111 2222 0123456789 0123	222222 3333 456789 0123	333333 456789	4444444444 5555 0123456789 0123	555555 6666 456789 0123	666666 7777 456789 0123
Ingroup Taxa							
L. aliciae	211002011	0101021211 0111	000000 0201	010100	1101011201 2201	102001 1001	110000 0010
L. amorimi	111000002	1202121211 1120	111111 1200	111100	1110011111 2100	013100 0000	012110 1120
L. babai	011012012	1200021211 0110	001000 0200	100000	11000100?1 2100	102000 0000	110000 2000
L. bifasciatus	011111100	1200010111 0100	001000 0110	100111	1010002100 0000	013010 0000	002230 0200
L. brandiae	011000011	1202121211 1120	111111 1200	111100	1100021110 1010	013000 0000	012110 1120
L. carnevalei	211002011	0101021211 0111	000000 0201	010100	1100011101 2201	102001 1001	110000 0010
L. chaseni	211012012	0210021211 0111	010001 ?2?1	000100	11011????? ????	?????? ????	?????? ????
L. couturieri	211002011	0101021211 0111	000000 0200	010100	1101011101 2201	102001 1001	110000 0010
L. crassipilus	211000012	100?121211 1121	111111 1200	110100	110001??11 2100	??2001 2002	01???0 ?220
L. crosskeyi	111002011	0101021211 0110	000000 0201	010100	1100011101 2101	102001 2002	110000 0010
L. eberhardi	211000012	1200121211 1121	111111 1200	110100	1100020111 3210	013000 0000	012120 1020
L. fasciculatus	112000012	1202121211 1120	111111 1200	111100	1110021111 2100	012100 0000	002110 1020
L. femoratus	112000012	1202121211 1120	111111 1200	111100	1110021111 3110	013100 0000	002110 1020
L. forcipatus	111100101	1100011110 0101	000001 1200	100010	1100022100 0000	011010 0000	001000 2121
L. furcatus	211000001	0100021210 0101	010010 1201	000100	1100021111 2200	013000 0000	001000 1120
L. gracilis	111002011	0101021211 0110	000000 0201	010100	1100011101 2101	102001 2002	110000 0110
L. grjebinei	211002012	0101021210 0121	001000 0201	010100	11000100?1 3101	102000 0000	110000 0010

Table 2. Continued.

	123456789	1111111111 2222 0123456789 0123	222222 456789	3333333333 0123456789	4444444444 5555 0123456789 0123	555555 456789	6666666666 0123456789	7777 0123
L. hyalinus	111010001	1201021211 0110	000000	0201000000	1100010011 2100	102000	0000110000	2000
L. magnificus	011111100	1200010110 0101	001000	0110100111	1010002100 0000	013010	0100002220	0100
L. mandelai	211000011	0101021111 0101	000000	0201000000	1100011101 2101	102001	1002110000	0110
L. medleri	211002011	0201021211 0111	000000	0201000100	1101011201 2201	102001	1001110000	0010
L. nebulosus	012111101	1200010110 0100	001000	0110100111	1010002100 0000	013010	0100002220	0100
L. neivai	211000002	1202121211 1121	111111	1200110100	1000021211 2100	013000	0000002110	1121
L. obscurus	111002011	0101021211 0110	000000	0201010100	1101011101 2101	102001	2002110000	0110
L. ornatus	211012011	0101021211 0111	001000	?1?0000100	11000????? ????	??????	??????????	????
L. panorpiformis	011111100	1200011110 0100	001000	0100100011	1010002100 0000	013010	0000002230	0200
L. perplexus	210001101	0000000000 0001	001000	?0?1000100	10000????? ????	??????	??????????	????
L. quadrimaculatus	011100101	1100011110 0100	000000	1200100011	1100012100 0000	011010	0000001000	2121
L. stigmatus	211002011	0101021211 0111	000000	0201000100	1100011101 2101	102001	1002110000	0110
L. subcaeruleus	011111100	1200010110 0100	001000	0110100111	1010002100 0000	013010	0100002220	0100
L. tabatius	211112011	0211021211 0111	010000	0201000000	1101111111 2201	203000	0010110001	0332
L. tagbanua	2?1010011	021?021211 0111	000000	0201000100	1101101111 2101	203000	0010110001	0332
L. titiwangsensis	211012012	0211020211 0111	001001	0200000100	1101011111 2100	102000	0010110000	0200
L. walkeri	211000101	0100011110 0101	000000	1200100010	1100021111 2100	012010	0000002110	2100
L. waodani	112000012	1202121211 1120	111111	1200111100	1110021111 3210	013100	0000002110	1020

Table 2. Continued.

		1111111111	2222222222 3333	333333 4444	444444	5555555555 6666	666666 7777
	123456789	0123456789	0123456789 0123	456789 0123	456789	0123456789 0123	456789 0123
Outgroup taxa							
Polylepta	000000000	1000000100	0000001000 0101	000111 0000	001110	000?000100 0000	00000? 0000
Neuratelia	000001000	1000000000	0000001000 0101	000111 0100	0000?0	000?000001 100?	00100? 0020
Allocotocera	000000000	0000000100	0001000000 0001	000011 0100	0000?0	000?000001 1002	0?1000 0020
Eudicrana	000000000	0000000000	0000000000 0100	100000 0000	0000?0	000?002000 0000	0?000? 0302

CONNECTING STATEMENT

Although *Leptomorphus* was found to be monophyletic (Chapter 2), its relationship with other genera in the tribe Sciophilini was relatively unknown. Previous phylogenetic work with a limited set of Sciophilini genera suggested a possible sister group relationship between *Leptomorphus* and either *Neuratelia* Rondani or *Allocotocera* Mik. However, given the small number of Sciophilini genera included in that study (12 of 34) these results were not conclusive. In order to clearly determine the relationships between the genera of the Sciophilini, including *Leptomorphus*, a phylogenetic analysis using all genera of the Sciophilini was required. This analysis, using morphological characters, was undertaken in Chapter 3 in order to define the monophyly and limits of the tribe, to explore the evolutionary relationships between the included genera and to confirm their monophyly. My work with *Leptomorphus* showed that there can be substantial variation in some morphology within a genus. This variation necessitated examination of multiple species of each genus of Sciophilini before selecting exemplar species and morphological characters for the tribal phylogenetic analysis.

CHAPTER 3. PHYLOGENY OF THE TRIBE SCIOPHILINI (DIPTERA: MYCETOPHILIDAE: SCIOPHILINAE)

Abstract

The monophyly and phylogenetic relationships within the species rich Sciophilini (Diptera: Mycetophilidae) were analyzed, based on 96 adult morphological characters. The cladistic analysis included 80 Sciophilini exemplar species (representing all but one of the 36 genera placed previously in the Sciophilini) and 11 outgroup taxa of other mycetophilid tribes. The monophyly of Sciophilini was supported in the parsimony analysis by four synapomorphies. The tribe now contains 34 genera: *Acnemia* Winnertz, *Acomoptera* Vockeroth, *Adicroneura* Vockeroth, *Afrocnemia* Matile, *Allocotocera* Mik, *Anaclileia* Meunier, *Aneura* Marshall, *Austrosciophila* Tonnoir, *Azana* Walker, *Baeopterogyna* Vockeroth, *Cluzobra* Edwards, *Drepanocercus* Vockeroth, *Duretophragma* Borkent **gen. n.**, *Eudicrana* Loew, *Leptomorphus* Curtis, *Loicia* Vockeroth, *Megalopelma* Enderlein, *Monoclona* Mik, *Morganiella* Tonnoir & Edwards, *Neoallocotocera* Tonnoir, *Neoaphelomera* Miller, *Neotrizygia* Tonnoir & Edwards, *Neuratelia* Rondani, *Paramorganiella* Tonnoir, *Paratinia* Mik, *Paratrizygia* Tonnoir, *Parvicellula* Marshall, *Phthinia* Winnertz, *Polylepta* Winnertz,*Sciophila* Meigen,*Stenophragma* Skuse, *Tasmanina* Tonnoir, *Taxicnemis* Tonnoir & Edwards, and *Trizygia* Skuse. Four genera placed previously in Sciophilini (*Coelophthinia* Edwards, *Impleta* Plassmann, *Speolepta* Edwards, and *Syntemna* Winnertz) are transferred to the Gnoristini. *Neoneurotelia* Shinji and *Neoparatinia* Shinji are considered **nomina dubia**. Diagnoses are given for all genera in the tribe. *Duretophragma* **gen. n.** is described for the following species (all of which are **comb. n.**): *Duretophragma andina* (Duret), *Duretophragma argentina* (Duret)**,** *Duretophragma glabanum* (Johannsen)**,** *Duretophragma*

humeralis (Edwards), *Duretophragma longifurcata* (Freeman) (type species), *Duretophragma morigenea* (Edwards), *Duretophragma naumanni* (Duret), *Duretophragma obscura* (Duret), *Duretophragma ochracea* (Freeman),and *Duretophragma pleuralis* (Edwards). Other new generic combinations include: T*rizygia albidens* (Oliveira & Amorim) **comb. n.**, T*rizygia alvesi* (Oliveira & Amorim) **comb.n.**, T*rizygia balbi* (Oliveira & Amorim) **comb.n.**, T*rizygia camargoi* (Oliveira & Amorim) **comb.n.**, and *Afrocnemia stellamicans* (Chandler) **comb. n**.

Introduction

The Mycetophilidae are a ubiquitous and diverse component of the dipteran fauna of forest ecosystems worldwide, where their larvae feed on fungal fruiting bodies, hyphae or spores. The family currently includes approximately 4100 described species in 180 genera (Pape *et al.,* 2011). Traditionally they are divided into three subfamilies: Sciophilinae, Manotinae, and Mycetophilinae although only the latter two are thought to be monophyletic (Söli, 1997b; Hippa *et al.,* 2004; Rindal & Söli, 2006). These subfamilies are further divided into four, one, and two tribes, respectively (Edwards, 1925; Tuomikoski, 1966). Recent phylogenetic work on the subfamily Mycetophilinae has further clarified the limits of each of its two tribes, and supports the monophyly of each tribe and the subfamily (Rindal & Söli, 2006; Rindal *et al.,* 2007, 2009a, 2009b). The five tribes within Sciophilinae (Gnoristini, Leiini, Metanepsiini, Mycomyiini, and Sciophilini) are less well defined, with only Sciophilini and Mycomyiini apparently monophyletic (Söli, 1996, 1997b; but see Rindal *et al.,* 2009b). The lack of phylogenetic resolution of tribal relationships in Sciophilinae (Söli, 1997b; Rindal *et al.,* 2009b) particularly between the Gnoristini and Sciophilini, led us to start with a traditional tribal classification of the Sciophilinae (Edwards, 1925; Söli, 1997b; Vockeroth, 2009) in this study, rather than raising the tribes to subfamily level as some authors have done (e.g., Matile, 1991; Amorim *et al.,* 2008).

The Sciophilini contains more than 520 extant species in 38 genera, and is an ancient group known to have occurred in the lower Cretaceous (Blagoderov, 1995). It is one of the four tribes described originally by Edwards (1925) within Sciophilinae and was defined as containing those genera with macrotrichia on the wing membrane and bristles on the mediotergite. However, the limits of Edwards' tribes are less than clear, as indicated by his frequent use of 'nearly', 'generally', and 'usually' in his descriptions (Edwards, 1925). Söli (1997b) suggested that

Sciophilini was monophyletic based on an analysis of the Sciophilinae that included 13 genera assigned to this tribe (from which two were removed by Söli (1997b): *Paratinia* Mik and *Syntemna* Winnertz). The clade with the remaining 11 genera was supported by 12 unambiguous character state changes (primarily characters involving presence/absence of setae on wings and legs). However, the genera included in the analysis represented only a third of the genera placed in this tribe and all were Palaearctic.

The Australasian/Oceanian region contains seven endemic Sciophilini genera. Though this might reflect divergence during the long isolation of the Australasian fauna from those of other regions, it may reflect the taxonomic approach of Tonnoir (1929). The six new genera described from Australia were not compared with the types of genera described previously from the region by Skuse (Tonnoir, 1929). The expectation was that future workers would compare this work to previous types and synonymise where needed. Unfortunately, this has not happened.

Other than Söli (1997b) most systematic studies on this tribe have been in the context of regional revisions, with no phylogenetic study of the relationships. Notable exceptions include a preliminary study of Sciophilini genera with a reduced posterior wing vein fork by Matile (1998) who suggested that these ten genera formed a monophyletic group, though no phylogenetic analysis was undertaken, and phylogenetic studies of *Cluzobra* Edwards (Matile, 1996), *Leptomorphus* Curtis (Borkent & Wheeler, in press) and the Afrotropical species of *Sciophila* Meigen (Söli, 1997a).

We conducted a generic level phylogenetic analysis of Sciophilini, using 80 exemplar species representing 35 of the 38 previously and currently included genera. The taxonomic limits of Sciophilini and the relationships between the genera are determined based on this analysis and new generic diagnoses are

provided, including the description of a new genus. This analysis provides a classification and phylogenetic framework for future generic revisions and phylogenies within the tribe.

Materials and Methods

Specimens of Sciophilini and outgroup mycetophilid genera were obtained from the following collections (including acronyms used in the text): Australian National Insect Collection, CSIRO, Canberra, Australian Capital Territory, Australia (ANIC); Bernice P. Bishop Museum, Honolulu, HI, USA (BPBM); California Academy of Sciences, San Francisco, CA, USA (CAS); Canterbury Museum, Christchurch, New Zealand (CMNZ); Canadian National Collection, Ottawa, ON, Canada (CNC); Iowa State University Insect Collection, Ames, IA, USA (ISUI); Lyman Entomological Museum, McGill University, Ste-Anne-de-Bellevue, QC, Canada (LEM); Muséum National d'Histoire Naturelle, Paris, France (MNHN); New Zealand Arthropod Collection, Landcare Research, Auckland, New Zealand (NZAC); National Museum of Natural History, Washington DC, USA (USNM).

Exemplars of 35 of the 38 genera assigned previously to the Sciophilini were obtained. No specimens of the monotypic genera *Neoneurotelia* Shinji and *Neoparatinia* Shinji could be located; the types apparently have been lost or were never deposited in a collection. No known specimens from Japan, the type locality for both genera, fit either genus description. These two names are therefore considered ***nomina dubia***. All specimens identified as *Neoallocotocera* Tonnoir that we examined were misidentified, and we were unable to obtain other specimens of this monotypic genus. Exemplar species for the remaining 35 genera included the type species, whenever possible, and additional exemplar species

from additional biogeographic regions in which a genus occurs, for a total of 80 ingroup species (Table 1). Exemplar species are listed after each generic diagnosis, along with the known distribution of the species. The following general regions, with abbreviations, were used for the distributions: Afrotropical (AF), Australasian/Oceanian (AU), Nearctic (NE), Neotropical (NT), Oriental (OR), and Palaearctic (PA). Eleven exemplar species representing all other mycetophilid subfamilies/tribes except Metanepsiini, were selected as outgroups: *Gnoriste bilineata* Zetterstedt, *G. macra* Johannsen (Gnoristini); *Allactoneura obscurata* Walker, *Leia oblectabilis* (Loew), *Tetragoneura pimpla* Coquillett (Leiini); *Mycomya marginata* (Meigen) (Mycomyiini); *Manota* n. sp. (Manotinae); *Exechia attrita* Johannsen, *E. fusca* (Meigen) (Mycetophilinae: Exechiini); *Mycetophila exstincta* Loew, *M. fungorum* (De Geer) (Mycetophilinae: Mycetophilini) (Table 1).

Morphological terminology follows Cumming & Wood (2009) in general and Söli (1997b) for some genitalic interpretations. The posterior wing veins CuA_1, CuA_2, and A_1 of Cumming & Wood (2009) are interpreted here as veins M_4, CuA, and CuP respectively (Saigusa, 2006; Amorim & Rindal, 2007).

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 three to five 15-second intervals in a microwave oven, 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.

Phylogeny

A matrix of characters was constructed using Mesquite 2.74 (Maddison &

Maddison, 2011) and a parsimony analysis was performed using TNT 1.1 (Goloboff *et al.,* 2003). A heuristic search was run with 500 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.

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.

Characters

The phylogenetic analysis was based on 96 characters (62 binary, 34 multistate). The plesiomorphic state (0) is given for each character (based on results of the analysis), followed by the apomorphic states (1, 2, 3) and, in parentheses, by the consistency index and retention index for each character.

