PHYLOGENY AND BIOGEOGRAPHY OF THE MAYFLY FAMILY LEPTOHYPHIDAE (INSECTA: EPHEMEROPTERA) WITH A TAXONOMIC REVISION OF SELECTED GENERA

A Dissertation

by

DAVID EUGENE BAUMGARDNER

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2008

Major Subject: Entomology

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Approved by:

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	James B. Woolley
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ABSTRACT

Phylogeny and Biogeography of the Mayfly Family Leptohyphidae (Insecta: Ephemeroptera) with a Taxonomic Revision of Selected Genera. (August 2008)

David Eugene Baumgardner, B.S., Baylor University;

M.S., University of North Texas

Chair of Advisory Committee: Dr. John D. Oswald

A cladistic analysis of the world genera of the mayfly family Leptohyphidae is presented. Analyses of a matrix of 58 ingroup and 9 outgroup species and 119 morphological characters strongly supports the monophyly of Leptohyphidae and its sister-group relationship with Coryphoridae. Larval and adult taxonomic keys are provided to the 11 recognized extant genera. A synonymical listing, differential diagnosis, list of proposed synapomorphies, diagnostic illustrations, and notes on distribution and included species are given for each genus. The following new synonyms of genus *Tricorythodes* are proposed: *Ableptemetes* **n. syn.,** *Cabecar* **n. syn.,** *Epiphrades* **n. syn.,** *Homoleptohyphes* **n. syn.,** *Macunahyphes* **n. syn.,** *Tricoryhyphes* **n. syn.** The former genus *Asioplax* is newly regarded as a subgenus of *Tricorythodes*. A species-level revision of North and Central American *Leptohyphes* is presented. A key to the 15 *Leptohyphes* species known as larvae is provided. In addition, detailed descriptions, diagnosis, and geographic distributions are given for all species of *Leptohyphes* known from North and Central America. Biogeographic analysis suggests that the family Leptohyphidae originated in South America, and that its North American species are the descendants of one or more ancestral species that crossed northward over the Panamanian land bridge.

The results of this research clearly show that the mayfly family Leptohyphidae is a strongly supported monophyletic clade supported by five unique synapomorphies. Currently recognized genera are also strongly supported; however, little support was found for subfamilies. The sister family is clearly Coryphoridae, which is supported by three unique synapomorphies. Biogeographic analysis indicates that Leptohyphidae originated in South American, with at least five independent invasions from South America to North and Central America during the evolution of Leptohyphidae.

DEDICATION

This work is dedicated to two eminent ephemeropteran systematists who passed away during the course of this research, Dr. George F. Edmunds, Jr. and Dr. William L. Peters. Both will be greatly missed by their many friends, associates, and students. They were not only leaders in their field but were outstanding individuals who contributed much to our knowledge of the world around us.

Dr. George F. Edmunds, Jr. (April 28, 1920 – March 04, 2006), whose career spanned more than 50 years, is generally considered the Father of North American ephemeropterology research. Dr. Edmunds completed his Ph.D. at the University of Massachusetts, under the guidance of Dr. Jay Traver. Dr. Edmunds began his teaching and research career at the University of Utah and retired from that university in 1989 as a professor of Biology. During his years in Utah, he was associated with research programs throughout the world, and was regarded by many mayfly specialists as the most influential ephemeropterist of his generation.

Dr. William L. Peters (27 June 1939 – 03 June 2000) was a student of Dr. Edmunds who had a long and successful career at Florida A&M University, Gainesville, where he made major contributions to the study of the Ephemeroptera. His scientific research focused on the cosmopolitan mayfly family Leptophlebiidae. Dr. Peters published more than 100 scientific papers and monographs, and established more than 60 new genera, subgenera, and species (Hubbard, 2003). He also encouraged, guided, and collaborated with many mayfly researchers throughout the world.

ACKNOWLEDGMENTS

Most systematists recognize the substantial sacrifices and contributions that their families make in support of their research. While we travel throughout the world in search of our critters and spend hours upon hours in the laboratory, our loved ones wait patiently. First, I would like to thank my wife, Abigail, for the many hours, days, weeks, months and years that she has endured my study and research. Her support, whether in the field, laboratory, or at home is always appreciated. Her patience has no bounds. And to my son Kirk, for all his support, understanding, and assistance on more than one field trip.

No graduate student would be able to complete their research without the constant oversight, support, and harassment of their committee. Drs. John D. Oswald, James B. Woolley, Jimmy K. Olson, and Merrill H. Sweet constantly supported and pushed me to be the best systematist possible. Their patience and understanding was greatly appreciated, especially during the 15 months that I was absent from the university in support of Operation Iraqi Freedom I.

Numerous friends and fellow scientists made substantial contributions to the completion of this research through their advice, time, and support. In particular, Mrs. Jan Peters and Dr. Wills Flowers (Florida A&M University) were a tremendous resource for discussing various aspects of ephemeropteran systematics, loaning specimens, and hosting me during visits to Florida A&M University. Dr. Carlos Molineri (Universidad Nacional de Tucumán, Tucumán, Argentina) provided a substantial number of South

American leptohyphid specimens, which increased the depth and breadth of the study. Dr. Pat McCafferty (Purdue University) was of great assistance in discussing various aspects of ephemeropteran systematics. Drs. Jack Schuster (Universidad del Valle, Guatemala City, Guatemala) and Jean-Michel Maes (Museo Entomologico, Leon, Nicaragua) were of tremendous assistance during collecting trips to Guatemala and Nicaragua, respectively, where they arranged for permits, lodging, and guidance. The administrative assistance and support of the Instituto Nacional de Biodiversidad (Santo Domingo de Heredia, Costa Rica) while working in Costa Rica is also much appreciated. The donations of Cuban leptohyphid mayflies by Dr. Nikita Kluge (St. Petersburg State University, St. Petersburg, Russia) was greatly appreciated.

Loans from the California Academy of Sciences and Academy of Natural Sciences of Philadelphia were particularly significant for providing many type specimens and much additional study material. The tremendous curatorial support provided by Mr. Edward Riley (Texas A&M University) is greatly appreciated. And finally, the financial support of the Texas A&M University Entomology Graduate Student Organization, the L.T. Jordan Institute for International Awareness, and the Ernst Mayr Travel Grants in Animal Systematics from the Museum of Comparative Zoology, Harvard University, is gratefully acknowledged.

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CHAPTER I

INTRODUCTION: BIOGEOGRAPHY

Biogeography and the Panamanian Land Bridge

Biologists have long been interested in the study of the patterns of distribution of plants and animals, patterns that can provide information about dispersal and vicariance events that have shaped the distributions of faunas. Many 18th Century scientists considered plants and animals immutable and attempted to explain distributions using "centers of creation" and multiple creation events. However, by the 19th Century, significant contributions to the science of biogeography were challenging these long-held beliefs. Two of the most influential 19th Century naturalists, Charles Darwin and Alfred Wallace, recognized that many plants and animals possess distinct distribution patterns. Darwin (1859) and Wallace (1876) developed some of the earliest and most significant works in biogeography and evolutionary biology. They believed that one of the keys to understanding plant and animal distributions was to study their patterns of distribution. Many of these patterns were explained by hypothesizing long-distance dispersal. Later, the importance of geology and plate tectonics would be incorporated into ideas of biogeography, resulting in the development of the concept of vicariance and its affect on distributions. As early as 1858 in his book "Creation and its Mysteries

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This dissertation follows the style of Transactions of the American Entomological Society.

Revealed", Antonio Snider-Pelligrini provided evidence of continental movements; his ideas would not be largely accepted until almost 100 years later.

In 1957, Darlington provided an extensive discussion of zoogeographic patterns based upon several different groups of animals, incorporating primarily dispersal, but also discussing vicariance, as critical factors impacting the distribution of populations. In the decades since the publication of Darlington (1957), increased emphasis has come to be placed on the elaboration of techniques useful for more rigorously discriminating between dispersal- and vicariance-based patterns.

The continents of North and South America contain excellent examples of faunas that have been influenced by both dispersal and vicariant events. Only recently have these two continents become connected through the Panamanian land bridge. The biotic interchange via this corridor is often referred to as the "great American interchange." The Panamanian land bridge may have formed as early as the Pliocene, some 5.7 mya (million years ago) (Raven and Axelrod, 1974; Webb, 1997), although other researchers put the date of final closure closer to 2.5 mya (Webb, 1997). Although there were apparently earlier, probably incomplete linkages between the northern and southern American land masses during the mid-Tertiary and Early Cretaceous, these apparently had limited effect on the exchange of biotas between the land masses (Rosen, 1978).

Extensive studies of the biogeographic effects of the dynamic Panamanian corridor exist for vertebrates and plants. For land mammals, an apparently symmetrical interchange between the continents of North and South America began about 3 million years ago (Marshall *et al*., 1982), although other researchers have hypothesized a more asymmetrical movement of mammals primarily from North to South America. The movement of many groups of flowering plants (Simpson and Neff, 1985) and freshwater fishes (Bussing, 1985) was predominantly northward. Reptiles and amphibians, however, were little affected by the formation of the Panamanian land bridge (Vanzolini and Heyer, 1985), with only a few species of reptiles or amphibians utilizing it as a corridor for dispersal. Data on the avian fauna suggest that most taxa moved from North to South America across the Isthmus of Panama (Vuilleumier, 1985).

It is less clear whether or not insects show predominantly northward or southward movement through the Panamanian corridor. Halffter (1987) discussed the distribution of montane insects in Central America, hypothesizing that a number of faunal elements have contributed to the insect fauna of Central America. He noted that many of the montane insects north of the Isthmus of Tehuantepec (located in Oaxaca, Mexico) are clearly of Nearctic origin, while many insects south of the Isthmus to northern Costa Rica evolved in this “Central American Nucleus”, a geographic region which includes southern Mexico, Belize, El Salvador, Guatemala, Honduras and Nicaragua. This nucleus apparently received ancient contributions from both North and South America. In Panama and Costa Rica, the area immediately south of this Central American Nucleus, montane areas appear to have been colonized largely by taxa with phylogenetic affinities to lowland species derived primarily from South America.

Several attempts have been made to explain the biogeography of various groups of Neotropical aquatic insects (Brundin, 1966; Illies, 1969; Edmunds, 1975; Pescador and Peters, 1980; Savage, 1987; McCafferty *et al*., 1992; McCafferty, 1998; Domínguez, 1999); however, most of these studies were either very broad in scope (Brundin, 1966; Edmunds, 1975) or focused primarily on South America (Pescador and Peters, 1980; Savage, 1987; Domínguez, 1999).

The study of Domínguez (1999) is the most comprehensive and rigorous biogeographic study to date involving a cladistic analysis of mayflies. He studied the genus *Farrodes* (Ephemeroptera: Leptophlebiidae) and was able to demonstrate the existence of two distinct clades within this genus. One clade was largely endemic to Middle America and northern South America; the other was widespread in South America. Only the study of McCafferty (1998) has examined the mayfly fauna of the New World with a special emphasis on how the Middle American corridor may have affected the distribution of mayflies. One of the major conclusions of this work was that the Central American corridor has strongly favored the northward dispersal of South American genera, with relatively few North American genera having dispersed into Central and South America.

To reach his conclusions suggesting predominantly northward dispersal of mayfly taxa, McCafferty (1998) examined the overall distribution patterns of 35 New World mayfly genera, combined with limited cladistic data and deductive reasoning. Although this study was not grounded in rigorous phylogenetic hypotheses, it was the first large-scaled attempt to identify biogeographic patterns in the New World mayfly fauna, with an extensive synthesis of available data.

The research undertaken here seeks to test three hypotheses that could explain the presence of leptohyphid mayflies in North America; i.e., leptohyphid mayflies were:

(1) present only in South America before the formation of the Panamanian land bridge, and reached North America by northward dispersal of ancestors across the Panamanian land bridge; (2) present only in North America before the formation of the land bridge, with North American species as descendants of ancient Laurasian ancestors that reached South America by southward dispersal of ancestors across the Panamanian land bridge; (3) present in both North and South America before the formation of the land bridge, with species as descendants of ancient Gondwana ancestors, and with dispersal of ancestors both north and south across the land bridge. See Chapter 5, Biogeography, for discussion of the biogeography of the Leptohyphidae.

Study Group

Several facts make the family Leptohyphidae well suited for testing biogeographic hypotheses. First, the family is known only in the New World, which means there will be no confounding implications of Old World taxa. Second, species are found over large parts of both North and South America, and display a variety of distribution ranges. Third, the Leptohyphidae is a speciose group of approximately 125 described species, a sufficient number of species to test these hypotheses. Fourth, the family is a monophyletic group (McCafferty and Wang, 2000). Fifth, the adults have limited dispersal capacity, due to their very short adult life spans and the restriction of their immature stages to fresh water. These limited dispersal characters restrict their ability to quickly and extensively colonize large areas. This research also addresses taxonomic, biological, and life history issues in the family Leptohyphidae. Taxonomic issues addressed include the association of life stages, descriptions and re-descriptions of new or poorly-known species, and development of taxonomic keys for identification of larvae and adults. New biological, life history, distributional data, and notes on microhabitats are documented for numerous species. The following section summarizes pertinent information on general Leptohyphidae adult and larval morphology used in the cladistic analysis.

Morphological Overview

This section presents an overview of ephemeropteran morphology pertinent to the study. It is intended to supplement characters used in the cladistic analysis (Chapter II) and taxonomic revision (Chapter III), not as a comprehensive morphological analysis of mayfly morphology. See Kluge (2004) for an extensive and detailed analysis of ephemeropteran morphology.

Adult Morphology

Head (Figs. 1A – C)

Head well-developed in all species; mouthparts absent; compound eyes at posterolateral margin of head; three ocelli present; all female and most male species with compound eyes small and remote (Fig. 1A); some males with compound eyes enlarged (i.e. width of eye in dorsal view equal to or greater than distance between compound eyes); enlarged eyes may be entire (Fig. 1B) or divided (dioptic) (Fig. 1C); paired occipital tubercles absent or present (Fig. 1A, pot).

Thorax (Figs. 1D – G; 2A – H)

All three thoracic segments present and well-developed; coloration highly variable; mesothorax most well-developed and always with wings; anterior parapsidal suture (aps) fused to either posterior parapsidal sutures (Fig. 1D, pps), or transverse interscutal suture (Fig. 1E, tis); plumidium present (Fig. 1E, plu) or absent; metathorax with or without hind wings.

Forewings. Present on all adults, males and females; shape and venation vary among taxa and species and between males and females of the same species; venation complex, including both longitudinal and crossveins (Fig. 1F); vein CuP curved strongly towards A, meeting at, or near wing margin (Fig. 1G) or CuP not strongly curved towards A (Fig. 1F); vein iCu_2 absent (Fig. 2A), or arising from base of CuA (Fig. 1G) or CuP (Fig. 1F); vein iCu_1 absent (Fig. 2B), or forming intercalary (Fig. 2C), or arising from base of ICu_1; vein iMP arising from MP_1 (Fig. 1F), or free (Fig. 2B), or arising from CuA (Fig. 2A); vein iMP shorter than MP_2 (Fig. 1F), equal in length to MP_2, or longer than MP_2 (Fig. 2A).

Hind Wings. Present or absent; when present, costal projection (Fig. 2D, cp) present or absent; longitudinal and cross veins present or absent (Fig. 2D).

Legs. Present and well-developed on all thoracic segments; segmentation: coxa, trochanter, femur, tibia, and tarsus, composed of four or five tarsomeres and two claws (Fig. 2E); male imago foretarsal claw either dissimilar (one hooked, one blunt) (Fig. 2F) or similar (both blunt) (Fig. 2G); some species with sharp, robust setae present ventrally on male imago foretibiae (Fig. 2H).

Abdomen (Figs. 3A – H)

Abdomen well-developed, 10 segmented; coloration and patterning highly variable; two cerci and one median caudal filament present, projecting posteriorly from 10^{th} abdominal segment.

Male Genitalia. Genitalia present on abdominal segment 9; forceps present, two (Fig. 3A, fc) or three-segmented (Figs. 3B – E, fc); styliger plate (Fig. 3B, sp) with posterior margin rounded or truncate; with or without internal and/or external basal projections (Fig. 3C, ebp); penes variously modified (Figs. 3A – F, pe); penal spines present (Figs. 3A, D – E, ps) or absent (Fig. 3B – C); accessory dorsal structures present and variously modified (Figs. 3G – H, ads) or absent.

Larval Morphology

Head (Figs. 4A – F; 5A – B)

Head generally well sclerotized; two compound eyes present at posterolateral margins of head (Fig. 4A); three ocelli present between compound eyes (Fig. 4A, oce); antennae shorter than maximum width of head; dorsal surface with or without distinctive colors and/or patterns; frontoclypeal projections, when present (Fig. 4A, fcp), located at the anterolateral corner of the clypeus, visible in dorsal view; genal projections present (Fig. 4A, gp) or absent; ocellar tubercles present or absent, located at inner margin of the compound eyes (Fig. 4B, ot); median occipital tubercle, located approximately between bases of antennae, present (Fig. 4B, mot) or absent.

Mouthparts. All mouthparts present and well-developed; labrum rectangular with long, thick setae along lateral and anterior margins (Fig. 4C); labium (Fig. 4D) with glossae (gl) and paraglossae (pg) generally very reduced, with a three-segmented palp (lp); left (Fig. 4E) and right (Fig. 4F) mandibles with well-developed molar regions (mr), and inner (ii) and outer incisors (oi); maxilla (Fig. 5A) well-developed; maxillary palp (mp) varies from three-segmented to absent; distal margin (dm) with filiform setae; base of inner margin (bim) with variable setae; hypopharynx (Fig. 5B) with extensive setae along anterior margin (Fig. 5B).

Thorax (Figs. 4B; 5C – G)

All nota present and well-developed; pronotum with (Fig. 4B, pmt) or without medial tubercle, and with (Fig. 5C – D, alp) or without anterolateral projections; mesonotum with (Fig. 5C, mlp) or without mesolateral projections, and/or a medial tubercle (Fig. 4B, mmt).

Legs. Three pairs of legs present, with all segments (coxa, trochanter, femur, tibia, tarsus, and claw) present and well-developed (Figs. 5E - F), but variously modified; profemur with transverse row of variously modified setae on dorsal margin (Figs. 5E, 15A – C, H – I); mid- and hind legs with (Fig. 5F) or without longitudinal ridge (lr) and median elevated longitudinal ridge (mel); variously modified setae present or absent along inner and/or outer margins of femur, tibia, and/or tarsus (Figs. 5E – F); claws (Fig. 5G) present and well-developed on all legs, with or without submarginal denticles (smd) and/or marginal denticles (md).

Abdomen (Figs. 6A – I)

Abdomen present, well-developed, ten segmented; colors and color patterns highly variable; abdominal tubercles present (Fig. 6A, at) or absent; terga with (Fig. 6B, rpm) or without raised posterior margins; posterolateral projections of abdominal terga 7 – 8 or 7 – 9 either present and well-developed (longer than the medical length of respective terga) (Fig. 6C), weakly developed (no more than subequal to medial length of respective terga) (Fig. 6D) or absent; posterior marginal tergal spines (Fig. 6E) present or absent.

Gills. Abdominal gills absent on segments one and six or seven through ten; present on segments two through five or two through six; number of lamellae (thin, colorless plates) present on each gill variable, generally between two and eight (Fig. 6F); dorsal lamella of gill two operculate (Fig. 6G, H), variously shaped, inserted laterally or ventrally on abdominal segment two; basal beak-like process on first lamellae of operculate gill present (Fig. 6I) or absent.

CHAPTER II

CLADISTIC ANALYSIS

Methods and Data

Overview

Leptohyphid intergeneric relationships were determined cladistically. Fifty-eight (out of approximately 130 described species) representing all described leptohyphid genera, and nine outgroup species were evaluated based upon 119 morphological characters. The resulting data matrix (Table 1) was analyzed using the computer program TNT (Goloboff, 1996; 1999). The final cladogram of leptohyphid intergeneric relationships is given in Fig. 7, with all species collapsed into their respective genera, synapomorphies listed on branches leading to genera and major clades, and the two most immediate sister families to the Leptohyphidae.

Ingroup Selection Criteria

Since it was not practical, or possible, to score all species within the family Leptohyphidae for all characters, exemplar species were used. In determining which exemplar species would be used in the phylogenetic analysis, a list of selection criteria was developed. Although these were not strict criteria, they were useful in ensuring a more complete and balanced group of ingroup species. The more criteria a species satisfied, the more likely it was to be included in the analysis. The selection criteria were as follows: (1) species known from both the adult and larval stages; (2) species known to be designated as types for genera; (3) species that possess unique or apparently phylogenetically-important characters; (4) species from throughout the range of the family (to ensure the inclusion of species from North, Central, and South America and the Caribbean); (5) attempt to sample approximate equal portions of each recognized genus; (6) species available and accessible in collections.

In addition, species were more likely to be excluded from the study that fell into one or more of the following categories: (1) apparently very closely related species from same taxon; (2) poorly known species that are only known from a few specimens, or poor quality specimens; (3) specimens of species that were very difficult to obtain.

Based upon these critera, 57 ingroup species representing all 17 leptohyphid genera were selected for inclusion in the phylogenetic study. See Table 2 for a listing of all ingroup species used in the study, number of specimens studied, and associated museum depository information.

Outgroup Selection

The outgroup taxa included in the phylogenetic analysis constituted a diverse array of species selected from mayfly families found in North and South America, Africa, and southeast Asia. Unlike with the ingroup species, no specific selection criteria were developed to assist in determining what species to include as outgroups. This is because the selection of outgroup species was determined largely by the availability of specimens. Since many of the outgroup species are distributed throughout Africa and Asia, extensive collections are not readily available. Despite this limitation, it was possible to secure a good selection of outgroup species.

The monophyly of the suborder Pannota (which includes the Leptohyphidae) has been reasonably well established (McCafferty and Wang, 2000; Molineri *et al*., 2001; Molineri and Domínguez, 2003; Jacobus and McCafferty, 2006), even though its internal higher taxonomy continues to be debated. Two superfamilies are generally recognized within the suborder, Caenoidea and Ephemerelloidea (Jacobus and McCafferty, 2006). No outgroups from Caenoidea were included in the analysis, because they are far removed from the ingroup.

Ephemerelloidea contains between eight (McCafferty and Wang, 2000) and eleven families (Molineri and Domínguez, 2003; Jacobus and McCafferty, 2006), and includes Leptohyphidae, which has traditionally been placed as the most derived family within Pannota. For this study, nine species representing five of the Ephemerelloidea families were chosen as outgroups. See Table 2 for a complete list of outgroup taxa used in the study, number of specimens studied, and associated museum depository information. A listing of collection details for each outgroup species is given in Table 3.

Two outgroup species were chosen from the family Ephemerellidae, and one from the Austremerellidae. Both of these families are considered basal within the Pannota, and contain species with many apparent pleisomorphic characters (such as adult males with dioptic compound eyes). Three species were selected from the family Teloganodidae. This is a diverse family that is considered more derived than the Ephemerellidae or the Austremerellidae, but which still contains many apparent pleisomorphic characters.

The single known species from the family Coryphoridae, *Coryphorus aquilus* Peters, was also chosen as one of the outgroups. This family has only recently been recognized as a family (Molineri et al., 2001), because it possesses dissimilar propetarsal claws on the imago (as opposed to similar propretarsal claws known on all leptohyphid adults), and is considered the most closely related family to the Leptohyphidae by Molineri et al. (2001). Historically, *C. aquilus* has been placed within the family Leptohyphidae. And lastly, two species from the family Tricorythidae, were included as outgroups. Historically, this family was considered sister to Leptohyphidae, although it is now considered sister to the Coryphoridae by Molineri et al. (2001). Both of these families contain many highly specialized species with few plesiomorphies, which limits their usefulness in polarizing characters. However, because of their uncertain sister relationships to the Leptohyphidae, their presence in the analysis was considered important.

Computational Analysis

A cladistic analysis of the data matrix (Table 1) was used to estimate phylogenetic relationships within Leptohyphidae. No *a priori* weighing or ordering of character states was used. Ten thousand random addition sequences followed by TBR branch-swapping using the computer program TNT (Goloboff, 1996; 1999) were used to generate tree sets. Searches were also conducted using various options of combinations such as sectorial searches, ratchet, drift, and tree fusing (Goloboff, 1999). These options are often used with large data sets to reduce search times and improve the probability of finding shorter tree sets. Clade robustness was assessed using boot-strap, jackknife, and

Bremer support values. In order to calculate Bremer support values using TNT, suboptimal trees are calculated in consecutive stages, each stage retaining 1000 trees. Suboptimal trees were calculated at 5, 10, 20, 50, 100, and 200 steps suboptimal. Bremer support values are then determined from these suboptimal tree sets. Boot-strap and jackknife values were calculated using the 10,000 random addition sequences of the new technology search.

Two equally parsiminious cladograms of 800 steps each resulted from the analysis. The final cladogram with synapomorphies displayed on nodes and species collapsed into their respective genera is shown in Figure 7. See the "Cladistic Results" section, which follows the character discussions, for a detailed discussion concerning the construction and justification of the final cladogram. It is presented here because it is referenced in several of the character discussions below.

Characters

Investigations utilized comparative morphological techniques of both adults and larvae to explore characters and patterns of character distribution among species and clades. Traditional and previously unexplored character systems were used in the analysis. See Table 4 for a brief synopsis of all characters used in the analysis.

The 119 characters used in the cladistic analysis consisted of 63 multistate characters and 55 binary characters. Binary characters have the plesiomorphic state coded "0" and derived state coded "1", based upon the final cladogram given in Figure 7. Noncomparable and missing characters were both assigned a "?" entry in the data matrix. All character states were treated as unordered and equally weighted. The characters, their associated character states based upon mapping on the final cladogram (Figure 7), and results of the character analysis are discussed below. Characters are grouped below according to major body region and subregion. Each character treatment is composed of four sections: (1) the character number and name, (2) a brief description of each character state, (3) when needed, a "Comments" section containing notes and discussion pertinent to the character and its associated states, and (4) a "Results" section that contains postanalysis assessments of character state interpretations and distributions.

Adult Characters (Characters 0-34)

Head (Characters 0 – 1)

Character 0: *Compound eyes of male*.

(0) large (Fig. 1B) and dioptic (Fig. 1C);

(1) large (Fig. 1B), not dioptic (Fig. 1B);

(2) small (Fig. 1A), not dioptic.

Comments: Compound eyes are considered large when the width of the eye (in dorsal view) is equal to or greater than distance between the eyes (Fig. 1B); eyes are considered small and remote when the width of one compound eye is less than the distance between the two compound eyes.

Results: State (0) is the ancestral state and is present in the majority of the outgroups, including the six most basal taxa, and it persists into the two most basal leptohyphid genera, *Leptohyphodes* and *Amanahyphes*. Character states (1) and (2) first appear in the sister families Coryphoridae and Tricorythidae, and almost all leptohyphid taxa possess state (2). An apparent reversal to state (1) from state (0) occurs in three closely-related species in the highly-derived genus *Tricorythodes.*

Character 1: *Paired occipital tubercles*.

(0) absent;

(1) present, small, weakly developed (basal width approximately equal to height) (Fig. 1A);

(2) present, large and distinct (height approximately twice basal width).

Comment: When present, one pair of occipital tubercles is located on the vertex of the head between the lateral ocelli.

Results: States (1) and (2) are absent in all outgroups and most of the basal leptohyphid genera. State (1) is present in the genus *Lumahyphes,* in all known adult *Leptohyphes*, and in all known adults of the subgenus *Tricorythodes* (*Tricorythodes*). State (1) appears to have been independently derived in these three lineages. State (2) is also present and a synapomorphy of the subgenus *Tricorythodes* (*Asioplax*). It is unclear if State (2) is an independently-evolved character state, or simply a modification of Character State (1), because two equally-parsimonious solutions exist to explain its presence. The first hypothesis is that the transformation from state (0) to state (1) occurred leading to the genus *Tricorythodes*, staying as state (1) in the subgenus *Tricorythodes* (*Tricorythodes*), with state (1) transforming to state (2) in the subgenus *Tricorythodes* (*Asioplax*). A second explanation is that state (0) could have transformed to state (1) in the subgenus *Tricorythodes* (*Tricorythodes*), and directly from state (0) to state (2) in subgenus *Tricorythodes* (*Asioplax*).

Thorax (Characters 2 – 3)

Character 2: *Fusion of anterior and posterior parapsidal sutures*.

(0) anterior parapsidal suture (aps) fused with transverse interscutal suture (tis) (Fig. 1E);

(1) anterior parapsidal suture (aps) fused with posterior parapsidal suture (pps) (Fig. 1D).

Comment: These sutures are present on the dorsum of the mesonotum.

Results: State (1) is present only in the genera *Vacupernius* and *Tricorythodes*. Two possibilities exist to explain the transition from state (0) to state (1). First, state (1) could have first appeared at Node 10 (Fig. 7), then been lost in the genus *Tricorythopsis*. Or second, state (1) could have evolved independently in the genera *Vacupernius* and *Tricorythodes*, and never have been present in the genus *Tricorythopsis*. Both hypotheses require the same number of steps. Additional research into the musculature associated with the thorax and flight may help to determine the proper polarity for this character in the Leptohyphidae.

Character 3: *Plumidium*.

(0) absent (Fig. 1D);

(1) present (Fig. 1E).

Comments: The plumidium is a small, fleshy structure extending from the posterior of the metathorax. The function, if any, of the plumidium is unclear. It could represent non-functioning remnants of part of the hind wing, or it could be used in flight in a manner analogous to the halters in Diptera.

Results: The plumidium is absent in all but one outgroup (*Dicercomyzon costale*, Family Tricorythidae), and in the genus *Haplohyphes* and subgenus *Tricorythodes* (*Tricorythodes*), where it has apparently been lost. It is present in all other leptohyphid genera. State (1) has evidently been gained at least twice (in the families Tricorythidae and Leptohyphidae), but lost multiple times.

Legs (Characters 4 – 9)

Character 4: *Male imago propretarsal claw*.

(0) dissimilar (one hooked, one blunt) (Fig. 2F);

(1) similar (both blunt) (Fig. 2G).

Comments: This character must be examined in the male imago, not the subimago. In the family Leptohyphidae, subimago males exhibit state (0), while imago males exhibit state (1).

Results: State (1) is a synapomorphy for the family Leptohyphidae.

Character 5: *Tarsal segmentation*.

(0) four segmented;

(1) five segmented.

Results: Four-segmented tarsi are apparently ancestral, with five-segmented tarsi uncommon in the outgroups. Within the Leptohyphidae, a gain to five segmented tarsi has occurred independently in the basal genus *Leptohyphodes* and the derived genus *Tricorythodes*.

Character 6: *Male protarsus/protibia ratio (ppt).*

(0) tarsus longer than tibia [ppt >1.25];

(1) tarsus two-thirds to three-quarters length of protibia [.65 < ppt < .75];

(2) approximately one-half length of protibia [.45 < ppt < .55];

(3) tarsus and tibia approximately equal in length [0.95 < ppt < 1.05].

Results: Some of the outgroups could not be scored for this character due to missing forelegs and unknown adult stages, making the results difficult to interpret; however, state (0) appears to be the plesiomorphic condition since it occurs in the two most basal outgroups. State (2) is present in all known adult leptohyphid species, except *Tricorythopsis* and *Tricorythodes*. Most species of *Tricorythopsis* possess state (1), and a few state (2). Within the genus *Tricorythodes*, states (1), (2), and (3) are present, with state (2) the most common. This appears to be a character in which reversals and/or independent gains are common.

Character 7: *Male metafemur/(metatibia plus metatarsus) ratio (mmm).*

(0) metafemur approximately equal in length to metatibia plus metatarsus [.90 < mmm < 1.10];

(1) metafemur much shorter than metatibia plus metatarsus combined [mmm <.85].

Results: The basal state of this character could not be determined with confidence, because states (0) and (1) are both present in the outgroups, and four out of the nine outgroup species could not be scored due to missing legs or unknown adult stage. State (1) is present in all known leptohyphid adults, except *Vacupernius* (a single known species) and *Tricorythodes*, where the majority of species possess state (0).

Character 8: *Male, protibia, setae.*

(0) absent;

(1) present (Fig. 2H).

Comments: When present, these robust and sharply-pointed setae are located ventrally on the male protibia. This character is visible in both subimagos and imagos.

Results: State (1) is a synapomorphy for the genus *Leptohyphes*.

Character 9: *Male metatarsus/metatibia ratio (mmr).*

(0) metatarsus ca. one-third length of metatibia [mmr = .33];

(1) metatarsus ca. one-half to two-thirds length of metatibia [.50 < mmr < .66].

Results: State (0) is present in most outgroups and the majority of ingroup species. State (1) is a synapomorphy of Node 10 (Fig. 7) leading to the three most derived genera in the family (*Vacupernius, Tricorythopsis* and *Tricorythodes*). Within *Tricorythodes*, a few species have reverted to state (0).

Forewings (Characters 10-16)

Character 10: *Imago, hind margin fringe.*

(0) absent;

(1) present, extensive (covering posterior wing margin);

(2) present, restricted (confined to anal margin).

Comments: When present, a fringe of hair-like setae can be found along the posterior margin of the wing.

Results: State (2) is a synapomorphy of the genus *Haplohyphes.* State (0) is present in all outgroups except the Tricorythidae and Coryphoridae, where state (1) first appears. State (1) is then present in all known adult leptohyphid species, except for the genus *Haplohyphes*. A reversion to state (0) occurs in a small group of closely-related species of *Leptohyphes*.

Character 11: *iMP/MP$_2$ ratio.*

(0) iMP shorter than MP_2 (Fig. 1F);

(1) iMP equal in length to MP_2;

(2) iMP longer than MP_2 (Fig. 2A).

Results: State (0) is present in all outgroups and almost all species of Leptohyphidae. State (1) is very rare within the Leptohyphidae, only being found in three species in different genera, one each in *Amanahyphes*, *Lumahyphes*, and *Vacupernius*. State (2) is a synapomorphy of the genus *Tricorythopsis.*

Character 12: *Male, configuration of CuP and A.*

(0) CuP not curved sharply towards A (Fig. 1F);

(1) CuP strongly curved towards A (Fig 1G);

(2) CuP extremely reduced, much shorter than A, or absent (Fig. 8A).

Comments: This can be a difficult character to score because states (0) and (1) can be found in different genders of the same species, requiring that only one gender be used. Character state (1) will often occur in females of a species, but not in the males. Only male imagos were used to score this characters.

Results: State (1) is a synapomorphy of the genus *Haplohyphes*; however, it is also present in a few species in the genera *Traverhyphes* and *Allenhyphes*. State (2) is present, but rare, in the genus *Tricorythodes*. State (0) is present in all outgroup, and most ingroup species

Character 13: V*ein iCu$_1$*.

(0) present, arising from base of CuA (Fig 1G);

(1) present, arising from base of CuP (Fig. 1F);

(2) absent (Fig. 2B).

Results: State (0) is clearly the ancestral state. State (1) first appears in the Tricorythidae, and is found in the vast majority of leptohyphid species. A reversal to state (0) occurs in a number of species of *Leptohyphes*, at least two species of *Traverhyphes*, and one *Tricorythodes*. State (2) is a synapomorphy of the outgroup species *Coryphorus aquilus* (Family Coryphoridae).

Character 14: *Vein iCu$_2$*.

(0) present, forming short intercalary vein (Fig. 2C);

(1) present, arising from base of iCu$_1$ (Fig. 1F);

(2) vein presentand well-developed, but not connected to iCu$_1$ (Fig. 2A, 8A);

(3) absent (Fig. 2B).

Results: This was a highly-variable character, with states (0), (1) and (2) all present in the outgroups. However, state (0) is apparently the primitive state, because it is the most common and present in the most primative outgroup species. This character appears to have only limited phylogenetic information, with the exception of state (3), which is a unique synapomorphy for the sister family Coryphoridae.

Character 15: *Vein iMP*.

(0) arising from MP_1 (Fig. 1F);

(1) base free, not connected to MP_1 (Fig. 2B);

(2) arising from CuA (Fig. 2A).

Results: Character state (2) is a synapomorphy of the genus *Tricorythopsis*. Character state (0) is present in almost all species of Leptohyphidae, and most of the outgroups. Character state (1) is apparently a rare condition that evolved in parallel in five different species from five different genera, including one of the outgroup species.

Character 16: *Marginal intercalaries*.

(0) present (Fig. 2C);

(1) absent (Fig. 1F).

Comments: When present, these are small, usually single (infrequently paired) veins along the posterior margin of the forewing.

Results: Marginal intercalaries are present in all outgroups, except the for the outgroup families Tricorythidae and Coryphoridae. These veins are also absent in all known leptohyphid adults. State (1) is a synapomorphy of the Tricorythidae + Leptohyphidae.

Imago, Hind Wing (Characters 17-22)

Character 17: *Male, presence/absence*.

(0) present;

(1) absent.

Results: This character has an unusual distribution. State (0) is present in the basal outgroups, with loss of the hind wing (state 1) found in the sister families Tricorythidae and Coryphoridae. State (1) persists into the two most basal leptohyphid genera *Leptohyphodes* and *Amanahyphes*. The hind wing then re-appears and is present in all known species of the genera *Haplohyphes, Leptohyphes*, *Vacupernius*, and all genera in the *Traverhyphes* genera group. The hind wing is then lost again (state 1) in all known species of the genera *Tricorythopsis* and *Tricorythodes*. This is unusual in that there is a sequential loss-gain-loss of the hind wing.

Character 18: *Male, costal projection*.

(0) present, small and blunt (Fig. 8B);

(1) present, elongate (Fig. 2D);

(2) absent.

Results: Costal projections are either absent in the outgroups or are small and blunt. All species of Leptohyphidae which have a hind wing also have an elongate costal projection (*Haplohyphes, Leptohyphes*, *Vacupernius*, *Allenhyphes, Yaurina, Lumahyphes*, and *Traverhyphes*).

Character 19: *Female, presence/absence*.

(0) present;

(1) absent.

Results: Hind wings are present in females of all outgroups except those of the family Tricorythidae and Coryphoridae, the ingroup genus *Haplohyphes*, and in two species of *Leptohyphes*. In all other leptohyphid species, hind wings are absent in females. There are several equally parsimonious solutions that explain this stated distribution, each of which posits wing regains occurring at some point.

Character 20: *Posterior margin (imago).*

(0) not fringed with fine hairs;

(1) fringed with fine hairs.

Results: All known leptohyphid adults with hind wings also possess fine hairs along the posterior margin of the wing (state 1). State (1) is also present in one of the outgroups, Austremerellidae, where it is interpreted a parallel gain. State (0) is clearly the plesiomorphic condition, characterizing the most basal outgroup species.

Character 21: *Longitudinal veins*.

(0) present (Fig. 2D);

(1) absent.

Results: Longitudinal veins are present in hind wings of all outgroups which have hind wings. Almost all species of Leptohyphidae which have hind wings also have longitudinal veins associated with the hind wings. Only one species within the genus *Allenhyphes* lacks veins.

Character 22: *Number of longitudinal veins*.

(0) 4 or more;

(1) 3;

(2) 2.

Comments: The homology of longitudinal hind wing veins in leptohyphid mayflies is unclear. There has obviously been extensive loss of these veins as compared to the outgroups, in which homologies among remaining veins can often be traced. However, in leptohyphids, a lack of any clear venitational features in the hind wings (such as crossveins or vein fusions) prevents determining homologies of the remaining veins with confidence. Because of this fact, states for this character are recorded as simple counts, with no attempt to determine what homologies might exist among the remaining veins.

Results: The vast majority (>95%) of species within Leptohyphidae that have hind wings also have either two or three longitudinal veins. The outgroup species with hind wings generally have more than four veins. The apparent trend within the evolution of this character in the Leptohyphidae is a reduction in the number of veins.

Male Genitalia (Characters 23-34)

Character 23: *Number of forceps segments*.

(0) 3-segmented (Fig. 3B – E);

(1) 2-segmented (Fig. 3A).

Comment: Forceps are always present in males and are usually three-segmented. It is unclear if one of the segments has been lost or is fused with another segment. There are no morphological features such as spines on specific segments that might indicate which segment is no longer present. As a result, the two character states are simple counts, with no implications as to which segment is no longer present, or if it has been lost of fused. Additional research into the musculature associated with the forceps may help to determine the proper polarity this character in the Leptohyphidae.

Results: The basal condition is clearly state (0), and is present in all outgroups species, except in the sister families Tricorythidae + Coryphoridae, where state (1) is present. State (1) persists into the family Leptohyphidae, and is present in all known species of its three most basal genera, *Leptohyphodes, Amanahyphes*, and *Haplohyphes*. Three-segmented forceps (state 0) are present in all remaining species of Leptohyphidae, except for the genus *Tricorythopsis*, where all known species possess state (1), which could represent a reversal or independent change to state (1).