1. Head shape (anterior view, eye width and height from bottom margin of eyes to peak of occiput): wider than tall (0), subequal (1), taller than wide (2) (0.1, 0.44).

2. Medial eye margins: farther apart dorsally than ventrally (0), parallel or closer together dorsally than ventrally (1) (1, 1).

3. Antennal eye notch: deep, angular, at least 2-3 ommatidia deep (0), slight, margin concave at antenna no more than 1-2 ommatidia deep and not angular (1), absent or eye flattened adjacent to antenna (2) (0.13, 0.59).

4. Interommatidial setae: present between all ommatidia (0), sparse (1), absent (2) (0.15, 0.39).

5. Ocelli number: 3 (0), 2 (1) (0.11, 0.5).

6. Ocelli arrangement: triangular (0), median ocellus just anterior (1), linear (2) (0.13, 0.44).

7. Lateral ocelli distance from eye margin: at least 1.5X ocellar diameter from eye margin (0), <0.5X to <1.5X diameter from eye margin (1), at eye margin (2) (0.12, 0.69).

8. Lateral ocelli distance from median ocellus: 0.5-1X diameter of lateral ocellus) (0), >1-2.5X diameter of lateral ocellus (1), >2.5X diameter of lateral ocellus (2). If two ocelli present, half the distance between them was used to approximate the location of the median ocellus (0.13, 0.56).

9. Median ocellus: raised (0), flat or sunken (1) (0.14, 0.54).

10. Median ocellus orientation: anteriorly (0), anterodorsally (1), dorsally (2) (0.33, 0.5).

11. Straight line between lateral ocelli touches eye margin: no (0), yes (1) (0.08, 0.73).

12. Lateral ocelli on raised base: yes (0), no (1) (0.17, 0.69).

13. Ocellar triangle color (around ocelli): darker than background (0), same as background (1) (0.07, 0.54).

14. Frontal cleft: absent (0), from lateral ocelli to eye margin (ocelli touching eye margin are included here) (1), from frontal furrow to eye margin (2) (0.11, 0.51).

15. Frontal furrow (median ocellus to apex of frons): complete (0), partial (1), absent (2) (0.08, 0.51).

16. Occipital furrow (median ocellus to occipital foramen): present (0), absent (1) (0.17, 0.64).

17. Setae on frons: absent (0), present on entire frons (1), present ventrally (2) (0.22, 0.87).

18. Length of scape setae relative to length of scape: 0.5-1X (0), >1X (1) (0.08, 0.5).

19. Length of pedicel setae relative to length of pedicel: 0.5-1 (0), 1.1-2 (1), >2 (2) (0.1, 0.59).

20. Flagellomere 1 basal stalk: uniformly tapering (0), slightly offset (1), distinctly offset (2) (0.18, 0.7).

21. Flagellomeres: cylindrical (0), slightly laterally compressed (1), strongly laterally compressed (1) (0.4, 0.57).

22. Flagellomere 6 shape: longer than wide (0), subequal (1), wider than long (2) (0.14, 0.4).

23. Face length relative to clypeus length: 0.3-1X (0), 1.1-2X (1), >2X (2) (0.15, 0.69).

24. Face and clypeus: >1/3 of margin fused (0), <1/3 of margin fused (1), separate (2) (0.18, 0.64).

25. Acrostichal setae: present (0), absent (1) (0.5, 0.67).

26. Anepisternal bristles: absent (0), present (1) (0.25, 0.86).

27. Anepisternal bristle location: bare (0), up to dorsal half covered (1), more than half covered (2) (0.33, 0.8).

28. Anepisternal trichia: present (1), absent (0) (0.17, 0.55).

29. Anterior basalare: bare (0), with many bristles (1) (0.2, 0.6).

30. Anapleural suture: single (0), double (1), absent (2) (0.4, 0.67).

31. Anapleural suture: complete (0), reduced (1), absent (2) (0.5, 0.5).

32. Anterior end of (upper) anapleural suture relative to posterior end: dorsal (0), subequal (1), ventral (2) (0.13, 0.63).

33. Mediotergite bristles: absent (0), present (1) (0.33, 0.92).

34. Mediotergite with macrotrichia (hairs): absent (0), present (1) (0.33, 0.75).

35. Mediotergite trichia placement: absent (0), anteriorly (1), central patch (2) (0.67, 0.86).

36. Laterotergite with bristles: absent (0), present (1) (0.25, 0.83).

37. Laterotergite with trichia: absent (0), present (1) (0.33, 0.6).

38. Laterotergite shape: evenly rounded (0), protruding with keel (1) (0.25, 0.5).

39. Metepisternum: bare (0), with several setae, usually posteriorly (1) (0.13, 0.71).

40. Bristle(s) just posteromedial of halter base: present (0), absent (1) (0.25, 0.8).

41. Wing membrane macrotrichia: present (0), absent (1) (0.5, 0.95).

42. Wing membrane setae: present (0), absent (1) (1, 1).

43. Wing macrotrichia orientation: absent or decumbent to wing tip (0), reflexed (1) (0.5, 0.75).

44. Wing membrane microtrichia: present (0), absent (1) (0.11, 0.43).

45. Microtrichia arrangement: irregular or absent (0), parallel lines (1) (1, 1).

46. Distal median plate: bare (0), setose (1) (0.25, 0.89).

47. Humeral vein: oblique (0), curved (1) (0.5, 0.96).

48. Dorsal humeral setae: absent (0), present (1) (0.1, 0.65).

49. Ventral humeral setae: absent (0), present (1) (0.11, 0.74).

50. Subcostal vein: ending in C (0), free beyond sc-r (1), ending in sc-r (i.e. Sc ending in R) (2), free at wing base (3) (0.38, 0.55).

51. Subcostal vein: long (> 1/3 wing length) (0), short (1) (0.11, 0.74).

52. sc-r: present (sometimes reported as Sc ending in R) (0), absent (1) (0.14, 0.68).

53. sc-r ending: before Rs or Sc ending near level of Rs if sc-r absent (0), at or very near Rs (1), beyond Rs (2) (0.14, 0.45).

54. Ventral surface of subcostal vein: bare (0), setose (1) (0.33, 0.91).

55. Ventral base of subcostal vein: bare (0), setose (1) (0.17, 0.83).

56. Dorsal surface of subcostal vein: bare (0), setose (1) (0.33, 0.88).

57. Dorsal base of subcostal vein: bare (0), setose (1) (0.17, 0.82).

58. bM dorsally: bare (0), setose (1) (0.13, 0.81).

59. bM ventrally: bare (0), setose (1) (0.09, 0.73).

60. C ending: beyond (0), at R_5 (1) (0.13, 0.5).

61. R_1 ventrally: bare (0), setose (1) (0.14, 0.57).

62. R_{2+3}: present (0), absent (1) (0.08, 0.65).

63. R_5 ventrally: bare (0), setose (1) (0.17, 0.55).

64. M_{1+2} length relative to anterior fork: shorter or absent (0), subequal (1), longer or reaching wing margin (fork absent) (2) (0.25, 0.67).

65. M_{1+2} dorsally: bare (0), setose (1) (0.08, 0.68).

66. M_{1+2} ventrally: bare (0), setose (1) (0.1, 0.71).

67. Anterior fork (M_1+M_2): present (0), absent (1) (0.5, 0).

68. Anterior fork origin: arising after posterior fork (0), subequal to posterior fork (1), before posterior fork or posterior fork absent (2), absent (M_{1+2} reaching wing margin) (3) (0.3, 0.82).

69. Base of M_1: strong (reaching M_{1+2} as thick as medial portion of M_2) (0), weak (reaching M_{1+2} as thinning vein (<0.5X medial thickness), crease, or setae) (1), free or absent (2) (0.18, 0.31).

70. M_1 ventrally: bare (0), setose (1) (0.14, 0.78).

71. Base of M_2: strong (reaching M_{1+2} as thick as medial portion of M_2) (0), weak (reaching M_{1+2} as thinning vein (<0.5X medial thickness), crease, or setae) (1), free or absent (2) (0.33, 0.78).

72. M_2 ventrally: bare (0), setose (1) (0.13, 0.75).

73. Posterior fork (M_4 and CuA): present (0), absent (M_4 missing) (1) (0.25, 0.88).

74. M_4 extent: joining bM (0), joining CuA (1), free or absent (2) (0.25, 0.8).

75. M_4 dorsally: bare (0), setose (1) (0.2, 0.2).

76. M_4 ventrally: bare (0), setose (1) (0.5, 0.5).

77. CuA dorsally: bare (0), setose (1) (1, 1).

78. CuA ventrally: bare (0), setose (1) (0.14, 0.4).

79. CuP extent: ending after posterior fork (0), ending at posterior fork (1), ending before posterior fork, or posterior fork absent and CuP short (2) (0.15, 0.7).

80. Halter knob color: same as stalk (0), darker than stalk (1) (0.06, 0.63).

81. Hind coxa, row of strong erect setae from base to apex on posterior margin: present (0), absent (1) (0.25, 0).

82. Extent of strong setal row on hind coxa: complete (0), partial (1), none (2) (0.13, 0.68).

83. Hind coxa, apical patch of setae: present (0), absent (1) (0.17, 0.58).

84. Arrangement of vestiture of tibia (exclusive of large setae): irregular (0), apical portion with parallel lines (1), all in parallel lines (2) (0.33, 0.6).

85. Mid tibial organ: absent (0), weak bare line dorsally or posterodorsally (1), present (2) (0.18, 0.71).

86. Base of hind tibial bristles: on surface (0), at base of short depression (1) (0.14, 0.63).

87. Vestiture arrangement on tarsomeres (dorsal view): irregular (0), in parallel lines (1) (0.2, 0.67). Note: some when viewed laterally appear to be in helical parallel lines.

88. Foretarsomere I length relative to foretibia length: <0.9 (0), 0.9-1.1 (1), >1.1 (2) (0.12, 0.67).

89. Empodium: well-developed (0), reduced/absent (1) (0.11, 0.65).

90. Abdominal sternite fold lines: absent (0), one (1), two (2) (0.5, 0.87).

91. Male segment 7: >0.5X length of segment 6 (0), 0.5X or less length of segment 6 (1), reduced/not visible (sternite 7 sometimes visible, tergite 7 always reduced (2) (0.13, 0.65).

92. Male segment 7: not retractable (0), retractable (1) (0.2, 0.6).

93. Sternite 8: <2X length of tergite 8 (0), >2X length of tergite 8 and partially covering genitalia (1) (0.08, 0.65).

94. Gonostylus with apically-feathered, spatulate, megasetae: absent (0), present (1) (1, 1).

95. Male genitalia: visible beyond segment 8 (not strongly retracted) (0), completely or almost completely (90%) retracted within segment 7 (1) (1, 1).

96. Base of gonostylus: single lobe (0), thick lobe accompanied by 1-3 partially articulating, thinner processes, each usually bearing a variety of trichia and/or setae (1) (Fig. 3).

Results and Discussion

Monophyly of the Sciophilini

The phylogenetic analysis resulted in 12 equally parsimonious trees (length = 777, C.I. = 0.17, R.I. = 0.68). Tree support values (Bremer (Br) and bootstrap >50%) are shown on the branches of the strict consensus tree (Fig. 1). One of the 12 equally parsimonious trees was selected as the basis for classification and character state changes are shown on this tree (Fig. 2).

Exemplars of four genera placed previously by some authors within Sciophilini (*Coelophthinia* Edwards, *Impleta* Plassmann, *Speolepta* Edwards, and *Syntemna* Winnertz) were placed consistently outside the tribe (Fig. 1). Söli (1997b) found a similar result, although *Impleta* was not included in his analysis. These four genera therefore are assigned to the Gnoristini as suggested by Vockeroth (1980), Väisänen (1986) and Söli (1997b).

The monophyly of Sciophilini is supported (Br = 2, Fig. 1A) by one uniquely derived synapomorphy (Fig. 2A): at least several adjacent sternites with two mediolateral fold lines, and by three homoplasious character states: lateral ocelli 0.5-1.5X their own diameter from eye margin (7:1), frontal cleft running from lateral ocelli to eye margin (14:1), and frontal furrow only running part of the distance to apex of frons (15:1). The sternite fold lines are unique within the Mycetophilidae. Rindal and Söli (2006) considered this character state present in most Mycetophilinae; however, in the Mycetophilinae we examined there was a secondary sclerotization of the membrane between the sternites and tergites. Rindal and Söli may have considered the dividing line between the membrane and sternite homologous with fold lines on the sternite.

Relationships within Sciophilini

Although the general structure of the Sciophilini phylogeny is mostly pectinate, there are six monophyletic groups containing two or more genera. These clades are referred to as the *Acomoptera* Vockeroth*, Aneura* Marshall*, Allocotocera* Mik*, Leptomorphus* Walker*, Cluzobra* Edwards*,* and *Parvicellula* Marshall clades.

The *Acomoptera* clade is placed as the sister group to the remaining Sciophilini (Figs 1A, 2A). Of the four included genera, two were included previously in Gnoristini (*Drepanocercus* Vockeroth, and *Acomoptera*) as they lacked macrotrichia or setae on the wing membrane. This clade is supported by two homoplasious character states. The *Acomoptera* clade retains several plesiomorphic character states and should be included as an outgroup in future phylogenetic studies of the Sciophilinae, particularly with regards to generic relationships within the Gnoristini.

The monotypic genus *Drepanocercus* is the basal member of the *Acomoptera* clade and is supported by six homoplasious character states (Fig. 2A). The remaining three genera form a clade supported by one uniquely derived synapomorphy: medial eye margins parallel or closer together dorsally than ventrally (2:1), and three homoplasious character states. The genus *Acomoptera* is weakly supported by two homoplasious character states (Figs 1A, 2A). The double anapleural suture is found in only two other genera within Sciophilini, *Phthinia* Winnertz and *Polylepta* Winnertz.

Loicia Vockeroth and *Paratinia* Mik are sister genera (Figs 1A, 2A) supported by a synapomorphy: wing membrane with setae (42:0), and two homoplasious character states, and the two genera are monophyletic, each supported by multiple character states (Figs 1A, 2A). The remaining Sciophilini genera form a clade supported by one unique synapomorphy: wing membrane macrotrichia present

(41:0) and four homoplasious character states.

The *Aneura* clade, containing *Aneura* and *Taxicnemis* Tonnoir & Edwards, is supported by four homoplasious character states. *Taxicnemis* is supported by 21 character states (Fig. 2A) including two unique synapomorphies: subcostal vein ending free beyond sc-r (50:1) and arrangement of vestiture of tibia (exclusive of large setae) in parallel lines (84:2). *Aneura* is supported also by multiple character states.

The remainder of the Sciophilini form a well supported monophyletic group based on eight character state changes including one unique synapomorphy: bristle(s) just posteromedial of halter base absent (40:1) (Figs 1A, 2A). This clade corresponds closely to Edwards (1925) concept of the Sciophilini as all the members have bristles on the mediotergite, except *Baeopterogyna* Vockeroth which has trichia (33:1), and macrotrichia on the wing (41:0). Outside Sciophilini mediotergite bristles are found only in some *Coelophthinia* and *Mycomya* Rondani. All members of this clade except *Duretophragma* gen. n. and *Stenophragma* Skuse also have the distal median plate of the wing setose (46:1), a state only found within two tribes of Mycetophilidae, the Sciophilini and Mycetophilini.

Phthinia is supported by 16 character states including one unique synapomorphy: dorsal surface of subcostal vein bare (56:0) (Figs 1A, 2A). Another unique synapomorphy occurs within some of the *Phthinia* included in the analysis: apical vestiture of tibia (exclusive of large setae) in parallel lines (84:1). *Phthinia* is placed basal to the remaining genera, which are united by three homoplasious character states (Figs 1A, 2A).

Neuratelia is the sister group to the remaining Sciophilini and the monophyly of the genus is supported by 6 character states (Figs 1A, 2A).

The clade above *Neuratelia* is united by five homoplasious character states (Figs 1A, 2A). This clade includes *Adicroneura* Vockeroth, previously included in the Gnoristini. *Adicroneura* is the sister genus to the remaining genera (Fig. 2A). The monophyly of the remaining Sciophilini genera is supported by five character states (Figs 1A, 2A).

Anaclileia is supported by five homoplasious character states and is the sister group to the remaining Sciophilini, which are supported by three character states (Figs 1A, 2B).