Character 24: *Basal swelling of second forceps segment*.

(0) absent (Fig. 3A, 3C – E);

(1) present (Fig. 3B).

Results: The presence of the basal swelling, state (1), is a unique synapomorphy of the genus *Tricorythodes*. One species, *Tricorythodes australis*, has evidently lost the basal swelling.

Character 25: *First forceps segment*.

(0) shorter than second segment;

(1) longer than second segment;

(2) equal in length to second segment.

Results: State (0) is clearly the plesiomorphic condition, and is present in almost all outgroups, and in the majority of leptohyphid species as well. State (1) is very rare, known only from one outgroup and one ingroup species. State (2) has evidently evolved in parallel among ingroup species, where it is present in the genus *Haplohyphes* and the vast majority of *Tricorythopsis* and *Tricorythodes* species. Within *Tricorythodes*, there have been some reversals to state (0).

Character 26: *Shape of posterior margin of styliger plate.*

(0) convex (Fig. 3D);

(1) concave (Fig. 3B);

(2) truncate (Fig. 3A);

(3) deeply concave (Fig. 8A).

Results: This is a highly variable character among a number of different species and clades. State (0) occurs in all known adults of *Leptohyphes*, and state (1) occurs in all known adult species of *Tricorythodes*. However, states (0) and (1) also occur in other species in multiple genera.

Character 27: *Internal basal projection of styliger plate*.

(0) absent (Fig. 3B);

(1) present, acute (Fig. 3E);

(2) present, rounded (Fig. 3C).

Comments: This character refers to the paired projections located at the internal lateral margins of the styliger plate.

Results: Character state (1) is considered a synapomorphy in the *Traverhyphes* genera group, with subsequent loss of the projections in one species of the genus *Allenhyphes*. Character state (2) is present on a few species within the genus *Traverhyphes*.

Character 28: *Fusion of penes.*

(0) fused for approximately three-fourths the length or more (Fig. 3B – C, E);

(1) fused for one-half the length (Fig. 3D).

Results: State (1) is a synapomorphy of the genus *Leptohyphes*; but, it has also arisen in parallel in a single species in three other genera.

Character 29: *Penes width*.

(0) widest at apex (Fig. 3D);

(1) widest at middle (Fig. 8C);

(2) widest at base (Fig. 3B);

(3) similar for entire length (Fig. 3A).

Results: The plesiomorphic state for this character appears to be state (0), where it is most common among the outgroups, but states (1) and (3) are also present among the outgroups. Within the Leptohyphidae, state (3) is most common among the basal clades (*Amanahyphes, Traverhyphes* genera group), and an apparent reversal to state (0) occurs in the genera *Leptohyphes* and *Vacupernius*. State (2) is a unique and unshared synapomorphy of Node 11 (Fig. 7), leading to the sister genera *Tricorythopsis* and *Tricorythodes.*

Character 30: *Penal spines*.

(0) absent (Fig 2B – C);

(1) present (Fig. 3A, D – E).

Comments: Penal spines, when present, are located at, or near, the terminal end of the penes.

Results: Character state (1) represents a unique, unshared synapomorphy at node 4 (Fig. 7). Within Leptohyphidae, penal spines have been lost in the sister genera *Allenhyphes* and *Yaurina* (Node 8), and at Node 11 (Fig. 7) leading to the sister genera *Tricorythopsis* and *Tricorythodes.*

Character 31: *Penal spines position*.

(0) spines positioned on outer apical margin of penes, projecting posteriorly (Fig. 3A, D);

(1) spines positioned laterally on pens, extending anteriodorsally (Fig. 3E);

(2) spines positioned dorsally on penes, projecting anteriorly (Fig. 3G, 8C).

Results: State (0) represents the plesiomorphic condition and is present in the genera *Haplohyphes* and *Leptohyphes*, which are the two most basal genera among genera in which penal spines are present. State (1) is a synapomorphy of the genus *Lumahyphes*, and state (2) is independently-derived for the genera *Traverhyphes* and *Vacupernius*, and represents a synapomorphy of these two genera.

Character 32: *Accessory dorsal structure*.

(0) absent;

(1) present (Fig. 3G – H, ads).

Results: The presence of an accessory dorsal structure is a synapomorphy of the *Traverhyphes* genera group, with subsequent loss at Node 8 (Fig. 7) leading to the sister genera *Allenhyphes* and *Yaurina*.

Character 33: *Outer longitudinal processes of penes*.

(0) absent;

(1) present (Fig. 8D).

Comments: The outer longitudinal process of the penes is a pair of long spine-like appendages on the ventral side of penes.

Results: State (1) is a synapomorphy of the genus *Yaurina*.

Character 34: *Median caudal filament spine*.

(0) absent.

(1) present (Fig. 8E, mcf).

Comments: State (1) is a small, ventrally directed spine near the base of the median caudal filament, present only in males. It is probably used in some fashion to hold the female during copulation.

Results: State (1) is a synapomorphy of the genus *Allenhyphes*.

Larval Characters (Characters 35-117)

Head (Characters 35 – 38)

Character 35: *Frontoclypeal projections*.

(0) present, length more than three times width at base (Fig. 9A);

(1) absent;

(2) present, length of projection approximately equal to width at base (Fig. 4A).

Comments: When present, these projections are located at the anterolateral corners of the clypeus and are visible in dorsal view.

Results: The ancestral state (0) is present in the two most basal outgroups. All remaining outgroups and the vast majority of leptohyphids lack these projections (state 1). State (2) is a synapomorphy of the genus *Haplohyphes*. However, state (2) has also evolved in parallel in a group of three closely-related species in the genus *Tricorythodes.* These three species (*popayanicus, condylus,* and *primus*) were previously placed in the genus *Tricoryhyphes* (Wiersema and McCafferty, 2000), based upon this character (among others). The current analysis clearly shows *Tricoryhyphes* to be nested within *Tricorythodes*. Molineri (2002), in his analysis of the South American species of *Tricorythodes*, also showed *Tricoryhyphes* to be nested within *Tricorythodes.*

Character 36: *Genal projections*.

(0) absent;

(1) present (Fig. 4A).

Comments: When present, these projections are located at the antero-lateral margin of the head, in front of the compound eyes.

Results: Genal projections are absent in all outgroups and almost all species of Leptohyphidae (state 0). State (1) is a synapomorphy of the genus *Haplohyphes*. State (1) has also evolved elsewhere in parallel; it is present in the most basal species of *Leptohyphes*, and in the three species of *Tricorythodes* previously placed in the genus *Tricoryhyphes* (see the discussion of this genus in the "Results" section of Character 35).

Character 37: *Ocellar tubercles*.

(0) absent;

(1) present (Fig. 4B).

Comments: When present, these small to moderate sized tubercles are located at the inner margin of the compound eyes.

Results: State (1) has evolved in parallel in two leptohyphid genera (*Leptohyphes* and *Tricorythodes*), and is considered a synapomorphy of the genus *Coryphorus* (Family Coryphoridae).

Character 38: *Median occipital tubercle*.

(0) absent;

(1) present (Fig. 4B).

Comments: State (1) is a small tubercle located approximately between bases of antennae.

Results: State (1) has evolved in parallel in the outgroup species *Coryphorus aquilus* (Family Coryphoridae), and the ingroup species *Tricorythodes bullus*. State (1) is a synapomorphy of the Family Coryphoridae.

Mouthparts (Characters 39 – 59)

Character 39: *Setae along dorsal margin of labrum*.

(0) branched (Fig. 9B);

(1) unbranched (Fig. 9C);

(2) absent.

Results: All states of this character appeared in the outgroups, making a determination of character polarity extremely difficult. State (1) is present in most of the outgroups, but state (0) is present in the most basal outgroup. The trend appears to be the presence of unbranched setae in the more basal clades (such as *Leptohyphes* and *Haplohyphes*), and the presence of branched setae (state 0) in the more derived groups such as *Tricorythodes*. However, various gains and losses in this character appear to have occurred throughout the Leptohyphidae. This character appears to hold little useful phylogenetic information and much homoplasy.

Character 40: *Anteromedian emargination of labrum (ael), length to width ratio.*

(0) shallow, only slightly recessed (ael ≥ 0.95) (Fig. 4C);

(1) deeply recessed (ael < 0.95) (Fig. 9D).

Comment: The value ael is determined by dividing the length of the labrum at the middle from the anterior to the posterior margin (y) by the maximum width of the labrum at its widest point (x) (Fig. 9D).

Results: The ancestral state (0) is shared by the majority of leptohyphid species. A deep recession, state (1), occurs in a variety of taxa in several different genera. A reversal to state (0) appears to have occurred in the genus *Leptohyphes*, some *Tricorythodes*, the genus *Tricorythopsis*, and a few other species. This character appears to hold little useful phylogenetic information.

Character 41: *Postmentum, length to width ratio (plw).*

(0) Broad (plw > 1.75) (Fig. 4D);

(1) Narrow (plw between 1.0 and 1.50) (Fig. 9E);

(2) Extremely narrow (plw < 1.0) (Fig. 9F).

Comments: The value of plw = maximum length of postmentum from the anterior to the posterior margin (x) / maximum width of the postmentum (y) (Fig. 9E).

Results: Character state (1) is a synapomorphy of the genus *Haplohyphes*.

Character 42: *Branched setae along lateral margin of postmentum.*

(0) absent;

(1) present.

Results: State (1) is an autapomorphy for three terminal taxa of *Tricorythodes* and one outgroup taxon. In this analysis, this character does not provide any phylogenetic information for the evolution of multispecies clades within the family Leptohyphidae.

Character 43. *Glossae and paraglossae, fusion ratio (gpf).*

(0) fused for approximately 90% their length (gpf ca. = .90) (Fig. 4D);

(1) fused for < ¾ their length (gpf < 0.75) (Fig. 9G);

(2) highly fused (gpf ca. = .95) (Fig. 10A);

(3) completely fused (gpf = 1) (Fig. 9F).

Comments: The value gpf equals length x divided by length y, where x = distance from fusion point of glossae to the anterior margin of the prementum, and y = distance from the apical margin of the paraglossae to the anterior margin of the prementum (Fig. 9G).

Results: The vast majority of ingroup taxa possess state (0). State (2) is a synapomorphy of the genus *Yaurina* and also occurs in one species of *Tricorythodes*. State (3) occurs in the outgroup sister families Tricorythidae and Coryphoridae.

Character 44: *Paraglossa and glossa, length ratio (pgr).*

(0) paraglossa subequal to glossa (pgr < 0.98) (Fig. 4D);

(1) paraglossae projects beyond glossae (pgr > 1.1) (Fig. 10B).

Comment: The glossae and paraglossae are extremely reduced in all species of Leptohyphidae and generally project to the same level; however, in some species the paraglossae project well above the level of the glossae. The value pgr was determined by measuring the straight line distance from the most anterior point of the paraglossa to the anterior margin of the postmentum / straight line distance from the most anterior point of the glossa to the anterior margin of the postmentum (Fig. 10B). This margin is normally horizontal, but in some instances it was curved. Where the margin was curved, a horizonal line was projected from the center of the anterior margin of the submentum and used as the reference point for both measurements (Fig. 10B).

Results: Character state (1) is an autapomorphy for two terminal taxa (*Leptohyphes cornutus* and *Tricorythodes bullus*). In this analysis, this character does not provide any phylogenetic information for the evolution of multispecies clades within the family Leptohyphidae.

Character 45: *Labial palps, ratio of segment one to segments two and three (lpr).*

(0) lpr < 3 (Fig. 4D);

(1) lpr > 5 (Fig. 9E).

Comment: The labial palps are 3-segmented in all known leptohyphids. The value lpr was determined by measuring the length of palp one and dividing by the combined length of segments two and three.

Results: State (1) is a synapomorphy of the ingroup genus *Haplohyphes* and the outgroup genus *Coryphorus* (Family Coryphoridae).

Character 46: *Left mandible, number of outer incisor denticles*.

(0) ≥ four denticles (Fig. 4E);

(1) three denticles;

(2) two denticles;

(3) one denticle.

Results: Reduction in the number of denticles, from the ancestral state of four to three or less, is common throughout genera and species in the Leptohyphidae. These reductions have occurred in parallel among species, with some species showing a reversal from three to four denticles. There appears to be only limited phylogenetic signal in this character, and extensive homoplasy.

Character 47: *Left mandible, number of inner incisor denticles*.

(0) two denticles (Fig. 4E);

(1) one denticle;

(2) three denticles.

Results: The ancestral state, state (0), is present in the vast majority of leptohyphid species. Reduction in the number of denticles has occurred independently in several *Leptohyphes* species. State (1) occurs in the family Tricorythidae, in at least two species of *Leptohyphes*, and in three closely-related genera (*Leptohyphodes, Coryphorus, Amanahyphes*). This character contains extensive homoplasy and does not appear to be useful for determining higher-level relationships within the Leptohyphidae.

Character 48: *Left mandible, prostheca*.

(0) present (Fig. 4E);

(1) absent.

Results: All species of Leptohyphidae examined in this study possessed the left mandible prostheca; however, it was absent in two of the outgroup species.

Character 49: *Right mandible, number of outer incisor denticles*.

(0) 3 denticles (Fig. 4F);

(1) 2 denticles;

(2) 1 denticle;

(3) ≥ four denticles.

Result: State (0) represents the ancestral state of three denticles, the condition possessed by the vast majority of leptohyphid species. Reduction from three to two denticles occurs in several terminal taxa in various clades. State (3) occurs in one species of *Leptohyphes*, one species of *Allenhyphes*, and in several of the outgroup taxa. The large amount of homoplasy in this character results in little useful phylogenetic information for the evolution of clades within the Leptohyphidae.

Character 50: *Right mandible, number of inner incisor denticles*.

(0) 1 denticle;

(1) 2 denticles (Fig. 4F);

(2) 3 denticles.

Results: A gain from the ancestral state of one denticle (state 0) to two or three denticles occurs independently at least seven times in terminal leptohyphid taxa. Because these changes are all in terminal taxa, no useful higher phylogenetic information is contained in this character for the examined taxa.

Character 51: *Right mandible, prostheca*.

(0) present;

(1) absent.

Result: State (1) occurs as an autaupmorphy in two terminal ingroup and two outgroup taxa, and does not provide any useful phylogenetic information for interspecific relationships within the family Leptohyphidae.

Character 52: *Right mandible, setae of prostheca*.

(0) present;

(1) absent.

Results: State (1) occurs as an autaupmorphy in four terminal ingroup taxa (one *Haplohyphes* and three *Leptohyphes*). It does not provide useful phylogenetic information for higher-level relationships.

Character 53: *Mandibles, setae along outer margin*.

(0) few (< 10), short, filiform setae or no setae (Fig. 4E, F);

(1) approximately 10-15 extremely long, elongate setae (Fig. 10C);

(2) many (> 20) filiform or elongate setae (Fig. 10D).

Results: State (0) occurs in the vast majority of ingroup and outgroup taxa. State (1) occurs in three sister species of the genus *Tricorythodes* that were previously placed in the genus *Tricoryhyphes* (see discussion in "Results" section of Character 35). Character State (2) occurs in one outgroup and rarely among the genus *Tricorythodes*.

Character 54: *Maxillary palp segmentation*.

(0) 3-segmented (Fig. 5A);

(1) 2-segmented (Fig. 10D);

(2) 1-segmented (Fig. 10E);

(3) absent, although terminal seta may be present (Fig. 10F).

Comments: Although it would be preferrable to code the states of this character as gains or losses of individual palpomeres, it is not possible at this point to determine which segments have been gained or lost. There are no apparent distinguishing morphological features on individual segments, which could be used to identify a lost or gain at a particular segment. Future research on the internal structure of the maxillary palp may help to determine individual segments that have been lost or gained.

Results: The large amount of homoplasy in this character results in little useful phylogenetic information for inferring clades within the Leptohyphidae. State (0) is apparently the basal condition, with segments being gained, lost, and perhaps fused, in numerous taxa and clades. Although the number of maxillary palpomeres is highly variable among species of *Tricorythodes* (varying from zero to three segments), all known species of *Leptohyphes* have three-segmented palps.

Character 55: *Maxillary palp, terminal seta*.

(0) absent (Fig. 5A);

(1) present (Fig. 10E – F).

Comment: When present, this seta is located at proximal end of the terminal maxillary palp.

Results: State (0) is apparently the ancestral state, with state (1) being present in some outgroup taxa and the genus *Haplohyphes*. State (1) is also present in numerous ingroup genera. The character apparently has been either gained and lost multiple times, or has arisen in parallel among several clades, or perhaps some combination of the two. There are numerous equally-parsimonious solutions for this character. Because of the high amount of homoplasy present in this character, little useful phylogenetic information can be deduced from it concerning relationships among clades within the Leptohyphidae.

Character 56: *Maxillary palp, lateral palp setae*.

(0) absent on palpomeres one and two;

(1) present on palpomere one (basal) only;

(2) present on palpomere two only;

(3) present on palpomeres one and two.

Results: Lateral palpomere setae are found in five terminal taxa (three ingroup and two outgroup). All state transitions for this character are autapomorphies of terminal taxa and do not provide any phylogenetic information concerning interspecific relationships. In addition, it is unclear which state represents the basal state.

Character 57: *Galea, number of long, curved filiform setae on distal margin*.

(0) setae absent (Fig. 10G);

(1) 1 to < 20 setae (Fig. 10F);

(2) 20 to 60 setae (Fig. 5A);

(3) > 100 setae (Fig. 10H).

Results: Because of the extensive homoplasy present in this character, it was not possible to determine a root state for this character. All states are present in the outgroups. Thus, the usefulness of this character in determine relationships among clades is very limited. There appear to be several reversals and independent multiple gains for different states of this character within the examined species.

Character 58: *Fusion between galea and lacinia.*

(0) present, extends greater than three-fourths length of maxilla (Fig. 5A);

(1) absent or extremely reduced, extending less than one-fourths of maxilla (Fig. 10E, F).

Results: The root state appears to be state (0), which is present in the most basal outgroups. State (1) occurs in several of the outgroups. Reduction of the suture (state 1) apparently occured in an ancestor basal to the Tricorythidae and continued into the Coryphoridae. Within the Leptohyphidae, a reversal (or perhaps an independent parallel gain) to state (0) occurs at Node 3 (Fig. 7) and the genera *Leptohyphes* and *Tricorythopsis*. State (0) is considered a synapomorphy for these three clades.

Character 59: *Maxilla, setae at base of inner margin.*

(0) one or two setae present (Fig. 10E);

(1) ≥ 3 setae present (Fig. 5A);

(2) setae absent.

Results: The root state is clearly state (0), which is present in all outgroups except Tricorythidae where state (2) is present. State (0) is also present in multiple terminal taxa from several genera within the Leptohyphidae, while state (1) is the most common character state. This character contains extensive homoplasy thus, its usefulness in determining phylogenetic relationships among clades is very limited.

Thorax (Characters 60 – 88)

Character 60: *Pronotum, medial tubercles;*

(0) absent;

(1) present (Fig. 4B, pmt).

Comments: When present, these tubercles are located near the mid-line of pronotum.

Results: This character provides no phylogenetic information because its derived state is present only as an autapomorphy in three different terminal ingroup taxa.

Character 61: *Pronotum, antero-lateral projections.*

(0) absent;

(1) present (Fig. 5C, D, alp).

Results: State (1) is present as an autapomorphy in one outgroup taxon and several ingroup terminal taxa. It appears to have developed in parallel among the different taxa where it is present. There is apparently no phylogenetic signal in this character for determing higher-level relationships within the Leptohyphidae.

Character 62: *Mesonotum, anterolateral tubercles.*

(0) absent;

(1) present (Fig. 5C, mlp).

Comments: When present, these tubercles are located at the anterior-lateral margins of the mesonotum.

Results: State (1) is absent in all outgroup taxa and present in five terminal taxa within the Leptohyphidae, where it has apparently evolved independently in each case. There is no useful phylogenetic signal in this character for assessing higher-level relationships amont the examined species of Leptohyphidae.

Character 63: M*esonoum, median tubercle.*

(0) absent;

(1) present, located near posterior margin of mesonotum;

(2) present, located near anterior margin of mesonotum (Fig. 4B, mmt).

Results: States (1) and (2) are derived independently as autapomorphies in three ingroup species. This character does not provide any support for higher-level relationships within the Leptohyphidae.

Character 64: *Proleg, femoral length/width ratio.*

(0) expanded (length 1.75x to 2.50x width) (Fig. 5E);

(1) greatly expanded (length 0.75x to 1.50x width) (Fig. 11A);

(2) narrow (length 2.75x to 3.25x width) (Fig. 11B);

(3) very narrow (length ≥ 4x width) (Fig. 11C).

Comments: The femoral length to width ratio was determined by dividing the length of the femur at its widest point by the width of the femur at its widest point.

Results: State (0) is clearly the ancestral state and is present in the majority (ca. 75%) of species within Leptohyphidae, and two-thirds of the outgroup species. State (2) is present irregularly throughout the family. State (1) is present in most species of the subgenus *Tricorythodes* (*Asioplax*). State (3) is a synapomorphy of the family Coryphoridae.

Character 65: *Profemur, form of setae in fore femoral band (dorsal surface).*

(0) filiform or acuminate (five or more times longer than broad) (Fig. 11D);

(1) elongate (approximately three to four times as long as broad) (Fig. 11E);

(2) robust (approximately twice as long as broad) (Fig. 11F);

(3) stout (approximately as wide as long) (Fig. 11G);

(4) absent.

Comments: The profemoral band of setae are located on the mid-dorsal surface of the femur.

Results: The plesiomorphic condition of this character is unclear, because states (4) and (1) occur in almost equal numbers in the outgroups. The vast majority of ingroup species share states (0) and (1), with states (2) and (3) occurring in a few terminal taxa. There is extensive homoplasy in this character. As such, there does not appear to be any useful phylogenetic signal in this character for determining higher-level relationships.

Character 66: *Profemur, number and arrangement of femoral band of setae*.

(0) numerous, evenly-space, forming a more-or-less complete arc across (Fig. 5E);

(1) few, scattered, forming an indistinct, or very short, row (Fig. 11H);

(2) numerous, forming an L – shaped arc (Fig. 11I).

Comments: The profemoral band of setae are located on the mid-dorsal surface of the femur.

Results: State (0) is clearly the ancestral condition and is present in almost all outgroup taxa and in the vast majority of leptohyphid species. State (2) is a synapomorphy of the *Traverhyphes* genera group, while state (1) is a synapomorphy of the genus *Haplohyphes*. State (1) also occurs in a few terminal ingroup and one outgroup taxa.

Character 67: *Profemur, form of setae along anterior (leading) margin* (Fig. 11H).

(0) elongate (Fig. 11E);

(1) robust (Fig. 11F);

(2) stout (Fig. 11G);

(3) filiform or acuminate (Fig. 11D);

(4) absent.

Comments: See Character 65 for explination of setal types.

Results: This is a highly variable character with extensive homoplasy. State (0) is apparently the ancestral state, present in the two most basal outgroup species. All other character states occurr throughout the ingroup taxa. There was no useful phylogenetic information in this character for determining relationships among the ingroup taxa.

Character 68: *Profemur, number of setae along anterior (leading) margin* (Fig. 10H).

(0) numerous (>15) (Fig. 11A);

(1) few (<10) (Fig. 11I).

Results: State (0) is the plesiomorphic condition, present in all outgroup species. Numerous terminal taxa in multiple genera possess state (1). This character does not provide any information concerning higher-level relationships within the family.

Character 69: *Profemur, form of setae along posterior margin* (Fig. 11H).

(0) absent;

(1) filiform/acuminate (Fig. 11D);

(2) elongate (Fig. 11E);

(3) robust (Fig. 11F).

Comments: See Character 65 for explination of setal types.

Results: This character contained extensive homoplasy and did not provide useful information concerning relationships among clades. State (2) was the most common character state with a number of terminal taxa possessing state (3).

Character 70: *Femora (all legs), outline of posterior margin*.

(0) smooth;

(1) serrated.

Results: State (0) is apparently the plesiomorphic state, present in almost all outgroup species. However, state (1) occurs in the most basal outgroup species. State (1) also occurs in a few terminal taxa in three different ingroup genera. This character did not provide any phylogenetic signal for higher-level relationships within the Leptohyphidae.

Character 71: *Profemur, tubercles of anterior margin*.

(0) present (Fig. 11J);

(1) absent.

Results: Tubercles are present only in the two most basal outgroup taxa; they are absent in all remaining outgroup and ingroup taxa.

Character 72: *Meso- and metafemora, longitudinal ridge*.

(0) absent;

(1) present (Fig. 5F).

Results: State (1) is an unshared synapomorphy of the genus *Leptohyphes*.

Character 73: *Meso- and metafemora, dorsal surface row of setae*.

(0) absent (Fig. 12A);

(1) present, 5-6 setae, forming longitudinal row (Fig. 12B);

(2) present, >15 setae, forming longitudinal row (Fig. 12C);

(3) present, 10 – 15 setae, scattered, not forming distinct longitudinal row (Fig. 5F);

(4) present, 5-6 setae, not forming longitudinal row (Fig. 12D).

Results: Character State (0) is clearly the plesiomorphic state, present in the majority of outgroup species and in approximately two-thirds of the ingroup taxa. States (1 – 4) are present in various terminal taxa throughout the ingroup and some outgroup taxa. This character provides only limited phylogenetic information concerning higher-level relationships within the ingroups.

Character 74: *Meso- and metafemora, basal setae*.

(0) absent;

(1) present, robust (Fig. 11F);

(2) present, elongate (Fig. 11D).

Comments: When present, these setae are located at the base of the meso- and metafemura.

Results: Because the basal setae are absent (state 0) in all but one outgroup species, it is clearly the plesiomorphic condition. The basal setae are also absent in the two most basal leptohyphid genera (*Leptohyphodes* and *Amanahyphes*). State (1) is a synapomorphy at Node 4 (Fig. 7), but with a reversal to state (0) at Node 7 (Fig. 7), which leads to the *Traverhyphes* genera group. State (1) occurs in almost all species of the genera *Haplohyphes* and *Leptohyphes*, with a very few species possessing state (2). State (2) occurs in all known species of the sister genera *Tricorythopsis* and *Tricorythodes*, where it is considered a synapomorphy at Node 11 (Fig. 7). State (2) has been independently-gained in a few species in the genera *Haplohyphes* and *Leptohyphes*.

Character 75: *Meso- and metatibiae, mediolongitudinal ridge*.

(0) absent;

(1) present (Fig. 5F, mel).

Comments: When present, the mediolongitudinal ridge is located on the dorsal surface of both the meso- and metatibiae. It forms a distinctive elevated ridge the entire length of the tibia.

Results: State (1) is an unshared synapomorphy of the genus *Leptohyphes*.

Character 76: *Meso- and metatibiae, median longitudinal row of setae*.

(0) absent;

(1) present, setae bipectinate (Fig. 12E);

(2) present, margins smooth, not bipectinate (Fig. 12F).

Results: State (0) is apparently the plesiomorphic state, being present in the majority of the outgroup taxa and persisting into the basal leptohyphid genera. State (1) is a synapomorphy of the *Traverhyphes* genera group, but with this state secondarily lost in some species. In the remainder Leptohyphidae, state (2) occurs in most species, but with apparent loss to state (0) in some taxa.

Character 77: *Metaleg, metatarsus/metatibia ratio (mmr).*

(0) mmr ≤ 0.5;

(1) mmr > 0.5.

Comments: The value of mmr is calculated by dividing the length of metatarsus by the length of metatibia.

Results: State (0) is clearly the plesiomorphic state, present in most outgroup taxa. State (1) is a synapomorphy for the outgroup family Coryphoridae, and Node 10 (Fig. 7) in the Leptohyphidae, which includes the genera *Vacupernius*, *Tricorythopsis*, and *Tricorythodes*. Within this three genera, a reversal to state (0) occurs among a few terminal taxa.

Character 78: *Metaleg, femur/(tibia + tarsus) ratio (fttr).*

(0) fttr > 0.90;

(1) 0.50 ≤ fttr ≤ 0.75.

Comments: The value fttr was calculated by dividing the length of the metafemur by the combined length of the metatibia and metatarsus.

Results: State (0) is evidently the plesiomorphic condition, present on the most basal taxon, and half the outgroups. State (1) is present in almost all ingroup taxa (>95%), with reversal to state (0) in a few terminal taxa.

Character 79: *Proleg and metaleg, profemur/metafemur ration (pmt).*

(0) 0.75 ≤ pmr ≤ 0.95;

(1) $0.50 \leq pmr \leq 0.65$;

(2) $pmr > 1.00$.

Comments: The value pmr is calculated by dividing the length of profemur by the length of the metafemur.

Results: State (0) is clearly the plesiomorphic condition, present in most of the outgroups, and evidently persists in the Leptohyphidae down through the most highly derived genus *Tricorythodes*. State (1) occurs in a few outgroup taxa in most species of the genus *Leptohyphes* and in most species within the *Traverhyphes* genera group. State (1) is independently derived in multiple clades, both in the ingroup and the outgroup.

Character 80: *Protibia, setae of anterior margin*.

(0) present, >20 setae (Fig. 12G);

(1) present, <15 setae (Fig. 12H);

(2) absent.

Comments: The plesiomorphic state (state 0) is most common among the outgroup taxa. State (1) first appears at Node 1 (Fig. 7), joining the Coryphoridae and Leptohyphidae. States (0) and (1) are present throughout the Leptohyphidae, although state (1) is the most frequent. There is apparently a reversal from state (1) to state (0) at Node 7 (Fig. 7) leading to the *Traverhyphes* genera group, and again at the subgenus *Tricorythodes* (*Asioplax*). This reversal is considered a synapomorphy at these two locations on the cladogram.

Character 81: *Protibia, highly-branched setae at distal end*.

(0) absent;

(1) present, one;

(2) present, more than one (Fig. 12I).

Comments: State (0), present in the outgroups, is the plesiomorphic state, and remains through the three basal genera of Leptohyphidae. At Node 5 (Fig. 7), the state changes from (0) to (2), and maintains that state throughout most of the Leptohyphidae. States (0) and (1) are also present in Leptohyphidae, but infrequent.

Character 82: *Protarsus, setae of mid-line/anterior margin.*

(0) absent;

(1) present, <6 setae (Fig. 11A);

(2) present, 8-15 setae (Fig. 12J).

Comment: State (0) is clearly the plesiomorphic state, present among most of the outgroups, with state (2) shared by Leptohyphidae and its sister families Tricorythidae and Coryphoridae (Fig. 7). State (2) is the most common state among the ingroup taxa, while state (1) is very rare. Within Leptohyphidae, the genera *Yaurina* and *Tricorythopsis* have reversed to state (0), along with numerous species of *Tricorythodes*.

Character 83: *Meso- and metatibia, setae of anterior margin.*

(0) present, numerous (>10), evenly dispersed (Fig. 12K);

(1) present, numerous (>10), clumped at distal end. (Fig. 12L);

(2) present, few (<5), scattered along margin.

Results: State (0), the plesimorphic condition, is the most common state among the outgroup species, as well as most of the ingroup species. States (1) and (2) occur infrequently in various terminal taxa of both the ingroup and outgroup.

Character 84: *Meso- and metatibia, setae of posterior margin.*

(0) present, many (≥8) (Fig. 12K);

(1) present, few (<5) (Fig. 12L);

(2) absent.

Results: The pleismorphic state, state (0), occurs in all outgroup species. State (0) also occurs in the vast majority of ingroup species. States (1) and (2) occur infrequently among taxa terminal taxa.

Character 85: *Meso- and metatarsus, setae of anterior margin*.

(0) present, few (<10) (Fig. 13A);

(1) present, many (≥10) (Fig. 13B);

(2) absent.

Results: State (0) is the ancestral state, present in almost all outgroup taxa, and the most common character state within Leptohyphidae. There appears to be numerous reversals and/or independent gains of States (1) and (2). This was a highly variable character with extensive homoplasy. There is evidently no useful phylogenetic signal in this character for determining clades within the ingroups.

Character 86: *Meso- and metatarsus, setae of posterior margin*.

(0) present, few (<10) (Figure 13A);

(1) present, many (≥10) (Figure 13B);

(2) absent.

Results: State (0), the ancestral state, is present in most ingroup taxa. States (1) and (2) are also present among a few of the outgroups. State (0) is also the most common character state within the Leptohyphidae, with states (1) and (2) present in various terminal taxa. This was a highly variable character with extensive homoplasy. There is evidently no useful phylogenetic signal in this character for determining clades within the Leptohyphidae.

Character 87: *Pretarsal claw, submarginal denticles* (Fig. 5D).

(0) absent;

(1) present, 1 denticle (Fig. 13C);

(2) present, >1 denticle, single row (Fig. 13D);

(3) present, one pair of denticles (Fig. 5G);

(4) present, more than one pair of denticles (Fig. 13E).

Comments: Submarginal denticles are distinguished from marginal denticles on the basis of four criteria. First, submarginal denticles are larger (taller and wider) than marginal denticles. Second, a gap is present between where the marginal denticles end and the submarginal denticles begin. Third, submarginal denticles are located at the apical margin of the claw, while the marginal denticles are located near the middle of the claw. And fourth, submarginal denticles are located mesolaterally on the claw, while marginal denticles are located medially on the claw.

The homology of one pair of submarginal denticles versus two pairs of submarginal denticles appears justified based upon structural and positional homology. First, the denticles in each row are almost identicial in shape and size, and second the denticles are directly across from each other.

Results: State (0) appears to be the the ancestral state, because it is most common among the outgroups. However, states (1), (3) and (4) are also present among some outgroups. Within the Leptohyphidae all states are present and are variable among the terminal taxa of different clades. Because of the extensive homoplasy within this character, there is evidently no useful phylogenetic information for determining higher-level relationships.

Character 88: *Pretarsal claws, number of marginal denticles.*

(0) 1 to 4;

(1) 5-8 (Fig. 5G, 13C);

(2) >10 (Fig. 13F);

(3) denticles absent (Fig. 13E).

Comments: See "Comments" associated with character 87 for an explanation of the differences between marginal and submarginal denticles.

Results: State (0) is most common among the outgroups, and apparently the ancestral state. However, states (1) and (2) are also present among the outgroups, but much less common than state (0). All character states are present in the ingroup species, and mixed within genera. State (3) is a synapomorphy for the genus *Haplohyphes*.

Abdomen (Characters 89 – 116)

Character 89: *Abdominal terga 1 – 6, posterior margin.*

(0) smooth, with few or no or serrations;

(1) distinctly serrated (Fig. 6E).

Comments: The serrated posterior margin of the abdominal terga in state (1) runs entire length of margin.

Results: State (0) is clearly the ancestral state, present in all but two outgroup species, with a transition to state (1) at Node 4 (Fig. 7) in the Leptohyphidae, where it is considered a synapomorphy. There are no changes of this character state within the Leptohyphidae, until the highly derived genus *Tricorythodes* where reversion to state (0) occurs.

Character 90: *Abdominal terga, setae at posterior submargin*.

(0) absent;

(1) robust, present on terga 2-9 (Fig. 6E);

(2) robust, present only on terga 3-6;

(3) elongate, present on terga 2-9 (Fig. 13G).

Comments: These setae are located on the posterior submargin, and project posteriorly. Homology of the character states is justified on the basis of position. When present, the setae are always located at the same location on the submargin.

Results: State (0) is the most common state among all outgroup and ingroup taxa. State (1) is present on numerous species of *Leptohyphes*, but also in a few other ingroup and outgroup taxa. States (2) and (3) are uncommon but widely dispersed among non-related ingroup taxa. This highly-variable character does not provide useful phylogenetic signal for determining higher-level relationships among examined ingroup taxa.

Character 91: *Abdominal terga, setae of sublateral margins*.

(0) absent;

(1) present on terga 2-9 (Fig. 13H, slms);

(2) present on terga 4-6.

Comments: When present, these setae are located lateral to the midline of the abdominal terga. They can become broken away and difficult to detect.

Results: State (0) is clearly the basal state, present on all outgroups except one. Within the Leptohyphidae, states (1) and (2) are present in about one-half of the species of *Leptohyphes*, and only in the apparnetly more derived species. Outside the genus *Leptohyphes*, state (1) does not occur and state (2) occurs only in the genus *Yaurina*, where it apparently evolved in parallel with its occurrence in *Leptohyphes*.

Character 92: *Abdominal sternites five through nine, tubercles*.

(0) absent;

(1) present (Fig. 6A).

Comments: When present, the tubercles are located medially on abdominal terga five through nine.

Results: Abdominal tubercles (state 1) are present in four outgroup taxa, and one ingroup taxon (*Leptohyphes tuberculatus*), where they have apparently evolved in parallel. Abdominal tubercules are absent (state 0) in all other ingroup and outgroup taxa studied. However, with many larval stages unknown, it is possible this character may occur in other species and provide some phylogenetic signal concerning intergenetic relationships.

Character 93: *Abdominal tergites, raised posterior margins*.

(0) absent;

(1) present (Fig. 6B, rpm).

Results: State (1) is present on one outgroup taxon and two ingroup taxa (*Tricorythodes undatus* and *T. melanobrancus*), where it has apparnelty evolved in parallel among the three species. This character does not provide any useful phylogenetic signal in determining intergenetic relationships within the Leptohyphidae.

Character 94: *Abdominal sternites 7 – 9, relative length of posterolateral projections*.

(0) shorter than, or equal to, medial length of associated tergites (Fig. 6D, plp);

(1) absent (Fig. 13I);

(2) longer than medial length of associated tergites (Fig. 6C, plp).

Comments: The length of the projections are determined by measuring, in a straight line distance, from the tip of the projection to the anterior margin of the tergite, then compared with the length of the tergite as measured medially from the the anterior to posterior margin.

Results: State (0) is the ancestral state, present in all outgroups except the leptohyphid sister families Tricorythidae and Coryphoridae, where they are absent (state 1). State (1) is found in the basal leptohyphid genera (*Haplohyphes* and *Leptohyphes*), then reverts back to state (0) at Node 5 (Fig. 7). State (2) occurs in all species of the subgenus *Asioplax*, except for the two most basal species, and *Tricorythodes serratus*.

Character 95: *Abdominal sternites, posterolateral projections (plp)*.

(0) present on segments 4-9 (12J);

(1) present only on segments 7-9 (Fig. 6C, D);

(2) present only on segments 8-9 (Fig. 14A);

(3) present only on segments 7-8 (Fig. 14B).

Results: The root state of this character appears to be state (0), with a loss of projections 4 – 6 early in the evolution of the outgroups. State (1) is present in the remaining outgroups, and in almost all ingroup taxa. State (2) is a synapomorphy of the genus *Tricorythopsis*. State (3) occurs infrequently among species in the genera *Traverhyphes* and *Tricorythodes*, where this state has apparently evolved in parallel.

Character 96: *Abdominal tergum 7, row of elongate setae on anterior margin*.

(0) absent;

(1) present, complete arc across terga (Fig. 14C);

(2) present, incomplete arc across terga (Fig. 14D).

Results: State (0) occurs in all outgroup and ingroup taxa except for the genera *Tricorythodes* and *Leptohyphodes*. Within the *Tricorythodes*, states (1) and (2) are present in various species, but without any clear phylogenetic pattern.

Character 97: *Cercus, cercomere joint setae*.

(0) longer than length of adjacent cercomeres (Fig. 14E);

(1) shorter than length of adjacent cercomeres (Fig. 14F).

Results: State (0) is clearly the ancestral state, present in almost all outgroup taxa, except for the two most immediate sister families (Tricorythidae and Coryphoridae) of the Leptohyphidae. A change from state (0) to state (1) occurs leading to the Family Tricorythidae. State (1) is found in all species of Leptohyphidae, until the highly derived genus *Tricorythodes*, where a change back to state (0) occurs. State (0) is found in almost all species of *Tricorythodes*, except for a few species which have character State (1).

Character 98: *Abdominal segment one, gill.*

(0) present;

(1) absent.

Results: Abdominal gill one is absent (state 1) on all ingroup species. It is also absent in all but two outgroup species, where the character has apparently been regained. The evolution of abdominal gill one is very unclear in the Pannota, as a number of species possess the gill. It was evidently lost early in the evolution of the Pannota, but has been regained in several taxa. However, it has apparnetly never been regained in the Leptohyphidae.

Character 99: *Abdominal somite 2, gill insertion.*

(0) present, inserted dorsolaterally on abdominal segment 2 (Fig. 14D)

(1) present, inserted ventrolaterally on abdominal segment 2 (Fig. 14G)

(2) absent

Results: State (1) is a unique synapomorphy of the genus *Haplohyphes*. State (0) is present on the vast majority of ingroup and outgroup taxa. State (2) is only present in a very few outgroup taxa.

Character 100: *Abdominal somite 2, operculate gill shape.*

(0) oval (Fig. 6H);

(1) subrectangular (Fig. 14H);

(2) triangular (Fig. 6G).

Comments: Oval gills are approximately twice as long as wide, without a distinctly straight edge along the inner margin. Triangular gills are approximately one-third longer than wide, with a distinct, nearly straight edge, along the inner margin. Subrectangular gills are also about twice as long as wide, but with a more distinct straight edge along the inner margin than on an oval gill. Measurements are made at the widest point of each metric.

Results: State (0) is present in almost outgroup taxa, and the majority of ingroup taxa. State (1) appears to have evolved in parallel in several clades. It is a synapomorphy of the genera *Leptohyphodes* and *Vacupernius,* and a synapomorphy for the *Traverhyphes* genera group at Node 7 (Fig. 7). State (0) occurs in approximately two-thirds of species in the genus *Tricorythodes,* with state (1) present among the remaining (and most highly derived) species.

Character 101: *Abdominal somite 2, operculate gill, beak-like basal process of first lamellae*.

(0) absent

(1) present (Fig. 6I)

Comments: This beak-like process is a small, colorless outgrowth of the underlying gill lamella. It is often referred to as a spine in older literature, but is clearly not a spine. Its homology is unclear, but it might be a reduced gill or some type of support structure for the operculate gill or lamellae. The function of this process is unknown.

Results: State (1) is an unshared synapomorphy of the genus *Leptohyphes*. All other ingroup and outgroup taxa possess the ancestral state (state 0).

Character 102: *Operculate gill, arrangement of setae along margin.*

(0) setae absent (Fig. 6H);

(1) setae crowded, present along most of gill margin (Fig. 6G);

(2) setae present, sparse, widely dispersed along margin (Fig. 14I).

Results: This character contained much homoplasy and does not provide any phylogenetic signal for determining higher-level relationships within the Leptohyphidae. All three character states are present throughout the Leptohyphidae. States (1) is the most common character state within Leptohyphidae, and apparently evolved well before its most common ancestor. States (0) is evidently a reversal among a few species within the Leptohyphidae. State (2) has apparently evolved in parallel in a number of leptohyphid clades.

Character 103: *Abdominal somite 2, gill.*

(0) non-operculate (Fig. 15A);

(1) semi-operculate (Fig. 15B);

(2) fully operculate (Figs. 13G, 14D).

Comments: A gill is considered non-operculate when it is approximately equal in size to other abdominal gills, and covers less than half of abdominal gill three (Fig. 15A). A semi-operculate gill is larger than all other abdominal gills, and covers between 50 and 90% of the succeeding abdominal gill. A fully operculate gill covers all other abdominal gills.

Results: All known ingroup species have fully-operculate gills (state 2). Most outgroup species possess a non-operculate gill two (state 0), with a few species possessing state (1). The evolutionary transformation is clearly from a non-operculate gill two, to a fully-operculate gill two, as demonstrated by the fact that no outgroup species possess fully operculate gills, which are only present among the ingroup species. No ingroup species have revered to semi- or non-operculate gills.

Character 104: *Abdominal somite 2, operculate gill, dorsal ridges*.

(0) absent (Fig. 6H);

(1) one, medial only (Fig. 6G; 15C);

(2) two, medial and anterior (Fig. 15D, E).

Results: State (0) is clearly the basal condition, present in most outgroups, and is found throughout the Leptohyphidae. State (1) occurs in a few basal ingroup species, but is most common in more highly-derived species in the genus *Tricorythodes*. State (2) occurs infrequently in species of the genera *Traverhyphes* and *Tricorythodes*.

Character 105: *Gills 3 – 6, ventral lamellae*.

(0) lamellae fimbrate, with numerous (>20), terminal filaments (Fig. 15F);

(1) lamellae entire, without filaments (Fig. 6F)

Results: State (1) is a unique synapomorphy of the family Leptohyphidae (Fig. 7, Node 1).

Character 106: *Gills, lamellar structure*.

(0) one lamella;

(1) two lamellae (dorsal and ventral).

Results: State (1) is present in all ingroup and all outgroup taxa except the outgroup *Dicercomyzon* (Family Tricorythidae).

Character 107: *Gill 2, ventral inferior lamella*.

(0) ventral lamella well-developed, parallel to dorsal lamella (Fig. 6I; 15G);

(1) ventral lamella well-developed, perpendicular to dorsal lamella (Fig. 15H);

(2) ventral lamella extremely reduced, parallel to dorsal lamella (Fig. 16A).

Results: State (0) is clearly the plesiomorphic condition, present in all outgroups. State (1) is a synapomorphy of the Leptohyphidae (Fig. 7, Node 2). A reversal from state (1) to state (0) occurs in the genera *Leptohyphes* and *Tricorythopsis*. This reversal is a synapomorphy of each of these genera. State (2) is a synapomorphy of the genus *Leptohyphodes*.

Character 108: *Gills 3 – 5, basal flap of dorsal lamellae*.

(0) absent (Fig. 16B);

(1) present (Fig. 16C).

Comments: The basal flap is a small, basal extension of the most exterior lamella.

Results: State (1) is independently derived as a synapomorphy in the genera *Leptohyphodes* and *Haplohyphes*, and in the subgenus *Tricorythodes*. State (1) is also present in two species in the subgenus *Tricorythodes* (*Asioplax*). State (0) is present in all other outgroup and ingroup taxa.

Character 109: *Gills 3 – 5, dorsal projection of ventral lamella*.

(0) absent (Fig. 16B);

(1) present (Fig. 16C).

Results: State (1) is an independently-derived synapomorphy of the genera *Leptohyphodes* and *Haplohyphes*, and the subgenus *Tricorythodes* (*Tricorythodes*).

Character 110: *Gill 2, number of lamellae*.

(0) ≥4 lamellae (Fig. 15F; 16D);

(1) 2 or 3 lamellae (Fig. 6I; 15G, 15H);

(2) 1 lamella (Fig. 16E).

Comments: The operculate gill is considered homolgous with the other lamellae and is counted as one lamella in the total count of gill lamellae.

Results: State (0) is clearly the pleisomorphic condition, present in all outgroup species (except *E. excrucians* and *D. lata*, where abdominal gill two is absent). Within the Leptohyphidae, state (1) is present in the vast majority of species. State (0) is very rare among ingroup taxa, being present in only two terminal taxa, and evidently represents a reversal to State (0). Among ingroup taxa, state (2) occurs infrequently in the genus *Leptohyphodes*, and in several species in the genus *Tricorythodes*. The trend is clearly that of a reduction in the number of lamellae on abdominal gill two. State (1) is considered a synapomorphy of the family Leptohyphidae.

Character 111: *Gill 3, number of lamellae*.

(0) ≥8 lamellae (Fig. 16F);

(1) 4-7 lamellae (Fig. 16B);

(2) 2-3 lamellae (Fig. 16C).

Results: State (0) is clearly the pleisomorphic state, present in all outgroups, with a transition to State (1) at Node 2 (Fig. 7), which is considered a synapomorphy of the family Leptohyphidae. Most species of Leptohyphidae exhibit state (1), with a transition to state (2) occuring in the genera *Vacupernius, Leptohyphodes*, and *Tricorythodes*, where state (2) evolved in parallel and is considered a synapomorphy for each genus. State (2) also occurs in species in the *Traverhyphes* genera group. The transition to state (2) is unclear in this genera group due to equally-parsimonious solutions. The transition may have occurred at Node 7 (Fig. 7), with reversals to state (1) among some species in the group, or state (2) may have evolved in parallel among different genera. The repeated trend for this character in the family Leptohyphidae is clearly one of reduction in the number of gill lamellae.

Character 112: *Gill 4, number of lamellae.*

(0) ≥8 lamellae (Fig. 16F; 16G);

(1) 4-6 lamellae (Fig. 16B);

(2) 2 -3 lamellae (Fig. 16C).

Results: State (0) is clearly the pleisomorphic state, present in most outgroup species, with a transition to state (1) at Node 2 (Fig. 7), which is considered a synapomorphy of the family Leptohyphidae. Another transition occurs, from state (1) to state (2), at the base of the Leptohyphidae at Node 3 (Fig. 7). State (1) is maintained within the genera *Haplohyphes, Leptohyphes, Tricorythopsis*, and in the subgenus *Asioplax*. Within the *Traverhyphes* genera group, the genera *Traverhyphes* and *Yaurina* transition to state (2), synapomorphies for these two genera. A reversal from state (2) to state (1) evidently occurs for the genus *Allenhyphes*. All species within the subgenus *Tricorythodes* (*Tricorythodes*), except for two of the most basal species, possess the state (2). The trend for this character is clearly one of reduction in the number of gill four lamellae.

Character 113: *Gill 5, number of lamellae*.

(0) ≥8 lamellae (Fig. 16F; 16G);

(1) 4-6 lamellae (Fig. 6F; 16B);

(2) 2-3 lamellae (Fig. 16C).

Results: State (0) is clearly the ancestral state, present in all outgroups, except the sister family Tricorythidae where a transition to state (1) occurs. A parallel transition from state (0) to state (1) also occurs at Node 1 (Fig. 7), a synapomorphy uniting Coryphoridae + Leptohyphidae as sister families. A transition from state (1) to state (2) occurs in parallel at Nodes 3 and 6 (Fig. 7), which includes all leptohyphid genera except *Haplohyphes* and *Leptohyphes*, where state (1) is retained.

Character 114: *Gill 6, presence/absence*.

(0) present;

(1) absent.

Results: Almost all species in the ingroup and outgroup possess gill six (state 0). The loss of gill six (state 1) occurrs independently in several places. Among the outgroup species, it has been lost in the two most basal species. Gill six has been lost in parallel in the Family Coryphoridae, and in the Leptohyphidae at Node 3 (Fig. 7), which unites the sister genera *Leptohyphodes* and *Amanahyphes*. Losses at these two places are considered synapomorphies.

Character 115: *Gill 6, number of lamellae*.

(0) ≥ 5 lamellae (Fig. 16F; 16G);

(1) 2-3 lamellae (Fig. 16H);

(2) 1 lamella (Fig. 16I).

Results: State (0) is clearly the pleisomorphic state, present in most outgroups, with a transition to state (1) at Node 4 (Fig. 7). State (2) is a unique synapomorphy of the genus *Tricorythopsis*.

Character 116: *Gill 7, presence/absence*.

(0) present;

(1) absent.

Results: Gill 7 is absent in all known larval species of Leptohyphidae, and present only in the two most basal outgroup families.

Body Shape (Characters 117 – 118)

Character 117: *Abdomen / thorax, length ratio (atlr)*.

(0) atlr < 0.9;

(1) atlr > 1.1;

(2) 0.9 ≤ atlr ≤ 1.1.

Comment: The value atlr is determined by dividing the length of thorax by the length of abdomen.

Results: State (0) is clearly the pleisomorphic state, occurring in almost all outgroup species. State (2) is most common within the Leptohyphidae. State (1) occurs infrequently among some of the outgroup and ingroup taxa.

Character 118. *Body shape*.

(0) not dorsally/ventrally flattened;

(1) dorsally/ventrally flattened.

Results: Dorsal flattening of the body (state 1) has occurred independently in some outgroup species and in the subgenus *Tricorythodes* (*Asioplax*), where it is considered a synapomorphy. The vast majority of ingroup and outgroup taxa possess state (0).

Cladistic Results

Cladograms

The parsimony analysis resulted in two cladograms of 800 steps each, with only minor differences among some of the terminal taxa. The final cladogram is given in Fig. 7, with all species collapsed into their respective genera, synapomorphies listed on branches leading to genera and major clades and the two most immediate sister families to the Leptohyphidae. In this cladogram, the species have been excluded from the cladogram for several reasons. First, the study focuses upon intergeneric relationships, not upon species relationships. Second, this figure more clearly shows the synapomorphies and each genus and their relationship with other genera without the visual distractions of each species. And third, since much of the homoplasy occurs among species within the genera, there are several polytomies, which do not provide any additional resolution. Only the two most closely-related sister families to the Leptohyphidae are shown, because they are discussed below under the heading "Sister Family to the Leptohyphidae." Figure 17 contains all ingroup and outgroup species used in the analysis. Figure 18 displays various branch support values for different clades, including jackknifing, bootstrap, and Bremer support values. Only Bootstrap and Jackknife values above 50% are reported.

Although the genus *Traverhyphes* resolves as paraphyletic (Fig. 17), it is treated as a monophyletic unit in Figure 7. Molineri (2004) clearly showed *Traverhyphes* to be a strongly supported monophyletic taxon based upon a cladistic analysis of larval and adult characters of all known species in the genus, and three other closely related genera. Because *Traverhyphes* (and its closely-related sister genera) are almost entirely South American, only a limited number of specimens of this genus were available for this study, and it is possible that the current results are a result of under sampling of species within this and closely related genera. It is also possible that the genus could indeed be paraphyletic. However, pending additional analysis of the genus and its closely-related sister genera, a conservative approach is followed herein in recognizing the genus as monophyletic based upon the results of Molineri (2004).

Proposed Taxonomy and Classification of Leptohyphidae

A new generic classification of the Leptohyphidae is proposed here, based on the monophyletic groups identified by the cladistic analysis (Fig. 7). This classification is given in full in Table 4. Due to the weak support values for several "higher level" nodes within the cladogram, genera are not assigned to subfamilies or tribes at this time. In his phylogenetic study of the South American Leptohyphidae, Molineri (2006) was faced with very similar issues. Strong support was found for most genera, but higher-level relationships were unclear and poorly supported. This study and Molineri's study (2006) recovered nearly identical results in terms of intergeneric relationships. The current study clearly recovered two distinct subgenera within the genus *Tricorythodes,* while Molineri (2006) did not recover these subgenera. Molineri did not examine the genus *Amanahyphes*, which was unavailable at that time. Molineri also reported the results of two slightly different cladograms, one calculated under implied weighting, the other using self weighting. The current analysis did not use a weighted approach, but used the equal weighting. Neither study recovered clades corresponding to the subfamilies proposed by Wiersema and McCafferty (2000). Although these authors stated that their classification was cladistically based, they did not include a matrix, a list of characters, or a phylogenetic branching diagram.

The proposed classification given in Table 4 makes several changes to the current taxonomy of the family. First, the genera *Ableptemetes, Cabecar, Epiphrades, Macunahyphes, Homoleptohyphes,* and *Tricoryhyphes* are all considered synonyms of the genus *Tricorythodes*. All are shown to be paraphyletic in Figure 17. And second, the currently-recognized genus *Asioplax* is reduced to a subgenus of *Tricorythodes* and a second subgenus of *Tricorythodes*, the subgenus *Tricorythodes*, is recognized Both are supported by synapomorphies (Fig. 7), and each is supported by a Bremer Support value of two (Fig. 18).

Discussion

Monophyly of the Leptohyphidae

The family Leptohyphidae was first proposed by Landa and Soldán (1985). It was based upon a detailed study of the internal morphology of multiple lineages of Ephemeroptera, although no formal synapomorphies were proposed for it. Several characters have since been proposed as putative synapomorphies to support the monophyly of the Leptohyphidae; however, many of these characters have evidently become reversed to pleisomorphic states or lost throughout the family (McCafferty and Wang, 2000; Molineri and Domínguez, 2003). For example, in the larval stage, loss of the maxillary palp, labial palp three, and gill seven are considered synapomorphies (McCafferty and Wang, 2000). In the adult stage, McCafferty and Wang (2000) consider the loss of hind wings and the condition of vein MP_2 being distinctly shorter than vein CuA as a synapomorphy supporting Leptohyphidae. Molineri and Domínguez (2003) considered the similar, blunt, fore-tarsal claws of the male imago a strong synapomorphy supporting the monophyly of Leptohyphidae, a character shared with few other taxa outside Leptohyphidae. All known male imagos of Leptohyphidae possess this claw character.

The current cladistic analysis strongly supports the monophyly of the Leptohyphidae, identifying five uniquely derived synapomorphies (one adult character and four larval characters) supporting the monophyly of the Leptohyphidae. The first of these is the presence of two similar (blunt) propretarsal claws in male imagos (Character 4, state 1), a character previously identified by Molineri *et al.* (2001). The second character, 107 (State 1), is a change in the position of the ventral inferior lamellae of abdominal gill two from parallel to perpendicular to the dorsal lamellae (Fig. 15H). A third character is the reduction from four or more lamellae on abdominal gill two to three or less lamellae (Character 110, state 1). Fourth is a reduction in the number of lamellae on abdominal gill three from eight or more lamellae to less than eight lamellae (Character 111, State 1). And fifth is Character 112 (State 1), which is a reduction in the number of lamellae on abdominal gill four from eight or more to six or less.

Sister Family to the Leptohyphidae

Over the last several years, there has been much research, but little agreement, as to the sister group of the Leptohyphidae. McCafferty and Wang (2000) proposed that the sister group of the Leptohyphidae was the Tricorythidae, which had generally been recognized as the sister family for many years. Members of these two clades share the synapomorphic forewing condition of a deep cubital fork and a well-developed $iCuA_2$ vein, though reversals in both characters are known within both families (McCafferty and Wang, 2000).

Coryphorus aquilus was described by Peters (1981) and placed in the subfamily Machadorythinae of the family Tricorythidae. At the time, Machadorythinae was a monotypic African subfamily containing the genus *Machadorythus*. Because of the unusual number of morphological features in *Coryphorus*, the assignment of *Coryphorus aquilus* to Machadorythinae was considered tentative. Because the adults of *Machadorythus* had the derived wing character of Tricorythidae and developing wings in larvae of *Coryphorus* lacked this character, Peters and Peters (1993) transfered the genus *Coryphorus* to the family Leptohyphidae. McCafferty and Wang (2000) suggested the genus *Coryphorus* might represent a separate subfamily within Leptohyphidae, but did not take any action, because they could not find any autapomorphies exclusive to the larval stage (the adult was still unknown).

Molineri et al. (2001) described the adult stage of *C. aquilus* and established the family Coryphoridae for the species, removing it from the Leptohyphidae. They established this new family because of several autapomorphies which included the loss of cubital intercalaries in the forewings, two-segmented forceps, dissimilar pretarsal claws on the proleg of the male imago, and the extreme reduction of labial palp segments two and three in the larva. Molineri and Domínguez (2003) evaluated the higher level relationships of Pannota and demonstrated that Coryphoridae was the sister family to the Leptohyphidae, and the Tricorythidae as the sister to Coryphoridae + Leptohyphidae. Jacobus and McCafferty (2006) re-evaluated Pannaota relationships and concluded that *Coryphorus* was part of the family Leptohyphidae and recognized the Family Machadorythidae as the sister-group to the Leptohyphidae, with the Tricorythidae sister to Machadorythidae + Leptohyphidae.

The current study strongly supports the family Coryphoridae as the sister family of the Leptohyphidae and agrees with by Molineri *et al* (2001) in placing Coryphoridae as the immediate sister family to the Leptohyphidae. Each of these families possess unique synapomorphies not shared between them. Three unique synapomorphies support the Coryphoridae: (1) the loss of vein iCu_1 (Fig. 2B); (2) the loss of vein iCu_2 (Fig. 2B); (3) the very narrow legs of the larvae, in which the femur is over four times longer than wide (Fig. 11C). Five unique synapomorphies support the family Leptohyphidae. In addition, there is strong Bremer support value for the Leptohyphidae (Fig. 18).

Subfamilies and Genera within the Leptohyphidae

Monophyletic groupings within the Leptohyphidae are unclear and there has been little agreement regarding phylogenetic relationships among described genera and subfamilies (McCafferty and Wang, 2000). Hypotheses of relationships made to date have been based on very incomplete and often highly speculative data, resulting in many apparently paraphyletic and polyphyletic groupings. A recent generic revision of the North and Central American Leptohyphidae extensively reorganized the family, including the establishment of several new genera (Wiersema and McCafferty, 2000). However, their phylogenetic assessment included a number of character systems of questionable utility and was not based on a rigorous cladistic analysis.

In his revision of the genus *Tricorythodes* in South America, Molineri (2002) synonymized several genera under *Tricorythodes* that had been proposed by Wiersema and McCafferty (2000). Molineri (2004) further modified the results of Wiersema and McCafferty (2002) in his analysis of the *Allenhyphes – Traverhyphes* group of South and Central America.

Molineri’s (2006) revision of the South American species of the Leptohyphidae failed to clearly define higher-level taxonomic units, included only a few North American species, and he did not present a single cladogram for the family. His results differed in many ways from those of Wiersema and McCafferty (2000). Firstly, Molineri (2006) did not recover as monophyletic either of the two subfamilies proposed by Wiersema and McCafferty (2000). He did, however, recover four well-supported clades that could be considered as subfamilies. Molineri (2006) chose not to formally describe these higher taxa until additional North and Central American taxa could be included in a more comprehensive analysis.

As with Molineri's (2006) analysis of the family Leptohyphidae, the current cladistic analysis failed to clearly define higher-level taxonomic units, although well-supported clades were recovered such as the *Traverhyphes* genera group (Fig. 7). Molineri (2006) also found strong support for the *Traverhyphes* genera group, which includes four closely-related genera (*Allenhyphes, Yaurina, Lumahyphes,* and *Traverhyphes*). One of the major differences between the two analyses was that Molineri (2006) recovered *Haplohyphes* sister to *Tricorythodes*, while the current analysis recovered *Tricorythopsis* sister to *Tricorythodes* (Fig. 7). Because of these conflicts, I prefer not to formally define higher-level clades recovered in the current analysis. As Molineri (2006) indicated, a more stable classification of the family will probably require extensive integration of the North American species with the South American species.

Notes on Selected Clades within Leptohyphidae

Three genera were recovered in the study which had extremely high support values. The genus *Haplohyphes* is a very strongly support clade with a jackknife value (JKV) of 92, a bootstrap (BTV) value of 96, and a Bremer support value (BSV) of 34. The genus possesses 12 synapomorphies (Fig. 7), four of which are unique and unshared with other clades (Character 10, State 2; 41 (1) , 88 (3), and 99 (1)). This genus has long been recognized as unique and distinct from other leptohyphid genera based upon both larval and adult characters.

The genus *Allenhyphes* is a strongly supported genus with a JKV of 58, a BTV of 58, and a BSV of 8. The genus possesses one unique, unshared synapomorphy (Character 34 State 1) present in the adult male. *Allenhyphes* was only recently established (Hofmann *et al.*, 1999) based upon this synapomorphy. Its sister genus, *Yaurina*, is very strongly supported with a JKV of 94, a BTV of 96, and a BSV of 21. It possesses three synapomorphies, one of which is unique and unshared (Character 33, State 1). This synapomorphy, present in the adult male, was recognized as unique by Molineri (2001b) when he first described the genus.

The genus *Tricorythopsis* is the most strongly support genus in the family, with a JKV value of 98, a BTV of 99, and a BSV of 34. Members of the genus share six synapomorphies, four of which are unique and unshared with other genera [Character 11 State 2; 15 (2); 96 (2); and 115 (2)]. The genus has a number of unique characters in the adult (genitalia, wing venation) and larval stage.

The *Traverhyphes* genera group (Fig. 7), which contains four closely related genera (*Allenhyphes, Yaurina, Lumahyphes*, and *Traverhyphes*) possesses eight synapomorphies, three of which are unique and unshared [Character 32 State 1; 66 (2); 76 (1)]. Molineri (2006) also recognized this genera group as unique and well-supported. It has not yet been given a formal taxonomic rank due to the uncertainty of relationships among higher-level clades. The genera group could easily be considered either a subfamily or tribe, depending on how other groups of higher-level clades are defined.

Discussion of Character Systems

A variety of larval and adult characters were used in the cladistic analysis, with varying levels of phylogenetically useful information. There was extensive homoplasy in both adult and larval characters; however, it was most prevalent in larval than adult characters. In the adult stage, characteristics of the male genitalia provided the most phylogenetically useful signal, with seven of the twelve characters possessing three or fewer steps. Among the most useful genital characters were those that contained accessory structures (such as characters 32 through 34), number of forceps segments, and presence of basal swelling at the base of the second forceps segment. Genitalia characters with extensive homoplasy included Characters 26 (shape of the posterior margin of the styliger plate) and 29 (pens width). Of the six leg characters, two possessed only one step (Characters 4 and 9), while the remaining characters contained extensive homoplasy. Characters of both fore- and hind wing veins were highly variable and only of limited use. However, at the generic and species level, a few characters were very useful, but were often reduction and/or loss characters. For example, *Coryphorus aquilus* (Family Coryphoridae) is easily recognized by the loss of veins iCu1 and iCu2.

Many larval characters were highly variable and also contained extensive homoplasy, much more so than many of the adult characters. Larval mouthparts accounted for many of the characters, but few contained phylogenetic signal, with the exception of some of the labium characters. Abdominal characteristics also accounted for many of the characters, but most also contained extensive homoplasy. A few characters of the gills (such as number of lamellae on individual abdominal segments) and legs did provide some phylogenetic signal in the larval stage. Considering that the larval stage accounts for the vast majority of the life cycle of a species where evolution likely excretes significant pressure, it is no surprising that there has been extensive modification of characters in order to adapt to a wide variety of environmental conditions and niches.

Many characters which contained high homoplasy were retained in the analysis for two reasons. Firstly, although some characters possessed several states and were highly variable at the species level, they were often useful at higher taxonomic levels, such as wing vein and genitalia characters. Secondly, many characters were used for the first time in this cladistic analysis of the Leptohyphidae and it is important to retain them so that future studies can have a basis for including or excluding them, or as a basis for additional studies. Future cladistic analysis of the Leptohyphidae should continue to include a wide variety of both adult and larval characteristics. Additional study of characters is needed in order to improve phylogenetic signal in the analysis. Additional studies of characters such include polarity of characters, ordering of character states, and a more detailed study of the internal morphological structure of structure such as the maxillary palp and forceps to try and determine if segments have been lost, fused, or were never present.

CHAPTER III

TAXONOMIC REVISION

Field Studies

Extensive new field collections of leptohyphid mayflies were made in the southwestern (Arizona, New Mexico, Texas) and eastern (Tennessee, North Carolina, Florida) United States and Central America (Mexico, Guatemala, Costa Rica, Nicaragua, Belize). These field investigations focused upon rearing larvae and collecting extensive series of individuals, both larvae and adults. The field collections were invaluable in providing fresh specimens of numerous species within the family.

Adult leptohyphid mayflies were collected in the early morning hours while swarming. The use of portable ultra-violet light traps often attracted large numbers of subimago adults, which were held until the final molt to obtain adults. Larvae were collected with dip nets and by hand picking from natural substrates. The larvae where most often found in the slower reaches of larger creeks and rivers, clinging to small stones and snag material. Mature larvae (indicated by large or dark wing pads) were collected live and placed in small, aerated containers and reared through subimago and adult stages. The associated larval cast skins were then used to associate larval and adult life stages. These rearing studies were critical in correlating adult and larval characters.

Museum and Laboratory Studies

Numerous museums contributed specimens for use in this study: Florida A&M University, Tallahassee, FL (FAMU); Purdue University, West Indianapolis, IN

(PERC); Cornell University, Ithaca, NY (CU); The California Academy of Sciences, San Francisco, CA (CAS); The Philadelphia Academy of Natural Sciences, Philadelphia, PA (ANSP); Texas A&M University, College Station, TX (TAMU); the Natural History Museum (formerly: British Museum of Natural History), London, England (BMNH); the Smithsonian National Museum of Natural History, Washington, D.C. (NMNH); Instituto-Fundación Miguel Lillo, San Miguel de Tucumán, Tucumán, Argentina (IFML).

The laboratory studies focused upon rearing larvae in order to associate both life stages and describing new species. During the course of the study, six new species of leptohyphid mayflies were described; two of these six species based upon both life stages (*Tricorythodes* (*Asioplax*) *numinuh* (Wiersema, McCafferty, and Baumgardner), 2001; *T. serratus* **(**Baumgardner and Ávila, 2006), and four from the larval stage only (*T.* (*Asioplax*) *isabelia* (Baumgardner, Meyer, McCafferty), 2006; *Leptohyphes mandibulus* Baumgardner, 2007; *T. kirki* Baumgardner, 2007; *T. primus* Baumgardner, 2007). Eight species which were previously known from only one life stage, have now been associated from both life stages (*L. ferruginus* Allen and Brusca; *L. zalope* Traver; *T. mirus* Allen; *T. sordidus* Allen; *T. fictus* Traver; *T. cobbi* Alba-Tercedor and Flannagan; *T. mosegus* Alba-Tercedor and Flannagan; *T. explicatus* (Eaton)).

Taxonomic History and Early Classification

The majority of research on the Leptohyphidae to date has been taxonomic in nature. The type genus *Leptohyphes* was established by Eaton (1882) based upon a single female imago from Argentina. Additional taxonomic literature includes Eaton

(1892), who first reported the genus from Central America, Ulmer (1920a, b), Needham and Murphy (1924), Traver (1943, 1958, 1959), Allen (1967, 1973, 1977, 1978), Mayo (1968), Allen and Roback (1969), Brusca (1971), Domínguez (1982, 1984), Allen and Brusca (1973), Kilgore and Allen (1973), Allen and Murvosh (1987), Lugo-Ortiz and McCafferty (1995), Wang *et al.* (1998), Molineri (1999a; 2001a, b, c; 2002, b; 2003a), Baumgardner and McCafferty (2000), Wiersema et al. (2001), Baumgardner (2003), Baumgardner *et al.* (2003) and Wiersema and McCafferty (2003).

The family Leptohyphidae has a complex taxonomic history, with many of its genera having traditionally been placed in the African family Tricorythidae. Leptohyphidae is generally known by its two speciose genera, *Leptohyphes* Eaton, 1882 and *Tricorythodes* Ulmer, 1920. A few other poorly known, but morphological distinctive genera were also described from South America, prior to its establishment as a family, such as *Haplohyphes* Allen, 1966 and *Tricorythopsis* Traver, 1958. As new taxa were described, the broad concepts of *Leptohyphes* and *Tricorythodes* became highly problematic, especially in North America, due to extensive interspecific and intraspecific variation among species.

Kluge and Naranjo (1990) and Lugo-Ortiz and McCafferty (1995) observed that some leptohyphid larvae possess characters that would place them in *Leptohyphes*, whereas their adult characters place them in *Tricorythodes*. Kluge and Naranjo (1990) suggested that the genera *Tricorythodes* and *Leptohyphes* were polyphyletic, and proposed that most leptohyphids be placed in the genus *Tricorythodes,* and that *Leptohyphes* be restricted to its type species. At that time, the type species of

Leptohyphes was known only from a single female subimago from Argentina, which had been thoroughly studied by Kluge (1992). McCafferty (1991) suggested this approach of Kluge and Naranjo (1990), which was characterized by the unequivocal synonymization of genera in Ephemeropteram, as had also been attempted in the Baetidae and Heptageniidae, was untenable. He argued that this approach to "cleaning up" taxonomic and phylogenetic questions would have the effect of masking discrete evolutionary lineages and ultimately the important biological information associated with such lineages. The root of this taxonomic problem is an insufficient understanding of the multiple lineages found within the family. McCafferty and Wang (2000) suggested that considerable additional study was required to clearly establish generic limits within the family. Molineri (2003b) clarified the status of the genus *Leptohyphes* by associating the female holotype with the adult male and larval stages, and established a more natural classification for the genus as part of his revision of the South American species.

Only recently has the family Leptohyphidae been studied using phylogenetic methodology. Wiersema and McCafferty (2000) were the first researchers that attempted to provide a phylogenetic framework for the family at least in North America. However, they did not include any South American taxa, which excluded a number of distinctive genera from their study. Several recent cladistic studies by Molineri (1996b; 2001a, b, c; 2002; 2003b; 2004) on the South American species of the Leptohyphidae have helped to more clearly differentiate clades within the family, and have provided a new framework for a phylogenetically-based generic classification. However, Molineri's (2006) revision of the South American species of Leptohyphidae failed to clearly define higher level taxonomic units, and included only a very few North American taxa. His results differed in many aspects from those of Wiersema and McCafferty (2000). Firstly, Molineri (2006) did not recover either of the subfamilies proposed by Wiersema and McCafferty (2000), but did recover four well supported, major taxonomic units which could be considered subfamilies. In addition, Molineri (2002, 2006) showed several genera proposed by Wiersema and McCafferty (2000) to be synonyms of the genus *Tricorythodes*, among other problems. Molineri (2006) chose not to formally describe these higher taxa until North and Central American taxa could be included in a more comprehensive analysis.

The current study further clarifies and supports generic limits within the family Leptohyphidae as established by Molineri (2006). However, as with Molineri's (2006) analysis of the South American fauna, higher-level relationships within the Leptohyphidae are still unclear. A cladistic analysis combining this study with Molineri's will probably be necessary before higher-level relationships can be determined.

Family Leptohyphidae Landa and Soldán, 1985

Differential Diagnosis

Leptohyphidae can be diagnosed from other mayfly families by the following combination of characters: (1) adults small, less than 6 mm in length (excluding cerci); (2) male imagos with dissimilar propretarsal claws; (3) forewing well-developed with numerous longitudinal and crossveins; (4) hind wing present or absent, but if present, then with an elongate costal process; (5) intercalaries absent in both fore- and hind wings; (6) males with two or three-segmented forceps; (7) genitalia highly variable, with or without penal spines, and with or without various accessory structures, (8) mature larvae between 3 mm and 10 mm in length (excluding cerci); (9) legs present, well-developed with highly variable setae and setal patterns ranging from stout spines to fine hairs; (10) abdominal gill one absent, gill two operculate and variously shaped, gills present on abdominal segments three through five or six; (11) larvae dorsally-ventrally flattened in some, but not most, species.

Taxonomy

The following keys distinguish all known male imagos and mature larvae (those with well-developed or black wing pads) to the level of genus (as recgonized herein). For additional characters, see the generic treatments for the individual genera.

Mature Larvae

Notes and Instructions

Because of significant variation among early and late instar larvae, only mature larvae (those with very mature or black wingpads) should be used. Couplets six through eleven are modified from Molineri, 2004.

1a. Abdominal gills inserted ventrally (Fig. 14G); postmentum narrowed

(Fig. 9E) .... *Haplohyphes*

1b. Abdominal gills inserted laterally (Fig. 14D); postmentum not narrowed

(Fig. 4D) 2

2a . Gill 6 present 4

2b. Gill 6 absent 3

3a. Operculate gills not touching on median line; lamellae of gills with numerous lobes (Fig. 15A) .... *Leptohyphodes inanis*

3b. Operculate gills touching on median line; lamellae of gills with a single side lobe (Fig. 15D) or none .... *Amanahyphes saguassu*

4a. Operculate gill with a basal beak-like process present at base on ventral side (Fig. 6I); dorsum of meso- and metafemora with longitudinal ridge (Fig. 5F); dorsum of meso- and metatibia with a median elevated ridge (Fig. 5F).. *Leptohyphes*

4b. Operculate gill without basal beak-like process at base on ventral side (Fig. 15G); dorsum of meso- and metafemora without a longitudinal ridge (Fig. 12A – B, D); dorsum of meso- and metatibia without a median elevated ridge (Fig. 12A – B, D) 5

5a. Hind wing pads present 6

5b. Hind wing pads absent 12

6a. Maxillary palp 1 or 2-segmented, with (Fig. 19A) or without an apical seta (Fig. 19B) 7

6b. Maxillary palp 3-segmented, without an apical seta (Fig. 19C) 10

7a. Gill 6 with one lamella (Fig. 16I)... 8

7b. Gill 6 with two (Fig. 16H) or three lamellae 9

8a. Maxillary palpomere without an apical seta (Fig. 19B) .... *Yaurina*

8b. Maxillaryp palpomere with an apical seta (Fig. 19A) .. *Traverhyphes* (*Byrsahyphes*)

9a. Maxillary palp 2-segmented, without an apical seta (Fig. 19B) . *Allenhyphes* (in part)

9b. Maxillary palp 1-segmented, with an apical seta

(Fig. 19E) .... *Traverhyphes* (s.g. *Traverhyphes*, *Mocohyphes*)

10a. Femoral spines with a slightly serrated, blunt apex (Fig. 19F) .... *Lumahyphes*

10b. Femoral spines with a smooth, rounded apex (Fig. 19G) 11

11a. Meso- and metatibiae with longitudinal row of branched setae

(Fig. 12E) .... *Allenhyphes* (in part)

11b. Meso- and metatibiae without longitudinal row of branched setae .... *Vacupernius*

12a. Gill 2 (operculate gill) with 4 ventral lamellae .... *Tricorythopsis*

12b. Gill 2 (operculate gill) with 1 (Fig. 16E) or 2 ventral lamellae

(Fig. 15H) .... *Tricorythodes*

Male Imagos

1a. Median caudal filament with a ventrally directed median spine at base

(Fig. 8I) .... *Allenhyphes*

1b. Median caudal filament without a ventrally directed median spine at base 2

2a. Forceps 2-segmented (Fig. 3A) 3

2b. Forceps 3-segmented (Fig. 3B – E)... 6

3a. Hind wings present (Fig. 2D) .... *Haplohyphes*

3b. Hind wings absent 4

4a. Vein iMP longer than vein MP_2; iMP fused basally with CuA

(Fig. 2A) .... *Tricorythopsis*

4b. Vein iMP equal in length to or shorter than vein MP_2; iMP free basally (Fig. 2B) or

fused basally with MP_1 (Fig. 1F) 5

5a. Penes with numerous ventrolateral spines

(Salles and Molineri, 2006: Fig. 9) .... *Amanahyphes saguassu*

5b. Penes without ventrolateral spines (Molineri, 2005: Fig. 8)...... *Leptohyphes inanis*

6a. Hind wings absent; segment two of forceps with a basal swelling (Fig. 2E)

(exception: *T. australis* lacks this basal swelling, but also lacks hindwings; it will

key to this couplet based upon the absence of hind wings) .... *Tricorythodes*

6b. Hind wings present; segment two of forceps without a basal swelling 7

7a. Protibia with distinct row of sharp spines (Fig. 2H) .... *Leptohyphes*

7b. Protibia without spines 8

8a. Penes with accessory dorsal structure present (Figs. 3G, H) 9

8b. Penes without accessory dorsal structure (Fig. 3A – E)....................................... 10

9a. Penal spines arising laterally, forming a ring (Fig. 3F)........................... *Lumahyphes*

9b. Penal spines arising dorsally, spine-like (Figs. 3G, H) .... *Traverhyphes*

10a. Penal spines arising ventrally, spine-like (Fig. 8G); elongate outer longitudinal

process absent .... *Vacupernius packeri*

10b. Penal spines absent; elongate outer longitudinal process present

(Fig. 8H) .... *Yaurina*

Generic Treatments

The following generic/subgeneric treatments are organized as follows:

1. Synonymical Listing. A brief taxonomic history of each genus, including a statement of the type species of the genus and a listing of synonymous names, if any. Also includes a reference list of taxonomic, revisional, and faunal works.

2. Diagnosis

3. Description. A listing of adult and larval characters that can be used to compare genera. A "gill formula" is given for each genus, which indicates the number of lamellae present in each abdominal gill. For example, a gill formula of 2/5-6/5-6/4/1 means that abdominal gill two is formed by two lamellae, gill three by five or six lamellae, gill four by five or six lamellae, gill five by four lamellae, and gill six by one lamella.

4. Proposed Synapomorphies

5. Species Included

6. Distribution

7. Comments

8. Type Material Examined

9. Other Material Examined

Genus *Leptohyphodes* Ulmer, 1920

1. Synonymical Listing. *Leptohyphodes* Ulmer, 1920:50 (Type species: *Potamanthus inanis* Pitctet, 1843:232): Ulmer, 1920b (generic discussion); Ulmer, 1933 (generic key); Traver, 1944 (larval description); Traver, 1958 (generic review);

Domínguez et al., 1992 (generic taxonomic key); Domíguez et al., 2001 (generic taxonomic key); Molineri, 2005 (generic revision, stage descriptions); Molineri, 2006 (family revision).

2. Diagnosis. Differentiated from other leptohyphid genera by the following combination of characters: *Adult:* (1) compound eyes enlarged, completely divided into an upper dorsal and lower ventral portion (Fig. 1C); (2) anterior parapsidal suture fused with transverse interscutal suture (Fig. 1E); (3) hind wings absent in both sexes; (4) plumidium present (Fig. 1E); (5) forceps two-segmented (Fig. 3C), directed ventrally; (6) penes wide, fused medially for at least half their lengths. *Larvae:* (1) labrum with a deep median cleft (Fig. 8D); (2) ventral lamellae of gills two through four with dorsal projections (Fig. 15C); (3) gill six absent; (4) pretarsal claws with five to six marginal denticles and a double row of two to three submarginal denticles (Fig. 19H).