The three genera in the *Allocotocera* clade are united by three homoplasious character states (Figs 1A, 2B). *Allocotocera* is the sister group to the remaining two genera and is supported by nine character states including one unique synapomorphy: male genitalia completely or almost completely (90%) retracted within segment 7 (95:1) (Figs 1A, 2B). The remaining two genera, *Baeopterogyna* and *Tasmanina* Tonnoir, share five homoplasious character states. *Baeopterogyna* is supported by 17 homoplasious character states and *Tasmanina* is supported by two (Fig. 2B).

The *Allocotocera* clade is basal to the remaining genera, which form a monophyletic group supported by five homoplasious character states (Figs 1A, 2B).

The *Leptomorphus* clade is supported by two character states (Figs, 1A, 2B). *Polylepta* is the sister group to the other two genera and is supported by nine character states (Figs, 1A, 2B). *Eudicrana* and *Leptomorphus* are sister genera, supported by seven character states including one unique synapomorphy: mediotergite with trichia placed anteriorly (35:1). *Eudicrana* is supported by eight character states and *Leptomorphus* by eight including one unique synapomorphy: acrostichal setae absent (25:1).

Above the *Leptomorphus* clade the remaining Sciophilini genera are united (Figs 1B, 2C) by four homoplasious character states. *Duretophragma* **gen. n.** is the sister group to the remaining genera and is supported by three character states. The remaining genera are supported by two homoplasious character states.

In the strict consensus tree (Fig. 1B) a tritomy is formed by *Stenophragma* Skuse, *Megalopelma* Enderlein and the remaining genera. For our discussion of character state placement we have chosen one of the 12 most parsimonious trees that places *Stenophragma* as sister to the remaining genera. This placement occurs in 50% of the trees, with the alternative being a monophyletic *Stenophragma* plus *Megalopelma* that is sister to the remainder. *Stenophragma* is supported by seven homoplasious character states (Figs 1B, 2C). The remaining genera are a monophyletic group supported by five homoplasious character states.

The sister group to the remaining genera is *Megalopelma* Enderlein which is supported by six homoplasious character states (Figs 1B, 2C). The other Sciophilini genera are united by four character states (Figs 1B, 2C).

The monotypic genus *Austrosciophila* Tonnoir is sister to the remaining genera and is supported by five character states (Fig. 2C). The clade of remaining genera is supported (Figs 1B, 2C) by six homoplasious character states. This apical clade contains all but one (*Adicroneura*) of the genera of the Sciophilini that have strong reduction or loss of longitudinal wing veins. This group corresponds to the expanded view of Matile's (1998) '*Azana* group' suggested by Amorim *et al.* (2008).

Monoclona Mik is basal to the remaining genera and is supported by five homoplasious character states (Figs 1B, 2C). The remaining clade is supported by five character states.

The *Cluzobra* clade (*Acnemia* Winnertz, *Cluzobra, Afrocnemia* Matile,

Neoaphelomera Marshall) is sister to the remaining genera and is supported by two character states (Figs 1B, 2D). *Acnemia* is the sister group to the other three genera based on one unique synapomorphy: base of gonostylus a thick lobe accompanied by 1-3 short to long, partially articulating, thinner processes, each usually bearing a variety of trichia and/or setae (96:1) (Figs 1B, 2D).

The monophyly of the remaining three genera is supported by five homoplasious character states (Figs 1B, 2D). *Cluzobra* is the sister group to *Afrocnemia* and *Neoaphelomera*, and is supported by four character states. The remaining two genera are united by two homoplasious character states. *Afrocnemia* is supported by eight character states and *Neoaphelomera* by five (Figs 1B, 2D).

The remaining genera of the Sciophilini (*Sciophila* Meigen + *Parvicellula* clade) form a monophyletic clade supported by four homoplasious character states (Figs 1B, 2D). *Sciophila* is monophyletic based on seven character states, including one unique synapomorphy: gonostylus with apically-feathered, spatulate, megasetae (94:1).

The monophyly of the *Parvicellula* clade is supported (Figs 1B, 2D) by three homoplasious character states. *Parvicellula* is the sister group to the remainder of the clade and is supported by eight character state changes (Figs 1B, 2E). The monophyly of remainder of the clade is supported by three character states.

The monotypic genus *Morganiella* is sister to the remaining genera and is supported by ten homoplasious character states (Fig. 2E). The remainder of the clade is supported by six character states (Figs 1B, 2E). *Azana*, sister group to the remaining genera is supported by seven character states (Figs 1B, 2E), including one unique synapomorphy: subcostal vein ending free at wing base (50:3).

The remaining genera in the *Parvicellula* clade are supported by two character states (Figs 1B, 2E). The monotypic genus *Neotrizygia* is sister to the remaining

three genera and is supported by five character states (Fig. 2E), including one unique synapomorphy: subcostal vein ending in sc-r. The rest of the genera form a monophyletic group supported by three character states (Figs 1B, 2E).

Paramorganiella, a monotypic genus, is the sister group to *Trizygia* plus *Paratrizygia*. The genus is supported by 12 character states (Fig. 2E). *Trizygia* and *Paratrizygia* are monophyletic, supported by four character states (Figs 1B, 2E). *Trizygia* is supported by five character state changes. *Paratrizygia* is supported strongly by ten character states. This justifies retaining *Paratrizygia* as a separate genus from *Trizygia* (Oliveira & Amorim, 2010; Amorim *et al.,* 2011).

Although the above unweighted parsimony analysis produced the preferred tree, we explored the data using implied weighting in a parsimony analysis in TNT (using the same parameters). This type of analysis gives higher weight to characters with lower homoplasy when choosing between conflicting arrangements. The weight is determined by the constant of concavity values (K) with lower values giving higher weights to fewer characters (Goloboff, 1993). We used K values of 6-20 which all supported the majority of Sciophilini genera being monotypic. The only exception to this was *Stenophragma* or *Megalopelma*, both of which were problematic in the unweighted analysis as well (*Duretophragma* was still considered monotypic). The overall arrangement and order of genera from base to apex generally was similar as well, though a few of the larger clades were broken up in some results, and a few genera placed in slightly different relationships (*e.g. Polylepta* removed from *Leptomorphus* clade and united with *Phthinia*; *Baeopterogyna* and *Tasmanina* forming their own clade and *Allocotocera* placed individually; movement of a couple of genera between the *Cluzobra* and *Parvicellula* clades). The other noticeable difference under implied weighting when K<16, was the removal of the *Acomoptera* clade from the Sciophilini to the Gnoristini and the accompanying placement of *Syntemna* as

the sister group to the remainder of the Sciophilini. This was not unexpected, based on the plesiomorphic nature of the *Acomoptera* clade, as discussed above.

Generic Diagnoses

***Acnemia* Winnertz**

Acnemia Winnertz, 1863: 798. Type species: *Leia nitidicollis* Meigen, 1818: 255 (subsequent designation by Johannnsen, 1909):

Diagnosis: Distinguished by: macrotrichia decumbent, wing membrane without microtrichia in some species, sc-r placed before origin of Rs, anterior fork present and complete, posterior fork absent (M_4 missing), male abdominal segment 7 less than 0.5X length of segment 6, and base of gonostylus a thick lobe accompanied by 1-3 short to long, partially articulating, thinner processes, each usually bearing a variety of trichia and/or setae (Zaitzev, 1982a, b).

Distribution: AF (Uganda), NE, NT, OR (Sri Lanka), PA.

Material examined: Acnemia falkei Matile & Vockeroth; *Acnemia fulvicollis* (Philippi); *Acnemia nitidicollis* (Meigen); *Acnemia vockerothi* Zaitzev.

***Acomoptera* Vockeroth**

Acomoptera Vockeroth, 1980: 534. Type species: *Eudicrana plexipus* Garrett, 1925: 4 (original designation).

Diagnosis: Distinguished by: medial eye margins closer together dorsally than ventrally, frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, wing membrane without macrotrichia, sc-r placed before origin of Rs, R_{2+3} present and forming a cell ~3X as long as tall, anterior

and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork after origin of posterior fork, and male abdominal segment 7 more than 0.5X length of segment 6 (Kerr, 2011).

Distribution: NE, PA.

Material examined: Acomoptera plexipus (Garrett); *Acomoptera vockerothi* Kerr.

Adicroneura Vockeroth

Adicroneura Vockeroth, 1980: 535. Type species: *Adicroneura biocellata* Vockeroth, 1980: 536 (original designation).

Diagnosis: The only genus in Sciophilini with wing vein M_{1+2} not forking and a complete posterior fork (M_4 and CuA). 2 or 3 ocelli, wing membrane with microtrichia and macrotrichia present (macrotrichia sometimes sparse and difficult to discern), sc-r absent, and male abdominal segment 7 more than 0.5X length of segment 6 (Matile, 1995).

Distribution: NE (western), NT (Chile).

Material examined: Adicroneura biocellata Vockeroth.

Afrocnemia Matile

Afrocnemia Matile, 1998: 390. Type species: *Afrocnemia whitfieldae* Matile, 1998: 391 (original designation).

New combinations: Afrocnemia stellamicans (Chandler) **comb. n.**

Diagnosis: Distinguished by: sc-r present or absent, sc-r placed before origin of

Rs when present, anterior fork present, posterior fork absent (M_4 missing), stem of anterior fork (M_{1+2}) shorter than fork, male abdominal segment 7 less than 0.5X length of segment 6.

Distribution: AF, PA (Israel).

Material examined: Afrocnemia whitfieldae Matile.

Comments: Based on the description and the figures of the genitalia (Chandler, 1994) *Acnemia stellamicans* belongs to this genus, though sc-r is present, unlike the remaining species.

***Allocotocera* Mik**

Eurycera Dziedzicki, 1885: 166. Type species: *Eurycera flava* Dziedzicki, 1885: 167 [= *Leia pulchella* Curtis, 1837], (monotypy) [preoccupied de Laporte, 1833.]

Allocotocera Mik, 1886: 102 (nom. n. for *Eurycera*).

Euryceras Marshall, 1896: 291. Type species: *Euryceras anaclinoides* Marshall, 1896: 291, (monotypy).

Diagnosis: Distinguished by: anepisternum setose, anterior basalare setose, metepisternum setose, wing membrane without microtrichia in some species, sc-r placed before origin of Rs, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than or equal to fork length, base of M_1 usually strong but sometimes weak or free, origin of anterior fork after origin of posterior fork, male abdominal segment 7 more than 0.5X length of segment 6, and male genitalia completely or almost completely (90%) retracted within segment 7.

Distribution: AU (NZ, undescribed species in Australia (Tonnoir, 1929)), NE, NT, PA.

Material examined: Allocotocera dilatata Tonnoir; *Allocotocera flavicoxa* Freeman; *Allocotocera parvula* (Coquillett); *Allocotocera pulchella* (Curtis).

Anaclileia Meunier

Anaclileia Meunier, 1904: 146. Type species: *Anaclileia anacliniformis* Meunier, 1904: 146 (subsequent designation by Johannsen, 1909).

Paraneurotelia Landrock, 1911: 161. Type species: *Paraneurotelia dziedzickii* Landrock, 1911: 161 (original designation).

Diagnosis: Distinguished by: sc-r present or absent, sc-r placed before origin of Rs when present, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, base of M_1 free, origin of anterior fork same as or after origin of posterior fork, and male abdominal segment 7 more than 0.5X length of segment 6 (Bechev, 1990a; Coher, 1995)

Distribution: NE, OR, PA.

Material examined: Anaclileia nepalensis Bechev; *Anaclileia vockerothi* Bechev.

Aneura Marshall

Aneura Marshall, 1896: 287. Type species: *Aneura boletinoides* Marshall, 1896: 288 (monotypy).

Diagnosis: Distinguished by: frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, sc-r placed before origin of Rs, R_{2+3} present or absent, when present forming a cell that is ~3X as long as tall, anterior and posterior fork present, stem of anterior fork (M_{1+2}) longer than fork,

origin of anterior fork after origin of posterior fork, and male abdominal segment 7 less than 0.5X length of segment 6 (Duret, 1975; Zaitzev, 2001).

Distribution: AU (NZ), NT (Patagonia)

Material examined: Aneura boletinoides Marshall; *Aneura longistila* Freeman.

Austrosciophila Tonnoir

Austrosciophila Tonnoir, 1929: 604 (*Sciophila* subg). Type species: *Sciophila (Austrosciophila) solitaria* Tonnoir, 1929: 604 (original designation).

Diagnosis: Distinguished by: metepisternum setose, wing membrane without microtrichia, sc-r placed well after origin of Rs, R_{2+3} present, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork before origin of posterior fork, and male abdominal segment 7 less than 0.5X length of segment 6.

Distribution: AU (Australia).

Material examined: Austrosciophila solitaria (Tonnoir).

Azana Walker

Azana Walker, 1856: 26. Type species: *Azana scatopsoides* Walker, 1856: 26 (monotypy), [= *anomala* (Staeger)].

Diagnosis: Distinguished by: 2 or 3 ocelli, anepisternum setose, subcostal vein ending free at wing base, sc-r absent, anterior fork usually present (M_{1+2} running to wing margin in NT species) but incomplete (M_2 free in apical portion of wing),

posterior fork absent (M_4 missing), and male abdominal segment 7 less than 0.5X length of segment 6 (Kerr, 2010).

Distribution: AF, NE, NT, OR, PA.

Material examined: Azana anomala (Staeger); *Azana asiatica* Senior-White; *Azana* sp. n. (Ecuador).

Baeopterogyna **Vockeroth**

Baeopterogyna Vockeroth, 1972: 1529. Type species: *Baeopterogyna nudipes* Vockeroth, 1972: 1532 (original designation).

Diagnosis: Distinguished by: mediotergite bare of setae but with macrotrichia, metepisternum setose, sc-r placed before origin of Rs, C not produced beyond the apex of R_5, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, base of M_1 weak, origin of anterior fork after origin of posterior fork, and male abdominal segment 7 less than 0.5X length of segment 6 and retractable.

Distribution: NE (northern), PA (western).

Material examined: Baeopterogyna nudipes Vockeroth.

Cluzobra **Edwards**

Cluzobra Edwards, 1940: 463. Type species: *Acnemia binocellaris* Edwards, 1934: 362 (original designation).

Diagnosis: Distinguished by: 2 or 3 ocelli, sc-r absent, anterior fork present,

posterior fork absent (M_4 missing), stem of anterior fork (M_{1+2}) shorter than fork, and male abdominal segment 7 less than 0.5X length of segment 6 (Matile, 1996; Coher, 1997; Amorim & Oliveira, 2008).

Distribution: NE (southern), NT.

Material examined: Cluzobra antennullata Coher; *Cluzobra plaumanni* Edwards.

Drepanocercus **Vockeroth**

Drepanocercus Vockeroth, 1980: 538. Type species: *Drepanocercus ensifer* Vockeroth, 1980: 539 (original designation).

Diagnosis: Distinguished by: frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, wing membrane without macrotrichia, distal median plate bare, sc-r placed before origin of Rs, R_{2+3} present and forming a cell ~3X as long as tall, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork after origin of posterior fork, M_4 almost reaching wing base before ending free, and male abdominal segment 7 more than 0.5X length of segment 6.

Distribution: NE (eastern).

Material examined: Drepanocercus ensifer Vockeroth.

Duretophragma **Borkent**

Duretophragma Borkent **gen. n.** Type species: *Stenophragma longifurcata* Freeman, 1951: 57. (present designation).

Included species: Duretophragma andina (Duret) **comb. n.**, *Duretophragma argentina* (Duret) **comb. n.**, *Duretophragma glabanum* (Johannsen) **comb. n.**, *Duretophragma humeralis* (Edwards) **comb. n.**, *Duretophragma longifurcata* (Freeman) **comb. n.**, *Duretophragma morigenea* (Edwards) **comb. n.**, *Duretophragma naumanni* (Duret) **comb. n.**, *Duretophragma obscura* (Duret) **comb. n.**, *Duretophragma ochracea* (Freeman) **comb. n.**, *Duretophragma pleuralis* (Edwards) **comb. n.**

Diagnosis: The genus can be distinguished by the following combination of characters: flagellomere 1 with a distinctly offset basal stalk, metepisternum setose, wing hyaline or with light shading on apical ¼, distal median plate bare, sc-r placed well after origin of Rs (at least halfway along cell created by R_{2+3}), R_{2+3} present forming a rectangular cell longer than wide, anterior and posterior fork present, stem of anterior fork (M_{1+2}) much shorter than fork (sometimes missing), origin of anterior fork before origin of posterior fork, male abdominal segment 7 more than 0.5X length of segment 6, and gonocoxites bearing apicolateral projection (with one to several apical long setae) (Duret, 1976, 1979).