3. Description. *Imago:* Length. Body, 5.5 – 7.5 mm; forewings, 7.0 – 8.0 mm. General coloration dark reddish brown, abdomen whitish. Head. Reddish brown, shaded with gray; eyes of male large (in dorsal view, distance between eyes less than distance across any one eye), divided into an upper dorsal and lower ventral portion (Fig. 1C); eyes of female small, not divided. Thorax. Reddish brown, shaded with gray, surrounded by white band; anterior parapsidal suture fused with transverse interscutal suture (Fig. 1E); plumidium present (Fig. 1E). Wings: forewing membrane hyaline, shaded with gray along costal and subcostal veins; hind wings absent in both sexes; hind margin of forewings fringed with setae; veins A and CuP not meeting at margin (Fig. 1F); iCu_2 free (Fig. 8C) at proximal end; MP_2 not united to MP1. Legs: brownish yellow to whitish yellow; tarsi of all legs five-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G). Abdomen. Whitish translucent, shaded with brownish gray along lateral segments; sterna whitish. Genitalia: forceps two-segmented; penes fused except for apical excavation.

Larva: Length. Body, 8.0 – 8.5 mm; caudal filaments, 3.0 – 3.5 mm. General coloration reddish-brown to gray. Head. Grayish in color. Labium with a circular submentum; prementum elongated; labial palp three-segmented, terminal segment small. Labrum with a deep anteriomedian cleft. Maxilla with a well-developed suture between galea and lacinia; palp reduced to a single, elongate seta. Outer incisor of right mandible with two denticles; inner incisor with one denticle. Outer incisor of left mandible with three denticles, inner incisor with one denticle. Thorax. Reddish brown, shaded with gray, fringed with setae. Pronotum with well-developed anterolateral projections. Legs elongate, extensively covered with elongate setae, yellowish in color. Claws with five to six marginal denticles, and a double row of two to three submarginal denticles. Abdomen. Whitish translucent, shaded with reddish brown and gray. Gills present on abdominal segments two through five only; absent on segment six. Ventral lamellae of abdominal gills with small lobes on outer margins (Fig. 15A). Operculate gill subrectangular, inserted laterally, with a weak transverse medial ridge.

4. Proposed Synapomorphies. Adult: None. Larvae: (1) [Character 107*; State transition 1-2] ventral inferior lamellae of abdominal gill 2 extremely reduced and parallel to dorsal lamellae (Fig. 16A) (ventral inferior lamellae of abdominal gill 2 well-developed, parallel or perpendicular to dorsal lamellae); (2) [100; 0-1] operculate gill subrectangular (Fig. 14H) (not oval or triangular); (3) [108; 0-1] basal flap of dorsal lamellae on gills 3 – 5 present (Fig. 16C) (basal flap of dorsal lamellae absent); (4) [109; 0-1] dorsal projection of ventral lamellae on gills 3 – 5 present (Fig. 16C) (dorsal projection of ventral lamellae absent); (5) [111; 1-2] abdominal gill 3 composed of 3 lamellae (Fig. 16C) (abdominal gill 3 composed of ≥4 or more lamellae).

5. Species Included (1). *Leptohyphodes inanis* (Pictet) [Brasil; A, L].

6. Distribution. Known only from northeastern Brasil.

7. Comments. Although no specimens of this genus were available for this study, the detailed revision of this genus by Molineri (2005) allowed for scoring of characters using the figures published in this paper. In addition, C. Molineri was consulted for clarification when there was any uncertainty concerning character scoring.

8. Type Material Examined. None

9. Other Material Examined. None

Genus *Amanahyphes* Salles and Molineri, 2006

1. Synonymical Listing. *Amanahyphes* Salles and Molineri 2006:2 (Type Species: *Amanahyphes saguassu* Salles and Molineri, 2006:9).

2. Diagnosis. Differentiated from other leptohyphid genera by the following combination of characters: *Imago*: (1) compound eyes enlarged, divided into a large upper and small lower section (Fig. 1C); (2) anterior parapsidal suture fused with transverse interscutal suture (Fig. 1E); (3) hind wings absent in both sexes; (4) plumidium present (Fig. 1E); (5) forceps two-segmented (Fig. 3C); (6) penes fused except for apical furrow; ventrolateral margin with numerous spines. *Larvae:* (1) legs long, slender (see Molineri, 2005, Figs. 14 - 16); (2) abdominal gill six absent.

3. Description. *Subimago* (imagos damaged, missing all appendages): Length. Body: 2.5 – 3.5 mm; forewings, 3.5 – 4.0 mm. General coloration yellow shaded with gray. Head. Whitish yellow, shaded with black. Eyes of male large (distance between eyes less than distance across any one eye), divided into an upper dorsal and lower ventral portion (Fig. 1C); eyes of female small, not divided. Thorax. Yellowish gray; anterior parapsidal suture fused with transverse interscutal suture (Fig. 1E); plumidium present (Fig. 1). Wings: forewings whitish; shaded with gray along costal and subcostal veins; hind wings absent in both sexes; hind margin of forewings fringed with setae; vein CuP not strongly curved towards A (Fig. 2B); iCu_2 free at proximal end (Fig. 8C); MP_2 not united to MP1; MP_2 and iMP free at proximal end. Legs: generally whitish shaded with gray; tarsi of all legs four-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G). Abdomen. Translucent whitish, shaded with yellow. Genitalia: forceps two-segmented; penes fused except for apical excavation.

Larva: Length. Body: 3.0 – 3.5 mm; caudal filaments 2.0 mm. General coloration whitish, with gray and black markings. Body relatively long, slender, without tubercles. Head. Whitish with gray marks. Labium with a laterally rounded submentum; prementum with slightly-differentiated glossae and paraglossae; labial palp three-segmented, terminal segment small. Labrum with a moderately deep anteriomedian cleft. Maxilla with a well-developed suture between galea and lacinia;

palp reduced to a single, elongate seta. Outer and inner incisors of right mandible with two denticles; outer incisor of left mandible with four denticles, inner incisor with one denticle. Thorax. Whitish, shaded with gray. Pronotum without anterolateral projections. Legs very long, slender. Dorsal surface of femora with elongate, spatulate setae; tibia with three rows of elongate setae. Claws with four to six marginal and a double row of one to three submarginal denticles. Abdomen. Whitish translucent, shaded with gray. Gills present on abdominal segments two through five, absent on segment six. Ventral lamellae of abdominal gills with two pairs of small lobes on outer margins (Fig. 15D). Operculate gills subquadrate, inserted laterally, overlapping, with a weak medial ridge.

4. Proposed Synapomorphies. None.

5. Species Included (1). *Amanahyphes saguassu* Salles and Molineri [Brasil, Peru; A, L].

6. Distribution. Known from Brasil and Peru (new country record).

7. Comments. Although no synapomorphies were identified for this genus in the current analysis, it does possess a striking assemblage of characters that readily distinguish it from other genera of the Leptohyphidae. The genus is provisionally maintained as valid here until evidence can be presented to justify or refute its synonymy with *Leptohyphodes*, its apparent sister genus.

Salles and Molineri (2006) noted that this genus appeared to occupy a rather basal position within the Leptohyphidae, and that it shared a number of characteristics with the genus *Leptohyphodes*, indicating a possible sister-group relationship. The current analysis supports both of these observations. Molineri (2006), in his revision of the South American leptohyphids, did not have *Amanahyphes* available for his analysis. The two genera share the derived conditions of male imagos with enlarged compound eyes, hind wings absent, and penes fused except for a small apical furrow. The larvae share the conditions of thin, elongate legs and absence of abdominal gill six. With additional study, this genus may prove to be synonymous with *Leptohyphodes*.

Although adult specimens of this genus were not available for this study, the excellent illustrations and description of the single species by Salles and Molineri (2006), and personal communications with C. Molineri, allowed for an accurate scoring of adult characters.

8. Type Material Examined. None.

9. Other Material Examined. PERU: Quebrada Mauisapa Cicra (S12.53761°; W70.116441°; elev. 231 m), 23.viii.2006, 2L, Flowers, Funk, Sweeney [FAMU]; Quebrada Ati 8 (S12°37.279'; W69°04.330'; elev. 134 m), 17.viii.2006, 2L, Flowers, Funk, Sweeney [FAMU].

Genus *Haplohyphes* Allen, 1966

1. Synonymical Listing. *Haplohyphes* Allen, 1966:566 (Type species: *Leptohyphes huallagas* Allen, 1966:567): Domínguez 1984 (new species description, *H. baritu* and *H. furtiva*); Lugo-Ortiz and McCafferty 1995 (new species description, *H. aquilonius*); Molineri 1999a (new species description, *H. dominguez*).Wiersema and McCafferty, 2000 (generic review); Molineri, 2003a (generic revision).

2. Diagnosis. Differentiated from other leptohyphid genera by the following combination of characters: *Imago*: (1) compound eyes small and remote; (2) anterior and posterior parapsidal sutures meet after transverse interseutal suture; (3) forewing with veins CuP and A_1 strongly converging at wing margin; (4) forewing with sparse setae along hind margin, mostly confined to anal region (5) two-segmented forceps (both segments approximately equal in length); (6) hindwings present (both sexes), with elongate, curved costal process; (7) plumidium absent. *Larvae:* (1) operculate gills inserted ventrally; (2) postmentum constructed, widest at base (Fig. 9E); (3) basal labial palpomere at least 5x longer than second and third segments combined; (4) frontoclypeal projections present, well-developed; (5) profemoral band of setae filiform, forming an indistinct row; (6) submarginal denticles present in two rows; marginal denticles absent or highly fused.

3. Description. *Imago:* Length. Body, 4.0 – 6.5 mm; forewings, 3.5 – 4.5 mm; hind wings 1.0 – 2.0 mm. General coloration yellowish-white to dark reddish brown. <u>Head.</u> Brown to reddish brown, shaded with gray; eyes small (distance between eyes two to three times greater than distance across any one eye). <u>Thorax.</u> Generally yellowish-white, shaded with black or gray; anterior parapsidal suture fused with transverse interscutal suture (Fig. 1E); plumidium absent. Wings: membrane hyaline, shaded with gray along costal and subcostal veins; hind wings present in both sexes; hind margin of forewings sparsly fringed with setae; vein CuP strongly (Fig. 1G) or not strongly (Fig. 1) curved towards A; iCu_2 merged with iCu_1 (Fig. 1G); iCu_1 joined with CuA near wing base (Fig. 1G); MP_2 united to MP_1 (Fig. 1G); iMP connected to MP_1 by crossvein (Fig. 1G). Legs: brownish yellow to whitish yellow; tarsi of all legs four-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G). Abdomen. Whitish to yellowish translucent, shaded with gray; sterna whitish. Genitalia (Fig. 3A): forceps two-segmented; penes fused for approximately two-thirds their distance; penal spines present.

Larva: Length. Body, 5.0 – 10.0 mm; caudal filaments 4.0 – 7.0 mm. General coloration yellowish, with black markings. Head. Yellow, with black markings along posterior margin. Labium (Fig. 9E); postmentum narrowed apically, widest basally; basal palpomere at least five times longer than second and third combined. Labrum with a shallow anteriomedian cleft. Maxilla with well-developed crown, and numerous, elongate setae; suture between galea and lacinia absent; palp variable, from one to three segments, and with or without a terminal seta. Outer incisor of right and left mandibles with two or three denticles. Thorax. Yellowish or white, shaded with black and/or gray. Pronotum without anterolateral projections. Legs yellow to white with gray or black markings, extensively-covered with elongate setae, yellowish in color. Claws with extremely reduce marginal denticles, numbering between zero and three, and a double row of two to four submarginal denticles. Abdomen. Yellowish with transverse black bands on tergites; sternites pale. Operculate gill oval, inserted ventrally, with lateral and transverse medial ridges (Fig. 19I). Gills present on abdominal segments two through six. Gill formula: 2-3/5-6/5-6/3-5/1-2.

4. Proposed Synapomorphies. Adult: [Character 10*; State transformation 0-2] forewing with sparse setae along hind margin, mostly confined to anal region (setae present along most of hind wing margin); [12; 0-1] vein CuP strongly curved towards A (Fig. 1G) (CuP not curved sharply towards A); [25; 0-2] first forceps segment approximately same length as second forceps segment (first forceps segment shorter than second forceps segment). Larva: [35; 0-2] frontoclypeal projections present and well-developed (Fig. 4A) (frontoclypeal projections absent or weakly developed); [36; 0-1] genal projections present, well-developed (Fig. 4A) (genal projections absent); [41*; 0-1] postmentum narrowed apically, broadest at base (Fig. 9E) (postmentum not narrowed, broadest at middle [Fig. 4D]); [45; 0-1] labial palpomere one at least five times longer than second and third segments combined (Fig. 9E) (labial palp one only two to three times longer than second and third segments combined [Fig. 4D]); [66; 0-1] forefemoral band of setae few, scattered, forming indistinct row across dorsal surface (Fig. 11B) (forefemoral band of setae numerous, evenly-space, forming a more-or-less complete arc across dorsal surface; [88; 1-3] marginal denticles absent (Fig. 13E) (marginal denticles present (Fig. 13C)); [99; 0-1] operculate gill inserted ventrolaterally on abdominal segment 2 (Fig. 14G) (operculate gill inserted dorsllaterally on abdominal segment 2 (Fig. 14D)); [108; 0-1] basal flap of dorsal lamellae on gills 3 – 5 present (Fig. 16C) (basal flap of dorsal lamellae on gills 3 – 5 absent); [109; 0-1] dorsal projection of ventral lamellae on gills 3 – 5 present (Fig. 16C) (dorsal projection of ventral lamellae on gills 3 – 5 absent).

5. Species Included (6). *H. aquilonius* Lugo-Ortiz and McCafferty [Colombia, Costa Rica; A, L]; *H. dominguezi* Molineri [Ecuador; A]; *H. baritu* Dominguez [Argentina, Bolivia; A, L]; *H. huallaga* Allen [Peru; A]; *H. mithras* Traver [Costa Rica; A]; *H. yanahuicsa* Molineri [Bolivia; A, L].

6. Distribution. Nicaragua south to southern Argentina [Argentina, Bolivia, Colombia, Costa Rica, Ecuador, Nicaragua, Panama, Peru]. Four species known exclusively from South America, one from Central America, and one from Central and northern South America.

7. Comments. Molineri (2003a) provided updated information for the genus, including new stage descriptions and a key for all known larvae and adults. Of the six known species, three are known from both life stages, and three are known only from the adult stage.

The type species of the genus, *Haplohyphes huallaga*, was examined; however, because of the extremely poor condition of the three male imago paratypes available for study, the species was not included in the analysis. It does clearly appear to belong to *Haplohyphes* because the male genitalia of this species are typical of the family.

8. Type Material Examined. *Haplohyphes aquilonius* Lugo-Ortiz and McCafferty: PARATYPE: COSTA RICA: Puntarenas Prov., Río Bellavista, ca 1.5 km NW Las Alturas (N8.951°; W82.846°; elev. 1400 m), 15-17.vi.1986, 1L, Holzenthal, Heyn, Armitage [FAMU]. *Haplohyphes huallaga* Allen: PARATYPES: PERU: Huanuco Prov; Río Huallaga, Tingo Maria, 29-31.vii.1963, 3♂ imagos, W.L. Peters

[CAS]. *Haplohyphes mithras* (Traver): PARATYPES: COSTA RICA: Río Pedregoso, ii.1939, 4♂ and 2♀ imagos, D. Rounds [CAS].

9. Other Material Examined. *Haplohyphes aquilonius* Lugo-Ortiz and McCafferty: same as paratype but, 18.ii.1986, 1L [FAMU]. *Haplohyphes furtiva* Dominguez: ARGENTINA: Salta, Paque Nacional El Rey, A Los Puestos (S24°47'48"; W64°37'19"), 24.iii.1999, 3♂, 3♀ imagos, Molineri y Romero [TAMU]; Jujuy, San Salvador de Jujuy, Rio Yala, 26.vi.1997, 5L, C. Molineri [TAMU]. *Haplohyphes mithras* (Traver): COSTA RICA: Puntarenas Prov, Río Sinigri, ca. 2 km S Finca Helechales (9.057°N; 83.082°W, elev. 720m), , 21.ii.1986, 10♂ imagos, Helzenthal, Morse, Fasth [TAMU]; NICARAGUA: Zelaya Norte, Cerro Saslaya (N13°44'; W85°01', elev. 700m), iv.1996, 35♂ and ♀ imagos, J.M. Maes & J. Hernadez [TAMU].

Genus *Leptohyphes* Eaton, 1882

1. Synonymical Listing. *Leptohyphes* Eaton, 1882:208 (Type species: *Leptohyphes eximius* Eaton, 1882:208); Eaton, 1884 (generic description); Ulmer, 1920a (new species); Needham & Murphy, 1924 (taxonomic key, new species); Ulmer, 1933 (order key to families and genera); Taver, 1943 (new species); Traver, 1944 (new species); Traver, 1958 (generic description, new species); Edmunds et al., 1963 (family key to genera); Roback, 1966 (species records and descriptions); Allen, 1967 (new species); Mayo, 1968 (new species); Allen and Roback, 1969 (new species); Brusca, 1971 (new species); Allen, 1973 (new species); Allen and Brusca, 1973 (new species); Kilgore and Allen, 1973 (new species); Edmunds, et al., 1976 (generic review); Allen, 1978 (generic revision); McCafferty, 1985 (new records); Allen and Murvosh, 1987 (new species); Kluge, 1992 (generic description); Lugo-Ortiz and McCafferty, 1995a (new species, records); Wang et al., 1998 (new species); Hofmann et al., 1999 (new species); Baumgardner and McCafferty, 2000 (new synonyms); Wiersema and McCafferty, 2000 (generic review); Molineri, 2003a (generic revision); Molineri, 2006 (family revision); Molineri and Zúñiga, 2006 (new species); Baumgardner, 2007 (new species).

2. Diagnosis. Differentiated from other leptohyphid genera by the following combination of characters: *Imago*: (1) compound eyes small and remote; (2) anterior parapsidal suture fused with posterior parapsidal suture (Fig. 1E); (3) male imago protibia ventrally with sharp, robust setae (Fig. 2H); (4) claws of male imago prolegs similar, blunt (Fig. 2G); (5) hind wings present on all males and most females, with elongate curved costal process (Fig. 2D); (6) plumidium present (Fig. 1E); (7) forceps three-segmented (Fig. 3D); (8) penes fused for approximately half their length, in the shape of a “Y” (Fig. 3D). *Larva*: (1) maxilla well-developed three-segmented palp and without an apical seta (Fig. 5A); (2) suture between galea and lacinia complete (Fig. 5A); (3) longitudinal ridge present on meso- and metafemora (Fig. 5F); (4) median elevated longitudinal ridge present on meso- and metatibia (Fig. 10F); (5) basal beak-like process on internal lamella of operculate gill (Figs. 6I; 15G); (6) ventral inferior lamellae of abdominal gill 2 parallel to dorsal lamellae (Fig. 6I; 15G).

3. Description. *Imago:* Length. Body, 5.0 – 8.0 mm; forewings, 7.0 – 8.0 mm; hind wings (when present), 2.0 – 3.0 mm. General coloration variable from pale to dark reddish brown; abdomen generally paler than thorax. Head. Compound eyes small (distance between eyes greater than distance across any one eye); two lateral ocelli, larger than median ocellus; occiput with a pair of small tubercles. Thorax. Coloration variable, but generally red to reddish-brown, with gray and black maculation; anterior parapsidal suture fused with transverse interscutal suture (Fig. 1E); plumidium present (Fig. 1E). Forewing (Fig. 19J): membrane hyaline, often tinged with yellowish or yellowish-brown; longitudinal veins hyaline to pale yellowish-brown; costal and subcostal veins often shaded with gray or reddish-brown; vein CuP not strongly curved towards A; vein iCu_2 free or united basally with iCu_1; iCu_1 attached basally with CuP, free, or attached to CuA or CuP by crossveins; MP_2 united basally to MP_1 or CuA by cross vein; hind wings present on all males, absent on most females; when present, with elongate costal process, and two to four longitudinal veins (Fig. 2D); hind margin of fore- and hind wings fringed with filiform setae. Legs: coloration highly variable; legs often reddish-brown with gray, black, or brown shading; tarsi of all legs five-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically-hooked (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G); foretibia of males with sharp spines along ventral surface (Fig. 2H). Abdomen. Translucent, shaded with grayish, blackish, or reddish. Genitalia (Fig. 3A): forceps three-segmented; first segment short, stout; second segment elongate; third segment small, globular. Penes with basal half fused, distal parts divergent, “Y” shaped; lateral margins sclerotized from base, extended to apex as a short spine; each spine medially to each membranous lobe. Cerci and median caudal filament present, well-developed.

Larva: Length. Body, 8.0 – 8.5mm; caudal filaments 3.0 – 3.5mm. General coloration reddish-brown to gray. Head. Coloration highly variable, often yellowish light brown to red, shaded with gray or black. Labrum (Fig.20A): dorsally with filiform setae along lateral margins; two rows of acuminate setae recessed from anterior margin; ventrally with single longitudinal row of acuminate setae near midline, interspersed with filiform setae; anterior and lateral margins with dense filiform and acuminate setae. Labium (Fig.20B): submentum moderately-developed (approximately twice as wide as long), with regularly-spaced acuminate setae along lateral margins; ventrally with numerous robust setae most abundant near midline; prementum ventrally with numerous filiform setae; labial palp three-segmented with numerous filiform setae; basal palpomere no more than two to three times longer than second and palpomeres combined; glossae and paraglossae subequal, fused except distally, with smooth or slightly serrated outer margins; glossae slightly recessed, rounded, and with robust setae; paraglossae with numerous filiform setae. Hypopharynx (Fig.20C): lingua apically rounded with numerous filiform and acuminate setae present on anterior margin; superlinguae oval, with numerous filiform and acuminate setae along anterior and lateral margins. Left Mandible (Fig.20D): outer incisor with two to four denticles, fused almost their entire distance; inner incisor with one or two denticles; prostheca arising at base of inner incisor, with highly branched setae projecting towards molar region. Right Mandible (Fig.20E): outer incisors with one to three denticles; inner incisors with one to denticles; prostheca arising at base of inner incisor with elongate setae projecting towards molar region; denticles of molar region mostly fused. Maxilla (Fig. 5A): suture between galea and lacinia present, complete; distal margin with numerous elongate and filiform setae; two or more setae at base of inner margin; palp elongate, three-segmented, without apical seta. Thorax. Coloration variable, often reddish-brown; some species yellowish to pale yellow; often shaded with black. Pro- and mesonotum (Fig. 5C) with or without well-developed anterolateral projections, and with (Fig. 4B) or without median tubercle. Legs: coxae sometimes with dorsal projections; profemur with transverse row of stout or elongate setae along dorsal surface, and anterior and posterior margins with or without variously modified setae (Figs. 5E; 22A – E); meso- and metafemur with longitudinal ridge (Fig. 5F), and variously modified and arranged setae along outer and/or inner margins and dorsal surface (Figs. 5F; 12A – B; 22F – G; 23A; 23B); tibia and tarsus of proleg with scattered setae along inner and/or outer margin (Figs. 5E; 22A – B, G; 22D), and with or without row of stout or elongate setae along dorsomedian surface; tibia of meso- and metaleg with median elevated ridge (Fig. 5F), with or without single row of stout or elongate setae along dorsoventral surface (Fig. 21F – G), and with or without scattered, elongate and/or filiform setae along inner and/or outer margins (Figs. 5G; 22F – G, 21C; 23A – B – C); claws with two to eight marginal and usually one marginal denticle (Figs. 24D – G) marginal denticle rarely absent or composed of three to five denticles. Abdomen. Coloration highly variable from pale yellow to dark reddish-brown; posterolateral projections sometimes present on segments seven through nine; gills present on segments two through six; operculate gill oval; ventral inferior lamella with basal beak-like process; gill formula: 2-3/6-10/6-8/5-8/1-5.

4. Proposed Synapomorphies. Adult: [Character 8*; State transformation 0-1] male imago foretibia with sharp, robust setae ventrally (Fig. 2H) (without sharp, robust setae); [28; 0-1] penes fused for one-half its length (Fig. 3D) (fused for approximately three-fourths its length or more [Fig. 3B, C]). Larva: [58; 1-0] suture between galea and lacinia present, complete (Fig. 5A) (suture absent or extremely [Fig. 10E, F]); [72*; 0-1] longitudinal ridge present on meso- and metafemora (Fig. 5F) (longitudinal ridge absent on femora II and III); [75*; 0-1] median elevated longitudinal ridge present on meso- and metatibia (Fig. 10F) (median elevated longitudinal ridge absent on mid- and hind tibia); [101*; 0-1] basal beak-like process on internal lamella of operculate gill (Figs. 6I, 15G) (beak-like process absent from internal lamella of operculate gill [Figs. 15H, 16E]); [107; 1-0] ventral inferior lamellae of abdominal gill two parallel to dorsal lamellae (Fig. 6I; 15G) (ventral inferior lamellae of abdominal gill two perpendicular to dorsal lamellae [Fig. 14H]).

5. Species Included (41). *L. albipennis* Molineri & Zúñiga [Colombia; A,L]; *L. alleni* Brusca [Mexico; L]; *L. berneri* Traver [Mexico, A]; *L. brevissimus* Eaton [Guatemala; A]; *L. brunneus* Allen and Brusca, 1973 [Mexico, Guatemala, L]; *L. castaneus* Allen, 1967 [Mexico, Guatemala, Costa Rica; L]; *L. carinus* Allen [Peru; L]; *L. coconuco* Molineri and Zúñiga 2006 [Colombia; A, L]; *L. cornutus* Allen [Argentina, Brazil; A, L]; *L. ecuador* Mayo [Ecuador; L]; *L. eximius* Eaton (= *L. bruchi* Navás, *Bruchella nigra* Navás, *L. nigra* (Navás), *L. niger* (Navás) [Argentina; A, L]; *Leptohyphes guadeloupensis* Hofmann and Sartori 1999 [Guadeloupe; A, L]; *L. illiesi* Allen [Peru; L]; *L. invictus* Allen [Peru; L]; *L. jamaicanus* Allen, 1973 [Jamica; L]; *L.*

jodiannae Allen [Peru; L]; *L. lestes* Allen and Brusca, 1973 [Mexico, Honduras; L]; *L. liniti* Wang, Sites & McCafferty [Ecuador; L]; *L. maculatus* Allen (= *L*. sp. 2 Roback, *L*. sp. 3 Roback, *L*. sp. 4 Roback, *L*. sp. Illies, *L. comatus* Allen, *L. hirsutus* Allen & Roback, *L. myllonotus* Allen & Roback 1969) [Peru; L]; *L. mandibulus* Baumgardner 2007 [Costa Rica; L]; *L. mollipes* Needham & Murphy [Bazil; A]; *L. murdocki* Allen, 1967 [Costa Rica; Panama; L]; *L. musseri* Allen, 1967 [Guatemala, Honduras; L]; *L. nigripennis* Molineri and Zúñiga 2006 [Colombia; A, L]; *L. nigripunctus* Traver (= *L. nigripunctum* [spelling]) [Venezuela, Mexico; A]; *L. peterseni* Ulmer [El Salvador, Guatemala, Brazil, Bolivia, Argentina; A]; *L. petersi* Allen (= *L*. Nymph no. 2 Needham and Murphy) [Peru; A]; *L. pilosus* Allen and Brusca [Mexico; L]; *L. populus* Allen [Brazil; L]; *L. plaumanni* Allen (= *L. pereirae* Da Silva) [Argentina, Brazil; A, L]; *L. priapus* Traver [Mexico; A]; *L. rolstoni* Allen, 1973 [Dominican Republic, L]; *L. sabinas* Traver, 1958 [Mexico; A, L]; *L. setosus* Allen (= *L*. sp. 3 Roback, *L*. sp. 5 Roback, *L. echinatus* Allen & Roback 1969) [Peru; A, L]; *L. spiculatus* Allen and Brusca, 1973 [Mexico, L]; *L. tacajalo* Mayo (= *L. albus* Mayo) [Ecuador; L]; *L. tarsos* Allen and Murvosh, 1987 [Mexico, L]; *L. tuberculatus* Allen (= *L*. sp. 6 Roback) [Peru; L]; *L. vulturnus* Allen, 1978 [Honduras; L]; *L. zalope* Traver, 1958 [United States, Mexico, Guatemala, Honduras, Nicaragua, Costa Rica; A, L].

6. Distribution. Eastern and southwestern United States, and all countries of Middle and South America. Several species are also known from Caribbean Islands.

7. Comments. *Leptohyphes* was described by Eaton (1882), based upon a very brief description of a dried adult female from Cordova, Argentine Republic. Eaton

(1884) provided a more extensive, but still brief, description of the genus and its associated type species. Kluge (1992) provided a detailed description of the type species, a female imago, and clarified the status of the genus. Molineri (2003b) reared and described the male and associated the larval stage clarifying the taxonomic status of the genus. Most species are known from either the larval or adult stage.

NOTE. Only South American material studied is listed here. The North and Central American material is listed under each individual species in the revision given in Chapter IV.

8. Type Material Examined. *Leptohyphes illies* Allen: PARATYPES: PERU: Río Sihuas near Arequipa, 17.v.1958, 4L, J. Illies [CAS]; Station 2, Río Chillon, 3.v.1958, 6L, J. Illies [CAS]; Station 3, Río Chillon, 3.v.1958, 1L, J. Illies [CAS]; Andamago River near Ongoro, 16.v.1958, 5L, J. Illies [CAS]; Station IV, Río Chillon, 3.v.1958, 4L, J. Illies [CAS]; Río Chillon, Station 5, 3.v.1958, 4L, J. Illies [2L CAS; 2L FAMU]; irrigation canal, near Hacienda Ongoro, 16.v.1958, 7L, J. Illies [CAS]. *Leptohyphes jodiannae* Allen: PARATYPES: PERU: San Martin, Rio Supte Grande, 10 km. E. Tingo Maria, , 26, vi, 1963, 13L, W.L. Peters [CAS]. *Leptohyphes petersi* Allen: PARATYPES: PERU: Huanuco, Río Rondos, km 14 on Monzon Road, 25.vi.1986, 4L, W.L. Peters [FAMU]; Rio Huallaga, Tingo Maria., 1.viii.1963, 54♂ imagos, W.L. Peters [FAMU]; same but, 14/16.viii.1963, 1♂ [FAMU]. *Leptohyphes plaumanni* Allen: PARATYPES: BRASIL: Ariranha River, Nova Teutonia, xi.1961, Fritz Plaumann, 2L [CAS]; Río Serra Mantequeira, Aquas de Prata, 23.vi.1958, J. Illies, 1L [CAS]; Nova Teutonia, iii.1962, F. Plaumann, 5L [CAS]. *Leptohyphes setosus*

Allen: PARATYPES: PERU: Huanuco Prov, Rio Huallaga, Tingo Maria, 29/31.vii.1963, 5, Larvae and 1 Adult, W.L. Peters [FAMU]; same but, 4/16.viii.1963, 1L [FAMU]; same but, 26.vii.1963, 3L [FAMU]. *Leptohyphes tacajalo* Mayo: PARATYPES: Ecuador, Cotopaxi, Macuchi, Braden Quebrada, 6.vi.1945, 17L, V.K. Mayo (FAMU). *Leptohyphes tuberculatus* Allen: PARATYPES: PERU: Huanuco Prov, Río Huallaga, Tingo Maria, 14/16.viii.1963, 1 slide, W.L. Peters [FAMU]; same but, 29/31.vii.1963, 3 3 slides, W.L. Peters [FAMU]; same but, 26.vii.1963, 4L [FAMU].

9. Other Material Examined. *Leptohyphes cornutus* Allen: BRASIL; Santa Catarina, Xanxere, Rio Toldo, 2L (2 slides, #DB05ix2502 and #DB05ix2503) [IFML]; ARGENTINA: Misiones, Parque Prov. Urugua-i A Uruzu, Ruta Prov. 19, 7-11.xii.1999, Molineri, 4♂, 1♀ imagos [TAMU]. *Leptohyphes eximius* Eaton: ARGENTINA: Jujuy; Sierra de Santa Barbara, Río entre El Fuerte y Palma Sola, 16.ix.1998, 7L, Dominguez, Molineri, and Ubero [TAMU]. *Leptohyphes plaumanni* Allen: ARGENTINA: Misiones, R.P. 7 - Aristobulo del Valle, Rio Cuna Piru, 19/20.xi.1998, Dominguez et al, 2L, 3♂ imagos [TAMU]; *Leptohyphes guadeloupensis* Hofmann and Sartori: Guadeloupe, Pled Grande Chute, 3.xi.1997, 2L (TAMU);

Genus *Allenhyphes* Hofmann and Sartori, 1999

1. Synonymical Listing. *Allenhyphes* Hofmann and Sartori, 1999 in Hofmann *et al.*, 1999:67 (Type Species: *Leptohyphes flinti* Allen, 1973); Allen, 1967 (new species description, *Leptohyphes asperulus*); Allen and Roback, 1969 (new species description, *Leptohyphes spinosus*); Allen, 1973 (new species description, *Leptohyphes flinti*) Allen, 1978 (new species description, *Leptohyphes vescus*); Hofmann & Sartori in: Hofmann *et al*., 1999 (original generic description, stage description); Molineri and Flowers, 2001 (distribution records); Baumgardner, 2003 (new synonym); Wiersema and McCafferty, 2000 (generic review); Molineri, 2004 (generic revision).

2. Diagnosis. Differentiated from other leptohyphid genera by the following combination of characters: Adult: (1) compound eyes small and remote; (2) anterior parapsidal suture fused with posterior parapsidal suture (Fig. 1E); (3) hind wing present (males only), with elongate costal process (Fig. 2D); (4) forceps three-segmented; (5) penes fused for one-half to three-fourths their length, without penal spines; (6) large, ventrally-directed spine present at base of median caudal filament (Fig. 8E). Larvae: (1) maxillary palp two-segmented with an apical seta (Fig. 19D), or three-segmented; (2) operculate gill ovoid and relatively small.

3. Description. *Imago:* Length. Body, 3.0 – 4.0 mm; forewings, 2.5 – 3.5 mm; hind wings 0.5mm. General coloration pale brown, abdomen translucent. Head. Tan to brown, with black maculation and brown lines; eyes small, black (distance between eyes greater than distance across any one eye); three ocelli whitish, black basally; antennae white. Thorax. Pronotum translucent with dark stippling; meso- and metathorax tan or brown; plumidium present. Forewings: membrane hyaline, longitudinal veins dark brown; vein CuP strongly curved toward A (Fig. 1G); vein iCu_2 free (Fig. 8A), or fused with iCu_1 (Fig. 1G); vein iCu_1 attached basally to CuP; vein MP_2 connected basally to CuA and MP_1 by crossveins (Fig. 1G), or only to MP_1 by crossvein; vein iMP free, or connected to veins MP2 and MP1 by crossveins; hind wings present on males, absent on females, with elongated costal process (Fig. 2D), and two longitudinal veins; hind margin of fore- and hind wings fringed with setae. Legs: tan to brown with dark brown lines; tarsi of all legs four-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G). Abdomen. Segments 1 – 8 translucent; segments 9 – 10 tan; ventrally directed spike present at base of median caudal filament (Fig. 8E). Genitalia: forceps three-segmented; penes narrow, fused for approximately one-half to three-fourths its distance.

Larva: Length. Body, 3.0 – 4.0 mm; caudal filaments 2.0 – 3.0 mm. General coloration light brown; body relatively long, delicate, without tubercles. Head. Light brown with brown markings; labium (Fig.23A) with an expanded and laterally rounded submentum; prementum with slightly differentiated glossae and paraglossae; labial palp three-segmented, terminal segment small, about as long as segment two. Labrum with a moderately deep anteriomedian cleft; ventrally with a longitudinal row of elongate setae; branched setae present along dorsal margin and anteriolateral margin. Maxilla (Fig.23B) lacking well-developed suture between galea and lacinia; palp two-segmented with an apical seta (Fig. 19D) or three-segmented; elongate, branched setae present on apical margin; outer apical surface with numerous hair-like setae. Right mandible with four outer and three inner incisor denticles; left mandible with three inner and outer incisor denticles. Thorax. Light brown with brown markings; tubercles absent. Legs pale; dorsal mediolongitudinal row of branched setae on mid- and hind tibiae (Fig. 11E); profemora with transverse row of spatulate setae dorsally; claws with four to six marginal and single row of four to six submarginal denticles. Abdomen. Light brown with dark brown markings. Gills present on segments two through six; operculate gills oval, inserted dorsally on abdomen; gill formula: 3/3-4/3-4/3/2

4. Proposed Synapomorphies. Adult: [Character 34*; State transition 0-1] male with large, ventrally directed spine present at base of median caudal filament (Fig. 8E) (median caudal filament without ventrally directed spine). Larva: None.

5. Species Included (4). *A. asperulus* (Allen) [Peru; L]; *A. flinti* (Allen) [Dominica, Guadeloupe, Montserrat, Panama, Venezuela; A, L]; *A. spinosus* (Allen) [Peru; L]; *A. vescus* (Allen) [Guatemala, Mexico, United States; A, L].

6. Distribution. Two species are known only from Peru in South America, one from the south-central United States (Texas), Mexico and northern Central America, and one from northern South America and several Caribbean islands.

7. Comments. In their review of the family Leptohyphidae, Wiersema and McCafferty (2000) included eleven species in the genus. One species, *A. michaeli* Allen, was synonymized with *A. vescus* (Baumgardner 2003), leaving ten species. Molineri (2004) showed the genus to be paraphyletic, with most of the species proposed by Wiersema and McCafferty (2000) being transferred to other genera such as *Tricorythopsis* and *Traverhyphes*. Four species are currently included in the genus, although two (*A. asperulus*, and *A. spinosus*) are doubtfully included (Molineri 2004). Once the adult stages are known for these two species, their correct placement can be confirmed. Although adult males are easily recognizable due to the presence of a large spine at the base of the median caudal filament, larvae can be difficult to distinguish from other closely-related genera such as *Traverhyphes* and *Yaurina*. Two species are known from only the larval stage, two from both life stages.

8. Type Material Examined. *Allenhyphes asperulus* (Allen): PARATYPE: PERU: San Martin Prov., Río Pendescia, Tulumayo Valley, 24 km E. Tingo Maria, vi-viii.1963, 1L, W.L. Peters [CAS]. *Allenhyphes flinti* (Allen): PARATYPE: DOMINICA: Springfield Est., 20-26.vii.1963, 1L, OS Flint [(FSCA/FAMU E2036]. *Leptohyphes vescus*: HOLOTYPE: Texas: Uvalde Co.; Rio Sabinal at Utopia, 2-viii-68, R.K. Allen; 2 slides [CAS, #13607].