Distribution: NE, NT.

Material examined: Duretophragma glabanum (Johannsen); *Duretophragma longifurcata* (Freeman); *Duretophragma ochracea* (Freeman).

Generic description:

Fig. 4, see also figures in Duret (1976, 1979)

Total length: 5-6.5 mm. Wing length: 4-5 mm.

Color: Head brown to black, mouthparts and palps yellow to brown, antenna mostly dark brown with scape and pedicel yellow to brown. Thorax yellow to dark brown, scutum sometimes with two to three darker longitudinal

stripes. Legs yellow to dark brown. Abdomen brown, tergites sometimes with light brown or yellow patches or bands anteriorly and posteriorly on each tergite. Genitalia light to dark brown.

Head: Circular in anterior view. Pedicel and scape bearing several bristles. Flagellomere 1 with a distinct, offset, basal stalk. Flagellomeres at least 1.5X longer than wide. Face and clypeus separate and subequal in length. Frons with ventral bristles, frontal furrow present, frontal cleft absent. Palpus with five segments, typically increasing in length from base to apex, segment 1 small and often hidden behind eye.

Compound eye with indentation (2-3 ommatidia deep) on medial margin just above level of antennae; interommatidial setulae present on entire eye surface. Three ocelli present on a dark background and almost in a straight line (median slightly in front of lateral ocelli), with lateral ocelli 1-1.5X own diameter from eye margin and 1.5X own diameter from median ocellus.

Thorax: Scutum with acrostichal and dorsocentral setae present and covered with small setae. Scutellum with large and small setae. Mediotergite with several bristles posteriorly and sometimes with small setae or appressed hairs medially. Laterotergite with several bristles and setae, sometimes with trichia as well. Anepisternum bare or with small dorsal patch of short trichia, metepisternum with several setae posteriorly. Anterior basalare bare. Anapleural suture with slight ventral curve on anterior portion.

Legs: Coxae with setae on dorsal margin, hind coxa with complete or partial row of strong setae on posterior margin. Tibiae with bristles and irregularly arranged, small, setae. Tibial spurs 1:2:2. Foretibia with anteroapical depressed area present. Midtibia with weak dorsal or posterodorsal bare line. Tarsi covered with irregularly arranged macrotrichia. Foretarsomere I subequal in length to

foretibia. Empodium present.

Wing: (Fig. 3B) Hyaline, rarely with apical ¼ lightly shaded. Membrane with both irregularly arranged microtrichia and macrotrichia, macrotrichia sparser near wing base and dense near apex. C extending barely beyond R_5.Humeral vein joining C close to wing base. Sc ending in C. sc-r present and joining R_1 just before or after R_{2+3}.R_{2+3} present and forming rectangular cell longer than broad.M_{1+2} forking into M_1 and M_2 immediately after origin at r-m (sometimes M_{1+2} absent).Origin of posterior fork (M_4 and CuA) after origin of anterior fork. Petiole of posterior fork (bCuA) shorter or longer than either M_4 or CuA. CuP ending at or beyond origin of posterior fork.A_1 absent to faintly present as crease. Distal median plate bare. Dorsal surfaces of Sc, R_1, R_5, all M veins, CuA, and CuP setose. Dorsal and ventral surface of humeral vein bare. Ventral surface of Sc, R_1, R_5, M_1, CuA setose, and of M_2, bare.M_4 bare or setose ventrally. Halter stem yellow, knob dark.

Abdomen: Abdominal segments 1-6 unmodified, segment 1 ~½ size of remainder. Segment 7 0.5 – 0.7X length of segment 6 and not retractable. Segment 8 reduced in size and at least partially retracted inside segment 7.

Male genitalia: Sternite 9 setose or bare, ranging from small (<¼ length of gonocoxite) triangular sclerite at base of genitalia, to thin oval or rectangular sclerite as long as medial length of gonocoxites, posterior margin concave, rounded or with medial point. Tergite 9 prominent, at least as long as rest of genitalia (often extending beyond), composed of two parts: basal rectangular or oval component, covered with sparse setae, making up ~¾ of length, and apical component (may be a remnant of tergite 10) densely covered in both small and long setae (concentrated on the apex) and frequently rectangular but sometimes tapering to a point. Gonocoxites large and setose, forming largest portion of genitalia and with an apicolateral protrusion ventrally, bearing one to several long

apical setae. Gonostylus with two to three broad lobes, bearing one to several combs of medially directed setae, as well as a group of short, thick, setae. Several long setae usually also present on medial margin. Aedeagus variable though apodemes appearing to fuse with gonocoxal apodemes.

Female genitalia: Tergite 9 lightly sclerotized. Sternite 9 bearing gonopore subapically, apical margin sclerotized. Tergite 10 a thin band at base of cerci. Sternite 10 sclerotized, setose and extending at least half length of cerci I. Cerci I large, cerci II usually small (though almost as long as cerci I in some species).

Etymology: The genus is named for Dr. José Pedro Duret (1913-2007) in recognition of his legacy of studies on the Mycetophilidae, including members of this new genus. The suffix indicates the close relationship between this genus and *Stenophragma*.

Comments: This genus is in need of revision. Some species have been assigned to *Duretophragma* based solely on published descriptions and examination of material is recommended to confirm their placement.

***Eudicrana* Loew**

Eudicrana Loew, 1870: 142. Type species: *Eudicrana obumbrata* Loew, 1870: 141 (monotypy).

Pareudicrana Tonnoir, 1929: 600. Type species: *Pareudicrana monticola* Tonnoir, 1929: 600 (original designation).

Diagnosis: Distinguished by: 2 ocelli, flagellomere 1 with a distinctly offset basal stalk, R_{2+3} present, wing membrane without microtrichia in some species, sc-r

placed near or well after origin of Rs, C not produced beyond the apex of R_5, R_{2+3} present and forming a cell ~3X as long as tall, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork after or at origin of posterior fork, and male abdominal segment 7 less than 0.5X length of segment 6.

Distribution: AU (Australia), NE, NT, PA.

Material examined: Eudicrana basinerva Freeman; *Eudicrana nicholsoni* (Tonnoir); *Eudicrana obumbrata* Loew.

***Leptomorphus* Curtis**

Leptomorphus Curtis, 1831: 365. Type species: *Leptomorphus walkeri* Curtis, 1831: 365 (monotypy).

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

Gymnoscutum Matile 1977: 144 (subgenus of *Leptomorphus*). Type species: *Leptomorphus obscurus* Matile 1977: 152 (original designation).

Austroleptomorphus Matile 1977: 145 (subgenus of *Leptomorphus*). Type species: *Leptomorphus grjebinei* Matile 1977: 154 (original designation).

Diagnosis: Species of *Leptomorphus* are distinguished by the following combination of characteristics: interommatidial setulae absent or very sparse and short, frons bare or with a few setae ventrally, flagellomere 1 with a distinctly offset basal stalk, flagellomeres slightly laterally compressed, anepimeron and preepisternum II bare, antepronotum and proepisternum setose, acrostichal bristles absent, wing membrane without microtrichia, sc-r (when present) placed

before or at origin of Rs, C not produced beyond the apex of R_5, R_{2+3} present or absent, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, base of M_1 complete, origin of anterior fork after origin of posterior fork, tibial bristles short, no more than half thickness of tibia in length, and male abdominal segment 7 more than 0.5X length of segment 6. (Papp & Ševčík, 2011; Borkent & Wheeler, in press).

Distribution: AF, AU (Only in NW, not reaching Australia), NE, NT, OR, PA.

Material examined: Leptomorphus medleri Matile; *Leptomorphus neivai* Edwards; *Leptomorphus walkeri* Curtis; (Most other described species in this genus were also studied, see Borkent & Wheeler (in press))

Loicia **Vockeroth**

Loicia Vockeroth, 1980: 530. Type species: *Loicia basifurca* Vockeroth, 1980: 531 (original designation).

Diagnosis: Distinguished by: medial eye margins parallel, frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, wing membrane without macrotrichia but with setae, distal median plate bare, sc-r placed before origin of Rs, R_{2+3} present and forming a cell ~3X as long as tall, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork after origin of posterior fork, M_4 joining bM near wing base, and male abdominal segment 7 more than 0.5X length of segment 6.

Distribution: NE (BC).

Material examined: Loicia basifurca Vockeroth.

***Megalopelma* Enderlein**

Megalopelma Enderlein, 1910: 165. Type species: *Megalopelma planiceps* Enderlein 1910: 166 (original designation).

Diagnosis: Distinguished by: metepisternum setose in some species, wing membrane macrotrichia reflexed towards wing base, sc-r placed well after origin of Rs, R_{2+3} present or absent, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork before origin of posterior fork, and male abdominal segment 7 less than 0.5X length of segment 6.

Distribution: NE, NT, PA.

Material examined: Megalopelma nigroclavatus (Strobl); *Megalopelma platyura* Edwards.

***Monoclona* Mik**

Staegeria Wulp, 1876: xlix (preoccupied Rondani, 1856). Type species: *Sciophila halterata* Staeger, 1840: 275 (monotypy) [= *rufilatera* (Walker)].

Monoclona Mik, 1886: 279 (*n. n*. for *Staegeria* Wulp).

Diagnosis: Distinguished by: 2 or 3 ocelli, metepisternum setose, wing membrane macrotrichia reflexed towards wing base, sc-r placed before origin of Rs, R_{2+3} present or absent, anterior fork present, posterior fork absent (M_4 missing), and stem of anterior fork (M_{1+2}) shorter than fork (Zaitzev, 1983).

Distribution: NE, NT, OR, PA.

Material examined: Monoclona bicolor (Enderlein); *Monoclona floridensis* Fisher; *Monoclona furcata* Johannsen; *Monoclona rufilatera* (Walker).

Morganiella Tonnoir & Edwards

Morganiella Tonnoir & Edwards, 1927: 817. Type species: *Morganiella fusca* Tonnoir *in* Tonnoir & Edwards, 1927: 817 (original designation).

Diagnosis: Distinguished by: anepisternum setose, wing membrane without microtrichia, sc-r placed well after origin of Rs, anterior and posterior fork present but posterior fork incomplete (M_4 free in apical portion of wing), stem of anterior fork (M_{1+2}) shorter than fork, base of M_1 and M_2 weak, and male abdominal segment 7 less than 0.5X length of segment 6.

Distribution: AU (NZ).

Material examined: Morganiella fusca Tonnoir.

Neoallocotocera Tonnoir

Neoallocotocera Tonnoir, 1929: 601. Type species: *Neoallocotocera fusca* Tonnoir, 1929: 601 (original designation).

Diagnosis: Distinguished by (based on Tonnoir 1929): eyes with numerous ommatidial setae, antennal segments wider than long and somewhat laterally compressed, anepisternum with bristles, anterior basalare bare, sc-r absent, R_5 sinuous, anterior and posterior wing forks complete, stem of anterior fork (M_{1+2}) shorter than fork, anterior fork origin just before origin of posterior fork, and male abdominal segment 7 long.

Distribution: AU (Tasmania).

Material examined: none.

***Neoaphelomera* Miller**

Aphelomera Skuse, 1888: 1206. Type species: *Aphelomera sydneyensis* Skuse, 1888: 1207 (monotypy) [preoccupied Stephens, 1833].

Neoaphelomera Miller, 1945: 72 (nom. n. for *Aphelomera*).

Diagnosis: Distinguished by: wing membrane macrotrichia reflexed towards wing base, sc-r absent, anterior fork present but incomplete (M_2 free in apical portion of wing), posterior fork absent (M_4 missing), stem of anterior fork (M_{1+2}) weak or free at base, and male abdominal segment 7 less than 0.5X length of segment 6.

Distribution: AU, NT (southern).

Material examined: Neoaphelomera cristata Freeman; *Neoaphelomera skusei* (Marshall); *Neoaphelomera sydneyensis* (Skuse).

***Neotrizygia* Tonnoir & Edwards**

Neotrizygia Tonnoir & Edwards, 1927: 816. Type species: *Neotrizygia obscura* Tonnoir *in* Tonnoir & Edwards, 1927: 816 (original designation).

Diagnosis: Distinguished by: anepisternum setose, anterior basalare setose, subcostal vein ending in sc-r, sc-r placed well after origin of Rs, anterior fork present but incomplete (M_2 free in apical portion of wing), posterior fork absent (M_4 missing), male abdominal segment 7 less than 0.5X length of segment 6.

Distribution: AU (NZ).

Material examined: Neotrizygia obscura Tonnoir.

Neuratelia Rondani

Neuratelia Rondani, 1856: 195. Type species: *Mycetophila nemoralis* Meigen 1818: 265 (original designation).

Anaclinia Winnertz, 1863: 770. Type species: *Mycetophila nemoralis* Meigen 1818: 265 (monotypy).

Odontopoda Aldrich, 1897: 187. Type species: *Odontopoda sayi* Aldrich 1897: 187 (monotypy).

Diagnosis: Distinguished by: flagellomere 1 with a distinctly offset basal stalk in some species, sc-r placed before origin of Rs, C not produced beyond the apex of R_5, R_5 sinuous, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, base of M_1 free, and origin of anterior fork after origin of posterior fork.

Distribution: NE, NT, OR (India), PA

Material examined: Neuratelia nemoralis (Meigen); *Neuratelia sayi* (Aldrich); *Neuratelia scitula* Johannsen.

Paramorganiella Tonnoir

Paramorganiella Tonnoir, 1929: 606.
Type species: *Paramorganiella adventurosa* Tonnoir, 1929: 606 (original designation).

Diagnosis: Distinguished by: anepisternum setose, metepisternum setose, sc-r placed well after origin of Rs, anterior and posterior fork present, but anterior fork

incomplete (M_2 free in apical portion of wing), and male abdominal segment 7 more than 0.5X length of segment 6. Males of *Paramorganiella* are the only Mycetophilidae with strongly modified palpi (see Jaschhof *et al.,* 2010).

Distribution: AU (Australia).

Material examined: Paramorganiella adventurosa Tonnoir.

Paratinia **Mik**

Paratinia Mik, 1874: 333.
Type species, *Paratinia sciarina* Mik 1874: 331 (monotypy.)

Diagnosis: Distinguished by: medial eye margins parallel, frons bare, mediotergite and laterotergite bare, bristle(s) present just posteromedially of halter base, wing membrane without macrotrichia but with setae, distal median plate bare, sc-r placed before origin of Rs, R_{2+3} present and forming a cell ~3X as long as tall, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork after origin of posterior fork, and male abdominal segment 7 more than 0.5X length of segment 6.

Distribution: NE, PA.

Material examined: Paratinia recurva Johannsen; *Paratinia sciarina* Mik.

Paratrizygia **Tonnoir**

Paratrizygia Tonnoir, 1929: 605. Type species: *Paratrizygia conformis* Tonnoir, 1929: 605 (original designation).

Diagnosis: Distinguished by: sc-r absent, R_{2+3} present or absent, anterior fork present but incomplete (M_2 free in apical portion of wing), posterior fork absent (M_4 missing), male abdominal segment 7 less than 0.5X length of segment 6, and setae scattered on apicoventral surface of male tergite nine.

Distribution: AU (Australia), NT.

Material examined: Paratrizygia conformis Tonnoir; *Paratrizygia setifera* Freeman; *Paratrizygia spinulosa* Freeman.

Comments: Amorim *et al.* (2011) in redescribing the holotype of *P. conformis* retained their recently described *Paratrizygia* species (Oliveira & Amorim, 2010) in this genus, based on the presence of parallel rows of spines on the ventral apex of tergite nine. Unfortunately the genitalia of the holotype are permanently mounted in lateral view. We have studied other material of *P. conformis* in which the genitalia in lateral view correspond to those of the holotype. However, in ventral view it is clear that the setae present on the ventral apex of tergite nine are not in parallel rows but are scattered, as in Freeman (1951: fig. 123). The arrangement of setae seen in the holotype is apparently coincidental due to the aspect of preservation. Based on this observation as well as other characteristics (i.e. anepisternum setose) the *Paratrizygia* species described from Brazil are transferred to *Trizygia* (see below).