9. Other Material Examined. *Allenhyphes flinti* (Allen): DOMINICA: Blenheim River, Blenheim Estate, 16.vi.1996, D. Bass, 3L (TAMU); same but, Check Hall River, Springfield Estate, 8-9.vi.1996, 6L (TAMU); same but, Banana Gutter Creek, Stonefield Estate, 11.vi.1996, 3L, 1 slide (TAMU); same but, Lor River, Fond Melle, 2L (TAMU). GUADELOUPE: Riv. Petit David Premier Bras, Aire pic-nic, 13.ix.1997, P.L. Martin, 8L; Troubleau, Bassins 29, Riv. uatre Bois, 29.iii.1997, 40 adults (TAMU); same but, Troubleau, Bassins 29, Riv. uatre Bois, 29.iii.1997, 8L, [TAMU]. MONTSERRAT: Lawyers River, Woodlands, 22.vi.1996, D. Bass, 1L, 1 slide (TAMU). PANAMA: Chiriquí, Fortuna, Río Chiriquí (N08°44’W44°15’, elev. 3100, ft), 4.xii.1977, >100 ♂ and ♀ imagos, R.W. Flowers [TAMU]; Bocas del Toro, Corriente Grande, Río Changuinola (N09°17’30”; W82°31’41”, elev. 50m), 20-26.ii.1980, 25♂ imagos, H. Waida [TAMU]. ST. KITTS: West Farm Gut, West Farm Estate, 19.v.1997, D. Bass, 2L (TAMU). *Allenhyphes vescus* (Allen): GUATEMALA: El Progreso: Quebrada Las Pericas at Hwy. 17, 11.1 Km W. from jct. with Hwy. CA 9

(14º54'54"N; 90º5'52"W), 1040 ft., 11L, 5 ♂ (reared), 1♀ (reared), 12.vii.2001, D.E. Baumgardner (TAMU); Río Hato at CA Hwy. 9, ca. 5.9 Km E. from jct. with Hwy. 17, Magdalena (14º55'11"N; 89º57'56"W), 1040 ft, 5L, 14.vii.2001, D.E. Baumgardner (TAMU); Zacapa: Río Cayo at CA Hwy. 9, 2.3 Km E. Santa Cruz, (15º0'54"N; 89º39'9"W), 830 ft, 6L, 14-vii-2001, D.E. Baumgardner (TAMU). MEXICO: Nuevo Leon: Río Cabazones at Hwy. 85, 15 mi. N. Linares, 16.v.1995, 1L, D.E. Baumgardner [TAMU]; Tamaulipas: spring (at local park) (at Hidlago Ave?) near town of Jaumave, off Hwy. 101; 16.v.1995, 2♂, D.E. Baumgardner; R. Guayaalejo (Tamasi) off Hwy 247nr. San Ingnacio, 26.v.1993, B. Henry, 18L. UNITES STATES: Texas: Bandera Co; Medina 3 mi. NW, Medina River, 26.v.1991, 3♂, DE Bowles [UNT]; Medina R. at TX. Hwy. 16, 1 mi. N. Medina (N25°48'59"; W99°15'33"), 23.vi.1990, 20♂, DE Bowles [UNT]; Medina R. at Horse Valley Ranch, 7 mi. NW TX 16 & FM 2107, 12.iv.1992, 1L, D.E. Baumgardner [UNT]; same but, 29.v.1991, 2♂, DE Bowles [TAMU]; Seco Ck., Just S. of FM 470, 11.iv.1993, 1L, L. Gilpin, V. Castillo [SWTS]; same but, 18.iii.1993, 1L, L. Gilpin, V. Castillo [SWTS]; Campe Verde, Verde Creek, 08.viii.1992, 11♂, DE Bowles [TAMU]. Comal Co., Honey Ck. in Honey Ck. St. Natural Area in Guadalupe R. State Pk. (N29º51'34.8"; W98º29'4.1"), 08.iii.1997, 2♂ (reared), 1♀ (reared), 9L [TAMU]; same but, 02.ix.1995, 1♀ (reared); Guadalupe River, Golden Crossing, Balconian, 10.vii.1991, 1♂, DE Bowles [UNT]. Kimble Co., Llano R. @ Texas Tech Field Station, 07.xi.1998, D.E. Baumgardner, 1♂ (reared) [TAMU]. Jct. Llano River and RR 385, Balconian (N30°35'17"; W99°35'58"), 01.vi.2000, 3L, EG Riley [TAMU]. Mason Co.; James River, 19.vi.1993, 6L, JL Cook [TAMU]. Menard

Co.; San Saba R. at FM 864 low water bridge, FT. McKavitt, 11.iv.1992, 4L, D.E. Baumgardner [TAMU]. Real Co.; Nueces R. at Tx. Hwy. 55 (Barksdale), 12.iv.1992, 2L, D.E. Baumgardner [UNT]; West Frio R. at US 83, ca. 1 mi. N. Leaky, 12.iv1992, 1L, D.E. Baumgardner [TAMU]. Val Verde Co., Dolan Falls Preserve, Devils River; The Nature Conservancy (N29º53'0.7"; W100º59'37.7"), 08.xi.1998, D.E. Baumgardner, 1♂ (TAMU). Val Verde Co., Devils River, Dolan Falls, 19.x.1993, C.R. Nelson (#6017) & S.M. Stringer, 2L (UT). Williamson Co., Georgetown, San Gabriel Park, riffles belowthe little dam on the San Gabriel River, 2 Oct. 1996, N. Wiersema, 1L (NW); Brushy Creek, 09.vi.1998, 1L, R. Fields & L. Tolley [TAMU].

Genus *Yaurina* Molineri, 2001

1. Synonymical Listing. *Yaurina* Molineri 2001b:338 (Type Species: *Yaurina yuta* Molineri, 2001); Molineri, 2004; Allen, 1967 (new species description, *Leptohyphes rallus*); Wiersema and McCafferty, 2000 (transfer of *Leptohyphes rallus* to *Allenhyphes*); Molineri, 2001b (original generic description and new species, *Y. mota, Y. yapa*, and *Y. yuta*). Molineri, 2004 (phylogeny of *Yaurina*, and transfer of *Allenhyphes rallus* (Allen) to *Yaurina*).

2. Diagnosis. Differentiated from other leptohyphid genera by the following combination of characters: Adult: (1) compound eyes small and remote; (2) anterior parapsidal suture fused with posterior parapsidal suture (Fig. 1E); (3) hind wing present (males only), with elongate costal process (Fig. 2D); (4) forceps three-segmented; (5) internal basal projections of styliger plate present (Fig. 3C) and acute; (6) penes long and slender with a pair of long spine-like appendages present on venter (Fig. 8D). Larvae:

(1) labium with glossae and paraglossae almost completely fused (Fig. 10A); (2) outer incisors of left mandibles formed by 3 denticles; (3) maxillary palp two-segmented, apical setae absent (Fig. 16B); (4) submarginal denticles arranged in single row.

3. Description. *Imago:* Length. Body, 3.5 – 3.5 mm; forewings, 3.0 – 3.5 mm; hind wings, 0.40 – 0.50 mm. General coloration light yellowish-orange to pale; abdomen whitish translucent. Head. Whitish with gray and brown maculation; compound eyes small, remote (distance between eyes at least three times greater than distance across any one eye). Thorax. Coloration variable, yellowish-white to light brown, extensively shaded with gray and black; anterior and posterior parapsidal sutures fused with transverse interscutal suture (Fig. 1E); plumidium present. Forewings: membrane hyaline, shaded with brown; longitudinal veins grayish-brown; gray along costal and subcostal veins; vein CuP strongly curved towards A; vein iCu_2 free, arising from base of $ICu_{1;}$ vein MP_2 united basally to veins CuA and MP_1 by cross vein; hind wings present, with elongate costal process, and two weakly-developed longitudinal veins. Legs: yellowish-white with light brown shading; tarsi of all legs four-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G). Abdomen. Whitish translucent, shaded with gray; sterna whitish. Genitalia: forceps three-segmented, basal segment short and stout; penes elongate, completely fused except for a small apical furrow (Fig. 8D); pair of long, spine-like appendages present along ventral side of penes (Fig. 8D).

Larva: Length. Body 3.0 – 4.5 mm; caudal filaments 1.5 – 2.5 mm. General coloration pale yellowish to yellowish light brown. Head. Yellowish light brown, shaded with gray. Labium (Fig. 10A) with greatly-expanded submentum; labial palp three-segmented, terminal segment small; glossae and paraglossae almost completely fused. Labrum with deep anteriomedian cleft; elongate setae present along lateral margins. Maxilla with galea – lacinia completely fused, except on apical furrow; basal inner margin with four to six elongate setae; distal margin densely covered with filiform setae; inner margin with six to seven elongate spines; palp two-segmented (Fig. 19B). Outer and inner incisor of right mandible each with two denticles; prostheca present, well-developed; outer margin strongly convex. Outer incisor of left mandible with three denticles, inner incisor two denticles; prostheca present, well-developed, with elongate setae projecting towards molar region. Thorax. Pale yellow, shaded with gray and black. Pro- and mesonotum without well-developed anterolateral projections. Legs: profemur with transverse row of elongate setae along dorsal surface; meso- and metafemur with elongate setae along outer margin; tibia and tarsus of proleg with elongate setae along inner margin; tibia of meso- and metaleg with two rows of elongate setae along inner and one row of elongate setae along outer margin; tarsi of all legs with one row of elongate setae along inner margin; claws with four to five marginal and five to six submarginal denticles. Abdomen. Whitish translucent, shaded with yellow and brown; gills present on segments two through six; operculate gill oval, with a weak transverse and medial ridge; gill formula: 2/3/3/3/1.

4. Proposed Synapomorphies. Adult: [Character 33*; State transformation 0-1] pair of long spine-like appendages present on venter on venter of penes (Fig. 8D) (penes without pair of long spine-like appendages). Larvae: [43; 0-2] glossae and paraglossae highly fused (Fig. 10A) (glossae and paraglossae not highly fused); [112; 1-2] abdominal gill four with two lamellae (abdominal gill four with four to six lamellae).

5. Species Included (4). *Y. mota* Molineri [Argentina; A,L]; *Y. ralla* (Allen) [Peru; L]; *Y. yapa* Molineri [Ecuador; A subimago]; *Y. yuta* Molineri [Argentina; A,L].

6. Distribution. All four species are known only from South America.

7. Comments. Two species (*Y. mota* and *Y. yuta*) are known from both life stages, *Y. ralla* only from the larval stage, and *Y. yapa* only from the male imago. According to Molineri (2004), larvae are indistinguishable at the species level. Larvae of *Yaurina* are most similar in appearance to *Allenhyphes* larvae, due to their thin, elongate bodies. Molineri (2004) provides taxonomic keys to larvae and adults of the genus.

8. Type Material Examined. *Yaurina mota* Molineri: PARATYPES: ARGENTINA: Jujuy; El Carmen, Camino de Cornisa, Rio Las Lanzas (S24d27"27'; W65d17"48'; 1250, meters), 2L, 1♂ and 1♀ imago, 3.iii.2000, coll. Cuezzo, Romero, Manzo, Molineri [IFML].

9. Other Material Examined. *Yaurina yuta* Molineri: BOLIVIA: La Paz: A entre Caranavi y Guanai (S15°40'18"; W67°42'04", elev. 500 m), 27.xi.2000, 5♂, 5♀ [TAMU].

Genus *Lumahyphes* Molineri, 2004

1. Synonymical Listing. Molineri 2004 in Molineri and Zúñiga 2004:20 (Type species: *Lumahyphes guacra* Molineri 2004:25); Molineri and Zúñiga, 2004 (original generic description, new species); Molineri, 2004 (generic revision, new species).

2. Diagnosis. Differentiated from other leptohyphid genera by the following combination of characters: Adult: (1) compound eyes small and remote; (2) anterior parapsidal suture (aps) fused with transverse interscutal suture (tis) (Fig. 1E); (3) vein CuP not strongly curved towards A (Fig. 1F); (4) vein ICu_2 free (Figs. 2A; 8A); (5) hind wing present (males only), with elongate costal process (Fig. 2D); (6) internal basal projections of styliger plate present (Fig. 3C) and acute; (7) penal spines present, inserted laterally, extending anteriorly (Fig. 3E – F); (8) forceps three-segmented. Larvae (1) maxillary palp three-segmented, without an apical setae; (2) profemora with a transverse row of long bifid spines.

3. Description. *Imago:* Length. Body, 2.5 – 3.5 mm; forewings, 2.5 – 3.5 mm; hind wings, .35 – .65 mm. General coloration whitish light brown to orangish yellow. Head. Brownish gray to yellowish white; compound eyes small, remote (distance between eyes less greater than distance across any one eye). Thorax. Translucent whitish to light brown with gray and black bands; anterior parapsidal suture fused with posterior parapsidal suture (Fig. 2D); plumidium present (Fig. 2D). Forewings: membrane hyaline, shaded with light brown; longitudinal veins grayish-brown, costal and subcostal veins darker; vein CuP not strongly curved towards A (Fig. 1F); vein iCu_2 shorter than iCu_1, free at base (Fig. 2A; 8A); iCu_1 united basally to veins CuP and CuA by crosveins; MP_2 united basally to CuA and MP_1 by crossvein; iMP free at base or united basally to MP_2 by crossvein; hind wings present in male, absent in female, with elongate costal process, and two longitudinal veins. Legs: yellowish-white with light brown shading; tarsi of all legs four-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G). Abdomen. Translucent yellowish white, shaded with gray on submedian and sublateral longitudinal bands. Genitalia (Fig. 3E): forceps three-segmented; penes almost completely fused, except apical furrow (Fig. 3F); apex of penes with two pairs of membranous lobes (Fig. 3F), and a pair of long curved spines directed anteriodorsally (Fig. 3D).

Larva: Length. Body, 3.5 – 4.5 mm; caudal filaments 1.5 – 2.5 mm. General coloration yellowish orange to brownish yellow with gray and black markings. Head. Yellowish, shaded with gray or black; without tubercles or spines. Labium (Fig. 10A) with greatly-enlarged submentum; labial palp three-segmented, terminal segment small; glossae and paraglossae almost completely fused, ventrally covered with elongate and bipectinate setae; paraglossae with pointed apex. Labrum with shallow anteriomedian cleft, and double row of elongate setae ventrally; elongate and filiform setae present on dorsum and lateral margins. Maxilla with galea – lacinia mostly fused, except on apical furrow; basal inner margin with five or six elongate setae; distal margin covered with filiform setae; subapical inner margin with row of seven spines; palp three-segmented, without an apical seta. Outer and inner incisor of right mandible each with two denticles; prostheca present, well-developed. Outer incisor of left mandible with three denticles, inner incisor with two denticles; prostheca present, well-developed, with elongate setae projecting towards molar region. Thorax. Yellowish, shaded with gray and black. Pro- and mesonotum without anterolateral projections. Legs: profemur with transverse row of elongate, bifid spines along dorsal surface; elongate, bifid spines along outer margin; meso- and metafemur with elongate, bifid spines along outer margin; tibia and tarsus of proleg with double row of elongate setae along inner margin; tibia of meso- and metaleg with double row of elongate setae along inner and one row of elongate setae along outer margin; tarsi of all legs with one row of elongate setae along inner margin; claws with eight marginal and double row of one to four submarginal denticles in each row. Abdomen. Whitish translucent, shaded with gray; gills present on segments two through six; operculate gill oval, with a weak transverse ridge; gill formula: 2/4/4/3/2.

4. Proposed Synapomorphies. Adult: [Character 31*; State transition 0-1] penal spines present, inserted laterally, extending anteriodorsally (forming a ring in some species) (penes without penal spines extending anteriodorsally). Larvae: None

5. Species Included (3). *Lumahyphes guacra* Molineri [Argentina, Bolivia; A, L]; *Lumahyphes pijcha* [Bolivia, Colombia; A, L]; *Lumahyphes yagua* Molineri and Zúñiga [Colombia; A, L].

6. Distribution. Known only from South America; an undescribed species has been reported from Chihuahua, Mexico (Molineri and Zúñiga, 2004).

7. Comments. Larvae of *Lumahyphes* can be difficult to distinguish from larvae of *Leptohyphes*. Characters of femoral spines and other details must be carefully reviewed. Molineri (2004) provides taxonomic keys to larvae and adults of the genus. All three species are known from both life stages.

8. Type Material Examined. None

9. Other Material Examined. *Lumahyphes guacra* Molineri: BOLIVIA: Río Blanco, cerca de 11%, camino entre Sta. Cruz y Trinidad (S15°21'40"; W63°17'29", elev. 250 m), 14.vi.2000, 3♂ and 3♀ imagos, Dominguez [TAMU].

Genus *Traverhyphes* Molineri, 2001

1. Synonymical Listing. Molineri, 2001:130 (Type species: *Leptohyphes indicator* Needham and Murphy, 1924:33); Needham and Murphy, 1924 (species description); Allen, 1967 (species description); Allen, 1978 (species records); Hubbard, 1982 (species records); Wiersema and McCafferty, 2000 (species listings); Molineri, 2001 (original generic description); Molineri, 2004 (new species, stage descriptions, cladistic analysis).

2. Diagnosis. Differentiated from other leptohyphid genera by the following combination of characters: *Imago*: (1) compound eyes small and remote; (2) anterior and posterior parapsidal sutures fused with transverse interscutal suture (Fig. 1E); (3) veins CuP strongly curved towards A (Fig. 1G); (2) hind wing present (males only), with elongate costal process (Fig. 2D); (3) forceps three-segmented (Fig. 3C); (4) internal and/or external basal projections of styliger plate present (Fig. 3C) and rounded or acute; (5) accessory dorsal structure present (Fig. 3G – H); (6) penal spines present, short, inserted dorsally or dorsolaterally (Fig. 3G – H). *Larvae:* (1) maxillary palp one- or two-segmented (Fig. 19A, E), with or without apical setae; (2) gill six with one or two lamellae; (3) profemur with a transverse row of elongate spines, bifid or smooth along apical margin.

3. Description. *Imago:* Length. Body, 2.5 – 4.5 mm; forewings, 3.0 – 4.5 mm; hind wings, 0.40 – 0.90 mm. General coloration light yellowish-brown, gray or white shaded with gray or black. Head. Yellowish, shaded with brown, gray, or black; compound eyes small, remote (distance between eyes at least three times greater than distance across any one eye). Thorax. Coloration variable, generally yellowish-brown with gray or black coloration; some species translucent; anterior parapsidal suture fused with posterior parapsidal suture (Fig. 2D); plumidium present (Fig. 2D). Forewings: membrane hyaline, shaded with yellow; longitudinal veins yellowish-brown; costal and subcostal margins sometimes shaded with brown; vein CuP curved (Fig. 1G) or not curved towards A (Fig. 1F); vein iCu_2 free (Fig. 2A) or arising from base of iCu_1 (Fig. 1G); vein iCu_1 united basally with CuP or CuP and CuA by crossvein (Fig. 8A); vein MP_2 united basally to vein CuA or CuA and MP_1 by cross vein (Fig. 1G); hind wings present, with elongate costal process (Fig. 2D), and two longitudinal veins. Legs: yellowish-white, shaded with gray and/or black; tarsi of all legs four-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G). Abdomen. Translucent yellowish white, shaded with gray or black. Genitalia: forceps three-segmented (Fig. 3C); internal and/or external basal projections of styliger plate present (Fig. 3C) and rounded or acute; accessory dorsal structure present (Fig. 3G – H); penal spines present, short, inserted dorsally or dorsolaterally (Fig. 3G – H).

Larva: Length. Body, 2.5 – 4.0 mm; caudal filaments 2.0 – 4.0 mm. General coloration yellowish-brown, often with gray, black, or purplish markings. Head.

Yellowish-light brown to reddish-brown, often shaded with gray or black. Labium with greatly expanded submentum (Fig. 10A), and sparse elongate setae; labial palp three-segmented, terminal segment small, densely covered with elongate setae on all segments; glossae and paraglossae almost completely fused. Labrum with deep anteriomedian cleft (Fig. 9D); elongate setae present along lateral margins; sparse setae present along dorsal margin. Maxilla with galea – lacinia completely fused, except on apical furrow; basal inner margin with five to eight elongate setae; distal margin densely covered with filiform setae; inner margin with five to eight thick and elongate spines; palp one (Fig. 19E) or two-segmented (Fig. 19A), with apical seta. Outer incisor of right mandible with two or three denticles; inner incisor with one or two denticles; prostheca present, with elongate seta projecting towards molar region; outer margin slightly convex. Outer incisor of left mandible with three or four denticles; inner incisor with one or two denticles; prostheca present, well-developed, with elongate setae projecting towards molar region; some species with small tooth-like projection present at base of molar region. <u>Thorax.</u> Coloration variable, often pale brownish to dark reddish-brown; often shaded with gray and black. Pro- and mesonotum without tubercles or anterolateral projections. Legs: profemur with transverse row of elongate setae along dorsal surface, and scattered filiform and elongate setae along inner (anterior) and outer (posterior) margins (Fig. 11I); meso- and metafemur with filiform setae along inner margin, and elongate setae along outer margin; tibiae of all legs with two rows of elongate setae along inner margin, and filiform seta along outer margin; metatibia also with elongate setae along outer margin; tarsi of all legs with row of elongate setae along inner margin, and scattered filiform seta along outer margin; claws with seven to ten marginal denticles, and two rows of submarginal denticles (one row with single denticle, other row with four to six denticles). Abdomen. Yellowish light brown to dark reddish-brown; gills present on segments two through six; operculate gill oval, with a transverse ridge; some species also with medial ridge (Fig. 14D); gill formula: 3/3 – 4/3 – 4/3/1 – 2.

4. Proposed Synapomorphies. Adult: [Character 31; State transformation 0-2] Penal spines inserted dorsally on penes (Fig. 3D). Larva: [112; 1-2] abdominal gill 4 with 2 – 3 lamellae.

5. Species Included (7). *Traverhyphes chiquitano* Molineri [Bolivia; A, L]; *Traverhyphes edmundsi* (Allen) [Argentina, Brazil; A, L]; *Traverhyphes indicator* (Needham and Murphy) [Argentina, Brazil; A, L]; *Traverhyphes nanus* (Allen) [Costa Rica, Colombia; A, L]; *Traverhyphes pirai* Molineri [Brazil; male subimago]; *Traverhyphes yuati* Molineri [Argentina; A, L]; *Traverhyphes yuqui* Molineri [Bolivia; A].

6. Distribution. Known from South America north to Costa Rica.

7. Comments. The genus is widely distributed across South America, with only one species known from Middle America, and none from north of Costa Rica. Molineri (2004) provides taxonomic keys to larvae and adults of the genus. Most species are known from both life stages. Only two species, *T. pirai* and *T. yuqui*, are known from one life stage, in this case the adult.

8. Type Material Examined. *Leptohyphes nanus*: PARATYPE: CANAL ZONE: Rio Camaron, N. edge Fort Clayton on Chiva-Chiva Road, 9.ix.1963, W.L.

Peters & M. McKeen, 1L, 1 slide [CAS]. *Leptohyphes edmundsi*: PARATYPE: BRAZIL: Parana State, Rio Catiras, Morrestes, iv.1965, 9L, F. Plaumann [CAS].

9. Other Material Examined. *Traverhyphes edmundsi* (Allen): ARGENTINA: Misiones, Parque Prov. Urugua-i A Uruzu, Ruta Prov. 19, 7-11.xii.1999, 4L, 4♂ imagos, Molineri [TAMU]. *Traverhyphes indicator* (Needham and Murphy): ARGENTINA: Misiones, Parque Prov. Urugua-i A Uruzu, Ruta Prov. 19, 7-11.xii.1999, 4♂ imagos, 4L, Molineri [TAMU]; 25 Km al S. de El Soberbio, 21.xi.1998, 5♂ imagos, 5L, Dominguez, Molineri, Nieto [TAMU]. *Traverhyphes nanus* (Allen): COSTA RICA: Alajuela; 3 km SE Rio Cuarto, Hwy. 140, Río Hule (N10°20'; W84°12'), 15.i.2000, 3L, WDS [TAMU]; N of Bijagua, Río Zapote (N10°44'45"; W85°05'29"), 6.vi.2000, 3L, WDS [TAMU]. Puntarenas; Río Jaba at Las Cruses Biological Station, ca. 14 Km. S. San Vito (elev. 4000 ft.), 23-24.vi.2001, 1L, D.E. Baumgardner [TAMU]; Quebrada Culebra at Las Cruses Biological Station, ca. 14 Km S. San Vito, 24.vi.2001, 12L, D.E. Baumgardner [TAMU]; 1 Km S Coloradito Norte, Rio Coloradito at Hwy. 2 (N08°36'10"; W82°54'07"), 17.vi.2000, 1L, WDS [TAMU]; Río Baru at Baru, ca. 5 Km NE Dominical, 22.vi.2001, 1L, D.E. Baumgardner [TAMU]; 14.5 Km N. Ciudad Neily, unnamed stream (N08°42'44"; W82°56'05", elev. 1070 m), 17.vi.2000, 1L, WDS [TAMU]. Guanacaste; Est. Maritza, Quebrada Marilin (SWRC tray #93) (N10°57'04"; W85°29'24", elev. 600 m), 3L, 1♂ imago (reared) [IFML]; Rincon de la Vieja Pk., trail, 18.i.2000, 2L, WDS [TAMU]. HONDURAS: El Paraiso; 50 km. E. Danli, Trib. Rio Guayambre at Junct. Hwy. #4, 3.ix.1964, 2L, J.S. Packer [CAS]; 38 km. E. Zamorano on Hwy. #4, stream 31.x.1964, 1L, J.S. Packer [CAS].

HONDURAS: 1964, 1L, J.S. Packer [CAS]. PANAMA: Canal Zone, Pipeline Rd., Quebrada Juan Grande (elev. 20 m), 25.xii.1977, R.W. Flowers, 1L (TAMU). Bocas del Toro, Quebrada Bonyic, nr. mouth, 25.iv.1985, 1L, R. Flowers and A. Glnzalez [TAMU]. Chiriquí, Fortuna, Río Chiriquí (N08º44'; W82º15', elev. 1000 m), 4.xii.1977, 1L, R.W. Flowers [TAMU]; same but, 28.xi.1977.

Genus *Vacupernius* Wiersema and McCaffety, 2000

1. Synonymical Listing. *Vacuperinus* Wiersema and McCafferty, 2000:345 (Type Species: *Leptohyphes packeri* Allen, 1967:350); Allen, 1973 (new species, *Leptohyphes rolstoni*); Allen, 1978 (synonyms); Henry, 1986 (stage description, *Leptohyphes packeri*); Baumgardner, 2003 (synonyms).

2. Diagnosis. Differentiated from other leptohyphid genera by the following combination of characters: Adult: (1) compound eyes small and remote; (2) anterior parapsidal suture fused with posterior parapsidal suture (Fig. 1D); (3) hind wing present (males only), with elongate costal process (Fig. 2D); (4) plumidium present (Fig. 1E); (5) forceps three-segmented (Fig. 8C); (6) styliger plate deeply concave, with acute internal basal projections (Fig. 8G); (7) penes wide with laterally projecting spines at posterior margins (Fig. 8G). Larvae: (1) maxillary palps three-segmented (Fig. 19C); (2) suture between galea and lacinia absent; (3) submentum expanded; (4) claw with six to eight marginal, and three to four submarginal denticles, arranged in single row.

3. Description. *Imago:* Length. Body, 3.0 – 4.0 mm; forewings, 3.0 – 3.5 mm. General coloration pale brown; abdomen translucent with dark shading. Head. Dark brown to black, shaded with gray; eyes small (distance between eyes greater than distance across any one eye); ocelli whitish; antennae white. Thorax. Tan with black macula; anterior parapsidal suture fused with posterior parapsidal suture (Fig. 1D); plumidium present (Fig. 1E). Forewings: membrane hyaline, costal area shaded with dark brown; veins brown; hind margin of fore- and hind wings fringed with setae; vein CuP not strongly curved towards A; vein iCu_2 free basally (Fig. 2A); vein iCu_1 fused basally with CuP (Fig. 1F); vein MP_2 connected basally to CuA and MP_1 by crossveins (Fig. 19J); vein iMP free at basal end; hind wings present in males, with elongated costal process (Fig. 1G), and two longitudinal veins, absent in females. Legs: yellowish-gray with black maculation; tarsi of all legs four-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G). Abdomen. Whitish translucent, covered with black maculation; sterna whitish. Genitalia: forceps three-segmented; penes fused for most its distance; two median folds on ventral surface, each lobe with a posteriorly directed spine near posterior origin of fold (Fig. 7G).

Larva: Length. Body, 3.5 – 4.5 mm; caudal filaments 3.0 – 4.0 mm. General coloration yellow to brown with pale markings. Head. Brown, dark band between lateral ocelli. Labium with greatly expanded submentum (10A), fringed with sparse filiform setae along lateral margins; glossae relatively well-developed; palp three-segmented. Labrum with shallow anteriomedian cleft (Fig. 4C); elongate setae present along lateral margins. Maxilla with galea – lacinia completely fused; basal inner margin with four to six elongate setae; distal margin densely covered with filiform setae; inner margin with six to seven elongate spines; palp three-segmented. Outer incisor of right mandible with three denticles; inner incisor with one denticle; prostheca present, well-developed with elongate setae projecting towards molar region; outer margin strongly convex. Outer incisor of left mandible with three denticles, inner incisor with two denticles; prostheca present, well-developed. Thorax. Brown with pale markings; tubercles absent. Legs: profemur with transverse row of elongate setae along dorsal surface; inner (anterior) margin with sparse stout setae; outer (posterior) margin with elongate setae along distal half; meso- and metafemur with scattered filiform and elongate setae along inner and outer margins; tibia and tarsus of all legs with scattered filiform and elongate setae along inner and outer margins; scattered stout setae present along inner margins; claws with six to ten marginal and three to six submarginal denticles, arranged in single row. Abdomen. Unicolorous yellowish-brown; gills present on segments two through six; operculate gill subrectangular, without basal beak-like process, transverse or medial ridge; gill formula: 2/3/3/3/1.

4. Proposed Synapomorphies. Adult: [27; 0-1] internal basal projection of styliger plate present (Fig. 3C), acute (internal basal projections of styliger plate absent); [31; 0-1] penal spines inserted dorsally (Fig. 8G) (penal spines absent, or inserted laterally or ventrally). Larvae: [100; 0-1] operculate gill subrectangular (operculate gill triangular or oval); [111; 1-2] abdominal gill three composed of two to three lamellae (abdominal gill three composed of four to six lamellae); [112; 1-2] abdominal gill four composed of two lamellae (abdominal gill four composed of four to six lamellae).

5. Species Included (2). *Vacupernius packeri* (Allen) [Belize, Costa Rica, Guatemala, Honduras, Mexico, United States; A, L]; *Vacupernius rolstoni* (Allen) [Dominican Republic; L].

6. Distribution. *Vacupernius packeri* is widely distributed throughout Central America and into the southwestern United States. *Vacupernius rolstoni* is known only from the type locality in the Dominican Republic.

7. Comments. Although not specifically mentioned by Wiersema and McCafferty (2000), the uniquely-shaped genitalia were apparently the primary character used in establishing the genus *Vacupernius*. The inclusion of *V. rolstoni* by Wiersema and McCafferty (2000) can only be considered tentative until the adult is associated.

8. Type Material Examined. *Leptohyphes paraguttatus* Allen: HOLOTYPE (larva): Geronimo Cr., Guadalupe Co., Tex., 18-v-73, Michael Peters; three associated slides (CAS #13603).

9. Other Material Examined. BELIZE: Stann Creek; North Stann Creek at Hummingbird Hwy., ca. 3 Km SE Middlesex (N17°00'39"; W88°28'33", elev. 90 m), 18.iii.2005, 5L, D.E. Baumgardner [TAMU]; Toledo; unnamed ck. at Southern Hwy., 11 Km S. Medina Bank (N16°21'15"; W88°47'56", elev. 50 m), 17.iii.2005, 14L, D.E. Baumgardner [TAMU]. **COSTA RICA:** Guanacaste; Río Diria at unnamed road, ca. 1 Km. E. of intersection with Hwy. 21 (N10°20'05"; W85°34'04", elev. 70 m), 15.vi.2001, 1L, D.E. Baumgardner [TAMU]. Heredia; La Selva Biological Station, SW Puerto Viejo, Sura Creek at Rio Puerto Viejo, (N10°25'49"; W84°00'06", elev. 35 m), 09.vi.2001, 2L, D.E. Baumgardner [TAMU]; Río Isla Grande at Hwy. 4, ca. 5 Km. W. of Rio Frio, (N10°23'31"; W83°5804", elev. 70 m), 10.vi.2001, 5L, D.E. Baumgardner

[TAMU]. Limon, Río Shiroles at Shiroles (N09°34’50”; W82°57’27”, elev. 95 m), 12.vi.2001, 1♀ imago (reared), D.E. Baumgardner [TAMU]. Puntarenas, Río Caracol at CA Hwy. 2, ca. 7.3Km E. Rio Claro (N08°39’47”; W83°00’41”, elev. 30 m), 23.vi.2001, 2♂ imagos (reared), 15L, D.E. Baumgardner [TAMU]; Río Balsar at Hwy. 34, ca. 8 Km NW Palmar Norte (N08°59’05”; W83°31’01”, elev. 65 m), 22.vi.2001, 15L, D.E. Baumgardner [TAMU]; Unnamed creek at Hwy. 34, ca 37.5 Km SE Dominical (N09°03’04”; W83°37’00”, elev. 35 m), 22.vi.2001, 2L, D.E. Baumgardner [TAMU]. San José; Río Pedregoso at Hwy. 243, ca. 4 Km S. San Isidro de El General (N09°21’15”; W83°43’35”, elev. 680 m), 22.vi.2001, 7L, D.E. Baumgardner [TAMU]. **GUATEMALA:** Alta Verapaz; Río Stainkreec, .8 Km E. from jct. of Hwy. 9&10, Río Hondo (N15°02’23”; W89°35’14”, elev. 200 m), 15.vii.2001, 4L, D.E. Baumgardner [TAMU]; Baja Verapaz; Río La Estancia at Hwy. 17, Salana (N15°05’54”; W90°18’18”, elev. 1000 m), 13.vii.2001, 1L, D.E. Baumgardner [TAMU]; El Progreso, Quebrada Las Pericas at Hwy. 17, 11.1 Km W. from jct. with Hwy. CA 9 (N14°54’54”; W90°05’52”, elev. 350 m), 12.vii.2001, 1♀ imago (reared), 6L, D.E. Baumgardner [TAMU]; Río Hato at CA Hwy. 9, ca. 5.9 Km E. from jct. with Hwy. 17, Magdalena (N14°55’11”; W89°57’56”, elev. 340 m), 14.vii.2001, 16L, D.E. Baumgardner [TAMU]; Zacapa; Río Cayo at CA Hwy. 9, 2.3 Km E. Santa Cruz (N15°00’54”; W89°39’09”, elev. 270 m), 14.vii.2001, 15L, D.E. Baumgardner [TAMU]. **HONDURAS:** Comayagua; Taulabe, Río Tamalito, 1.5 Km from Bogran House (N14°41’; W87°55’), 14.iii.2002, 1L, R. Caesar, A. Cognato, A. Harlin, J. Torres [TAMU]. **MEXICO:** Nuevo Leon; Cabazones R. at Hwy. 85, 15 mi. N. Linares, 16.v.1995, 2L, D.E. Baumgardner [TAMU].

UNITED STATES: Arizona: Yavapai Co; Wet Beaver Creek at FR 618, Coconino Nat. Forest (N34°40'09"; W111°42'52", elev. 1,275 m), 25.v.2004, 2L, D.E. Baumgardner [TAMU]; Wet Beaver Creek at Wet Beaver Creek Campground (N34°40'8"; W111°42'47"), 24-25.v.1999, 1L, D.E. Baumgardner [TAMU]. Texas: Bandera Co; Winans Cr. @ TX 16, ca. 4 mi. N. Bandera, 12.iv.1992, 6♂ and 2♀ subimagoes, Moulton & Stewart [TAMU]; Campe Verde, Verde Creek, 8.viii.1992, 13♂ and 17♀ imagos, DE Bowles [TAMU]; Medina R. at TX. Hwy. 16, 1 mi. N. Medina (N25°48'59"; W99°15'33"), 08.viii.1996, 1♂ imago, D.E. Baumgardner and DE Bowles [TAMU]. Bexar Co; Salado Creek, 14.vii.1999, 2L, DE Bowles [TAMU]. Brazos Co; Navasota R., 09.vi.1998, 1L, R. Fields and L. Tolley [TAMU]. Comal Co.; Sattler, Rio Raft Co., Guadalupe River at 5.5 mi. below Canyon Dam below 4th X-ing., 26.x.1996, 1L, N. Wiersema [TAMU]; Guadalupe River at Hwy. 311, 20.vi.1993, 3L, J.L. Cook [TAMU]. Hays Co.; San Marcos R. at Co. Rd. 101 (Caners Crossing), 1 mi. below conf. with Blanco R., in San Marcos City Limits, at Hays/Caldwell Co. Line, 21.ii.1997, 4L, DE Baumgardner and DE Bowles [TAMU]. Kerr Co.; Fessenden Ck. at Hwy. 41, Heart of the Hills Research Station, TPWD (N30°09'28"; W99°20'41"), 19.iv.1997, 3L, D.E. Baumgardner & DE Bowles [TAMU]. Kimble Co.; Junction, South Llano River (N30°28'45", W99°,45'45"), 21.x.1997, 2L, NA Wiersema [TAMU]. Medina Co.; Seco Creek, 6 mi. S. of D'Hanis, 25.iv.1993, 3L, L. Gilpin & V. Castillo [SWTS]; same but, 13.v.1993, 16L [SWTS, TAMU]; same but, 27.vi.1993, 8L [SWTS, TAMU]. Milam Co.; Rockdale, San Gabriel R. at 487 x-ing, 16.xi.1996, 2L, N. Wiersema [TAMU]; San

Gabriel R., 08-vi-1999, 2L, DE Bowles [TAMU]. Williamson Co.; Brushy Creek, 9.v.1998, 8L, R. Fields and L. Tolley [TAMU].

Genus *Tricorythopsis* Traver, 1958

1. Synonymical Listing. *Tricorythopsis* Traver, 1958:491 (Type Species: *Tricorythopsis artigas* Traver, 1958:492); Traver, 1958; Allen, 1967 (*T. gibbus*; *T. undlatus*); Allen, 1973 (*T. minimus*); Molineri, 1999b (generic revision, new species descriptions, *T. volsellus, T. sigillatus*); Wiersema and McCafferty, 2000:355 (review of genus); Molineri, 2001c (generic revision, new combinations, new stage and species descriptions, *T. chiriguano, T. yacutinga*); Dias and Salles, 2005 (new species descriptions, *T. araponga, T. baptistai, T. pseudogibbus*).

2. Diagnosis. Distinguished from other leptohyphid genera by the following combination of characters: Adult: (1) forceps two-segmented (Fig. 3A); (2) hind wings absent in both sexes; (3) plumidium present (Fig. 1E); (4) eyes small and remote; (5) anterior parapsidal suture fused with transverse interscutal suture (Fig. 1E); (6) vein iMP longer than MP_2, fused with CuA (MP_2 forms an intercalary) (Fig. 2A). Larva: (1) suture between galea and lacinia present, complete; (2) distal margin of galea with few (10 or less) setae; (3) base of inner margin of maxilla with 1 or 2 setae; (4) less than 10 seta along anterior margin of meso- and metatarsi; (5) setae extremely sparse, or absent, from margin of operculate gill; (6) abdominal gills three and four each with four lamellae.

3. Description. *Imago:* Length. Body, 1.25 – 3.0 mm; forewings, 1.5 – 3.0 mm; General coloration light whitish-yellow to orange, often with black, gray, or red markings; to pale; own, abdomen whitish translucent. Head. Whitish translucent, often with gray and brown markings; compound eyes small, remote (distance between eyes at least three times greater than distance across any one eye). Thorax. Hyaline to pale yellowish-white, often shaded with black; anterior parapsidal suture fused with transverse interscutal suture (Fig. 1E); plumidium present (Fig. 1E). Forewings: membrane hyaline; veins whitish translucent, except Sc and R often shaded with gray; vein CuP not strongly curved towards A (Fig. 2A); vein iCu_2 free basally, not connected with vein iCu_1 (Fig. 2A); vein iCu_1 fused at base with A (Fig. 2A); iMP longer than MP_2, fused at base with CuA (Fig. 2A); anal margin of wing with numerous elongate hairs; hind wings absent in both sexes. Legs: yellowish-white with blacks bands; tarsi of all legs four-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in forelegs of male imagos, both blunt (Fig. 2G). Abdomen. whitish translucent, often with black markings or shaded with gray. Genitalia (Fig. 3A): forceps two-segmented, approximately equal in length; distal segment often directed outwardly; penes elongate, narrow, fused between one-half to almost entire length; penal spines present at posterolateral margin of penes.

Larva: Length. Body, 1.5 – 3.5 mm; caudal filaments 1.5 – 2.5 mm. General coloration pale with brownish markings. Head. Pale, often shaded with brown. Labium: submentum rounded with sparse stout setae along lateral margins; labial palp three-segmented; glossae and paraglossae mostly fused; filiform and elongate setae present along anterior margin. Labrum with shallow anteriomedian cleft (Fig. 4C); filiform and elongate hairs present along lateral and anterior margins. Maxilla with galea – lacinia mostly fused, except on apical furrow; basal inner margin with one or two elongate setae; distal margin with tuft of a few filiform setae; apex with four to six thick, heavy spines; palp one or two-segmented, with apical seta. Left mandible: outer incisor with three denticles, inner with two denticles; prostheca present, projecting towards molar region. Right mandible: outer incisor with three denticles, inner with one denticle; prostheca present, projecting towards molar region. Thorax. Pale yellowish-brown, shaded with gray and black. Pro- and mesonotum without tubercles or anterolateral projections. Legs: profemur with transverse row of stout or elongate setae along dorsal surface; inner (anterior) margin with few scattered, stout setae, occasionally absent; outer (posterior) margin with few stout or elongate setae mostly confined to distal end; meso- and metafemur with scattered stout setae on dorsal surface; stout setae present along most of inner and outer margins; tibia and tarsus of proleg with elongate setae along inner margin; tibia of meso- and metaleg with two rows of elongate setae along inner margin; few, scattered setae sometimes present along outer margin; tarsi of meso- and metalegs with single row along inner margin; outer margin with few, filiform setae or absent; claws with five to eight marginal denticles; two rows of submarginal denticles present along ventral margin, each with two to five denticles. Abdomen. Pale, often shaded with yellow and brown; gills present on segments two through six; operculate gill oval; gill formula: 4/4/4/2/1.

4. Proposed Synapomorphies. Proposed Synapomorphies: Adult: [Character 11; State transition 0-2*] vein iMP longer than MP_2 (Fig. 2A) (vein iMP shorter than MP_2); [15*; 0-2] vein iMP fused with CuA (Fig. 2A) (vein iMP free basally, or fused with MP_1). Larva: [50; 1-0] inner incisor of right mandible with one denticle (inner incisor of right mandible with more than one denticle); [58: 1-0] fusion between galea and lacinia present, well-developed (Fig. 5A) (fusion between galea and lacinia extremely reduced or absent (Figs. 10D – F)); [96*; 1-2] only abdominal segments eight and nine with posterolateral projections (Fig. 14A) (abdominal segments seven through nine (Figs. 6C – D) with posterolateral projections); [107; 1-0] ventral inferior lamellae of abdominal gill two parallel to dorsal lamellae (Fig. 6I; 14G) (ventral inferior lamellae of abdominal gill two perpendicular to dorsal lamellae (Fig. 14H); [115*; 1-2] abdominal gill six with one lamella (abdominal gill six with more than one lamella);

5. Species Included (11). *T. araponga* Dias and Salles [Brazil; L]; *T. artigas* Traver [Argentina; Brazl; Uruguay; A, L]; *T. baptistai* Dias and Salles [Brazil; L]; *T. chiriguano* Molineri [Bolivia; A, L]; *T. gibbus* (Allen) [Brazil, Argentina; A, L]; *T. minimus* (Allen) [Brazil, Argentina; A, L]; *T. pseudogibbus* Dias and Salles [Brazil; L]; *T. sigillatus* Molineri [Brazil; A]; *T. undulatus* (Allen) [Argentina, Brazil; A, L]; *T. volsellus* Molineri [Venezuela; A]; *T. yacutinga* Molineri [Argentina; A, L].

6. Distribution. Known only from South America; five of the eleven species known only from Brazil.

7. Comments. Although the genus and types species were originally described by Traver (1958) based upon adults from Uruguay, nothing else was known of the genus until Molineri (1999) was able to describe the female adult and one larval exuviae from Argentina. The recent discovery of three new species in Brazil by Dias and Salles (2005) indicates that numerous additional species may await description. The small size of the adults and larvae, generally between 1.5 mm and 2.5 mm, makes them easly overlooked. Three species are known only from the larval stage (*T. araponga*, *T. baptistaia*, *T. pseudogibbus*), two from the adult (*T. sigillatus*, *T. volsellus*), and six from both life stages (*T. artigas, T. chiriguano, T. gibbus, T. minimus, T. undulatus, T. yacutinga*).

8. Type Material Examined. *Tricorythopsis chiriguano* Molineri: PARATYPES: ARGENTINA: Santa Cruz; Río de las Petas (S16°22"24"; W59°10'38", elev. 120 meters), 19.vi.2000, 3L, Dominguez (2 slides, #DB 05x2201, DB05x2202) [IFML]; PARATYPES: BOLIVIA: Río Bugress, 30 km W de San Matias (S16°22'14"; W58°42'60"; 100m), 19.vi.2000, 6♂ imagos, E. Dominguez [FAMU]; PARATYPES: BOLIVIA: Santa Cruz, Río de las Petas (S16°22'24"; W59°10'38", elev. 120m), 21.vi.2000, 10L, E. Dominguez [FAMU]. *Tricorythopsis minimus* (Allen): PARATYPE: BRAZIL: Arroio Lageado, Arroio Lageado, Rio Grande do Sul, xi.1964, 2L, F. Plaumann [CAS].

9. Other Material Examined. *Tricorythopsis artigas* Traver: ARGENTINA: Misiones, Alem, 5 Km W Cerro Agul R.N. 14, A Martires, 17.xi.1998, 3♂, 3♀ imagos, Dominguez, Molineri, and Nieto [TAMU]; Misiones, 25 Km al S. de El Soberbio, 21.xi.1998, 6♂, 6♀ imagos, Dominguez, Molineri, Nieto [TAMU]. *Tricorythopsis undulatus* (Allen): ARGENTINA: Misiones, Parque Prov. Urugua-i A Uruzu, Ruta Prov. 19, 7-11.xii.1999, 2♂ imagos, 2L, Molineri [TAMU].

Genus *Tricorythodes* Ulmer, 1920

1. Synonymical Listing. *Tricorythodes* Ulmer, 1920a:51 (Type Species:

Tricorythus explicatus Eaton, 1892:138); Eaton, 1892 (new species); Banks, 1903 (distributional records); Ulmer, 1920b (taxonomy); McDunnough, 1931 (distributional records); Kimmins, 1934 (taxonomy); Traver, 1935 (taxonomic key, generic review, new species); Taver, 1943 (new species); Berner, 1946 (new species); Burks, 1953 (new species, distributional records); Traver, 1958 (taxonomy); Traver, 1959 (new species); Allen, 1967 (new species); Allen and Roback, 1969 (new species); Allen, 1973 (new species); Allen and Brusca, 1973 (new species); Kilgore and Allen, 1973 (new species, distribution records); Allen, 1977 (new species, taxonomy); Allen, 1978 (distributional records); Domínguez, 1982 (new species); Allen and Murvosh, 1987 (taxonomy, distribution records); Berner and Pescador, 1988 (records); Kluge and Naranjo, 1990 (new species); McCafferty et al., 1993 (distributional records); Alba-Tercedor and Flannagan, 1995 (new species, distributional records); Lugo-Ortiz and McCafferty, 1995a (new species); Lugo-Ortiz and McCafferty, 1995b (distributional records); Lugo-Ortiz and McCafferty, 1995c (distributional records); Baumgardner et al., 1997 (distributional records); McCafferty et al., 1997 (distributional records); Randolph and McCafferty, 1998 (distributional records); Wang et al., 1998 (new species); Wiersema and McCafferty, 2000 (taxonomic changes); Randolph and McCafferty, 2000 (distributional records); Molineri, 2001d (new species); Wiersema et al., 2001 (new species – numinuh); Molineri, 2002 (generic revision); Baumgardner et al., 2003 (new stage descriptions, distribution records); Wiersema and McCafferty, 2003 (taxonomy); McCafferty et al., 2004 (distributional records); Baumgardner and Bowles, 2005 (distributional records); Dias et al., 2005 (taxonomy, new combinations); Molineri, 2005 (stage description); Wiersema and McCafferty, 2005 (taxonomy); Baumgardner and Ávila, 2006 (new species, stage description); Baumgardner et al., 2006 (new species); Molineri, 2006 (taxonomy); Molineri and Zúñiga, 2006 (new species); Baumgardner, 2007 (new species).

2. Diagnosis. Distinguished from other leptohyphid genera by the following combination of characters: Adult: (1) eyes small and remote; (2) anterior parapsidal suture fused with posterior parapsidal suture (Fig. 1D); (3) hind wings absent in both sexes; (4) plumidium absent (Fig. 1D); (5) forceps three-segmented, second segment of forceps with an enlarged basal swelling (Fig. 3B); (6) penal spines absent (Fig. 3B). Larva: (1) galea – lacinia suture absent (Figs. 10D – F); (2) proleg with transverse row of filiform setae; (3) abdominal gill two, with one or two ventral lamellae; when two present, unequal in size and shape (Fig. 15H); (4) operculate gill with numerous filiform setae along most of margin.

3. Description. *Imago:* Length. Body, 2.5 – 8.0 mm; forewings, 3.0 – 5.0 mm; hind wings absent. General coloration highly variable; light yellowish to dark reddish-brown, often with gray and black markings; abdomen whitish translucent to gray, often with black markings. <u>Head.</u> Typically pale yellowish to gray, with black markings; compound eyes small, remote (distance between compound eyes at least three times greater than distance across any one eye) or large (width of one compound eye (in dorsal view) is equal to or greater than distance between the compound eyes) and dioptic (Fig. 1C) or large, not dioptic (Fig. 1B); paired occipital tubercles present, small, weakly-developed (basal width approximately equal to height) (Fig. 1A) or present, large and distinct (height approximately twice basal width). Thorax. Coloration variable, yellowish-white to reddish-brown, often extensively shaded with gray and/or black; anterior parapsidal sutures fused with posterior interscutal suture (Fig. 1D); plumidium absent. Forewings (Fig. 1F): membrane hyaline, sometimes shaded with brown; longitudinal veins pale to grayish-brown; costal and subcostal veins often with gray or brown along margins of veins; most species with vein CuP not strongly curved towards A (Fig. 1F); rarely CuP strongly curved towards A (Fig. 1G); rarely, CuP greatly reduced, proximal half absent, or CuP completely absent; vein iCu_2 usually attached basally to iCu_1 (Fig. 1F); rarely, iCu_2 attached basally to CuP or free at basal end; vein iCu_1 usually attached basally to CuP (Fig. 1F); rarely attached basally to A; vein MP_2 free basally (Fig. 1F), or united basally to veins CuA and MP_1 by cross vein (Fig. 1G), or attached only to CuA or iMP (Fig. 2A); hind wings absent in both sexes. Legs: yellowish-gray to reddish brown, often with black markings; tarsi of all legs five-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2A), except in forelegs of male imagos, both blunt (Fig. 2C). Abdomen. Coloration highly variable; whitish translucent to gray to dark reddish-brown, shaded with gray or black. Genitalia: forceps three-segmented, second segment of forceps with an enlarged basal swelling (Fig. 3B); penal spines absent (Fig. 3B).

Larva: Length. Body, 4.0 – 8.0 mm; caudal filaments 2.0 – 4.0 mm. General coloration pale white to whitish-yellow, heavily shaded with gray, black, or greyish-black. Head. Yellowish, shaded with gray or black; genial projections present (Fig. 4A) or absent. Labium (Fig. 4D) with expanded submentum, and with filiform and elongate setae present along lateral and anterior margins; labial palp three-segmented, densely covered with filiform setae along margins; glossae and paraglossae almost completely fused. Labrum with shallow (Fig. 4C) or deep (Fig. 9D) anteriomedian cleft; filiform and elongate setae present along lateral margins; anterior margin with stout setae, often branched (Fig. 9D). Maxilla with galea and lacinia completely fused; basal inner margin with one to eight elongate setae; distal margin densely-covered with filiform setae; labial palp absent to three-segmented (Figs. 10D – F); terminal setae present (Figs. 10D – F) or absent. Outer incisor of right mandible with two or three denticles, inner incisor with one to three denticles; prostecha present, well-developed (Fig. 4E); Outer incisor of left mandible with three or four denticles, inner incisor with two denticles, prostecha present, well-developed, with elongate setae projecting towards molar region. <u>Thorax.</u> Coloration variable; pale yellow to dark reddish-brown, often shaded with gray or black. Pronotum with (Fig. 5C) or without anterolateral projections, and with or without median tubercle (Fig. 4B); mesonotum with or without mesolateral projections (Fig. 5C), and with (Fig. 4B) or without mesonotal tubercle. Legs: profemur with transverse row of elongate or filiform setae along dorsal surface (Figs. 11A; 24C – D); meso- and metafemur with variously arranged filiform (Fig. 12A; 24C – D;), elongate (Fig. 11A; 12B), or robust (Fig. 12C) setae along inner and outer margins; tibia and tarsus of all legs with one or two rows of variously arranged filiform (Fig. 23C – D), and/or elongate (Fig. 11A) setae along inner and outer margins, or without setae along inner and/or outer margins (Fig. 12A – B, D); claws with marginal denticles absent (see figs. 24, 97 Molineri, 2002) or with two (Fig. 23E) to fourteen (Fig. 13F) denticles; submarginal denticles present or absent (Fig. 13F); when present, a single denticle, or double row of one (Fig. 5G) or two to four denticles (Fig.23E) distolaterally. Abdomen. Coloration highly variable from whitish translucent to reddish-brown, often shaded with yellow, brown, grey, or black; gills present on segments two through six; operculate gill subtriangular (Fig. 6G) or oval (Fig. 6H; 13G), with or without a transverse and/or medial ridge (Fig. 15E); gill formula: 1-2/3/3/3/1-2.

4. Proposed Synapomorphies. Adult: [Character 24*; State Transformation 0-1] basal swelling at base of second forceps segment (Fig. 2E) (basal swelling absent at base of second forceps segment). Larva: [89; 1-0] posterior margin of abdominal terga one through six smooth (posterior margins serrated); [111; 1-2] number of lamellae on abdominal gill three composed of two or three lamellae (gill composed of four to seven lamellae); [98; 1-0] cerci with long, hair-like setae at each anulation (Fig. 14E) (cerci with short, thick setae at each annulation (Fig. 14F)).

5. Subgenera Included [2]. *Tricorythodes* (*Asioplax*) McCafferty and Wiersema; *Tricorythodes* (*Tricorythodes*) Ulmer. See each subgenus below for a complete listing of species included in each subgenus. Fifty-four species currently known in genus.

6. Distribution. Known from North, Central, and South America and the Carribean region. The genus equally diverse in North and South America.

7. Comments. The following new synonyms of genus *Tricorythodes* are proposed: *Ableptemetes* **n. syn**., *Cabecar* **n. syn.**, *Epiphrades* **n. syn**., *Homoleptohyphes* **n. syn**., *Macunahyphes* **n. syn**., *Tricoryhyphes* **n. syn**. The former genus *Asioplax* is newly-regarded as a subgenus of *Tricorythodes*. Based upon the cladistic analysis, all are shown to be paraphyletic in Figures 17 and 18.

Ableptemetes was described by Wiersema and McCafferty (2003) for two species (*melanobranchus* and *dicinctus*) known only from Middle America and originally placed in the genus *Leptohyphes*, then in *Tricorythopsis* (Wiersema and McCafferty, 2000). Although the adult stage is unknown for both species, they clearly fall within *Asioplax*, near the base of the group. The genus *Cabecar* was described by Baumgardner and Ávila (2006), for one Middle American species, and *Epiphrades* by Wiersema and McCafferty (2000) for two South American and one Middle America species. Molineri (2002), in his cladistic analysis of the South American leptohyphids, considered *Epiphrades* a synonym of *Tricorythodes*. The current cladistic analysis shows the two genera to be sister groups (Fig. 17) near the base of the genus *Tricorythodes*.

The genus *Homoleptohyphes* was first proposed as a subgenus of *Tricorythodes* by Allen and Murvosh (1987), and included three leptohyphid species in which the males possessed large compound eyes (Fig. 1B). Wiersema and McCafferty (2000) elevated it to full generic status. Molineri (2002) did not include any of these three species in his analysis of the South American leptohyphids, because they occur only in the United States and Mexico. This is the first cladistic analysis to include all three species of the genus *Homoleptohyphes*. It is clearly shown to be polyphyletic (Fig. 17) and a synonym of *Tricorythodes*. All three species are shown to be closely related sister species.

Tricoryhyphes was first proposed as a subgenus of *Tricorythodes* (Allen and Murvosh, 1987), and elevated to a genus by Wiersema and McCafferty (2002), who included five species, three known from South America, and one each from Middle America and the United States. The results of Molineri's (2002) cladistic analysis of the South American leptohyphids demonstrated that *Tricoryhyphes* was polyphyletic, and a synonym of *Tricorythodes*. The current cladistic analysis also shows *Tricoryhyphes* to be clearly polyphyletic (Fig. 17), and a synonym of *Tricorythodes*. The species originally included in the genus *Tricoryhyphes* are shown to be sister species.

Tricorythodes australis was originally described by Banks (1913) based upon adults and placed in the African genus *Tricorythus*. Traver (1958) redescribed the species and noted that the male lacked the swelling at the base of the second forceps, a character known in all other species of *Tricorythodes* which are known from the male life stage. Molineri (2002) noted that the species fell at the base of the genus *Tricorythodes* in his analysis of the South American *Tricorythodes*, and suggested that a new genus might be necessary to accommodate the species. Dias et al. (2005) formally proposed the genus *Macunahyphes* to include the single species *T. australis*, based in part, on the absence of a basal swelling at the base of the second forceps join. In his analysis of the family Leptohyphidae in South America, *T. australis* was shown to be nested within *Tricorythodes*, but no discussion of this result was included in the paper. In the current cladistic analysis, *T. australis* displays a similar position in the cladogram, as that of Molineri's (2006) cladogram. *Tricorythodes australis* clearly belongs in the genus *Tricorythodes*, with an apparent loss of the primary synapomorphy (basal swelling of the second forceps joint) defining the genus *Tricorythodes*.

The genus *Asioplax* was proposed by Wiersema and McCafferty (2000) to accommodate several species previously included in *Tricorythodes*, species known to occur in North and South America. Their primary justification for the new genus is the fact that larvae are dorsoventrally flattened, a unique characteristic within the Leptohyphidae. Molineri (2002) showed *Asioplax* to be highly derived within *Tricorythodes*, considered in paraphyletic, and synonymized it with *Tricorythodes*. Wiersema and McCafferty (2005) revalidated the genus, agreeing with Molineri that it is highly derived within *Tricorythodes* and deserving of generic status. The current cladistic analysis shows *Asioplax* to be a well supported clade, but as a subgenus within *Tricorythodes* (Fig. 17). However, it is shown to contain the most basal species of *Tricorythodes*, not the most derived species. The current analysis includes a much more complete sampling of species within *Asioplax* than was Molineri's (2002). Molineri included only three species, two from South America and one from Middle America. The current analysis includes seven species from North and Middle America, and Cuba.

8. Type Material Examined. Complete listing of all specimens examined given below in each subgenus.

9. Other Material Examined. Complete listing of all specimens examined given below in each subgenus.

Subgenus *Tricorythodes* (*Asioplax*) Wiersema and McCafferty, 2000

1. Synonymical Listing. *Asioplax* Wiersema and McCafferty, 2000:347 (Type

Species: *Tricorythodes edmundsi* Allen, 1967:370); Traver, 1935 (taxonomic key, generic review, new species); Traver, 1959 (new species); Allen, 1967 (new species); Allen, 1973 (new species); Allen and Brusca, 1973 (new species); Allen, 1977 (new species, taxonomy, distributional records); Allen, 1978 (distributional records); Kilgore and Allen, 1973 (new species); Kluge and Naranjo, 1990 (new species); McCafferty et al., 1993 (distributional records); Lugo-Ortiz and McCafferty, 1995a (new species); Lugo-Ortiz and McCafferty, 1995b (distributional records); Lugo-Ortiz and McCafferty, 1995c (distributional records); Baumgardner et al., 1997 (distributional records); McCafferty et al., 1997 (distributional records); Wang et al., 1998 (new species); Berner and Pescador, 1998 (records); Wiersema and McCafferty, 2000 (taxonomic changes); Randolph and McCafferty, 2000 (distributional records); Wiersema et al., 2001 (new species); Molineri, 2002 (generic revision); Wiersema and McCafferty, 2003 (taxonomy); McCafferty et al., 2004 (distributional records); Wiersema and McCafferty, 2005 (taxonomy); Molineri, 2006 (family revision); Baumgardner et al., 2006 (new species).

2. Diagnosis. Distinguished from *Tricorythodes* (*Tricorythodes*) by the following combination of characters Adult: (1) metafemora greater than three-fourths length of hindtibiae and hindtarsi combined (Wiersema and McCafferty, 2000); (2) paired occipital tubercles present, large and distinct (height approximately twice basal width). Larva: (1) body dorsoventrally flattened; (2) abdominal tergites seven and eight with posterolateral projections longer than medial length of associated tergites (Fig. 6C); (3) profemora greatly expanded (Fig. 11), width three-fourths or greater than length.

3. Description. *Imago:* Length. Body, 2.5– 4.0 mm; forewings, 2.5 – 3.5 mm; hind wings absent. General coloration pale; light yellowish to reddish-brown, often with gray or black markings; abdomen whitish to whitish translucent to gray, often with black markings. Head. Gray, with extensive black shading; compound eyes small, remote (distance between compound eyes at least three times greater than distance across any one eye); paired occipital tubercles present, large and distinct (height approximately twice basal width). Thorax. Yellowish-brown to dark reddish-brown, often extensively shaded with gray and/or black; anterior parapsidal sutures fused with posterior interscutal suture (Fig. 1D); plumidium absent. Forewings (Fig. 1F): membrane hyaline, sometimes shaded with brown; longitudinal veins pale to grayish-brown; costal and subcostal veins often with gray or brown along margins of veins; most species with vein CuP not strongly curved towards A (Fig. 1F); rarely CuP strongly curved towards A (Fig. 1G); rarely, CuP absent; vein iCu_2 usually attached basally to iCu_1 (Fig. 1F), or or free at basal end; vein iCu_1 usually attached basally to CuP (Fig. 1F); rarely attached basally to A; vein MP_2 free basally (Fig. 1F), or united basally to veins CuA and MP_1 by cross vein (Fig. 1G), or attached only to CuA or iMP (Fig. 2A); hind wings absent in both sexes. Legs: gray, extensively covered with black markings; tarsi of all legs five-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2A), except in forelegs of male imagos, both blunt (Fig. 2C); metafemora greater than three-fourths length of hindtibiae and hindtarsi combined. Abdomen. Coloration highly variable; whitish translucent to gray to dark reddish-brown, shaded with gray or black. Genitalia: forceps three-segmented, second segment of forceps with an enlarged basal swelling (Fig. 3B); penal spines absent (Fig. 3B); penes fused for approximately three-fourth their distance.

Larva: Length. Body, 2.5 – 3.5 mm; caudal filaments 1.5 – 2.0 mm. Body robust and dorsoventrally flattened. General coloration pale to dark reddish brown with black markings. Head: Pale brown with variable black markings to dark reddish brown; very small genal projections present; tubercles absent. Labium (Fig.23F): labial palp three-segmented, with numerous filiform setae; glossae and paraglossae fused except distially; numerous filiform setae present along anterior and lateral margins. Labrum with shallow anteriomedian cleft; dorsally with highly branched elongate setae recessed from the anterior margin; numerous filiform setae along lateral and anterior margins. Maxilla (Fig.23G) with galea – lacinia completely fused, except on apical furrow; basal inner margin with one or two elongate setae; distal margin densely covered with filiform setae; palp absent to three-segmented, with or without apical seta. Right mandible (Fig.24A): outer incisor with two or three denticles, inner incisor with one to three denticles; prostecha present, well-developed. Left mandible (Fig.24B): outer incisor with three or four denticles, inncer incisor with two denticles; prostecha present, well-developed, with elongate setae projecting towards molar region. Thorax. Pale to dark reddish-brown, often with extensive black shading; pronotum often with pair of small, sharp projections on anterior lateral margins; hindwing pads absent in both sexes. Legs: profemur rounded, with transverse row of elongate setae along dorsal surface (Fig. 11A), width three-fourths or greater than length; meso- and metafemur withwith numerous acuminate and filiform setae along anterior and posterior margins becoming shorter towards apex of femur; tibia and tarsus of proleg with with numerous acuminate and filiform setae along anterior and posterior margins; tibia and tarsus of meso- and metalegs with acuminate setae present along anterior and posterior margins; claws with five or six marginal denticles, and one pair of submarginal denticles or none. Abdomen. Generally reddish brown; some individuals with extensive black maculae; numerous filiform setae present along lateral margins of terga; posterolateral margins of abdominal segments seven through nine (Fig. 13G) greatly expanded; segments seven and eight reaching approximately mid-point of next segment; segment nine projecting to or beyond posterior margin of segment ten; gills present on segments two through six; operculate gill oval, with acuminate and filiform setae present along lateral margins; gill formula: 1-2/3/3/3/1-2.

4. Proposed Synapomorphies. Adult: [Character 1, State transition 0-2] paired occipital tubercles present, large and distinct (height approximately twice basal width) (paired occipital tubercles absent). Larvae: [73, 1-0] meso- and metafemora with longitudinal row of setae on dorsal surface absent (longitudinal row of setae present); [80, 1-0] protibia with greater than 20 setae of anterior margin (protibia with less than 15 setae on anterior margin); [118, 0-1] body dorsally/ventrally flattened (body not dorsally/ventrally flattened).

5. Species Included (12). *Tricorythodes.* (*Asioplax.*) *curiosus* Lugo-Ortiz and McCafferty [Costa Rica, Panama; L]; *T.* (*A.*) *dicinctus* (Allen and Brusca) [Belize, Guatemala; L]; *T.* (*A.*) *dolani* Allen [southeastern USA; L]; *T.* (*A.*) *edmundsi* Allen [western USA, Canada; L, A]; *T.* (*A.*) *isabelia* (Baumgardner, Meyer, and McCafferty)

[Nicaragua, Costa Rica; L]; *T.* (*A.*) *melanobranchus* (Allen and Brusca) [Costa Rica, Guatemala, Mexico; L]; *T.* (*A.*) *nicholsae* (Wang, Sites, and McCafferty) [Ecuador; L]; *T.* (*A.*) *numinuh* Wiersema, McCafferty & Baumgardner [southcentral USA, northeastern Mexico; L, A]; *T.* (*A.*) *santarita* Traver [Argentina, Brazil, Uruguay; A]; *T.* (*A.*) *sacculobranchis* (Kluge and Naranjo) [Cuba; L]; *T.* (*A.*) *texanus* Traver [Mexico, southwestern USA; A]; *T.* (*A.*) *zunigae* Molineri [Colombia; L, A].

6. Distribution. Known from North, Central, and South America and Cuba.

7. Comments. Molineri (2002) considers all the South American species of *Asioplax* congeneric with *Tricorythodes*, while Wiersema and McCafferty (2005) consider *Asioplax* a valid genus. Molineri (2002) based his conclusions on quantitative phylogenetic analysis, while Wiersema and McCafferty (2005) base their conclusion on non-quantitative cladistic analysis. *Asioplax* is herein considered a subgenus of *Tricorythodes*. See “Comments” under discussion of the genus *Tricorythodes* for detailed justifications.

Two species are tentatively assigned to the subgenus *Tricorythodes* (*Asioplax*), *T.* (*A.*) *santarita* Traver and *T.* (*A.*) *texanus* Traver. Both are known only from the adult life stage, and discovery of the larval stage will be necessary to confirm their correct placement in this subgenus. *Tricorythodes*. (*Tricorythodes*) *sierramaestrae* was originally assigned in *Asioplax* by Wiersema and McCafferty (2000), but considered provisional by these authors. This study confirms its placement in the subgenus *Tricorythodes* (*Tricorythodes*), as the most basal species (Fig. 17).

8. Type Material Examined. *Leptohyphes dicinctus* (Allen and Brusca): HOLOTYPES: **MEXICO:** Guerrero, Trib. Rio Papagayo nr. Tierra Colorado, 16.xi.1968, 1 larva, R.K. Allen [CAS]; PARATYPES: same data as holotype, 1L. *Leptohyphes dolani* Allen: HOLOTYPE (larva): Savannah River, Dikes above Ellenton, S.C., Station 1, 2.ix.1955, S.S. Roback (ANSP). PARATYPES: Savannah River, South Carolina-Georgia, Station 6A, SS Roback, 21.vii.1955, 1L (ANSP). Savannah River, Ga-S.C., Station 5, T.Dolan IV, X-23-51, 1L (ANSP). Following specimens originally unpublished - Savannah River, Georgia-South Carolina Station 1, Aiken Co., S.C., T. Dolan IV, VII-26-51, 3L (Survey SRP #1), 3 slides (ANSP). *Asioplax isabelia* Baumgardner, Meyer, and McCafferty: PARATYPES: Costa Rica: Limon; unnamed creek at Hwy. 32, ca. 3 Km W. of Pocora (N10º10’38”; W83º37’03”), 10.vi.2001, 1 larva, D.E. Baumgardner [TAMU]; Río Catarata at Hwy. 36, 4 Km East of Bribri (N09º37’50”; W82º49’06”), 11.vi.2001, 1 larva, D.E. Baumgardner [TAMU]; Heredia; La Selva Biological Station, SW Puerto Viejo, Sura Creek at Rio Puerto Viejo (N10º25’49”; W84º00’06”), 08-09.vi.2001, 2 larva, D.E. Baumgardner [TAMU]. *Leptohyphes melanobranchus* Allen and Brusca: HOLOTYPE (larva): Guatemala: Río Cartaga, between Esquintla and Taxisco, 25.x.1968, R.K. Allen [CAS]. *Tricorythodes saccullbranchis* Kluge: PARATYPE: CUBA: San Lorenzo, 11-12.vi.1985, 6 larvae, C. Naranjo [TAMU].

9. Other Material Examined. *Tricorythodes* (*Asioplax*) *curiosa* Lugo-Ortiz and McCafferty: **COSTA RICA:** Heredia Prov., La Selva Biological Station, SW Puerto Viejo, Sura Creek at Rio Puerto Viejo (N10°25’49”; W84°00’06”, elev. 30 m), 09.vi.2001, 1L, D.E. Baumgardner [TAMU]. Puntarenas Prov.; 1 Km S Coloradito Norte, Rio Coloradito at Hwy. 2 (N08°36'10"; W82°54'07"), 17.vi.2000, 1L, W.D. Shepard [TAMU]. **PANAMA:** Bocas del Toro, Rio Changuinola below mouth of Rio Teribe, Zegla, 24.iv.1985, 5L, R.W. Flowers [TAMU]. *Tricorythodes (Asioplax) dolani* (Allen): South Carolina: Newberry Co., Little River on Hwy. #56, 4.viii.1955, Hynes, 1L (FAMU). Texas: Montgomery Co., Peach Creek, 16-vi-1998, D.E. Bowles, 3L (TAMU); San Jacinto Co., Winters Bayou, Sam Houston National Forest, ca. 5 mi. NW Cleveland, 03.x.1999, D.E. Baumgardner, 2♀ (reared) (TAMU). *Tricorythodes* (*Asioplax*) *numinuh* Wiersema, McCafferty, and Baumgardner: **MEXICO:** Tamaulipas, Pilon R. at bridge off Hwy. 85, @ Villa Mainero (town), 16.v.1995, 2 larva, D.E. Baumgardner and B.C. Henry [TAMU]. *Tricorythodes* (*Asioplax*) *edmundsi* Allen: **USA:** California: Humboldt Co., Klamath River at Miners Creek, 28-29.vii.2003, 4 larvae [TAMU]; New Mexico: San Miguel Co, Pecos R. at Santa Ana FR, San Jose (N35º24'10"; W105º28'30"), 14.vii.2004, D.E. Baumgardner, 1 larvae [TAMU]; Arizona: Yavapai Co.; West Clear Creek at Clear Creek Campground, ca. 1 mi. from Hwy. 260, ca. 4 mi SE Camp Verde (N34º30'55"; W111º45'45"), 27-28.v.1999, D.E. Baumgardner, 1 larva [TAMU]; Colorado: Moffat Co.; Green River, Echo Park, Dinosaur NM, 24.vii.1992, DAW, 15 larvae [TAMU]. *Tricorythodes* (*Asioplax*) *melanobranchus* (Allen and Brusca): **COSTA RICA:** Alajuela, La Fortuna, Quebrada Burio (N10º 28'; W84º39'), 15.i.2000, W.D. Shepard, 1 larvae [TAMU]; 2.7 km S. La Fortuna, Rio Burro (N10º27'; W84º38'), 16.i.2000, W.D. Shepard, 1L [TAMU]; Guanacaste, Canas, Rio Canas (N10º26'; W85º06'), 23.i.2000,W.D. Shepard, 1 larva.

GUATEMALA: El Progreso, RÍo Hato at CA Hwy. 9, ca. 5.9 Km E. from jct. with Hwy. 17, Magdalena (N14º55’11”; W89º57’56”), 14.vii.2001, 27 larvae, D.E. Baumgardner [TAMU]; **MEXICO:** Morelos, Rio Cuautla at Cuautla, 13.xi.1968, 1 larva, R.K. Allen [CAS].

Subgenus *Tricorythodes* (*Tricorythodes*) Allen and Murvosh, 1987

1. Synonymical Listing. *Tricorythodes* (*Tricorythodes*) Allen and Murvosh, 1987:36 (Type Species: *Tricorythus explicatus* Eaton, 1892:138); Eaton, 1882 (new species); Banks, 1903 (distributional records); Ulmer 1920a (new species); McDunnough, 1931 (distributional records); Kimmins, 1934 (taxonomy); Traver, 1935 (taxonomic key, generic review, new species); Traver, 1943 (new species); Berner, 1946 (new species); Burks, 1953 (distributional records, new species); Traver, 1958 (taxonomy, new combinations); Traver, 1959 (new species); Allen, 1967 (new species); Allen and Roback, 1969 (new species); Allen, 1973 (new species); Allen and Brusca, 1973 (new species); Allen, 1977 (distributional records); Kilgore and Allen, 1973 (distribution records); Domínguez, 1982 (new species); Allen and Murvosh, 1987 (taxonomy, distribution records); Kluge and Naranjo, 1990 (new species); McCafferty et al., 1993 (distributional records); Alba-Tercedor and Flannagan, 1995 (new species, distributional records); Lugo-Ortiz and McCafferty, 1995a (new species); Lugo-Ortiz and McCafferty, 1995b (distributional records); Lugo-Ortiz and McCafferty, 1995c (distributional records); Baumgardner et al., 1997 (distributional records); McCafferty et al., 1997 (distributional records); Berner and Pescador, 1988 (records); Randolph and McCafferty, 1998 (distributional records); Wiersema and McCafferty, 2000 (taxonomic changes); Randolph and McCafferty, 2000 (distributional records); Molineri, 2001d (new species); Molineri, 2002 (generic revision); Baumgardner et al., 2003 (stage descriptions); McCafferty et al., 2004 (distributional records); Baumgardner and Bowles, 2005 (distributional records); Dias et al., 2005 (taxonomy, new combinations); Molineri, 2005 (stage description); Molineri, 2006 (family revision); Molineri and Zúñiga, 2006 (new species); Baumgardner, 2007 (new species); Baumgardner and Ávila, 2006 (new species).

2. Diagnosis. Distinguished from *Tricorythodes* (*Asioplax*) by the following combination of characters Adult: (1) metafemora approximately one-half length of hindtibiae and hindtarsi combined (Wiersema and McCafferty, 2000); (2) paired occipital tubercles absent, or present but, small, weakly developed (basal width approximately equal to height) (Fig. 1A); Larva: (1) body not dorsoventrally flattened; (2) abdominal terga seven and eight with posterolateral projections shorter than, or equal to, medial length of associated tergites (Fig. 6D); (3) profemora greatly expanded (Fig. 11), width less than one-half length (Figs. 12A – B; 24C – D).

3. Description. *Imago:* Length. Body, 4.0 – 8.0 mm; forewings, 3.0 – 5.0 mm; hind wings absent. General coloration highly variable; light yellowish to gray to dark reddish-brown, often with gray and black markings; abdomen whitish translucent to gray, often with black markings. <u>Head.</u> Typically gray or brownish, with black and/or gray markings; compound eyes small, remote (distance between compound eyes at least three times greater than distance across any one eye) or large (width of one compound eye (in dorsal view) is equal to or greater than distance between the compound eyes) and dioptic (Fig. 1C) or large, not dioptic (Fig. 1B); paired occipital tubercles present, small, weakly developed (basal width approximately equal to height) (Fig. 1A). Thorax. Coloration highly variable from pale yellowish-white to reddish-brown, often extensively shaded with gray, red, and/or black; anterior parapsidal sutures fused with posterior interscutal suture (Fig. 1D); plumidium absent. Forewings (Fig. 1F): membrane hyaline, sometimes shaded with brown; longitudinal veins pale to grayish-brown; costal and subcostal veins often with gray or brown along margins of veins; most species with vein CuP not strongly curved towards A (Fig. 1F); rarely CuP strongly curved towards A (Fig. 1G), often occurring in females; rarely, CuP greatly reduced, proximal half absent, or CuP completely absent; vein iCu_2 attached basally to iCu_1 (Fig. 1F), or CuP, or free at basal end; vein iCu_1 attached basally to CuP (Fig. 1F) or A; vein MP_2 free basally (Fig. 1F), or united basally to veins CuA and MP_1 by cross vein (Fig. 1G), or attached only to CuA or iMP (Fig. 2A); hind wings absent in both sexes. Legs: yellowish-gray to reddish brown, often with black markings; tarsi of all legs five-segmented; tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2A), except in forelegs of male imagos, both blunt (Fig. 2C). Abdomen. Coloration highly variable; whitish translucent to gray to dark reddish-brown, shaded with gray or black. Genitalia: forceps three-segmented, second segment of forceps with an enlarged basal swelling (Fig. 3B), absent in one species; penal spines absent (Fig. 3B); penes fused for greater than three-fourths their distance (Fig. 3B).

Larva: Length: 4.0 – 8.0 mm; caudal filaments 2.0 – 4.0 mm. General coloration highly variable from pale translucent yellow, to yellowish light brown, to dark reddish-brown. Head. Gray to light brown, often shaded with dark gray, red, brown, or black; genial and/or frontoclypeal projections present (Fig. 4A) or absent. Labium (Fig. 4D) with expanded submentum, and with filiform and elongate setae present along lateral and anterior margins; labial palp three-segmented, densely covered with filiform setae along margins; glossae and paraglossae almost completely fused. Labrum with shallow (Fig. 4C) or deep (Fig. 9D) anteriomedian cleft; filiform and elongate setae present along lateral margins; anterior margin with stout setae, often branched (Fig. 9D). Maxilla with galea and lacinia completely fused; basal inner margin with one to eight elongate setae; distal margin densely covered with filiform setae; labial palp present, one to three-segmented (Figs. 10D – E); terminal setae present (Figs. 10D – F) or absent. Outer incisor of right mandible with two or three denticles, inner incisor with one denticle, prostecha present, well-developed (Fig. 4F); outer incisor of left mandible with three or four denticles, inner incisor with two denticles, prostecha present, well-developed, with elongate setae projecting towards molar region (Fig. 4E); outer margins of mandibles with (Fig. 10C) or without elongate setae. Thorax. Coloration variable; pale yellow to dark reddish-brown, often shaded with gray or black. Pronotum with (Fig. 5C) or without anterolateral projections, and with or without median tubercle (Fig. 4B); mesonotum with or without mesolateral projections (Fig. 5C), and with (Fig. 4B) or without mesonotal tubercle. Legs: profemur with transverse row of elongate or filiform setae along dorsal surface (Figs. 24C – D); meso- and metafemur with variously arranged filiform or elongate (Fig. 12B) setae along inner and outer margins; tibia and tarsus of all legs with one or two rows of variously arranged filiform (Fig. 23C – D), and/or elongate setae along inner and outer margins, or without setae along inner and/or outer margins (Fig. 12B); claws with marginal denticles absent (see figs. 24, 97 Molineri, 2002) or with two (Fig.23E) to fourteen (Fig. 13F; 24E) denticles; submarginal denticles present or absent (Fig. 13F); when present, a single denticle, or double row of one (Fig. 5G) or two to four denticles (Fig.23E) distolaterally. Abdomen. Coloration highly variable from whitish translucent to dark reddish-brown, often shaded with yellow, brown, grey, or black; gills present on segments two through six; operculate gill subtriangular (Fig. 6G), with or without a transverse and/or medial ridge (Fig. 15E); gill formula: 1-2/3/3/3/1-2.

4. Proposed Synapomorphies. [Character 1; State transition 0-1] paired occipital tubercles present, small, weakly developed (Fig.1A) (paired occipital tubercles absent or present, large and well-developed); [108; 0-1] abdominal gills 3 – 5 with basal flap of dorsal lamellae present (Fig. 15C) (gills 3 – 5 with basal flap of dorsal lamellae on gills 3 – 5 absent (Fig. 15B)); [109; 0-1] abdominal gills 3 – 5, dorsal projection of ventral lamellae present (Fig. 15C) (abdominal gills 3 – 5, dorsal projection of ventral lamellae absent (Fig. 15B)).