Parvicellula **Marshall**

Parvicellula Marshall, 1896: 284. Type species: *Parvicellula triangula* Marshall, 1896: 284 (monotypy).

Diagnosis: Distinguished by: anepisternum setose, anterior basalare setose, wing membrane without microtrichia in some species, sc-r placed before origin of Rs,

R_{2+3} present, anterior fork present, posterior fork absent (M_4 missing), stem of anterior fork (M_{1+2}) shorter than fork, base of M_2 weak, male abdominal segment 7 less than 0.5X length of segment 6, and male with 1-2 pairs of processes arising from the distal margin of tergite nine and each bearing a comb of setae on apical margin.

Distribution: AU (NZ), NT.

Material examined: Parvicellula fascipennis Edwards; *Parvicellula flabellifera* Freeman; *Parvicellula producta* Freeman; *Parvicellula triangula* Marshall.

Phthinia **Winnertz**

Phthinia Winnertz, 1863: 779. Type species: *Phthinia humilis* Winnertz, 1863: 780 (subsequent designation by Johannsen, 1909: 83).

Diagnosis: Distinguished by: 2 or 3 ocelli, dorsal surface of subcostal vein bare, sc-r placed before origin of Rs, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork before origin of posterior fork, and mid tibial organ (sensory groove) clearly present (Zaitzev 1984).

Distribution: AU, NE, NT, PA.

Material examined: Phthinia furcata Freeman; *Phthinia humilis* Winnertz; *Phthinia longiventris* Tonnoir; *Phthinia* sp. n.; *Phthinia tanypus* Loew.

Polylepta **Winnertz**

Polylepta Winnertz, 1863: 745. Type species: *Polylepta undulata* Winnertz, 1863:

746 (subsequent designation by Johannsen, 1909: 43) [= *guttiventris* (Zetterstedt)].

Diagnosis: Distinguished by: flagellomere 1 with distinctly offset basal stalk, metepisternum setose, sc-r placed well after origin of Rs, R_{2+3} present, R_5 sinuous, anterior and posterior fork present, stem of anterior fork (M_{1+2}) equal to fork length, base of M_1 weak, origin of anterior fork after origin of posterior fork, mid tibial organ (sensory groove) clearly present, and male abdominal segment 7 more than 0.5X length of segment 6 (Bechev, 1990a; Kurina, 2003).

Distribution: NE, OR, PA.

Material examined: Polylepta borealis Lundström; *Polylepta guttiventris* Winnertz.

Sciophila **Meigen**

Sciophila Meigen, 1818: 245. Type species: *Sciophila hirta* Meigen, 1818, (subsequent designation by Curtis, 1837: 641).

Lasiosoma Winnertz, 1863: 748. Type-species: *Sciophila pilosa* Meigen, 1838: 42 (subsequent designation by Coquillett, 1910: 558) [=*hirta* Meigen, 1818].

Diagnosis: Distinguished by: anepisternum setose, wing membrane without microtrichia in some species, sc-r placed at or well beyond origin of Rs, R_{2+3} present, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork before origin of posterior fork, and gonostylus bearing apically-feathered, spatulate, megasetae (Zaitzev, 1982c; Söli, 1995, 1997a).

Distribution: AF, NE, NT, OR, PA.

Material examined: Sciophila adamsi Edwards; *Sciophila hirta* Meigen; *Sciophila* sp. n. (*intima* group); *Sciophila nepalensis* Zaitzev; *Sciophila rufa* Meigen.

Stenophragma **Skuse**

Homaspis Skuse, 1888: 1191. Type species: *Homaspis meridiana* Skuse, 1888: 1192 (monotypy) [preoccupied Förster, 1868].

Stenophragma Skuse, 1890: 612 (nom. n. for *Homaspis*).

Diagnosis: Distinguished by: 2 or 3 ocelli, flagellomere 1 with a distinctly offset basal stalk, metepisternum setose, wing with three to four ~parallel grey stripes (Matile 1991, Fig. 12), distal median plate bare, sc-r placed near Rs, R_{2+3} present or absent, anterior and posterior fork present, stem of anterior fork (M_{1+2}) missing (M_1 joining r-m), and origin of anterior fork before origin of posterior fork.

Distribution: AU (Australia, New Caledonia), OR (undescribed species from Indonesia, Malaysia).

Material examined: Stenophragma meridianum (Skuse); *Stenophragma papanorum* Matile.

Tasmanina **Tonnoir**

Tasmanina Tonnoir, 1929: 602. Type species: *Tasmanina gracilis* Tonnoir, 1929: 603 (original designation).

Diagnosis: Distinguished by: metepisternum setose, sc-r placed before origin of Rs, anterior and posterior fork present, stem of anterior fork (M_{1+2}) shorter than fork, origin of anterior fork after origin of posterior fork, and male abdominal

segment 7 more than 0.5X length of segment 6.

Distribution: AU (Australia).

Material examined: Tasmanina gracilis (Tonnoir).

Taxicnemis **Tonnoir & Edwards**

Taxicnemis Tonnoir & Edwards, 1927: 805. Type species: *Sciophila hirta* Marshall, 1896: 283 (original designation) [preoccupied Meigen 1818, = *Taxicnemis marshalli* Matile, 1989].

Diagnosis: Distinguished by: frons bare, mediotergite and laterotergite bare, metepisternum setose, bristle(s) present just posteromedially of halter base, distal median plate bare, subcostal vein ending free beyond sc-r, sc-r placed before origin of Rs, C not produced beyond the apex of R_5, R_{2+3} present and forming a cell ~3X as long as tall, anterior and posterior fork present, stem of anterior fork (M_{1+2}) equal to fork length, origin of anterior fork after origin of posterior fork, M_4 almost reaching wing base before ending free, vestiture of the tibia arranged in parallel lines, and male abdominal segment 7 less than 0.5X length of segment 6.

Distribution: AU (NZ).

Material examined: Taxicnemis marshalli (Marshall).

Trizygia **Skuse**

Trizygia Skuse, 1888: 1204. Type species: *Trizygia flavipes* Skuse, 1888: 1205 (monotypy).

New combinations: T*rizygia albidens* (Oliveira & Amorim) **comb. n.**, T*rizygia alvesi* (Oliveira & Amorim) **comb.n.**, T*rizygia balbi* (Oliveira & Amorim) **comb.n.**, *Trizygia camargoi* (Oliveira & Amorim) **comb.n.**

Diagnosis: Distinguished by: anepisternum setose, anterior basalare setose, sc-r placed near Rs when present, anterior fork present but incomplete (M_2 free in apical portion of wing), posterior fork absent (M_4 missing), male abdominal segment 7 less than 0.5X length of segment 6, and 2-4 parallel lines of thick setae present on ventral apex of tergite 9.

Distribution: AU (Australia), NT.

Material examined: Trizygia flavipes Skuse.

Comments: As discussed above, the *Paratrizygia* species described by Oliveira and Amorim (2010) belong in this genus based on the presence of a setose anepisternum and the parallel rows of strong setae present ventrally on tergite nine.

Conclusion

This study has provided the first complete phylogeny of the genera in the Sciophilini, revising the tribal limits and clarifying the placement of several genera placed previously both in the Sciophilini and Gnoristini. The tribe now includes 34 genera and over 520 described species. This phylogeny lays the foundation for future taxonomic and phylogenetic work within the tribe.

Much of the world's mycetophilid fauna remains to be discovered and described (Pape *et al.,* 2009), and genera of the Sciophilini and other tribes continue to be found in regions from which they were unknown previously (i.e. *Azana* (Amorim

et al., 2008) and *Leptomorphus* (Papp and Ševčík, 2011)), particularly in the Afrotropical, Australasian and Oriental regions. However, some general comments on biogeographic patterns of the Sciophilini can be made. The tribe is cosmopolitan except for Antarctica. Most genera have either a principally Holarctic or Gondwanan distribution, sometimes with dispersal into adjacent regions. *Acomoptera, Baeopterogyna, Drepanocercus, Loicia,* and *Paratinia* are exclusively Holarctic. *Acnemia, Anaclileia, Azana, Monoclona, Neuratelia, Phthinia, Polylepta* and *Sciophila* are most species-rich in the Holarctic but have a few representatives in other regions. Genera that are exclusively found in the southern hemisphere include: *Afrocnemia, Aneura, Austrosciophila, Morganiella, Neoaphelomera, Neotrizygia, Paramorganiella, Paratrizygia, Parvicellula, Tasmanina, Taxicnemis,* and *Trizygia. Allocotocera, Eudicrana,* and *Stenophragma* are most species-rich in the southern hemisphere but also have some species present in other regions. *Adicroneura, Cluzobra,* and *Duretophragma* are restricted to the new world; all three are most species-rich in South America, with one species present in the southern or western Nearctic. *Megalopelma* has equal numbers of described species from the Holarctic and Neotropical regions. *Leptomorphus* is the only genus known from all regions, though in the Australasian region it is restricted to the islands of the northwest of the region, and does not reach Australia or New Zealand. More generic revisions and species-level phylogenies within Sciophilini are required before robust hypotheses about historical dispersal and vicariance within the tribe can be proposed.

Most genera of Sciophilini are in need of revision, particularly outside of the Holarctic region, and these studies, when undertaken, will certainly reveal finer details of the relationships both within and between genera. Collection and description effort should be particularly concentrated in the Oriental, Afrotropical and Australasian regions because of the likely high diversity there.

Genera in particular need of revision are *Duretophragma, Megalopelma,* and *Stenophragma.* Revisions and phylogenies of these three genera may resolve the polytomy in the strict consensus tree (Fig. 1B). Most genera in the Australasian region would benefit from revisionary work as they have a greater diversity than is currently described (Tonnoir & Edwards, 1927; Tonnoir, 1929).

More information is also needed on the morphology and habits of immature stages of this and other tribes. This will provide further data to test the current hypothesis of relationships between genera as well as allowing the study of host associations of particular genera and their fungal hosts. This may, in turn, contribute to Mycetophilidae being used as a proxy for the diversity of fungi in a forest.

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Table 1. Character state matrix used for Sciophilini phylogenetic analysis. Missing character state data are indicated by "?".

	1 1234567890	1111111112 1234567890 123	2222222223 4567890 123	3333333334 4567890 123	4444444445 4567890
Ingroup Taxa					
Acnemia falkei Matile & Vockeroth	1000010100	0000211120	0102000000	0010010001	0101011110
Acnemia fulvicollis (Philippi) 100	0010100	0001011120	0012000000	0010010001	0100011110
Acnemia nitidicollis (Meigen) 100	0010100	0001011120	0112000000	0010010001	0101011110
Acnemia vockerothi Zaitzev 100	0021100	0001011120	0012000000	0210010001	0101011110
Acomoptera plexipus (Garrett) 010	1001100	1011100000	0000000001	0000000000	1100000000
Acomoptera vockerothi Kerr 010	1001100	1011100100	0000000001	0000000000	1100000000
Adicroneura biocellata Vockeroth 201	01?00??	0000212001	0002000000	0010010001	0100011000
Afrocnemia whitfieldae Matile 101	0021100	1001011121	0022000000	0210010001	0100011010
Allocotocera dilatata Tonnoir 000	0011100	1001112000	0202011010	0010010011	0101011000
Allocotocera flavicoxa Freeman 100	0011100	1001112000	2112011010	0010010011	0100011100
Allocotocera parvula (Coquillett) 100	0011100	1001012000	0112011010	0011210011	0101011110
Allocotocera pulchella (Curtis) 100	0011100	1001012000	1212011010	0011210011	0101011110
Anaclileia nepalensis Bechev 100	0010000	0010111100	0001000000	0010010001	0100011100
Anaclileia vockerothi Bechev 100	0000000	0000111100	0002000000	0010010001	0100011010
Aneura boletinoides Marshall 000	2011100	1001100000	0001000000	0000000000	0100001000
Aneura longistila Freeman 001	2012100	1001200000	0001000000	0000000000	0100001000
Austrosciophila solitaria (Tonnoir) 100	0011000	0000011111	0012000000	0010010011	0101011010
Azana anomala (Staeger) 201	0000100	0010011110	0102012000	0010010001	0100011003
Azana asiatica Senior-White 201	0000000	0000011110	0102012000	0010010001	0100011003
Azana n.sp.	10201?00??	0000111120	2222011000	0010010001	0100011013
Baeopterogyna nudipes Vockeroth 002	1010000	0011012100	0002000100	0001210011	0100011000
Cluzobra antennullata Coher 100	01?11??	0001212120	0012000000	0210010001	0100011010
Cluzobra plaumanni Edwards 100	01?01??	0001212110	0012000000	0210010001	0100011010
Coelophthinia curta (Johannsen)	1000021110	1011010100 000	1000000 011	0000001 110	0000000
Coelophthinia flavithorax (Freeman)	10?0021110	10?1010000 ?00	1000000 010	0000001 110	0000000
Coelophthinia thoracica (Winnertz)	1000021110	1011010000 000	1000000 021	0000001 110	0000000

Table 1. Continued.

	1 1234567890	1111111112 1234567890 123	2222222223 4567890 123	3333333334 4567890 123	4444444445 4567890
Drepanocercus ensifer Vockeroth 100	2001100	0001100110	0000000000	0000000000	1100000000
Eudicrana basinerva Freeman 101	01?21??	1001112002	1001000100	1211110001	0101011110
Eudicrana nicholsoni (Tonnoir) 001	01?21??	1001212???	??01000100	1211110001	0100011000
Eudicrana obumbrata Loew 101	01?21??	1001112002	1001000100	1211110001	0100011110
Impleta polypori (Vockeroth) 202	0012200	1011111020	0101000000	0000010000	1100000003
Leptomorphus medleri Matile 101	2010000	0002110012	1002100000	0011110001	0101011100
Leptomorphus neivai Edwards 101	2010000	0002110012	1002100000	0111111001	0101011100
Leptomorphus walkeri Curtis 201	1010000	0002112012	1002100000	0111110001	0101011100
Loicia basifurca Vockeroth 110	1001100	1000000010	0000000000	0000000000	1000000000
Megalopelma nigroclavatus (Strobl) 201	0010000	0000011010	0012000000	0210010011	0110011000
Megalopelma platyura Edwards 200	0010000	0000211010	0212000000	0210010001	0110011000
Monoclona bicolor (Enderlein) 100	01?00??	0000211120	0202000000	0110010011	0110011010
Monoclona floridensis Fisher 100	01?00??	0000211120	0202000000	0110010011	0110011010
Monoclona furcata Johannsen 100	0010000	0001211110	0012000000	0110010011	0110011010
Monoclona rufilatera (Walker) 100	0010000	0001211010	0212000000	0110010011	0110011010
Morganiella fusca Tonnoir 100	0020100	0010012000	0111011000	0010010001	0101011100
Neoaphelomera cristata Freeman 101	0010100	0010211120	0012000000	0210010001	0110011010
Neoaphelomera skusei (Marshall) 201	0020100	0010211020	0012000000	0210010001	0110011010
Neoaphelomera sydneyensis (Skuse) 101	0010101	0000211010	0012000000	0210010001	0110011010
Neotrizygia obscura Tonnoir 200	0010000	0010212000	0102011010	0?10010001	0100011002
Neuratelia nemoralis (Meigen) 101	0011100	0001112001	0011000000	1010010001	0100011110
Neuratelia sayi (Aldrich) 101	0011100	1011112001	0011000000	0010010001	0100011010
Neuratelia scitula Johannsen 101	0011100	1011112002	0012000000	0010010001	0100011010
Paramorganiella adventurosa Tonnoir 200	1010101	0010211000	0012011000	0010010011	0100011000
Paratinia recurva Johannsen 010	2011100	1011010000	0000000000	0000000000	1000000000
Paratinia sciarina Mik 010	2011100	10?1010000	0000000000	0000000000	1000000000

Table 1. Continued.

	1	1111111112	2222222223	3333333334	4444444445
	1234567890	1234567890 123	4567890 123	4567890 123	4567890
Paratrizygia conformis Tonnoir 200	0011211	1001111000	0102000000	0010010001	0100011000
Paratrizygia setifera Freeman 20?	0012111	1011211010	0002000000	0010010001	0100011000
Paratrizygia spinulosa Freeman 20?	0012111	1011211010	0002000000	0010010001	0100011000
Parvicellula fascipennis Edwards 100	0011100	1111211011	0012011110	0010010001	0101011110
Parvicellula flabellifera Freeman 100	0011100	1110211011	0012011010	0010010001	0100011100
Parvicellula producta Freeman 200	0011100	1111211001	0012011010	0010010001	0100011100
Parvicellula triangula Marshall 000	0021200	1111111011	0012011110	0010010001	0101011100
Phthinia furcata Freeman ?01	0021110	110??12001	0000000001	0210000001	0100010000
Phthinia humilis Winnertz 101	0021110	1110112011	0000000001	0210000001	0100010000
Phthinia longiventris Tonnoir 10?	11?11??	1101?12001	0000000001	0210010001	0100010000
Phthinia n.sp. 102	1021000	1001212001	0000000001	0210010001	0100010000
Phthinia tanypus Loew 101	0021110	1101212001	0000000001	0210010001	0100010000
Polylepta borealis Lundström 100	0020100	0010212012	0002000001	0210010011	0100011100
Polylepta guttiventris Winnertz 100	0020100	0110212012	0002000001	0210010011	0100011100
Sciophila adamsi Edwards 200	0020010	0001011010	0012011000	0010010001	0100011110
Sciophila hirta Meigen 200	0020000	0001011010	0012011000	0010010001	0100011110
Sciophila n.sp. (*intima* group)	2000020000	0001011010	0012011000	0010010001	0100011110
Sciophila nepalensis Zaitzev 100	0010000	0001011010	0012011000	0010010001	0100011110
Sciophila rufa Meigen 200	0020000	0001011010	0002011000	0010010001	0101011110
Speolepta leptogaster (Winnertz) 001	0010100	0010010100	0000000000	0000000000	1100000001
Stenophragma glabanum (Johannsen) 100	0011101	0000012012	0012000000	0210010011	0100001000
Stenophragma longifurcata Freeman 100	0010100	0000012002	0002000100	0210011011	0100001000
Stenophragma meridianum (Skuse) 200	01?11??	0001212012	0012000000	0010010011	0100001000
Stenophragma papanorum Matile 200	01?10??	0001002102	0?12000000	0210010011	0100001000
Syntemna hungarica (Lundström) 200	0010100	0000000000	0002000000	0000010010	0100000002
Tasmanina gracilis (Tonnoir) 100	2010100	0011012000	0002000000	0010010011	0100011000
Taxicnemis marshalli (Marshall) 001	1011112	0002000001	0012000000	0100000010	0100001001
Trizygia flavipes Skuse 200	0011111	1011011000	0102011010	0010010001	0100011100

Table 1. Continued.

	1 1234567890	1111111112 1234567890 123	2222222223 4567890 123	3333333334 4567890 123	4444444445 4567890
Outgroup taxa					
Allactoneura obscurata Walker 002	1020112	0100010000	0002000002	2?00010101	1100000000
Exechia attrita Johannsen 102	01?22??	1101111001	0102000100	0200011111	1100100003
Exechia fusca (Meigen) 102	01?22??	1101111011	0102000100	0200011111	1100100003
Gnoriste bilineata Zetterstedt	0001011000	1000000000	0002000000	0000000000	1100000000
Gnoriste macra Johannsen	0011010100	1000000000	0002000000	0000000000	1100000000
Leia oblectabilis (Loew)	1010022212	1101010010	0002000000	0000010101	1100000000
Manota n.sp.	1010011100	1100010000	0122100112	2?00010101	1100000003
Mycomya marginata (Meigen)	10001?00??	0002000011	1001000000	0200000000	1100000000
Mycetophila exstincta Loew	10201?22??	1101000011	0002012100	0200011111	1100110013
Mycetophila fungorum (De Geer)	10201?22??	1101000011	0002012100	0200011011	1100110013
Tetragoneura pimpla Coquillett	0020010100	0110000000	0111000000	0000000100	1100000002

Table 1. Continued.

555	5555556	6666666667	7777777778	8888888889	999999
123	4567890	1234567890	1234567890	1234567890	123456
Ingroup Taxa					
Acnemia falkei Matile & Vockeroth	1001111110	1110000200	0012??1021	0100010102	101000
Acnemia fulvicollis (Philippi) 000	1111110	1110100200	0012??1021	0100010102	101001
Acnemia nitidicollis (Meigen) 000	1111110	1110100200	0012??1021	0100010102	101001
Acnemia vockerothi Zaitzev 000	1111110	1110100200	0012??1021	0100010102	101001
Acomoptera plexipus (Garrett) 000	0010000	1010000001	0001011000	0000000002	000000
Acomoptera vockerothi Kerr 000	0010000	1010000001	0001011001	0000000102	000000
Adicroneura biocellata Vockeroth 01?	0010100	011210132?	2?01011020	00000?0112	000000
Afrocnemia whitfieldae Matile 110	1111110	1110100200	0012??1021	0000110202	101000
Allocotocera dilatata Tonnoir 100	1110110	1110110001	0101111000	0000110002	000010
Allocotocera flavicoxa Freeman 000	1110110	1110110001	0101011000	0000110002	000010
Allocotocera parvula (Coquillett) 000	1110110	1111110021	0101011000	0000110002	000010
Allocotocera pulchella (Curtis) 000	1110110	1111110001	0101011100	0000110002	000010
Anaclileia nepalensis Bechev 010	1011110	1110110121	0101011020	0000000102	000000
Anaclileia vockerothi Bechev 000	1010110	1110110021	0101011010	0000000002	000000
Aneura boletinoides Marshall 000	1010010	0102000000	0001011021	0110010102	101000
Aneura longistila Freeman 000	1010010	0002000000	0001011021	0110010202	101000
Austrosciophila solitaria (Tonnoir) 002	1110110	1010110201	0101011021	0100110102	???000
Azana anomala (Staeger) 110	????110	1112100200	2012??1021	0100010002	???000
Azana asiatica Senior-White 110	????110	1112100200	2012??1021	0100010002	101000
Azana n.sp.	1101111110	011210132?	2?12??1021	12000?0012	100000
Baeopterogyna nudipes Vockeroth 000	1110011	1110110011	0101111101	1200000002	110000
Cluzobra antennullata Coher 110	1110110	0100100200	0012??1021	0100010202	???000
Cluzobra plaumanni Edwards 110	1110110	1110110200	0012??1021	0100010202	101000
Coelophthinia curta (Johannsen) 100	0000000	0100000200	0001011021	0110200111	100000
Coelophthinia flavithorax (Freeman) 100	0000000	0100000200	0001011021	0110000111	100000
Coelophthinia thoracica (Winnertz) 100	0000000	0100000200	0001011021	0110200111	100000

Table 1. Continued.

555	5555556	6666666667	7777777778	8888888889	999999
123	4567890	1234567890	1234567890	1234567890	123456
Drepanocercus ensifer Vockeroth 000	0010000	1010000000	0002011000	0000010002	000000
Eudicrana basinerva Freeman 001	1110110	1010110001	0101011000	0000010212	100000
Eudicrana nicholsoni (Tonnoir) 002	1110010	1010110101	0101011000	0000010??2	100000
Eudicrana obumbrata Loew 002	1110110	1010010001	0101011001	0000010212	100000
Impleta polypori (Vockeroth) 110	0000110	1110000010	1001011020	0110000000	100000
Leptomorphus medleri Matile 000	1110111	1110110001	0101011001	0100110212	000000
Leptomorphus neivai Edwards 001	1110111	1010110001	0101011000	0100110212	000000
Leptomorphus walkeri Curtis 000	1110111	1110110001	0101011001	0000110212	000000
Loicia basifurca Vockeroth 000	0010000	0010100001	0100011000	0000010102	000000
Megalopelma nigroclavatus (Strobl) 002	1111000	1010000200	0001011021	0000110102	100000
Megalopelma platyura Edwards 002	1111000	1110010201	0101011021	0100110102	100000
Monoclona bicolor (Enderlein) 000	1111110	1110000200	0012??1021	0000110102	100000
Monoclona floridensis Fisher 000	1111110	1110??0200	0012??1021	0000110102	100000
Monoclona furcata Johannsen 000	1111110	1010000200	0012??1021	0000110102	000000
Monoclona rufilatera (Walker) 000	1111110	1010000200	0012??1021	0000110102	100000
Morganiella fusca Tonnoir 002	1111110	1110110210	1002011020	0000010002	100000
Neoaphelomera cristata Freeman 110	1111110	1112100200	2012??1021	0100110102	101000
Neoaphelomera skusei (Marshall) 110	1110110	1112100200	2012??1021	0100110102	210000
Neoaphelomera sydneyensis (Skuse) 110	1110110	1112100200	2012??1021	0100110102	2100000
Neotrizygia obscura Tonnoir 002	1111110	1112100200	2012??1021	0100010002	100000
Neuratelia nemoralis (Meigen) 000	1010001	1110000020	0001011100	0000010102	101000
Neuratelia sayi (Aldrich) 000	1110001	1110100020	0001011000	0000010102	001000
Neuratelia scitula Johannsen 000	1110001	1110100020	0001011100	0000010202	001000
Paramorganiella adventurosa Tonnoir 002	1111100	1111100100	2001011010	0100110002	000000
Paratinia recurva Johannsen 000	0010010	1010100001	0101111100	0000000102	000000
Paratinia sciarina Mik 000	0010000	1010000001	0101011110	0000000102	000000

Table 1. Continued.

555	5555556	6666666667	7777777778	8888888889	999999
123	4567890	1234567890	1234567890	1234567890	123456
Paratrizygia conformis Tonnoir 110	1111000	1012110201	2112??1120	0100010002	101000
Paratrizygia setifera Freeman 110	1111000	1112110201	2112??1121	0100010012	101000
Paratrizygia spinulosa Freeman 110	1110000	1112110201	2112??1121	0100010012	101000
Parvicellula fascipennis Edwards 100	1111110	1010110200	1012??1020	0000010002	???000
Parvicellula flabellifera Freeman 100	1111110	1010110200	1012??1021	0000010002	101000
Parvicellula producta Freeman 100	1111110	1010110200	1012??1021	0100010002	101000
Parvicellula triangula Marshall 100	1111110	1010100200	1012??1020	0000010002	101000
Phthinia furcata Freeman 000	1100010	0100010200	0001011021	0011201212	100000
Phthinia humilis Winnertz 000	1100010	0110010200	0001011021	0011201212	001000
Phthinia longiventris Tonnoir 000	1000010	0100000200	0001011021	0001201212	000000
Phthinia n.sp. 000	1100110	1110000200	0001011021	0000201212	000000
Phthinia tanypus Loew 000	1000010	1110000200	0001011021	0011201212	000000
Polylepta borealis Lundström 002	1110110	1011100010	0001011000	0000210112	000000
Polylepta guttiventris Winnertz 002	1110110	1011100010	0001011000	0000210112	000000
Sciophila adamsi Edwards 002	1111110	1010110200	0101011000	0100010002	101100
Sciophila hirta Meigen 001	1111110	1010110200	0101011000	0100010002	101100
Sciophila n.sp. (*intima* group) 002	1111100	1010110200	0001011021	0100010002	101100
Sciophila nepalensis Zaitzev 001	1111100	1010110200	0101011011	0100010102	001100
Sciophila rufa Meigen 001	1111110	1010110200	0101011000	0100010102	101100
Speolepta leptogaster (Winnertz) 100	0000000	0000000000	0001011021	0000200111	000000
Stenophragma glabanum (Johannsen) 001	1110110	1010100201	0001011021	0000110102	100000
Stenophragma longifurcata Freeman 002	1110110	1000??0200	0001111101	0100110102	000000
Stenophragma meridianum (Skuse) 001	1110100	1010000201	0101011021	0000010102	???000
Stenophragma papanorum Matile 001	1110100	1110000201	0101111021	0000110102	000000
Syntemna hungarica (Lundström) 001	0010000	1010100000	0001011000	0000010001	100000
Tasmanina gracilis (Tonnoir) 000	1110000	1110110001	0101111100	0000010002	000000
Taxicnemis marshalli (Marshall) 100	1010101	0011110001	0102011001	0002011012	101000
Trizygia flavipes Skuse 001	1111100	1112100200	2012??1020	0000010002	100000

Table 1. Continued.

555	5555556	6666666667	7777777778	8888888889	999999
123	4567890	1234567890	1234567890	1234567890	123456
Outgroup taxa					
Allactoneura obscurata Walker 100	1100001	1110000000	0000011000	1200010101	210000
Exechia attrita Johannsen 110	0000001	1110000200	0001000020	0102011111	211000
Exechia fusca (Meigen) 110	0000001	1110000200	0001000020	0102011111	211000
Gnoriste bilineata Zetterstedt	0000010000	1110000200	0001011000	0000010001	210000
Gnoriste macra Johannsen	0000010000	1110000000	0001001000	0000010001	210000
Leia oblectabilis (Loew)	1000000101	1110100000	0001011000	0111011100	101000
Manota n.sp.	1100000000	111???0?20	2001011001	1212011200	211000
Mycomya marginata (Meigen)	0020010001	1000000000	0001011000	0002011110	000000
Mycetophila exstincta Loew	1100000001	1110000000	0001011020	0112011101	210000
Mycetophila fungorum (De Geer)	1100000001	1110000000	0001011020	0112011101	211000
Tetragoneura pimpla Coquillett	1000000000	0000000010	0000011000	0000210101	211000

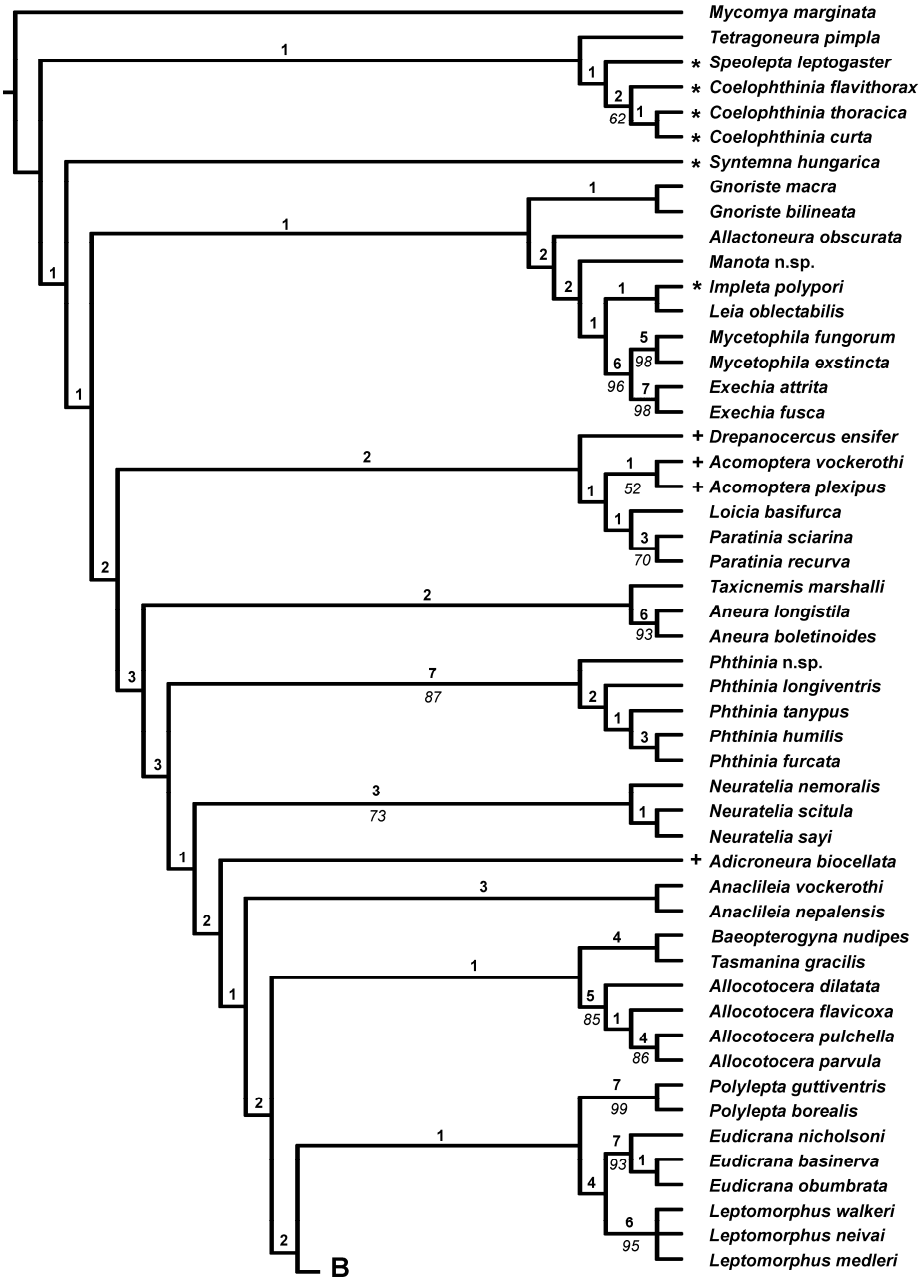

Figure 1A. Base of strict consensus tree of 12 equally parsimonious trees found in the phylogenetic analysis. Bremer support values are above the branches in bold; bootstrap values >50% are in italics below the branches. Taxa previously included in Sciophilini are noted with an '*' and new additions with a '+'.