5. Species Included (42). *Tricorythodes (Tricorythodes) albilineatus* Berner [United States; A, L]; *T.* (*T.*) *allectus* (Needham) [Canada, United States; A, L]; *T.* (*T.*) *arequita* Traver [Uruguay, Brazil, Argentinal; A, L]; *T.* (*T.*) *australis* (Banks) [Argentina, Brazil; A]; *T.* (*T.*) *barbus* Allen [Argentina, Brazil; L]; *T.* (*T.*) *bullus* Allen [Argentina, Brazil; L]; *T.* (*T.*) *cobbi* Alba-Tercedor and Flannagan [Canada, United States; A, L]; *T.* (*T.*) *comus* Traver, 1959 [Mexico; A]; *T.* (*T.*). *condylus* Allen [Mexico, United States; A L]; *T.* (*T.*). *costaricanus* (Ulmer) [Costa Rica; A]; *T.* (*T.*) *cristatus* Allen [Brazil; L]; *T.* (*T.*) *cubensis* Klug and Narnajo [Cuba; A, L]; *T.* (*T.*) *curvatus* Allen [United States; L]; *T.* (*T.*) *dimorphus* Allen (Mexico, United States; A, L]; *T.* (*T.*) *explicatus* (Eaton) [Mexico, United States; A, L]; *T.* (*T.*) *fictus* Traver [Mexico, United States; A, L]; *T.* (*T.*) *grallator*, Kluge and Narnajo, 1990; *T.* (*T.*) *griseus* Hofmann and Satori [Guadeloupe; A, L]; *T.* (*T.*) *hiemalis* Molineri [Argentina; A, L]; *T.* (*T.*) *kirki* Baumgardner [Costa Rica; L]; *T.* (*T.*) *lichyi* Traver [Venezuela; A]; *T.* (*T.*) *minutus* Traver [Canada, Guatemala, Mexico, United States; A, L]; *T.* (*T.*) *mirca* Molineri [Bolivia; A, L]; *T.* (*T.*) *mirus* (Allen) [Mexico, United States; A, L]; *T.* (*T.*) *montanus* Kluge and Naranjo [Cuba; A, L]; *T.* (*T.*) *mosequs* Alba-Tercedor and Flannagan [Canada, United States; A, L]; *T.* (*T.*) *mulaiki* (Traver) [Mexico; A]; *T.* (*T.*) *notatus* Allen and Brusca Mexico; [L]; *T.* (*T.*) *ocellus* Allen and Roback [Peru; A, L]; *T.* (*T.*) *popayanicus* Dominguez [Argentina; A, L]; *T.* (*T.*) *primus* Baumgardner [Costa Rica; L]; *T.* (*T.*) *quercus* (Kilgore and Allen) [United States; L]; *T.* (*T.*) *quizeri* Molineri [Bolivia; A, L]; *T.* (*T.*) *robacki* (Allen) [United States; L]; *T.* (*T.*). *serratus* (Baumgardner and Ávila) [Costa Rica; A, L]; *T.* (*T.*) *sierramaestrae* Kluge and Naranjo [Cuba; A, L]; *T.* (*T.*) *sordidus* Allen [Costa Rica, Guatemala, Nicaragua; A, L]; *T.* (*T.*) *stygiatus* McDunnough [Canada, United States; A]; *T.* (*T.*) *trifasciatus* Molineri and Zúñiga [Colombia; A, L]; *T.* (*T.*) *ulmeri* Allen and Brusa [Mexico; L]; *T.* (*T.*) *undatus* Lugo-Ortiz and McCafferty [Costa Rica, Guatemala; L]; *T.* (*T.*) *yura* Molineri [Bolivia; A, L].

6. Distribution. Species known from North, Central, and South America and the Carribean region.

7. Comments. This is perhaps the most commonly-encountered genus of leptohyphid mayflies in North and Central America. Larvae occur in a wide variety of habitats within a number of different lotic ecosystems.

8. Type Material Examined. *Leptohyphes baumanni* Kilgore and Allen (=*L. mirus*): HOLOTYPE (male larva): USA: Arizona: Santa Cruz Co.; Sonoita Creek, Highway 82, near Patagonia, 22.v.1970, R.W. Bauman [CAS, #13601]; PARATYPES, same data as holotype, 11L [CAS]. *Tricorythodes cobbi* Alba-Tercedor and Flannagan: PARATYPES: CANADA: Manitoba, Assiniboine River, St. Francois Xavier, Lido Plage Rd., 49°52'24"N; 97°30'35"W, 23.vii.1993, 14♀ imagoes (FSCA (FAMU) E2052). *Leptohyphes costaricanus* Ulmer: HOLOTYPE (female imago): COSTA RICA: San Jose [Bavariann State Collection, Zoology, Munich, Germany] (onlyelectronic images of holotypey examined). *Tricorythodes cubensis* Kluge: PARATYPE: CUBA: Sienfuegos, RÍo Caburni, 14-18.iv.1989, 5L, 1♂, 1♀ [TAMU]. *Tricorythodes curvatus* Allen: HOLOTYPE (larva): Arkansas: Independence Co.; White R., Sta. 2, ca. 2.8 mi. ENE Salado, 31.vii.1974, J.W. Richardson [ANSP]; PARATYPES: same data as holotype, 3L. *Tricorythodes dimorphus* Allen: HOLOTYPE (male larvae) and ALLOTYPE (female larva): UNITED STATES: Arizona: Yavapai Co., Beaver Creek at Beaver Creek Rangers Station, Coconino National forest, 7.vii.1964, RK Allen [CAS #10030]; PARATOPOTYPES: same data as holotype, 2L [CAS]. *Tricorythodes explicatus* (Eaton): LECTOTYPE (male imago).

MEXICO: N. Sonora, Morrison. *Tricorythodes fictus* Traver: HOLOTYPE (male imago): USA: Oklahoma; Murry Co., 20.iii.1932, A. Sandoz [CU]. *Tricorythodes kirki* Baumgardner: HOLOTYPE (larva): COSTA RICA: Alajuela Province, Río Guayabo at Hwy 140, 1.8 km E Venicia (N10º40'45N, W84º15'13", elev. 460 m), 09.vi.2001, DE Baumgardner [TAMU]; PARATYPES: same data as holotype, 5 larvae [4 larvae TAMU, 1 larva FAMU]; Heredia Province, unnamed creek at Hwy. 4, ca. 3 Km from jct. with Hwy. 32 (N10º15'10", W83º55'11"; elev. 200 m) 10.vi.2001, 2 larvae [TAMU]; La Selva Biological Station, SW Puerto Viejo, Sura Creek at Rio Puerto Viejo (N10°25'49"; W84°00'06", elev. 33 m), 09.vi.2001, 8L, DE Baumgardner, 8 larvae [5L TAMU, 3L FAMU]; Río Isla Grande at Hwy. 4, ca. 5 Km. W. of Rio Frio (N10°23'31"; W 83°58'04", elev. 65 m), 10.vi.2001, 1 larva [PERC]. San José Province; Río Pedregoso at Hwy. 243, ca. 4 Km S. San Isidro de El General (N09°21'15 W83°43'35", elev. 660 m), 22.vi.2001, 12 larvae [TAMU]. *Tricorythodes minutus* Traver: HOLOTYPE (male imago): UNITED STATES: Utah: Provo River, 22.vii.1926 (CU). PARATYPES: Same data as holotype; 8 male imagos. *Leptohyphes mirus* Allen: HOLOTYPE (male larva): USA: Arizona; Río Blanco, 3.iv.37, J.G. Needham, (FSCA (FAMU) E2017.T). ALLOTYPE: same data as holotype, 1 female larva (in same vial as holotype). PARATYPES: same data as holotype, 2L (CAS), 4L (FSCA (FAMU) E2017.T). *Tricorythodes montanus* Kluge: PARATYPE: CUBA: Santiago de Cuba, Sierra Maestra, Río Guama (Alcarraza-Sandor), 1-7.ii.1989, 3L, 1♂, 1♀, N. Kluge [TAMU]. *Tricorythodes mosegus* Alba-Tercedor and Flannagan: PARATYPE: CANADA: Manitoba, Assiniboine River, St. Francois Xavier, Lido Plage Rd., 49°52'24"N; 97°30'35"W, 09-vii-1993, 1 male imago (FSCA (FAMU) E2051). *Tricorythodes notatus* Allen and Brusca: HOLOTYPE: MEXICO: Oaxaca, stream 10 mi. N. Huajintlan de Leon, 7.xi.1968, 1L, RK Allen [CAS]. PARATYPES: same data as holotype, 29L [CAS]. *Tricorythodes primus* Baumgardner: HOLOTYPE (larva): COSTA RICA: Puntarenas Province; Río Caracol at CA Hwy. 2, ca. 7.3 Km E. Río Claro (N08º39'47", W83º00'41", elev. 80 feet), 23.vi.2001, DE Baumgardner [TAMU]. PARATYPES: COSTA RICA: Puntarenas: Río Coloradito at CA Hwy. 2, ca. 6.7 Km SE Ciudad Neily (N08º36'09", W82º52'02", elev. 180 feet), 23.vi.2001, DE Baumgardner, 1 larva [TAMU]. *Leptohyphes quercus* Allen: HOLOTYPE (female larva): USA: Arizona: Coconino Co., Oak Creek Canyon S. Flagstaff at Pine Flat Campground, 9.iv.1968, RW Koss and R. Baumann [CAS, #13605]. *Cabecar serratus*: HOLOTYPE (female larva): COSTA RICA: Limón Provience, unnamed creek at Hwy 32, ca. 3 km W Pocora (10º10'38"N, 83º37'03"W, 110 m), 10.vi.2001, DE Baumgardner [TAMU]. PARATYPES: Same data as holotype, 1 mature female larva [FAMU]; COSTA RICA: Puntarenas Prov.: Río Barú at Barú, ca. 5 km NE Dominical, 22.vi.2001, 3L, D.E. Baumgardner [TAMU]; Río Balsar at Hwy 34, ca. 8 km NW Palmar Norte (08º59'05"N, 83º31'07"W; 65m), 22.vi.2001, 1L, D.E. Baumgardner [PERC]; Golfito, Quebrada Km. 20 (ULS 285 950 N/566 000 E), 21.iii.2005, 1♂, S. Avila [TAMU]; Golfito, Río Claro, Golfito, Queb. Labarto (ULS 293 100N/564 700 E), 21.iii.2005, 2♂, 3♀, S. Avila, [TAMU]; Río Claro, Quebrada Chiricanos, puente de C.I.A. (ULS 292 200 N/566 500E), 12.iii.2005, 1♂ (reared), S. Avila, [TAMU]. Limón Prov.: Río Suzrez at Hwy 36, ca. 17 Km NW Bribri (09º43'36"N, 82º50'21"W; 20 m), 11.vi.2001, 1L, DE Baumgardner [INBio]. NICARAGUA: Dept. of Granada: unnamed creek at Domitila Field Station, ca. 30 km S Granada (11º42'09"N, 85º57'06"W; 80 m), 13-18.vi.2004, 2L, 1 slide (#DB04x3001) (8L TAMU, 2L each FAMU, PERC), DE Baumgardner. *Tricorythodes sierramaestrae* Kluge: PARATYPE: CUBA: Santiago de Cuba, Sierra Maestra, Rio Guama (Alcarraza-Sandor), 1-7.ii.1989, 4L, 1♀, N. Kluge [TAMU]. *Tricorythodes sordidus* Allen: HOLOTYPE (female larva): COSTA RICA: San Jose Prov.; San Jose, 9-viii-62, G.G. Musser [FSCA(FAMU) - E2003.1T]. PARATYPES: same data as holotype, 4L (CAS), originally designated paratopotypes. COSTA RICA: stream 11 mi. SE San Isidro del General, 200 ft., 22-vii-1962, G.G. Musser, 1L [FSCA(FAMU) - E2003. T]. *Tricorythodes ulmeri* Allen and Brusca: HOLOTYPE (larva): MEXICO: Morelos, Río Cuautla at Cuautla, 13.xi.1968, RK Allen [CAS]. PARATYPES: same data as holotype, 39L [CAS].

9. Other Material Examined. *Tricorythodes albilineatus* Berner: **UNITED STATES:** FLORIDA: Gadsden Co.; Rocky Comfort Creek, on dirt road at bridge, 6 mi. S. State Hwy. 268, 30.xi.1969, J. Jones, 10 larvae [TAMU]; Flat Ck. at CR 270A, i Km S. Chatt, 24.vii.19996, J. Jones and A.R. Robinson, 4 larvae [TAMU]; Dixie/Levy/Gilchrist Co.'s, Suwanee River at Hwy. alt. 27, 9.v.1975, P.H. Carlson, 3♂, 3♀ [TAMU]; Taylor Co.; Econfina R. at Hwy. 98, ca. 10 mi. W. Perry (N30 º09'; W83 º51'), 19.viii.1999, D.E. Baumgardner, 4 larvae [TAMU]. GEORGIA: Lowndes Co.; Withlacoochee R. at Hwy. 31(GA/FL state line), ca. 5 mi. Ne Pinetta, FL (30º38'N; 83º19'W), 21.viii.1999, D.E. Baumgardner, 6 larvae [TAMU]. *Tricorythodes allectus* (Needham): **UNITED STATES:** CONNECTICUT: Hartford Co.; Connecticut River, Kings Island Boat Ramp, Enfield (N41°57'46"; W72 °6'28"), 7.vi.2004, SK Burian, 1♂ (reared) [TAMU]. OKLAHOMA: Comanche Co.; Ft. Sill, East Cache Creek, South Boundry Rd., East Range, 19.ix.2003, Kondratieff & Znellig, 31 larvae, >50♂ imagoes [TAMU]; Custer Co.; Deer Creek 5 mi. N. Weatherford on Caddo Rd., 15.v.1999, DE Baumgardner, >100 larvae [TAMU]; Le Flore Co.; Kiamichi R. at unnamed road, 3 mi. E. Albion, 6.v.1995, DE Baumgardner, 1♂ (reared), 1♀ (reared), 1 larva [TAMU]; Kiamichi R. at Hwy. 259, ca. 1 mi. S. of Big Cedar, 20.vi.1993, DE Baumgardner, 1 larval cast skin [TAMU]; Pushmataha Co.; Kiamichi R. at Hwy. 2, 16.3 mi. N. of Hwy. 2-3 jct., 16.ix.1993, DE Baumgardner, 6♂ subimagoes [TAMU]; Cedar Ck. at unnamed road, ca. 1 mi. N. of Snow, 21.vi.1993, DE Baumgardner, 1♂ (reared) [TAMU]. TEXAS: Anderson Co.; REMAP Site #55, Box Creek, 10.vi.1998, DE Bowles, 1 larva [TAMU]; Austin Co.; REMAP Site #49, Mill Creek, 22.vii.1998, DE Bowles, 3 larvae [TAMU]; Bexar Co.; Salado Creek, REMAP Site No. 98, 14.vii.1999, DE Bowles, 1 larva [TAMU]; Brazos Co.; Navasota River, Democrate Crossing, 9.5 km ENE Kurten, 12.ix.2000, DE Baumgardner, 1 larva [TAMU]; Caldwell Co.; REMAP Site #34, Plum Creek, 7.vii.1998, DE Bowles & L. Tolley, 4 larvae [TAMU]; Comal Co.; Honey Ck. in Honey Ck. St. Natural Area in Guadalupe R. State Pk (N29°51'34"; W98°29'4"), 31.v.1997, DE Bowles, 1 larvae [TAMU]; Cooke Co.; Elm Fork of the Trinity R. @ FM 2071, S. Gainesville, 27.vii.1995, DE Baumgardner, 12 larvae [TAMU]; Grimes Co.; REMAP Site #48, Navasota River, 13.vii.1998, T. Jurgensen, 4 larvae [TAMU]; Hays Co.; Blanco R. @ Westerfield Crossing, in San Marcos, 21.ii.1997, D.E. Baumgardner and D.E. Bowles, 1♀ (reared) [TAMU]; San Marcos R. at Cape Road, San Marcos, 22.ii.1997, D.E. Baumgardner & D.E. Bowles, 1♂ (reared), 3♀ (reared) [TAMU]; San Marcos River, 09.ix.1999, 4 larvae [TAMU]; Hemphill Co.; Canadian R. at Hwy. 83, ca. 2 mi. N. Canadian (N35°56'09"; W100°22'15"), 29.v.2002, DE Baumgardner, 3 larvae [TAMU]; Milam Co.; Brazos River, Port Sullivan, 9Km W. Hearne (N30 °52'50”; W96 °41'35"), 20.ix.2002, DE Baumgardner, 1 larva [TAMU]; Montgomery Co.; Peach Creek, REMAP Site 57, 16.vi.1998, DE Bowles, 1 larva [TAMU]; Nacogdoches Co.; REMAP Site #25, Legg Creek, 9.vi.1998, DE Bowles, 2 larvae [TAMU]; San Jacinto Co.; Winter's Bayou, 5 mi. NE Cleveland, 1st bridge crossing from Lonestar trailhead (N30 °23'44"; W95 °09'25"), 26.ix.2004, DE Baumgardner, 25 larvae, 3♂ (reared), 11♀ (reared) [TAMU]; same but, 03.x.1999, 2 larvae [TAMU]; Winters Bayou, REMAP Site No. 111, 18.viii.1999, DE Bowles, 6 larvae [TAMU]; same but, 17.viii.1999, DE Bowles, 5 larvae [TAMU]; Winters Bayou, ca. 2 mi. SE Bear Ck. Cemetery (N30°27.00'; W95°13.26'), 05.ix.2005, EG Riley, 2 larvae [TAMU]; Travis Co.; Hamilton Pool and stream, 17.ii.1995, Jasper, Gibson, Moeller, 1 larva [TAMU]; Williamson Co.; Georgetown, San Gabriel Park, below little dam and bridge, 07.x.1996, Wiersema, 8 larvae [TAMU]; *Tricorythodes australis* (Banks): **BRASIL:** MATO GROSSO STATE; Río Jaurua on BR 174, 10 Km W de Cáceres, 8.iii.1986, 7♂ imagos [FAMU]; PARANÁ STATE, Río Paraná, Guairá, (elev. 220 m), 10.iii.1969, 4♂ imagos W.L. & J.G. Peters [FAMU]. *Tricorythodes bullus* Allen: **ARGENTINA:** MISIONES, 25 Km al S. de El Soberbio, 21.xi.1998, 2L, 6♂ imagos Coll. Dominguez, Molineri, Nieto [IFML]. *Tricorythodes cobbi* Alba-Tercedor and Flannagan: USA: CONNECTICUT; Harford County, Connecticut River at Kings Island boat ramp, Enfield (41º57'50"N; 72º36'30"W); 14.viii.1997, S.K. Burian, 1♂ (TAMU); same but, 15.viii.1999, 1♂ and 2♀(reared) (NEL, TAMU); same but, 30-vi-1998, 1♂ (reared) (TAMU); same but, 21.vii.1998, 1♂ (reared) (TAMU); same but, 20.vii.1997, ♂ and ♀ (TAMU); 14.viii.1997, 3♂ (1 reared), 2♀ (reared) (NEL, TAMU); same but, 30.vii.1998, 3♂, 2♀ (reared) (NEL); same but, 02.ix.1999, 1♂, 3♀ (reared) (TAMU, NEL); Harford County, Connecticut River at Kings Island boat ramp, sandy area at end of path (41º54'59"N; 72º36'30"W), 20-vii-1997, S.K. Burian, 1♂, 2♀ (NEL); Harford County, Connecticut River at Kings Island boat ramp, Enfield, upstr. Side of near island (41°57'46"N; 72º36'28"W), 24-vii-2000, S.K. Burian, 1♂, 2♀ (reared) (TAMU); New Haven County, Mill River, below broken dam, Sleeping Giant S.P., Hamden, vii-1996, S.K. Burian, 1♂ (reared) (TAMU). *Tricorythodes condylus* Allen: **MEXICO:** PUEBLA; Rt 130 La Esperanza, Río San Marcos 30 Km NE Villa, Juarez, 16.iv.1975, 1 larva, J. Bueno. MISSOURI: Crawford Co.; Huzzah Creek at Davisville; Red Bluff Campgd, 6.x.1992, B. Nichols, 20 larvae [TAMU]; Meramec River, MU Wurdack Farm at Cook Station, 21.vii.1992, B. Nichols, 30 larvae [TAMU]. TEXAS: Hays Co.; San Marcos River at Lions City Club Park, 23-vi-1984, Elise Anderson, 2 larvae [TMU]; San Marcos, 09.ix.1999, 4 larvae [TAMU]; TEXAS: Montgomery Co.; New Caney, Caney Creek & US 59, 08.iii.1997, N. Wiersema, 2 larvae [TAMU]; same but, 27.xii.1996, 12 larvae [TAMU]. *Tricorythodes dimorphus* Allen: **MEXICO:** QUERETARO; unnamed creek, nr. Huasquilico (N21˚10'; W99˚33'), 08.i.2001, 1 larva (male), D.E. Baumgardner [TAMU]. **UNITED STATES:** ARIZONA: Gila Co.; Haigler Cr. at Haigler Ck. Camp Ground (N34°13'08.8"; W110°57'31.4"), 28.v.1999, 1 larva, D.E.

Baumgardner [TAMU]; Coconino Co.; Oak Cr. at Pine Flat Camp Ground (N35°00'52"; W111°44'26"), 27.v.1999, 3 larvae, D.E. Baumgardner [TAMU]; same but, 03-05-vi-2000, 64 larvae, D.E. Baumgardner [TAMU]; Oak Cr. at Manzanita Camp Ground, Coconino Nat. Forest (N34°56'04.1"; W111°44'46.0"), 25-26.v.1999, 12 larvae, D.E. Baumgardner [TAMU]; Oak Creek at Hwy. 89, ca. 3 mi.N. Sedona, Coconino National Forest (N34°55'21.6"; W111°44'1.7"), 25.v.1999, 6 larvae, D.E. Baumgardner [TAMU]; Oak Creek at Bootlegger Camp Ground, Hwy. 89A, Oak Creek Canyon (N34°58'09.4"; W111°45'01.4", elev. 1,700 m), 23-24.v.2004, 75 larvae, 2♀ imagos (reared), D.E. Baumgardner [TAMU]; Navajo Co.; North Fork White River at SR 55, Whitewater (N33°49'47.4"; W109°57'36.5", , elev. 1,700 m), 23.v.2004, 6L, D.E. Baumgardner [TAMU]. Pinal Co., Aravaipa Creek, 14.iii.1976, Dale Bruns, 40+L [CAS]. Yavapai Co.; Wet Beaver Creek at Wet Beaver Creek Campground (N34°40'8.1"; W111°42'46.8"), 24-25.v.1999, 12L, 1♂ imago (reared), D.E. Baumgardner [TAMU]; Oak Creek at Red Rock Crossing, Coconino National Forest, 7-8.vii.1964, 2 larvae, RK Allen [CAS]. Stewart Campground, Cave Cr., nr. Portal, Arizona, 14.v.1964, SG Jewett, 1 larva [CAS]. CALIFORNIA: Los Angeles Co.; W. Fork San Gabriel R. N. of Rincon Forest Service Station (elev. 500 m), 14.vi.1965, 3L, WP Vann [CAS]; N. Fk. San Gabriel River, 23.iv.1965, W.P. Vann, 16L [CAS]; San Gabriel R., San Gabriel Canyon entrance by bridge, 13.viii.1965, W.R. Vann, 1L [CAS]; same but, 23-viii-1965, W.R. Vann 1♂ imago [CAS]; E. Fk. San Gabriel R. , W. of E. Fk. Bridge, 18.vi.1965, W.R. Vann, 12♂ imagos [CAS]; E. Fk. San Gabriel River at and around E. Fk. Bridge, 18.viii.1967,1 larva, D. Dollins [CAS]; stream in Cattle Cyn (elev. 650 m), 22.vii.1965, 4L, W.P. Vann [CAS]; same but, 14.vi.1965, 1 larva, W.P. Vann [CAS]; W. Fk. San Gabriel R. at or about 63 Rincon For. Serv. Sta, 13.viii.1965, 1 larva, WPV [CAS]; San Gabriel R., S. of E. Fk. Bridge and N. of San Gabriel Dam, 30.viii.1965, 7 larvae, W.P. Vann [CAS]. COLORADO: Delta Co.; Escalante Cr. at Rd. 6.50, ca. 4.1 mi. from jct. with Hwy. 50 (N38°44'41"; W108°15'28"), 01.vi.2000, 5 larvae, D.E. Baumgardner [TAMU]. NEW MEXICO: Catron Co.; Willow Creek at Willow Creek campground (Hwy. 159), ca. 35 mi. E. Glenwood, Gila National Forest (N33°24'37"; W108°34'20", elev. 2,400 m), 23-24.v.2000, 30 larvae, 3♂ and 5♀ imagos (reared), D.E. Baumgardner [TAMU]; Middle Fork Gilla R., Gila National Monument (N33°13'46.7"; W108°15'57.9", elev. 1,900 m), 18.v.2004, 2 larvae, D.E. Baumgardner [TAMU]; Whitewater Creek at Hwy. 174, 5 mi. NE Glenwood, Gila Nat. Forest (N33°22'23.9"; W108°50'29.1", elev. elev. 1,800 m), 21.v.2004, 1 larvae, D.E. Baumgardner [TAMU]; Grant Co.; Sapillo Crek near Lake Roberts on Highway 25, 21.vii,70, 21 larvae, R.K. Allen [CAS]; Taos Co.; Upper Red River, Carson National Forest, 28.vii.37, Tarzwell, >50 larvae [CAS]. *Tricorythodes minutus* Traver: **GUATEMALA:** BAJA VERAPEZ: Río La Estancia at Hwy. 17, Salana (N15°05’54”; W90°18’18”, elev. 3000 ft), 07.i.2007, 55 larvae, D.E. Baumgardner (TAMU). SANTA ROSA: unnamed creek at Hwy. 16, ca. 13.2 Km S. from Hwy. 16/CA 1 jct, between Km marker 78 & 79 (N14°11’51”; W90°21’38”, elev. 2095 ft), 06.i.2007, 14 larvae (TAMU). **MEXICO:** AGUASCALIENTES: Sabinolandia, Río San Pedro, El Salto de los Salados (N21.85; W02.49), 06.xii.1997, 2 larvae (TAMU). MEXICO: stream at 56 km. between Toluca and Zitaeuaro 4 km. N.E. Bosencheue (elev. 8200 feet), 24.viii.1977, 4 larvae, RK Allen

(CAS). QUERETARO: Puerta de Alegriax, Arroyo Los Zunigas (N20°20’28”; W100°07’10”, elev. 2000 m), 08.vii.2000, 1 larvae, WDS (TAMU); 1 km S. San Miguel Palmas, Rio Victoria (N21°05’13”; W99°57’10”), 09.vii.2000, 100+ larvae, WDS (TAMU); Bucareli, Río Estorax (N21°02’05”; W99°37’03”), 11.vii.2000, 12 larvae, WDS (TAMU); 1 Km. S. Huasquilico, Arroyo Jalpan (N21°09’04”; W99°34’42”, elev. 1725 m), 11.vii.2000, 1 larvae, WDS (TAMU). **UNITED STATES:** ARIZONA: *Cochise Co*.; San Pedro R., Luis Springs, 17.iv.2001, 22♂, D. Rees (TAMU); San Pedro River, Hereford Rd. Bridge, 26.xi.1999, 14♂, A.B. Richards (TAMU); San Pedro River, Rt. 80, Saint David, 1.v.1995, 21 larvae, BCK (TAMU); *Cochise Co*, San Pedro River, Riparian Nat. Cons. Area, Rt. 90, 30.iv.1995, >100♂, BCK (CSU). *Coconino Co*.; Oak Cr. at Hwy. 89A, ca. 5 mi. N. Sedona (N34°55'23"; W111°44'01"), 04.vi.2000, 4 larvae, D.E. Baumgardner (TAMU); Oak Cr. at Manzanita Camp Ground (Hwy. 89), Coconino Nat. Forest (N34°56'04.1"; W111°44'46.0"), 25-26.v.1999, 16 larvae, D.E. Baumgardner (TAMU); Oak Cr. at Pine Flat Camp Ground (Hwy. 89) (N35°00'52"; W111°44'26"), 03-05.vi.2000, 15 larvae, 3♀ (reared), D.E. Baumgardner (TAMU); Oak Creek at Bootlegger Camp Ground, Hwy. 89A, Oak Creek Canyon (N34°58'09.4"; W111°45'01", elev. 5210 ft.), 24.v.2004, 20 larvae, 2♀ (reared), 1♂ (reared), D.E. Baumgardner (TAMU). *Graham Co*.; Gila R. at Ft. Thomas Road, Ft. Thomas (N33°02'59"; W109°58'01, elev. 2660 ft.), 27.v.2004, 1 larvae, D.E. Baumgardner (TAMU). *Greenlee Co*.; San Francisco R. at FS Rd. 212, ca. 1 mi. N Clifton (N33°04'30"; W109°18'03", elev. 3700 ft.), 21.v.2004, >100 larvae, D.E. Baumgardner (TAMU). *Santa Cruz Co*.; Patagonia State Park, Sonoita Creek, 22.iii.1987, 3 larvae, R. Leschen (TAMU); Sonita

Cr. at Blue Haven Rd., just off Hwy. 82, ca 1 mi. SW Patagonia (N31°30'57"; W110°47'35"), 06.vi.2000, 2 larvae, D.E. Baumgardner (TAMU); Sonoita Cr., nr. Patagonia, 15.iii.1997, 1♂, J. Slusark & K. Byrnes (TAMU). *Yavapai Co*.; Bubbling Springs off Forest Service Rd. 134, ca. 1 kn N. Page Springs, 22.iv.1993, 4 larvae, S.R. Moulton and K.W. Stewart (TAMU); Oak Cr. at Page Springs Rd (Co. Rd. 50), Page Springs (N34°45'57"; W111°53'27", elev. 3455 ft), 25.v.2004, >75 larvae, D.E. Baumgardner (TAMU); Verde R. @ Hwy. 260, Camp Verde (N34°32'60"; W111°51'00", elev. 3140 ft.), 23.v.1999, 4♂, 8♀ (reared), 38 larvae, D.E. Baumgardner (TAMU); Verde R. @ Hwy. 260, Camp Verde (N34°32'60"; W111°51'00", elev. 3140 ft.), 23.v.1999, 6♂ (reared), 9♀ (reared), 25 larvae, D.E. Baumgardner (TAMU); Verde R. @ Perkinsville bridge, ca. 16 mi. N. Jerome on FSR 318, Prescott Nat. Forest, 6.vi.1993, 2 larvae, S.R. Moulton and K.D. Alexander (TAMU); Verde River @ US Hwy. 89A bridge, Cottonwood, 4-5.vi.1993, 38♂ and ♀ imagos, S.R. Moulton and K.D. Alexander (TAMU); West Clear Creek at Clear Creek Campground, ca. 1 mi. from Hwy. 260, ca. 4 mi SE Camp Verde (N34°30'55"; W111°45'45", elev. 3270 ft.), 26.v.2004, 11 larvae, D.E. Baumgardner (TAMU); East Verde River, Camp Verde, 29.iv.1995, 2 larvae, BCK (CSU); Oak Creek, Red Rock Crossing, 20.i.1988, 1 larvae, 1♂, 1♀, BCK (CSU). COLORADO: *Arapahoe Co*.; South Platte R., Mineral Rd., 23.v.1993, 25♂, S. Fitzgerald (TAMU). *Archuleta Co*, Piedra River, Rd. 193, 1.vii.1996, 26♂, BCK (CSU). *Boulder Co*.; South Boulder Creek, Baseline Rd., 3.x.1995, 16♂, BCK (TAMU). *Chaffee Co*, Trout Cr, F.R. 215 and US 285, 4.ix.1993, 5♂, BCK & R. Durfee (CSU). *Costilla Co*, Trinchera Creek, 12 Road, 30.vi.1996, 9 larvae, BCK (CSU). *Douglas Co.*; Deckers Resort, BLT, 23.viii.1988, 6♂, P.A. Opler (CU); South Plate, Trumbull, 10.ix.1993, 12♂, 10♀, K. Rogers, (CSU). *Garfield Co*, 31.viii.1975, 1♂, 1♀, D.E. Ruiter (CSU). *Gunnison Co.*; Gunnison River, Riverway Picnic Area, 3 mi. W. of Gunnison, 31.viii.1991, 22♂, BCK, R. Durfee (TAMU). *Jackson Co.*; Grizzly Creek, Peterson SWA, off Rt. 14, 28.vii.1991, 4 larvae, R. Durfee & B. Painter (TAMU); North Platte River, Verner SWA, 7 mi. SW of Walden, 22.viii.1991, 42♂, R. Durfee (CSU). *Kit Carson Co*, South Fork Republican, N of Stratton, 17.vii.1986, 4 larvae, 16♂, BCK (CSU). *Larimer Co.*; Buckhorn Creek, about 6 miles west of Horsetooth Reservior, 12ix.1986, 4♂, G.W. Gerlich (TAMU); Head of Spring Creek, Stream, 11.ix.1986, 4♂, D. Brigham (TAMU); Mail Cr., BLT, 14.x.1988, 3♂, P.A. Opler (TAMU); Poudre River, nr. N. Colorado Nature Area, 21.ix.1986, 6 larvae, 39♂, BCK (TAMU); Ft. Collins, 27.vii.1979, 2♂, D.E. Ruiter (CSU); Heatheridge & Prospect, 27.vii.1979, 6♂, D.E. Ruiter (CSU); Mail Creek, Fort Collins, 10.xiii.1989, 40♂, P.A. Opler (CSU); Poudre R., Shields St. Br. Ft. Collins, 14.ix.1986, 1 larva, 3♂, S. Klahn (CSU). *Moffat Co.*; Yampa River, Echo Park, Dinosaur NM, 19.vii.1993, 18♂, 4♀, 2 larvae, BCK & R. Durfee (CSU); Yampa River, Tee Pee Campground, Dinosaur NM, 28.vii.1995, 38♂ (TAMU); Green River, Echo Park, Dinosaur NM, 24.vii.1992, 2 larvae, DAW (CSU); Yampa R., Craig, 15 larvae, (CSU). *Montezuma Co*, Mancos River, Mancos Canyon, Mesa Verde NF, 10.vii.1998, 7 larvae, BCK (CSU); Mancos River, Rt. 666, 18.vii.1990, 53♂, BCK (CSU). *Rio Blanco Co.*; Douglas Creek @ Rt. 64, 19.vii.1996, 23 larvae, 18♂, 15♀, BCK & R. Durfee (TAMU). *Saguache Co*, Indian Springs NA, 15.viii.1999, 1♂, BCK (CSU). *Weld Co*, 9.ix.1986, 1♂, D. Thompson (CSU); Lone Tree Creek, Terry Ranch, 10 mi. NW Carr, , 17.vi.1989, 4♂, 1♂ , P.A. Opler (CSU). *Yuma Co.*; S. Fork Republican R., US Hwy. 385 bridge, 29.iv.1993, 18 larvae, BCK & R. Durfee (TAMU); Arikaree River, Bowman Ranch, 23.vi.1999, 1 larva, G. Doyle, (CSU). MISSOURI: *Dallas Co*., Niangua R. at Hwy. M, 3.5 mi. E. jct. with Hwy. 38 (N37°31'11"; W92°59'03", elev. 1,120 ft), 10.viii.2005, 3 larvae, D.E. Baumgardner (TAMU). MONTANA: *Big Horn Co*, Big Horn River, 5.ix.1991, 17♂, D.E. Ruiter (TAMU). NEBRASKA: *Garden Co*, Blue Ck, Rackett Rd., 22.v.1998, 3♂, 8♀, BCK (TAMU). *Keith Co*, Otter Ck., St. Hwy. 92, 22.v.1998, 11 larvae, 2♀, BCK (TAMU). *Sioux Co*, Sowbelly Canyon, 6 mi. NE of Harrison, 12.vi.1989, >300♂, BCK (CSU). NEW MEXICO: *Catron Co.*; San Francisco R., Gila National Forest, ca. 5 mi. S. Glenwood (N33°14'18"; W108°52'47, elev. 4560 ft.), 20.v.2004, 2♂ (reared), >100 larvae, D.E. Baumgardner (TAMU); creek at FS Road 233, ca. 5 mi. NE Reserve, Gila National Forest (N33°43'54"; W108°42'28", elev. 5960 ft.), 20.v.2004, 1 larva, D.E. Baumgardner (TAMU); Middle Fork Gila R., Gila National Monument (N33°13'47"; W108°15'58", elev. 5720 ft.), 18.v.2004, 7 larvae, D.E. Baumgardner (TAMU); Taylor Creek, above Wall Lake, 02.viii.1993, 12 larvae, >50 adults, R. Durfee (TAMU). *Grant Co.*; Gila R., Gila Riparian Reserve, Gila Wilderness, ca. 6.7 mi. NE Cliff (N33°02'39"; W108°31'47", elev. 4650 ft.), 19.v.2004, 6 larvae, D.E. Baumgardner (TAMU). *Lincoln Co.*; Río Ruidoso at Main St. in Ruidoso (N33°19'14"; W105°42'43", elev. 4000 ft), 22.v.2000, 5 larvae, D.E. Baumgardner (TAMU). *Sandoval Co.*; Jemez R. at Vista Linda Camp Sight (Santa Fe Nat Forest), Hwy. 4, ca. 5 mi. N. Jemez Puebloa (N35°43'02"; W106°43'17, elev. 5865 ft.), 12.vii.2004, >75 larvae, 5♂ (reared), 5♀ (reared), D.E. Baumgardner (TAMU); same but, 26,27.v.2000, 3♀ (reared), 17 larvae, D.E. Baumgardner (TAMU); Río Guadalupe at Hwy. 485, ca. 2 mi. N. Gilman (N35°44'11"; W106°45'52", elev. 6190 ft.), 12.vii.2004, 3 larvae, D.E. Baumgardner (TAMU). *San Miguel Co.*; Pecos R. at Santa Ana FR, San Jose (N35°24'10"; W105°28'30", elev. 6100 ft.), 14.vii.2004, 29 larvae, D.E. Baumgardner (TAMU). *Sierra Co.*; Palomas Creek, 5 mi. W. of Williamsburg, 24.iv.1994, 20 larvae, >100♂ imagos, R. Durfee (CSU). SOUTH DAKOTA: *Lawrence Co*, Boxelder Creek, Boxelder Forks Campground (N44°11'57"; W103°32'05"), 12.vii.1997, 9♂, Baumann and BCK (TAMU); Redwater River, S. of Belle Fourche (N44°35'36"; W103°52'10"), 13.vii.1997, 10♂, Baumann & BCK (TAMU). *Fall River Co*, Fall River, Hot Springs, 5.ii.1995, 3 larvae, 1♂, 1♀, BCK (CSU). TEXAS: *Brewster Co*.; Big Bend National Park, Santa Elena Canyon, Rio Grande (N29°09'55""; W103°36'39, elev. 2200 ft.), 23.iv.2004, 2♀ (reared), D.E. Baumgardner (TAMU); same but, 12.v.2002, 16 larvae, 1♂ (reared), 3♀ (reared) D.E. Baumgardner (TAMU); Calamity Cr. @ TX Hwy 118, ca. 22 mi. S. Alpine, 21.x.1993, 50♂ imagos, SR Moulton and JC Abbott (TAMU). *Comal Co*.; Sattler, Rio Raft Co., Guadalupe River @ 5.5 mi. below Canyon Dam below 4th X-ing, 26.x.1996, 2♂ imagos, N. Wiersema (TAMU). *Gillespie Co*.; Sandy Creek at Park Rd. 965, Enchanted Rock State Park, 07.iv.2001, 4♂ (reared), 14♀ (reared), 100+ larvae, D.E. Baumgardner (TAMU). *Hemphill Co*.; Canadian R. at Hwy. 83, ca. 2 mi. N. Canadian (N35°56'09"; W100°22'15, elev. 2321 ft), 29.v.2002, 1 larva, D.E. Baumgardner (TAMU). *Jeff Davis Co*.; Davis State Park, Limpia Creek, 17.x.2000, 34 larvae, D. Wood and K. Winther (TAMU); H.C. Espy