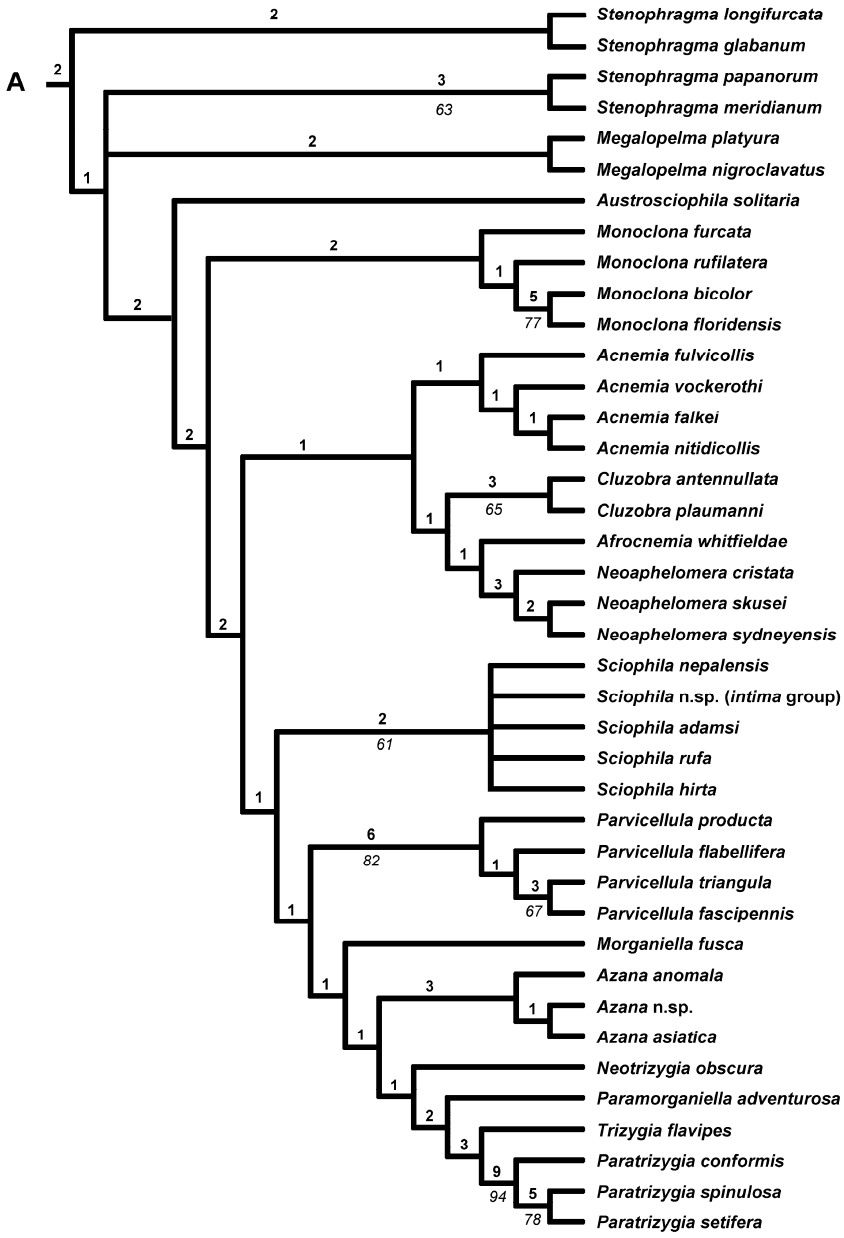

Figure 1B. Apex of strict consensus tree of 12 equally parsimonious trees found in the phylogenetic analysis. Bremer support values are above the branches in bold; bootstrap values >50% are in italics below the branches. Taxa previously included in Sciophilini are noted with an '*' and new additions with a '+'

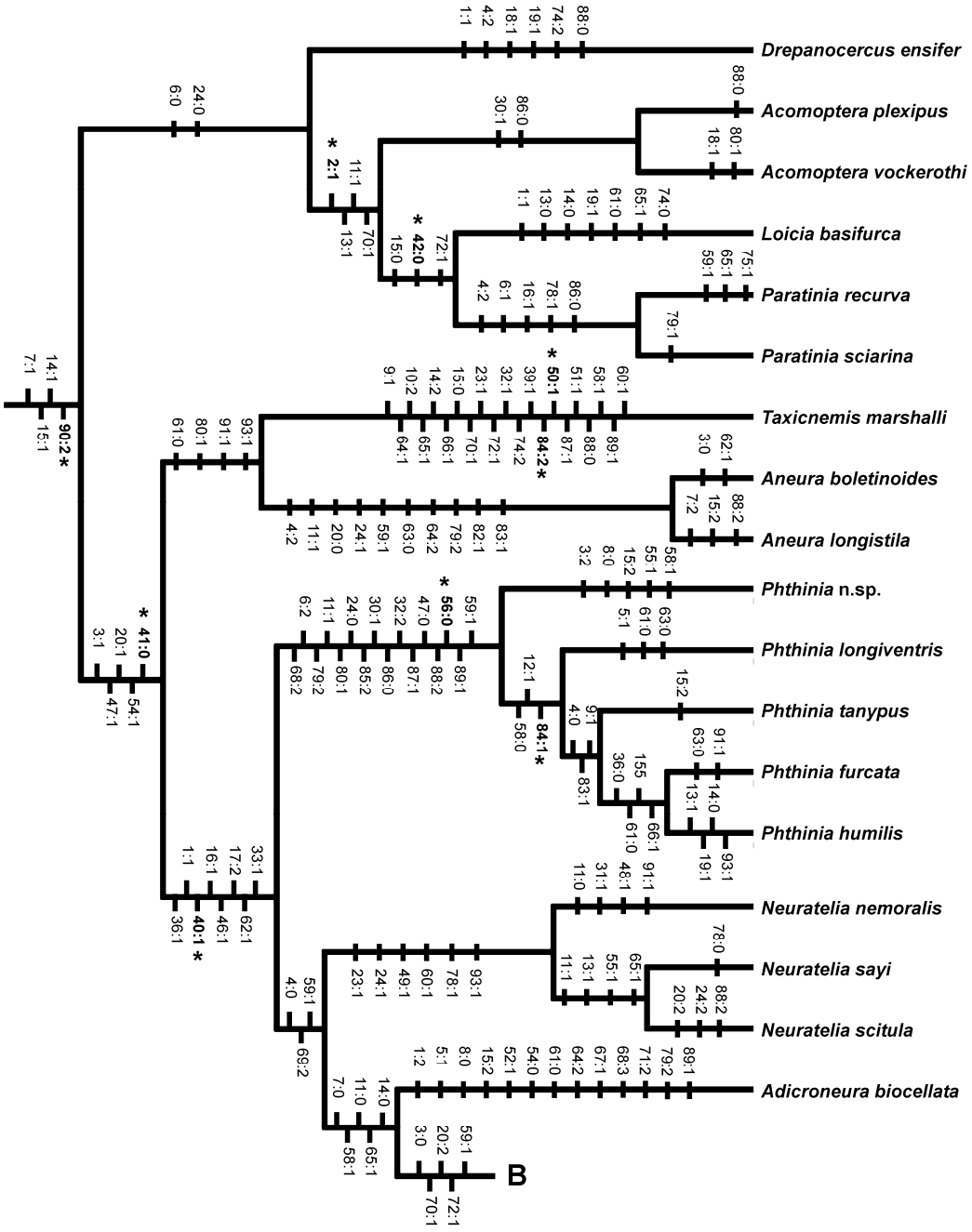

Figure 2A. One of 12 equally parsimonious trees showing relationships at the base of the tree (*Drepanocercus – Adicroneura*). Character state changes are indicated by black bars. Uniquely derived synapomorphies are in bold with an asterisk.

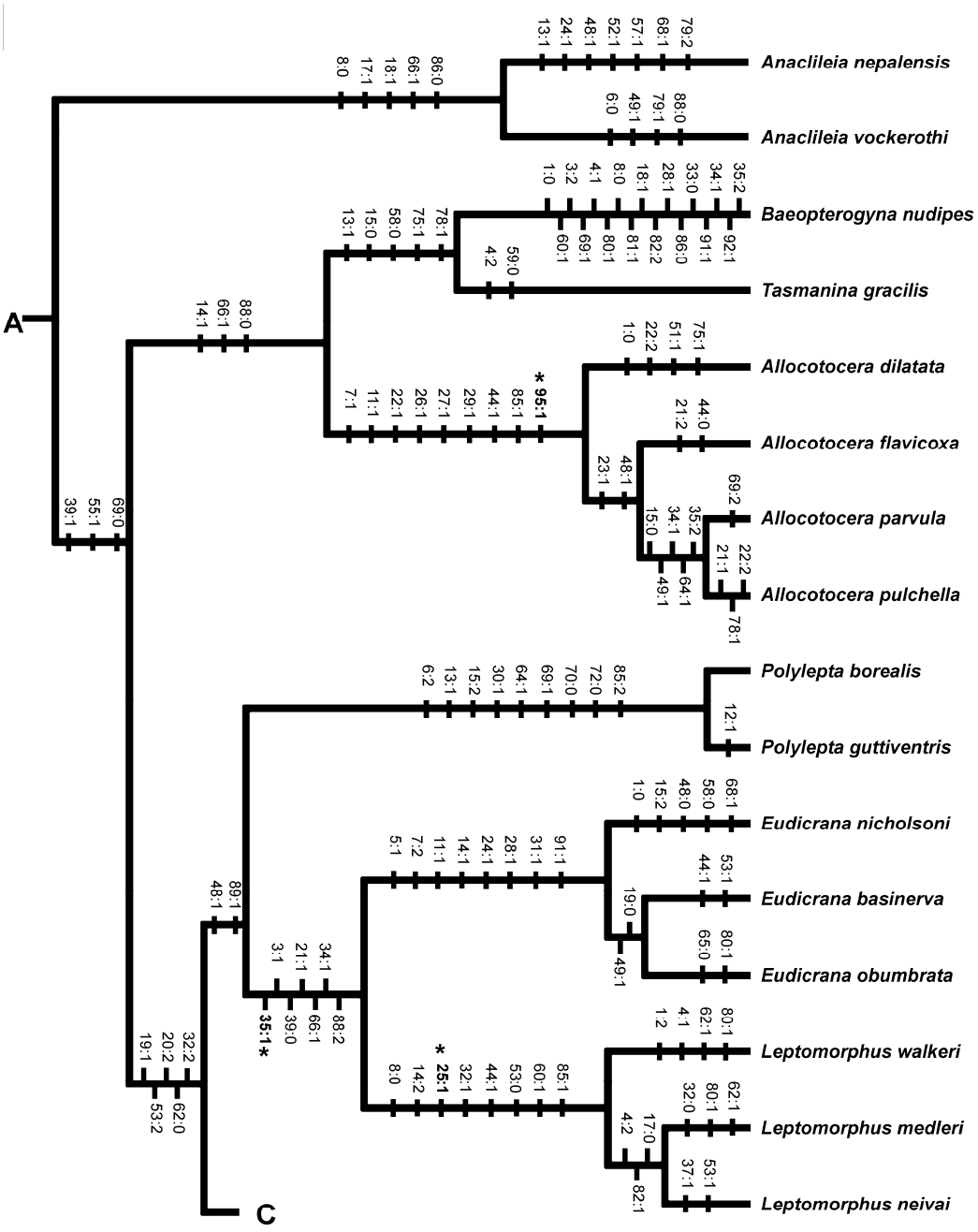

Figure 2B. Continuation of one of 12 equally parsimonious trees showing relationships from *Eudicrana* to *Polylepta*. Character state changes are indicated by black bars. Uniquely derived synapomorphies are in bold with an asterisk.

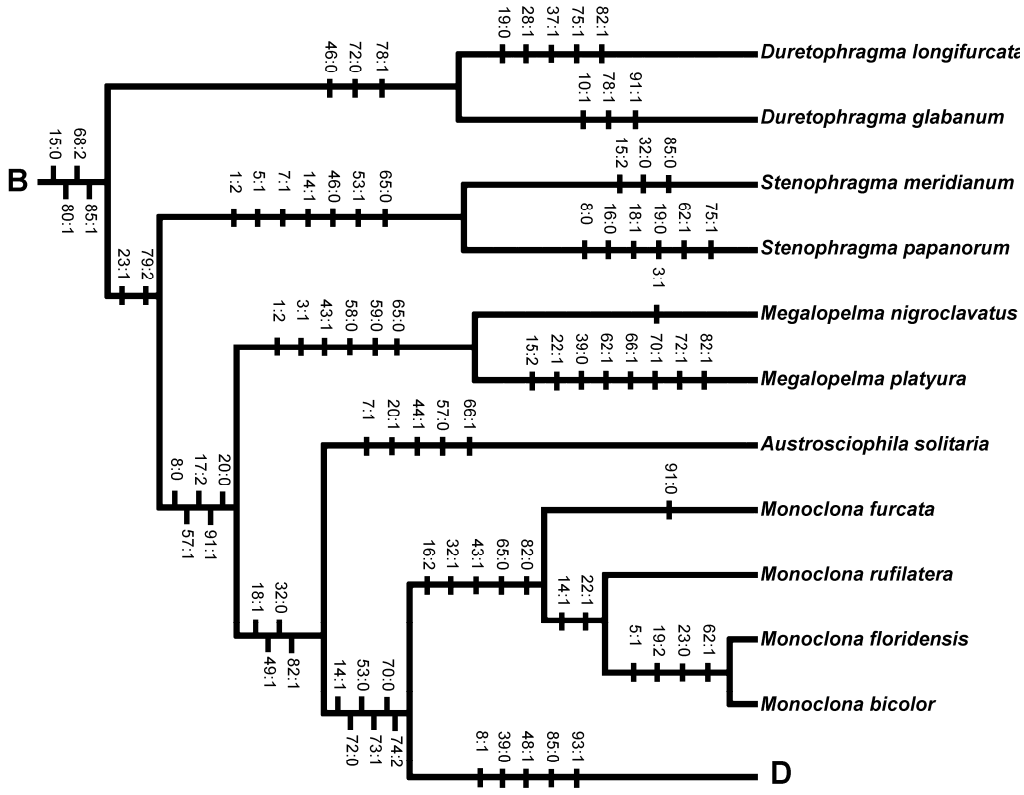

Figure 2C. Continuation of one of 12 equally parsimonious trees showing relationships from *Stenophragma* to *Monoclona.* Character state changes are indicated by black bars.

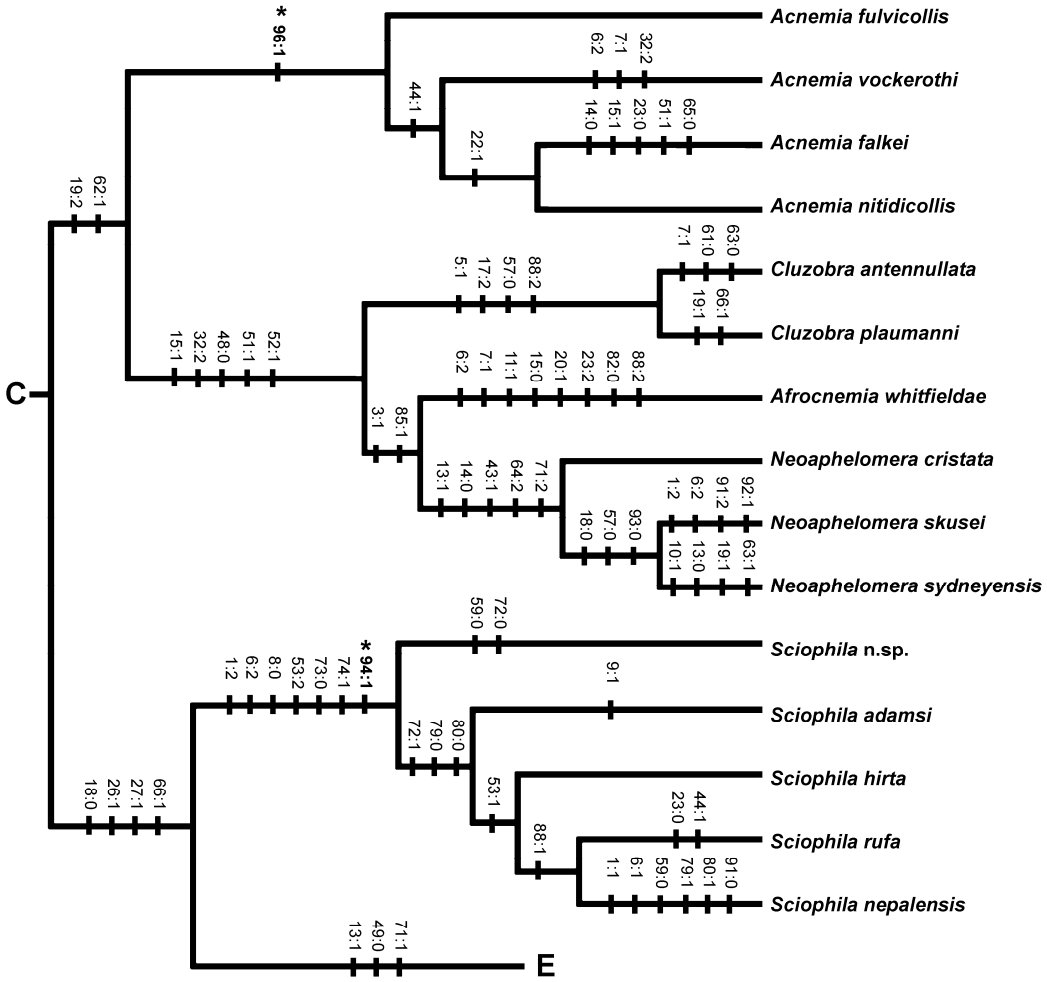

Figure 2D. Continuation of one of 12 equally parsimonious trees showing relationships within the *Acnemia* clade (*Acnemia – Neoaphelomera*) and *Sciophila.* Character state changes are indicated by black bars. Uniquely derived synapomorphies are in bold with an asterisk.

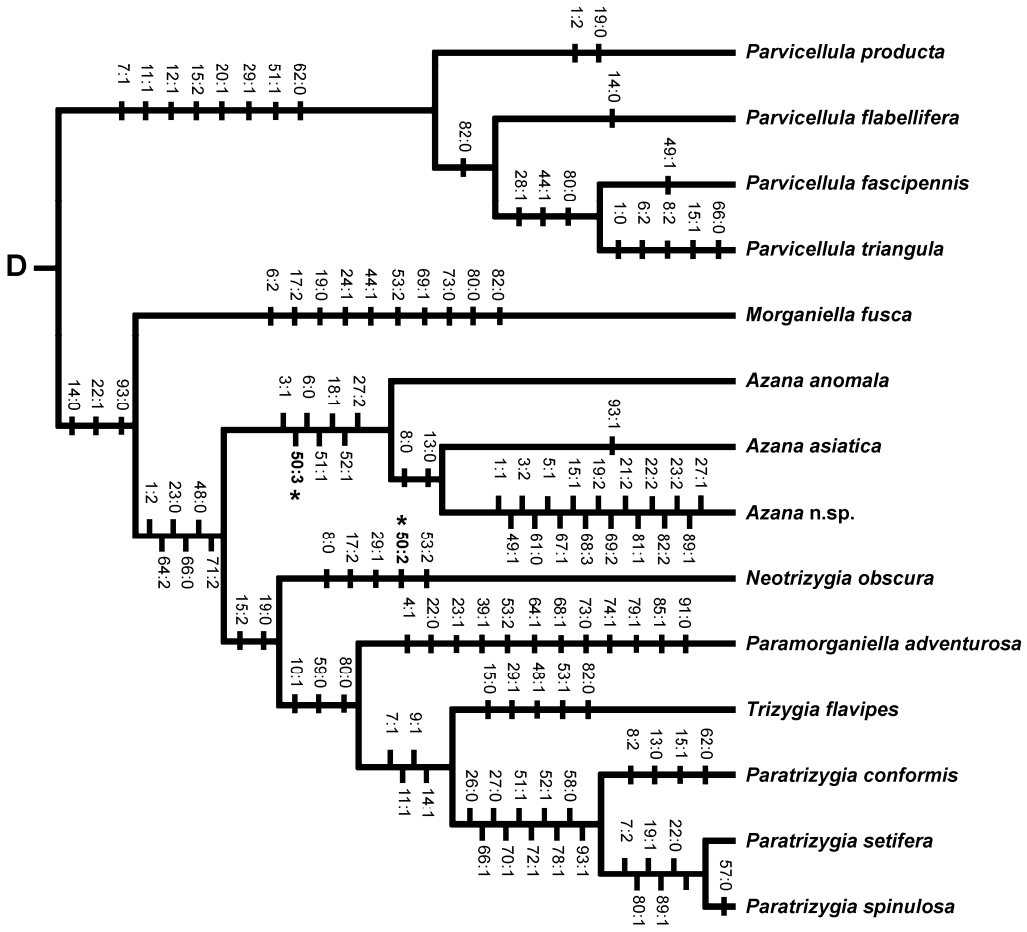

Figure 2E. Continuation of one of 12 equally parsimonious trees showing relationships at the apex of the tree (*Parvicellula – Paratrizygia*). Character state changes are indicated by black bars. Uniquely derived synapomorphies are in bold with an asterisk.

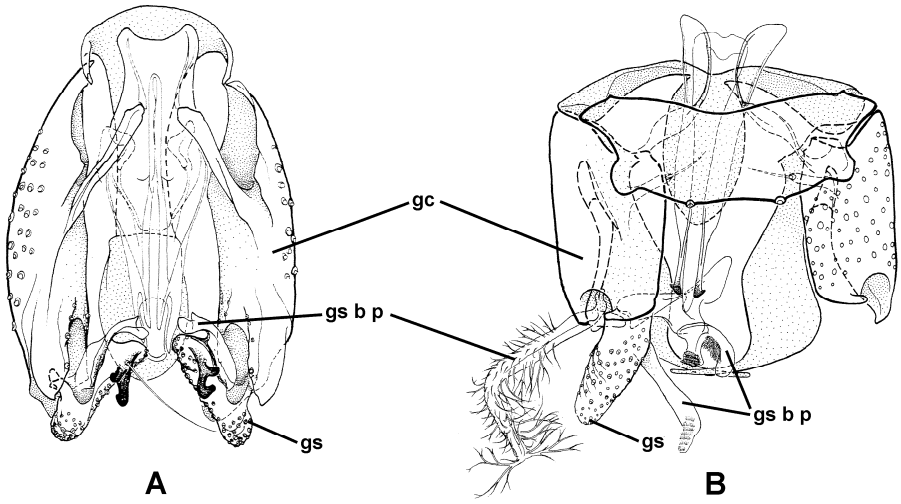

Figure 3. Male genitalia of *Acnemia*, showing presence of gonostylar basal processes (after Söli 1997b). A) *A. longipes*. B) *A. nitidicollis*. Abbreviations: gc = gonocoxite, gs = gonostylus, gs b p = gonostylar basal process.

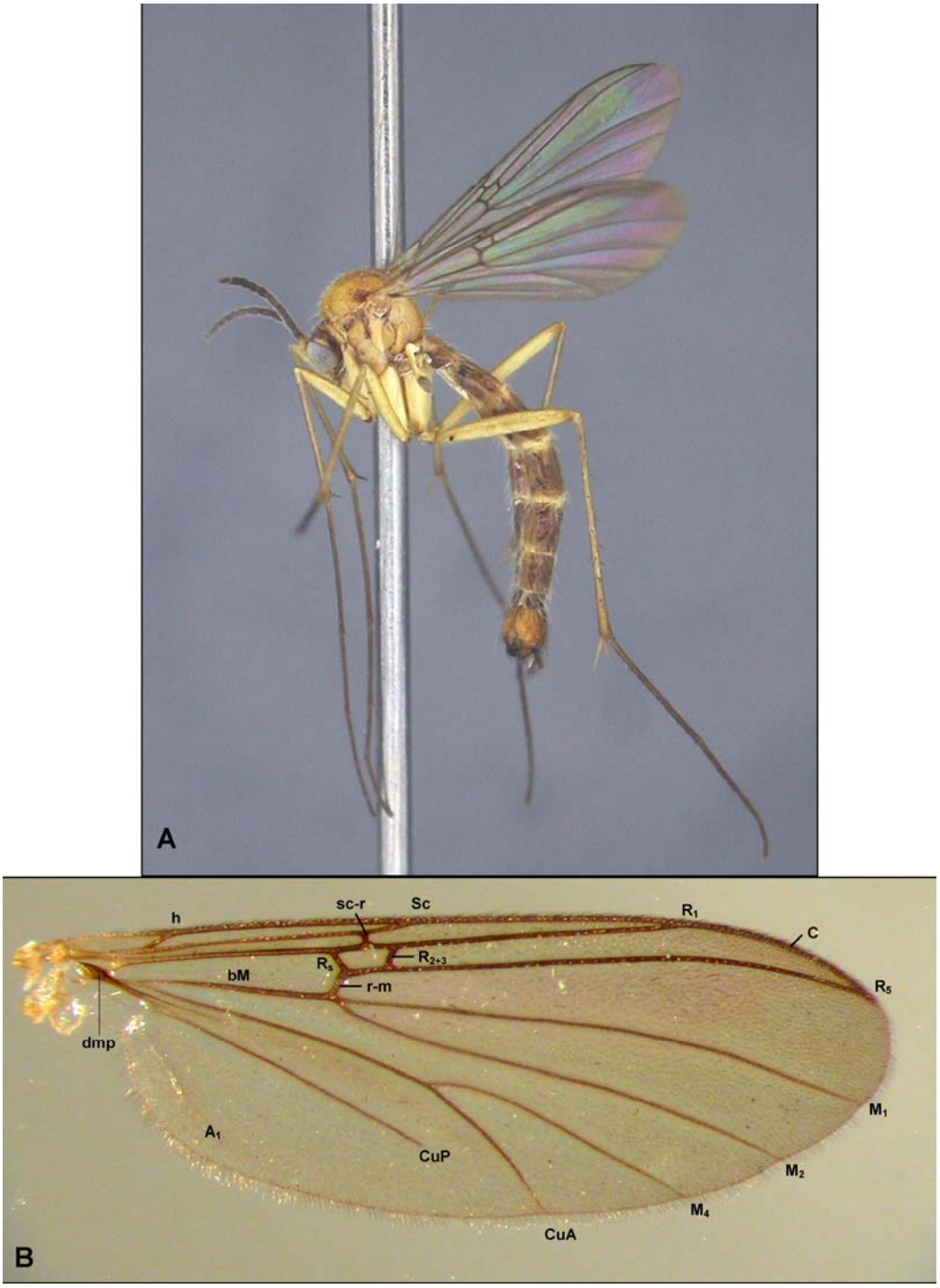

Figure 4. *Duretophragma glabanum*. A) Male habitus. B) Wing, ventral view. Wing length is 4.5 mm in both figures.

CHAPTER 4. GENERAL CONCLUSION

The studies presented in this thesis have been a major contribution to our understanding of the phylogeny of the tribe Sciophilini and the diversity and relationships within the genus *Leptomorphus*. It provides the first worldwide revision of *Leptomorphus*, including detailed descriptions, figures of morphology and distributions, and a key to species. Hypotheses of the phylogenetic relationships for all species of *Leptomorphus* and all genera of the Sciophilini were also presented for the first time.

The revision of *Leptomorphus* presented in Chapter 2 provides a comprehensive resource for future work on this genus, both in terms of biodiversity studies requiring identification tools and future taxonomic work on the genus. It is certain that new species of *Leptomorphus* will be discovered as more material is collected from under-sampled areas around the world. This revision provides the context necessary to determine if species are new, and to place them phylogenetically within the genus based on the characters they possess. The phylogeny of species relationships has confirmed the monophyly of the genus and has clarified the classification by synonymizing the previously erected subgenera and providing monophyletic species groups for phylogenetic discussions.

The relationships and species limits within the *Leptomorphus nebulosus* species group require further attention, as the males in this group have identical genitalia but can be separated based on colour patterns and a few other morphological characteristics. This group should be studied using molecular sequence data from multiple genes (e.g., COI, COII, 16s, CytB) to determine species limits and the relationships both within the species group and to other North American *Leptomorphus* species.

The phylogenetic analysis of the Sciophilini presented in Chapter 3 confirmed the limits of the tribe, removing four genera and adding three, and the monophyly of the contained genera (after the new genus *Duretophragma* Borkent was described). This is the first complete phylogeny of the Sciophilini, including 33 of the 34 genera, and multiple exemplars for most genera. It is expected that as genera within this tribe are revised, and therefore more species within genera are examined and discovered, new morphological characters will also be found that could change the topology of the phylogeny. Revisions of the genera *Duretophragma*, *Megalopelma* Enderlein and *Stenophragma* Skuse, would be particularly useful, as characters would likely be discovered resolving the polytomy between the latter two genera in the Sciophilini phylogeny.

Much work on the phylogeny of the Mycetophilidae remains, particularly with respect to the composition of the Gnoristini and Leiini. The phylogeny of the Leiini is currently being explored by S. Oliveira (USP, São Paulo, Brazil), but the Gnoristini has received no such study. A phylogenetic treatment of this tribe is necessary to resolve the relationships at the base of the Mycetophilidae and should be the next higher-level analysis undertaken within the family. The *Acomoptera* and *Aneura* clades should be included in any future phylogenetic analyses attempting to determine the relationships between the Gnoristini, Leiini, Mycomyiini and Sciophilini tribes, as these two clades are the most plesiomorphic of the Sciophilini and should help reveal relationships to the other tribes, while minimizing the amount of homoplasy.

Another source of characters for phylogenetic analysis is molecular data, and the relationships between the tribes would certainly benefit from analysis of sequence data. However, the small amount of previous work within the Mycetophilidae has produced conflicting and/or inconclusive results at this broader phylogenetic level (Bertone *et al.* 2008, Rindal *et al.* 2009b). New genes and primers are being

evaluated for use and hopefully these will provide more useful molecular data and clearer phylogenetic resolution (Gibson *et al.* 2011, Wiegmann *et al.* 2011).

The investigation of molecular data would provide another set of characters to evaluate the hypothesized relationships between the genera of the Sciophilini. Few studies using molecular data for phylogeny exploration in the Mycetophilidae have been undertaken (Rindal *et al.* 2007, 2009a, b, Martinsson *et al.* 2011). These studies used the mitochondrial genes COI, 16S and CytB and the nuclear genes 18s and 28s. Given the age of the tribe, mitochondrial genes will probably contain little useful data. The relatively low mutation rates of the nuclear genes make them a preferred choice for exploring the higher level relationships between the genera in the tribe. In Chironomidae the nuclear genes CAD and EF-1a have shown promise for studies of tribal phylogeny (Ekrem *et al*. 2010) and should be explored in the Mycetophilidae. The mitochondrial genes mentioned would be useful for investigating species level relationships.

The DNA barcoding region of COI will also be useful in future studies of both taxonomy and ecology in the Mycetophilidae, as it can be used for associating males and females of the same species (Kurina *et al.* 2011) and for associating immature stages with adults (e.g. Stur & Ekrem 2010). The association of immature and adult specimens will allow larval morphological characters to be added to phylogenetic studies, and the association of mycetophilid species with their host fungi without the trouble of rearing the larvae.

The Mycetophilidae have been considered an 'orphan taxa' (with no current workers) or poorly known in all of the world's biogeographic realms except the Palaearctic (Pape *et al.* 2009). However, in the last few years this trend has changed, as new students of mycetophilid taxonomy have been trained in the New World, and with the beginning of projects such as the Manual of Afrotropical Diptera, which aims to discover the diversity of Diptera in that region

(www.afrotropicalmanual.net). Interest continues to increase in the phylogeny and taxonomy of the Sciaroidea and it is hoped that the development of online resources such as www.sciaroidea.info and increased communication and collaboration between workers will increase this momentum.

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