Ranch, Farm Rd. 1832, 14.v.1973, 30♂, R.G. McClure (TAMU); Limpia Ck. @ Hwy. 118, ca. 1 mi. W. Ft. Davis (N30°36'17"; W103°53'51, elev. 4943 ft), 14.v.2002, 1 larva, D.E. Baumgardner (TAMU); roadside Pk., stream 2 mi. N. Ft. Davis at St. Rd. 17, 20.vii.1968, 28♂, K.W. Stewart, B. Stark, and G.L. Atmar (D.E. Baumgardner); Limpia Creek, Fort Davis, 10.iv.1935, 5 male imagos (pinned), INHS. *Presidio Co*.; Rio Grande, Grassy Banks Access Area on Big Bend Ranch State Park, 24.viii.1996, 1♀ (reared), D.E. Baumgardner & D.E. Bowles (TAMU); Big Bend Ranch State Park @ Ojito Adentro (N29°29'27.4"; W104°03'49.9), 24.viii.1996, 4 larvae, 1♂, D.E. Baumgardner (TAMU). *Reeves Co*.; unnamed ck., Hwy 17, Balmorhea (N30°59'13""; W103°44'35, elev. 3341 ft), 04.v.2002, 11 larvae, D.E. Baumgardner (TAMU). *Val Verde Co*.; Dolan Falls Preserve, Dolan Creek; The Nature Conservancy (N29°53'41", W100°59'11"), 08.xi.1998, 3♂, D.E. Baumgardner (TAMU). UTAH: *Uintah Co*, Green River, Cub Cr. Rd, 23.viii.1990, 12♂, BCK (CSU). VERMONT: *Bennington Co*.; Batten Kill R., Arlington at Rt. 7a (N45°5.8'; W73°8.5"), 17.vii.2004, 1♂ (reared), 2♀ (reared), S.K. Burian (TAMU). WYOMING: *Albany Co*, Laramie River, Hwy. 30, 2.ix.1989, 24 reared ♂, ♀ (imagos and subimagos), M. Harris (TAMU). *Carbon Co*, North Platte River, 1 mile above Treasure Island, 26.viii.1986, 1♂, 1 larva, Keith (CSU). *Platte Co*, Spring Fed pond, Warm Spring, Guernsey, 17.ix.1999, 20♂, 2 larvae, BCK & Doyle (TAMU); same but, 27.ii.2000, 1♂, BCK & Zuellig (CU); North Platte River, Camp Guernsey, 26.viii.2000, 15♂, 1♀, 3 larvae, BCK (CSU). *Tricorythodes fictus* Traver: OKLAHOMA: Murry Co., Honey Ck. at Turner Falls Pk., above Falls, 30-iv-1995, DE Baumgardner, 3♂, 2♀, 1♀ (reared) (TAMU). Same but, 21-iii-1995, 25 larvae (TAMU). Same but, 16-ii-1995, 4♂, 3 larvae (TAMU). Same but, 07-ii-1994, 3 larvae, 1♂ (reared) (TAMU). TEXAS: Bandera Co., Medina R. @ Hwy. 16, 1 mi. NW Medina, 08.iii.1997, DE Baumgardner & DE Bowles, 1♂ (reared), 4♀ (reared) (TAMU). Montgomery Co., New Caney, Peach Creek at FM 1485, 05-i-1997, NA Wiersema, 2♂. Hays Co., San Marcos R. @ Cape Rd., San Marcos, 22-ii-1997, DE Baumgardner, 11 larvae (TAMU). Kerr Co., Fessenden Ck. @ Hwy. 41, 19-iv-1997, DE Baumgardner and DE Bowles, 1♂ (reared), 6 larvae (TAMU). Comal Co., Guadalupe R @ Hwy. 311, 20-vi-1993, JL Cook, 3 larvae (TAMU). Val Verde Co., Devils River at Devils River State Park, 22-xii-1992, DE Baumgardner, 2 larvae, 2♂ (TAMU). Val Verde Co., Devils River at Dolan Creek Preserve (TNC), 08.xi.1998, DE Baumgardner, numerous larvae, reared adults (TAMU). *Tricorythodes mirus* (Allen): MEXICO: CHIHUAHUA: Río Satevo at Gral. Tris on Hwy. 16 (elev. 5100'), 13.viii.1977, 9 larvae, RK Allen [CAS]; Río Papagochic, 4 mi. E. Ciudad Guerrero on Hwy 16, 13.viii.1977, 2 larvae, RK Allen [CAS]; Río San Pedro at Meoqui on Hwy. 45, (elev. 3818'), 14.viii.1977, 6 larvae, RK Allen [CAS]; SINALOA: Río Baluarce at Rosarito, 13.i.1983, 1 larva, Allen and Murvosh [CAS]; stream 1 mi. N. El Viola, 18.i.1983, 6 larvae, Allen and Murvosh [CAS]; SONORA; Río Sonora 2 mi. SE Rte. 21 between Uras & Mazocahui, 14.i.1983, 1L, Allen & Murvosh (Slide #DB97060102) [CAS]; Río Bavispe, 3 mi. SW Colonia Moralia at dam, 2.i.1983, 12 larvae, Allen and Murvosh [CAS]; Río Altas at Tubutama, 13.i.1983, 5L, Allen and Murvosh [CAS]. **UNITED STATES:** ARIZONA: Santa Cruz Co.; Sonoita Cr., nr. Patagonia, 15.iii.1997, 30 larvae, 5♂ imagos, J. Slusark and K. Byrnes, [TAMU]; Sonita Cr. at

Blue Haven Rd., just off Hwy. 82, ca 1 mi. SW Patagonia (N31°30'57"; W110°47'35"), 06.vi.2002, >50 larvae, 3♂ and 2♀ imagos (reared), [TAMU]. TEXAS: Brewster Co.; Calamity Cr. @ TX Hwy 118, ca. 22 mi. S. Alpine, 24.viii.1996, 2 larvae, D.E. Baumgardner & DE Bowles [TAMU]. Jeff Davis Co.; Limpia Ck. at Hwy. 118, ca. 1 mi. W. Ft. Davis (N30°36'17"; W103°53'51", elev. 1,600 m), 14.v.2002, 76 larvae, D.E. Baumgardner [TAMU]; H.C. Espy Ranch, Farm Rd. 1832, 14.v.1973, 20 larvae, RG McClure [TAMU]. *Tricorythodes mosegus* Alba-Tercedor and Flannagan: **UNITED STATES:** CONNECTICUT; New Haven Co.; Bladdens Brk., Seymour @ jct. of Rt. 67 and Sokarat Rd., 22-vii-1996, S.K. Burian, 2♂ (reared) (NEL, TAMU); USA: Connecticut, Harford County, Connecticut River at Kings Island boat ramp, sandy area at end of path (41°54'59"N; 72°36'30"W), 20-vii-1997, S.K. Burian, 1♂ (reared), 1♀ (reared) (TAMU). *Tricorythodes popayanicus* Dominguez: **ARGENTINA:** SALTA; Paque Nacional El Rey, A Los Puestos (S24º47'48"; W64º37'19"), 24.iii.1999, 5 ♂,♀ imagos, Molineri Y Romero [TAMU]; Rio Grande de El Sauce 15.ix.1998, 5 larvae, Dominguez, Molineri y Ubero [TAMU]. *Tricorythodes quercus* (Kilgore and Allen): ARIZONA: Coconino Co.; Oak Cr. at Pine Flat Camp Ground (N35°00'52"; W111°44'26"), 03-05.vi.2000, 1 larva, D.E. Baumgardner [TAMU]. NEW MEXICO: Río Grande at Hatch, 11.viii.1977, 1 larva, RK Allen (elev. 3700', 78F), 1 associated slide (Slide #DB97060101) [CAS]. *Tricorythodes serratus* (Baumgardner and Ávila): **COSTA RICA:** PUNTARENAS PROV., 4.1 Km N Dominical on Hwy. 243, unnamed river (N09°16'51"; W83°50'55"), 14.vi.2000, 1L, W.D. Shepard [TAMU]. **NICARAGUA:** DEPT. OF RÍO SAN JUAN: Bartola Field Station, Río San Juan, ca. 3

km SE El Castillo (10º58'22"N, 84º20'24"W; 50 m), 19-24.vi.2004, 1L (immature), D.E. Baumgardner (DB 04-43) (TAMU). **PANAMÁ**: PANAMÁ, Capira, Río Capira, tierras bajas, 15-iv-1995, Coll. J. Coronado, 1L (TAMU). *Tricorythodes sordidus* Allen (all specimens deposited in TAMU)*:* **COSTA RICA**: ALAJUELA PROV.: NE of Bijagua, nr. Las Flores, Río Areuo (10°21’06”N; 85°21’05”W), 07.vi.2000, 2 larvae, WDS; 3 km SE Rio Cuarto, Hwy. 140, Río Hule (10°20’N; 84°12’W), 15.i.2000, 1 larva, WDS. GUANACASTE PROV.: 4.8 km N Canas, Hwy. 142, Río Santa Rosa, 17.i.2000, 4 larvae, WDS; Río Diria at unnamed road, ca. 1 Km. E of intersection with Hwy 21, (10°20’05”N; 85°34’04”W), 15.vi.2001, 3 larvae, D.E. Baumgardner; 6 km S San Miguel, Hwy 1, Quebrada Culvert (10°19’N; 85°03’W), 23.i.2000, 3 larvae, WDS; unnamed creek at Hwy. 18, ca. 8 Km NW Nicoya (10°10’00”N; 85°26’08”W), 16.vi.2001, 2L, D.E. Baumgardner. HEREDIA PROV: unnamed creek at Hwy 4, ca. 3 Km from jct. with Hwy 32 (10°15’10”N; 83°55’11”W), 10.vi.2001, 2L, D.E. Baumgardner. LIMÓN PROV.: Río Catarata at Hwy 36, 4 Km East of Bribri (09°37’50”N; 82°49’06”W), 11.vi.2001, 1 larva, D.E. Baumgardner; unnamed creek at Hwy 32, ca. 3 Km W of Pocora (10°10’38”N; 83°37’03”W), 10.vi.2001, 2L, D.E. Baumgardner; unnamed stream at road, ca. 2 Km NW Puerto Viejo (09°38’43”N; 82°47’12”W), 11.vi.2001, 1 larva, D.E. Baumgardner. PUNTARENAS PROV.: 1 Km S Coloradito, Río Coloradito at Hwy. 2 (08°36’10”N; 82°54’07”W), 17.vi.2000, 3L, WDS; 4.1 Km N Dominical on Hwy. 243, unnamed river (09°16’51”; N83°50’55”W), 14.vi.2000, 2 larvae, WDS; Río Jaba at Las Cruces Biological Station, ca. 14 Km. S San Vito, 23, 24.vi.2001, 1 larva, 1♂ (reared), D.E. Baumgardner; Estacion Biologica

Monteverde, Quebrada Moquina (10°19'N; 84°48'W), 24.i.2000, 2L, WDS; Río Baru at Baru, ca. 5 Km NE Dominical, 22.vi.2001, 1L, D.E. Baumgardner; 1 Km S Coloradito, Río Coloradito at Hwy 2 (08°36'10"N; 82°54'07"W), 17.vi.2000, 6 larvae, WDS; Quebrada Culebra at Las Cruses Biological Station, ca. 14 Km S. San Vito, 24.vi.2001, 2L, D.E. Baumgardner; NE Dominical, unnamed stream (09°16'48"N; 83°49'22"W), 19.vi.2000, 1 larvae, WDS; unnamed creek at Hwy. 34, ca 37.5 Km SE Dominical (09°03'04"N; 83°37'00"W), 22.vi.2001, 5L, D.E. Baumgardner; Río Caracol at CA Hwy. 2, ca. 7.3Km E. Río Claro (08°39'47"N; 83°00'41"W), 23.vi.2001, 3 larvae, D.E. Baumgardner; 5 Km SE Coloradito, unnamed river (08°34'41"N; 82°52'28"W), 17.vi.2000, 1 larva, WDS. San Jose Prov.: Río Pedregoso at Hwy. 243, ca. 4 Km S. San Isidro de El General (09°21'15"N; 83°43'35"W), 22.vi.2001, 1 larva, D.E. Baumgardner. **GUATEMALA:** CHIQUIMULA DEPT.: Río Anguiatu, Frontera a Anquiata, 13.vii.1995, 1 larva, Bryan Yates; EL PROGRESO Dept.: Río Hato at CA Hwy. 9, ca. 5.9 Km E. from jct. with Hwy. 17, Magdalena (14°55'11"N; 89°57'56'W), 14.vii.2001, 3 larvae, D.E. Baumgardner; Quebrada Las Pericas at Hwy. 17, 11.1 Km W. from jct. with Hwy. CA (09°14'54"N; 90°05'52"W), 12.vii.2001, 4 larvae, D.E. Baumgardner; IZABEL DEPT.: Río Cienega at CA Hwy. 13, ca. 4 Km. S. Shaila (15°43'53"N; 89°84'44"W), 16.vii.2001, 1 larva, D.E. Baumgardner; ZACAPA DEPT.: Río Cayo at CA Hwy. 9, 2.3 Km E. Santa Cruz (15°00'54"N; 89°39'09'W), 14.vii.2001, 1 larva, D.E. Baumgardner; Río Cayo at CA Hwy. 9, 2.3 Km E. Santa Cruz (15°00'54'N; 89°39'09'W), 14.vii.2001, 3 larvae, D.E. Baumgardner. **MEXICO:** NUEVO LEON: Río Cabazones at Hwy. 85, 15 mi. N. Linares., 5 larvae, 16.v.1995;

unnamed creek at road leading to Brownsville, nr. town of Galenana off Hwy. 60, 9L, 19.v.1995; QUERETARO: Puerta de Alegriax, Arroyo Los Zunigas (20°20'28"N; 100°07'10"W), 1 larvae, 08-vii-2000, WDS; 1 Km. S. Huasquilico, Arroyo Jalpan (21°09'04"N; 99°34'42"W), 7 larvae, 11.vii.2000, WDS; 1 km SSE San Pedro, Arroyo Real (21°07'07"N; 99°32'05"W), 12L, 11.vii.2000, WDS; Chuveje, Río Chuveje (21°10'13"N; 99°33'18"W), 12.vii.2000, 1 larvae, WDS; Pínal de Amoles, Agua Fria (UTM 2338413), 1 larvae, 28.viii.1997, R. Jones; SAN LUÍS POTOSI: Río Moctezuma at Tamazunchale on Hwy. 85, 2L, 18.viii.1977, R.K. Allen (CAS); TAMAULIPAS: Río San marcos nr. Ciudad Victoria, 14 larvae, 24/25.xi.1968, R.K. Allen (CAS); Branch of Río Chihue at Hwy. 101, ca. 12 mi. S Juamave, nr. kilo. marker #91, 10 larvae, 17.v.1995, D.E. Baumgardner. **NICARAGUA:** GRANADA: Unnamed river at Domitila Field Station, ca. 30 km S Granada (N11º42'09"; W85º57'06"), 13-18.vi.2004, 68L, 2 ♂ (reared), 7 ♀ (reared), D.E. Baumgardner. *Tricorythodes undatus* Lugo-Ortiz and McCafferty: **COSTA RICA**: LIMON, Río Shiroles at Shiroles (N09°34'50"; W82°57'27", elev. 95 m), 12.vi.2001, 4L, D.E. Baumgardner [TAMU]; Río Suarez at Hwy. 36, ca 17 Km NW Bribri (N09°43'36"; W82°50'21", elev. 20 m), 11.vi.2001, 10 larvae, D.E. Baumgardner [TAMU]; Shiroles Creek Blei, 30.iv.2000, 2 larvae, Bill McCamey [TAMU]. PUNTARENAS, Río Baru at Baru, ca. 5 Km NE Dominical, 22.vi.2001, 2 larvae, D.E. Baumgardner [TAMU]. **PANAMA**: CHIRIQUI, 7.5 Km N Chiriqui, Rio Gualaca (N08°26'; W82°17'; elev. 10 m), 17.i.2001, 1L, A. Gillogly [TAMU].

CHAPTER IV

A TAXONOMIC REVISION OF THE GENUS *LEPTOHYPHES* EATON IN NORTH AND CENTRAL AMERICA

Introduction

Significant progress has recently been made in understanding North and South America species within the diverse Western Hemisphere mayfly family Leptohyphidae (Lugo-Ortiz and McCafferty, 1995a; Baumgardner and McCafferty, 2000; Wiersema and McCafferty, 2000; Molineri 2003b, 2004; Baumgardner and Ávila, 2006; Baumgardner, 2007). A revision of the genus *Leptohyphes* in South America was given by Molineri (2003b). Research on this genus in North and Central America, except for species synonymies of Baumgardner and McCafferty (2000) and restriction of the generic concept by Wiersema and McCafferty (2000), has focused more on new species descriptions and range extensions (Lugo-Ortiz and McCafferty, 1995a; Baumgardner et al., 1993; Baumgardner and Ávila, 2006). As part of a comprehensive revision of *Leptohyphes* in North and Central America, we present here a number of new synonyms, species revalidations, a discussion of numerous descriptive errors associated with original species descriptions discovered, and one new adult description. Research on new collections, large sample sizes, and specimens from numerous locations has led to the resolution of most remaining taxonomic issues within North and Central American *Leptohyphes*.

Collections (and their acronyms) housing materials used in this study include: California Academy of Sciences, San Francisco (CAS); Florida A&M University, Tallahassee (FAMU); Purdue University, West Lafayette, Indiana (PERC), and Texas A & M University, College Station (TAMU). In material-examined summaries, larval collections are abbreviated by the capital letter "L", preceded by the number of specimens examined. Collectors are identified by the following initials: D.E. Baumgardner (David E. Baumgardner); RKA (Richard K. Allen); WDS (William D. Sheppard). Global positioning measures are given in longitude/latitude coordinates as degrees, minutes, seconds. Descriptive adjectives for setae follow Baumgardner and Ávila (2006).

Morphology

Many morphological characters of both the larvae and adults of North and Central American *Leptohyphes* are very similar, making species identifications difficult for both adults and larvae. In addition, limited material of many species and a lack of associations among the adult and larval stages of many species adds to the uncertainty of species limits. The only available taxonomic key to distinguish North and Central American *Leptohyphes* larvae is that of Allen (1978), which relies in large part to differences in body coloration and highly variable morphological features. Baumgardner and McCafferty (2000) discussed these shortcomings, and proposed a number of synonyms in the genus *Leptohyphes*, based upon morphological variations among populations. There are a number of morphological characters shared among all known male imagos and larvae of North and Central American *Leptohyphes*. Those characteristics are discussed in the following paragraph, and will not be repeated in individual species descriptions, unless stated otherwise. Detailed descriptions of the male imago and larval stages are given under each species.

The following characters occur in all the known *Leptohyphes* male imagos in North and Central America. The compound eyes are small (distance between eyes greater than distance across any one eye) (Fig. 1A). On the dorsal surface of the mesonotum, the anterior parapsidal suture is fused with the transverse interscutal suture, and the plumidium is present (Fig. 1E). Hind wings are present on all males, with an elongate costal process (Fig. 2D). Tarsi of all legs are five-segmented, with tarsal claws of all legs dissimilar, one blunt, the other apically hooked, (Fig. 2F), except in the forelegs of male imagos, where both are blunt (Fig. 2G); the foretibia of males possesses sharp spines along ventral surface (Fig. 2H). The forceps are three-segmented, with the first segment short and stout, the second segment elongate, and the third segment small and globular (Fig. 3D). The basal half of the penes is fused, distal parts divergent, "Y" shaped; lateral margins sclerotized from base and extended to apex as a short spine; each spine is medially to each membranous lobe.

With very few exceptions, there are no differences among the highly conserved mouthparts of larvae of the North and Central American species of *Leptohyphes*. Unless stated otherwise in the species descriptions, the following mouthpart descriptions apply to all North and Central American species of *Leptohyphes*.

Labrum (Fig. 20A): dorsally with filiform setae along lateral margins; two rows of acuminate setae recessed from anterior margin; ventrally with single longitudinal row of acuminate setae near midline, interspersed with filiform setae; anterior and lateral margins with dense filiform and acuminate setae. *Labium* (Fig.20B): submentum moderately developed (approximately twice as wide as long), with regularly-spaced acuminate setae along lateral margins; ventrally with numerous robust setae most abundant near midline; prementum ventrally with numerous filiform setae; labial palp three-segmented with numerous filiform setae; basal palp no more than 2-3 times longer than 2^{nd} and 3^{rd} palps combined; glossae and paraglossae subequal, fused except distally, with smooth or slightly serrated outer margins; glossae slightly recessed, rounded, and with robust setae; paraglossae with numerous filiform setae. *Hypopharynx* (Fig.20C): lingua apically-rounded with numerous filiform and acuminate setae present on anterior margin; superlinguae oval, with numerous filiform and acuminate setae along anterior and lateral margins. *Left Mandible* (Fig.20D): outer incisor with two to four denticles, fused almost their entire distance; inner incisor with one or two denticles; prostheca arising at base of inner incisor, with highly-branched setae projecting towards molar region. *Right Mandible* (Fig.20E): outer incisors with one to three denticles; inner incisors with one to denticles; prostheca arising at base of inner incisor with elongate setae projecting towards molar region; denticles of molar region mostly fused. Maxilla (Fig. 5A): suture between galea and lacinia present, complete; distal margin with numerous elongate and filiform setae; one or more setae at base of inner margin; palp elongate, three-segmented, without apical seta.

Additionally, all larvae possess the following morphological structures unless specifically mentioned otherwise in individual species discussion. Meso- and metalegs with a single transverse row of stout or robust setae basally (Fig. 5E); dorsal surface of femur with a longitudinal ridge (Fig. 5F); anterodorsal surface of tibia with a median elevated ridge (Fig. 5F). Abdominal terga two through ten with robust setae along posterior margins (Fig. 6E); sternites seven and eight with posterolateral projections shorter than, or equal to, medial length of associated tergites (Fig. 6D). Operculate gill on abdominal segment two oval (Fig. 6H); inner lamella with a small, colorless ventrolateral projection (Fig. 15G); gills present on abdominal segments two through six.

Descriptive adjectives for setae follow Baumgardner and Ávila (2006). A "gill formula" is given for each species, which indicates the number of lamellae present in each abdominal gill. For example, a gill formula of 2/5-6/5-6/4/1 means that abdominal gill two is formed by two lamellae, gill three by five or six lamellae, gill four by five or six lamellae, gill five by four lamellae, and gill six by one lamella.

Species Accounts

Leptohyphes alleni Brusca

Leptohyphes alleni Brusca, 1971:146; Allen, 1978:543.

Diagnosis: Based upon the original description, larvae of *L. alleni* are distinguished from other known *Leptohyphes* larvae by the presence of numerous small, pale spots (see "Discussion" below for comments concerning this character) on the head, body, and appendages, which are absent in all other species, except *L. murdochi*, which also possesses pale spots on the body. *Leptohyphes murdochi* larvae can be distinguished from *L. alleni* larvae due to the presence of a distinct apical concavity on the middle and hind femora, which are absent on *L. alleni* larvae.

Description: *Male Imago*: Unknown. *Larva*: Length. Body, 4.5 – 5.5 mm; caudal filaments, 4.0 – 5.0 mm. General coloration very pale yellowish-brown. Head: pale yellowish; antennae pale. Thorax: pale yellowish-brown; without anterolateral projections and median tubercle. Legs. Proleg (Fig.21A): femur with transverse row of robust setae and numerous, small, shallow circular depressions on dorsal surface; anterior and posterior margins with few, scattered filiform setae; tibia with evenly spaced row of filiform setae along anterior margin, and single row of elongate setae along anterolateral margin; posterior margin with few, scattered filiform setae; tarsus with evenly spaced filiform setae along inner margin; posterior margin with a few, scattered filiform setae along outer margin. Meso- and metalegs (Fig.21F): femora densely covered with numerous, small, shallow circular depressions on dorsal surface; setae absent from dorsal surface; anterior margin with few, scattered stout setae; basal half of posterior margin with scattered filiform, and elongate setae along most of distal margin; tibiae with elongate setae present along most of anterior and posterior margins; tarsus with setae absent from anterior margin, and single row of filiform setae along posterior margin. Claws of all legs with three to four marginal denticles (Fig.22D); submarginal denticle absent. Abdomen: terga pale yellowish-brown; sublateral margins of tergites seven and eight without setae (Fig.24D); operculate pale; gill formula 2/5/5/5/2.

Distribution: Known only from the type locality in Oaxaca, Mexico.

Discussion: *Leptohyphes alleni* was described by Brusca (1971) on the basis of four larvae from a single location in Oaxaca, Mexico. No additional collection records of it have been reported in the literature since its original description. The holotype (a mature female larva) and paratypes of *L. alleni* are badly faded and show no "pale spots", as described in the literature. What appear as pale spots on the abdominal tergites of the holotype female larva are the underlying eggs. The dorsal surface of all femora are densely covered with small, shallow depressions which are paler than the surrounding coloration of the leg. These depressions, or pits, are mostly readily visible under very high magnification (400x), and often only barely discernable under low magnification. These pits may have been the "pale spots" to which Allen was referring in the original description. However, no similar structures could be found on the head or body. The exact function of these pits is unclear, but may function in some type of chemical reception.

The type specimens are all badly faded and do not show any of the darker reddish-brown coloration as described in the original description (Brusca, 1971), or by Allen (1978). In addition, none of the black markings are present as originally described, such as the black band between the compound eyes, or black markings on the thorax, abdomen, or operculate gills. Coloration in the above description is based upon the current coloration of the larvae.

All legs have been removed from the holotype, and possibly mounted on slides associated with the type series; however, it is unclear which slides are associated with the holotype, and which with the paratypes. Tarsal claw denticulation and shape of the profemur do agree with the original description.

Type Material Examined: *Leptohyphes alleni* HOLOTYPE (larva): MEXICO, Oaxaca, stream 10 miles N. Huajuapan de Leon (elev. 5,400 ft), 07.xi.1968, RKA [CAS #13600]. PARATYPES: same data as holotype, 3L, 5 slides (unknown which slides belong with holotype and which belong with paratypes) [CAS].

Other Material Examined: None

Leptohyphes apache Allen

Leptohyphes apache Allen, 1967:352; Allen, 1978; Lugo-Ortiz and McCafferty, 1995b.

Leptohyphes hispidus Allen and Brusca, 1973:89; Baumgardner and McCafferty, 2000 (syn. of *Leptohyphes zalope*); Lugo-Ortiz and McCafferty, 1995a. **new synonym**

Leptohyphes lumas Allen and Brusca, 1973:91; Allen, 1978:547 (syn of *Leptohyphes hispidus*); Lugo-Ortiz and McCafferty, 1995c (re-validated); Baumgardner and McCafferty, 2000 (syn. of *Leptohyphes zalope*) **new synonym**

Leptohyphes spiculatus Allen and Brusca, 1973:92; Allen, 1978 **new synonym**

Leptohyphes succinus Allen 1978:555; Baumgardner and McCafferty, 2000 (syn of *Leptohyphes zalope*) **new synonym**

Diagnosis: Larvae of *L. apache* can be differentiated from other species of *Leptohyphes* in North America by a complete absence of setae on the sublateral margins of the abdominal terga (in rare cases, a few (< 5) setae may be present). In addition, the dorsal surface of the meso- and metafemora are without setae. As in *L. zalope*, mature larvae are typically large (5-8 mm in length), dark reddish-brown in color, and with extensive black shading over much of the body. *Leptohyphes apache* larvae also have a vertex pattern very similar to that of *L. zalope*.

Description: *Male Imago*: Unknown. *Larva*: Length. Body, 5.5 – 7.0 mm; caudal filaments, 4.0 – 6.0 mm. General coloration light brown to reddish-brown with dark brown markings. Head: brown with complex black pattern on vertex, and thick black band on frons between compound eyes and at base of antennae (Fig.24C); antennae pale. Thorax: brown to reddish-brown, with irregular dark brown and black markings; without anterolateral projections and median tubercle. Legs. Proleg (Fig.21B): femur with transverse row of stout and elongate setae along dorsal surface; anterior margin with scattered robust setae; posterior margin with stout setae distally, and few scattered filiform setae in basal half; tibia with rows of filiform setae along anterior margin, and elongate setae along anterolateral margin; posterior margin with few, scattered filiform setae or none; tarsus with scattered filiform and elongate setae along inner margin, and a single row of elongate setae along anterolateral margin; posterior margin with a few filiform and elongate setae along distal outer margin. Meso- and metalegs (Fig.21G): femora with setae absent from dorsal surface; anterior margin with few, scattered stout setae; posterior margin with fairly regularly-spaced elongate setae along most of margin; tibiae with elongate setae present along most of anterior and posterior margins; tarsus with few, scattered filiform setae along anterior and posterior margins, or none; single row of elongate setae present medially. Claws of all legs with four to eight marginal, and a single submarginal denticle (Fig.22E). Abdomen: terga light brown to reddish-brown with irregular brown and black markings along posterior margin; sublateral margins of tergites seven and eight without setae (Fig.24D); operculate gill brown, with pale markings apically; gill formula 2/5/5/4/1.

Distribution: *Leptohyphes apache* is known from Arizona, New Mexico, Utah, and Texas in the United States, throughout Mexico, and south to Guatemala. Some records of *L. zalope* from the Southwestern United States and Central America may be attributable to *L. apache*.

Discussion: *Leptohyphes apache* was described by Allen (1967) on the basis of larvae from Arizona, New Mexico and Utah. No discussion was given how the larvae differed from other species of *Leptohyphes.* Allen and Brusca (1973) described *L. hispidus*, *L. lumas*, and *L. spiculatus* based upon larvae from various locations in Mexico. *Leptohyphes hispidus* was distinguished from other *Leptohyphes* by the presence of small black spicules on the body, *L. lumas* by its dark coloration, and *L. spiculatus* by the presence of scattered spicules on the head, body and appendages. In addition, both *L. lumas* and *L. spiculatus* were described as having numerous setae on the abdominal terga (see figure 29, Allen and Brusca 1973). Examination of the holotype and paratypes of all three of these species, however, clearly show they completely lack any setae on the abdominal terga. No morphological features could be found to separate the species from each other.

Allen (1978) recognized the equivalency of *L. hispidus* and *L. lumas*, and synonymized *L. lumas* with *L. hispidus*, stating only minor morphological differences separate them. Evidently the original description of *L. lumas* with “abdominal terga 1-10 with scattered short spines and long paired submedian spines on posterior margin”, and the abdominal terga of *L. spiculatus* as "terga with numerous long spines" were incorrect. Figure 29 of Allen and Brusca (1973) is more similar to that of *L. zalope* than *L. spiculatus*.

The use of the term "spicules" to distinguish *L. spiculatus* from other species is not reliable for two reasons. First, spicules are not actually present on the body of *L. spiculatus*. The body possesses only a rough surface that could give the appearance of spicules under low magnification. This surface feature can best be described as scabriculous. Second, a scabriculous surface is common to many species of *Leptohyphes*, and can also be variable among individuals of the same species.

Type Material Examined: *Leptohyphes apache* Allen; HOLOTYPE Larva: ARIZONA: Navajo Co., N. Fk. White River at White River, Fort Apache Indian Reservation, 5-VII-64, R.K. Allen [CAS]. PARATYPES: AZ: Navajo Co., N. Fk. White River at White River, Fort Apache Indian Reservation, 5.VII.64, R.K. Allen, 14L, 1 associated slide (4L in one vial, 10L in second vial, all at CAS). AZ: Navajo Co., stream 8 mi N. White River, 25.vi.51, S.J. Preece, 1L [FAMU, #E2012.T] 2 associated slides [CAS]; AZ: Navajo Co., White River, 4 mi N. White River, 25.vi.51, S.J. Preece, 4L [FAMU, #E2012.T], 2 associated slides [CAS]; NM: Taylor Creek, Santa Fe Natl. Forest, 26-VIII-37, C.M. Tarzwell, 11L, 4 associated slides [CAS]; UT: Virgin River, Zion's Natl. Park, VI.47, G.F. Edmunds, Jr, 3 slides [CAS]; AZ: Yavapai Co., Beaver Creek at Beaver Creek Rangers Station, 7-VII-64, R.K. Allen, 2L [CAS]; AZ: Greenlee Co., San Francisco River at Clifton, 4-VII-64, R.K. Allen, 2L [CAS]. *Leptohyphes hispidus* Allen and Brusca; HOLOTYPE Larva: Mexico: Vera Cruz, stream 5 miles south Ciudad Mendoza, 7-XI-68, R.K. Allen, [CAS Type #11975]. PARATYPES: 42L, same data as holotype [CAS]. Mexico: Vera Cruz, Rio Jamapa, 3 miles northeast Coscomatopec, 8.xi.68, R.K. Allen, 14L [CAS]; 2 slides included with type series, unknown which slides belong with which specimens [CAS]. *Leptohyphes lumas* Allen and Brusca: HOLOTYPE Larva: MEXICO, Chiapas, stream 7 miles north Arriaga on Highway 190, 20-VII-1966, R.K. Allen [CAS]. PARATYPES: 16L, same data as holotype [CAS]. MEXICO, Chiapas, stream 7 miles north Arriaga on Highway 190, 23.x.1968, R.K. Allen, 7L [CAS]. Chiapas, stream at Santa Isabel, 12 miles above Arriaga on Highway 190, 23.x.1968, R.K. Allen, 3L [CAS]. Chiapas, Rio Teapa near Ishuatann, 18.vii.1966, R.K. Allen, 3L [CAS]. Oaxaca, Rio Grande, 3 miles south Gualatao, 6.xi.1968, R.K. Allen, 2L [CAS]. Tabasco, Rio Grifalva at Teapa, 18.vii.1966, R.K. Allen, 1L [CAS]. Chiapas, Rio Huitla, 14 miles north Tapachula, 1.xi.1968, R.K. Allen, 1L [CAS]. Vera Cruz, Rio Jamapa, 3 miles northeast Coscomatepec, R.K. Allen, 8.xi.1968, 7L [CAS]. Same but, 14.vii.1966, 2L [CAS]. Vera Cruz, Rio Tecolapan, Santiago Tuxtla on Highway 180, 16.vii.1966, R.K. Allen, 2L [CAS]. Vera Cruz, Rio San Marcos at Apapantilla, 3 miles southeast Villa A. Camacho, 12.xi.1968, R.K. Allen, 5L [CAS]. *Leptohyphes spiculatus* Allen and Brusca; HOLOTYPE Larva: Mexico; Morelos; Rio Amacuzuc at Huajintlan on Hwy. 95, 14-xi-1968, R.K. Allen [CAS #11980]. PARATYPES: same data as holotype, 8L. *Leptohyphes succinus* Allen; HOLOTYPE Larva: TEXAS, Hays Co., San Marcos River, 3-IV-1973, Michael Peters [CAS #13606]. PARATYPES: 4 larvae, same data as holotype [CAS]; 8 larvae, 6.vi.1973, other data same as holotype, [CAS].

Other Material Examined: GUATEMALA: **Alta Verapaz**: Río Cahabon at Hwy. 7E, San Julian (N15°19'09; W90°19'06", elev. 4700 ft.), 14.vii.2001, D.E. Baumgardner, 45L [TAMU]. **MEXICO:** Queretaro: Ayutla, Río Ayutla (N21°23'29"; W99°35'10"), 14.vii.2000, WDS, 3L [TAMU]; 1 km SSE San Pedro, Arroyo Real (N21°07'07"; W99°32'05", elev. 1685 m), 11.vii.2000, WDS, 3L [TAMU]; unnamed creek, nr. Huasquilico (N21°10'; W99°33'), 26.ii.1999, R. Jones, 1L [TAMU]; Neblinas, Rio Verdito (N21°15'56"; W99°03'25"), 13.vii.2000, WDS, 100+L [TAMU]; Pinal de Amoles, Agua Fria (UTM 2338413), 28.viii.1997, R. Jones, 5L [TAMU]. Verz Cruz: Rio Metlac nr. El Fortin, 17.xii.1948, H.B. Leech, 2L [CAS]. **UNITED STATES:** Arizona: Coconino Co.; Oak Cr. at Manzanita Camp Ground (Hwy. 89), Coconino Nat. Forest (N34°56'04"; W111°44'46"), 5.vi.1993, Moulton & Alexander, 1L [TAMU]; same but, 25,26.v.1999, D.E. Baumgardner, 20L [TAMU]; Oak Creek at Hwy. 89, ca. 3 mi.N. Sedona, Coconino National Forest (N34°55'21"; W111°44'2"), 25.v.1999, D.E. Baumgardner, 30L [TAMU]; Oak Cr. at Hwy. 89A, ca. 5 mi. N. Sedona (N34°55'23"; W111°44'01), 04.vi.2000, D.E. Baumgardner, 57L [TAMU]; Oak Creek at Bootlegger Camp Ground, Hwy. 89A, Oak Creek Canyon (N34°58'09"; W111°45'01", elev. 5210 ft.), 24.v.2004, D.E. Baumgardner, 8L, [TAMU].

Leptohyphes berneri Traver 1958

Leptohyphes berneri Traver, 1958:84; Allen, 1978.

Diagnosis: Traver (1958) distinguished this species from other adult *Leptohyphes* based upon a pale reddish brown body. Figures of the hind wing and genitalia given by Traver (1958) in the original description are typical of other species of

Leptohyphes, as is the described body coloration. The limited knowledge of the adult stages of *Leptohyphes* prevent a diagnosis of this species from others in the genus.

Description: *Male Imago*: Length. Body, 3.5 – 4.5 mm; forewings, 4.0 – 5.0 mm; hind wings, 1.0 – 1.5 mm. General coloration reddish-brown, with black and grey shading. Head: light reddish-brown; black markings along posterior and lateral margins; antennae yellowish. Thorax: pronotum reddish-brown, shaded with gray and black; meso- and metathorax light reddish-brown, with gray and black shading. Legs: femora yellowish to pale reddish-brown; tibia and tarsus grey. Forewing: membrane very pale brown; veins pale reddish-brown; Sc and R light brown; vein CuP not strongly curved towards A; vein iCu_2 united basally with iCu_1; iCu_1 attached basally to CuA by crossvein; MP_2 united basally to CuA and iMP by cross veins. Hind wing: membrane very pale brown; three longitudinal veins present; costal process well-developed; hind margin of fore- and hind wings fringed with filiform setae. Legs: yellowish to pale reddish-brown to grey, with basal blackish shading. Abdomen. Pale reddish-brown; black transverse bands on along posterior margin of basal and middle tergites; sternites paler than tergites. Genitalia pale reddish-brown, forceps three-segmented, penes with basal half fused, distal parts divergent, "Y" shaped; cerci and median caudal filament present, well-developed. *Larva*: Unknown.

Distribution: Known only from Veracruz, Mexico.

Discussion: *Leptohyphes berneri* was described by Traver (1958) on the basis of adults from Metlac, Mexico, evidently in the state of Veracruz (Allen, 1978). The holotype and paratypes are deposited at FAMU. Additional rearings and research of

Leptohyphes species will be necessary to clarify the identity of this species. There remains a strong possibility that a previously-described species of *Leptohyphes* known only from the larval stage, may prove to be synonymous with this species. The type locality was described as a clear, cold swiftly flowing stream, fed by snowmelt, with adults emerging just before dark "by the thousands" (Traver, 1958).

Type Material Examined: PARATYPE: *Leptohyphes berneri* Traver: MEXICO: Metlac, 25.xii.1940, 4♂ imagos, H.H. Hobbs [CAS].

Other Material Examined: None

Leptohyphes brevissimus Eaton 1892

Leptohyphes brevissimus Eaton, 1892:12; Traver, 1958; Allen, 1978.

Diagnosis: Because only three females are available, it is not possible at this time to diagnosis this species from others in the genus.

Description: *Male Imago*: Unknown. *Female Imago* (pinned): Length. Body, 2.0 mm; forewing, 4.0mm. Body dark brown to black. Legs brown becoming pale brown distally. Forewing (Fig.24E): reddish-brown; vein CuP not strongly curved towards A; vein iCu_2 free; iCu_1 attached basally to CuA by crossvein; MP_2 united basally to iMP by cross veins. Legs: yellowish to pale reddish-brown to grey, with basal blackish shading. Hind wing absent. Abdomen. Dark brown with black markings. *Larva*: Unknown

Distribution: Known only from the type locality in Zapote, Guatemala.

Discussion: Little is known concerning this species, which was described from Guatemala on the basis of three dried female adults. The type locality, Zapote, is located in the state of Escuintla, 12 km. northwest of the town of Escuintla (N14°23'; W90°52') (Selander and Vaurie, 1962). The original description was very vague, and consisted of only three sentences. It is highly questionable if a male or larva can ever be associated with this species. As is the situation with *Leptohyphes berneri*, there is a strong possibility that a previously described species of *Leptohyphes* known only from the larval stage may be synonymous with this species.

During a collecting trip to Guatemala in 2007, the type locality of this species (the Río Zapote, near the town of Zapote) was located with the assistance of a Guatemalan entomologist. The Río Zapote is about 8 meters wide, swiftly flowing, with rock/rubble substrate, ranges in depth from a few centimeters to over a meter, and flows through numerous coffee plantations. Numerous *Leptohyphes* larvae were collected from the type locality, representing at least three species of *Leptohyphes.* Until rearing studies can be conducted and the larva associated with the adult, the status of this species will be very uncertain.

Primary Type Material Examined: *Leptohyphes brevissimus*, 1 female imago (pinned), designated as a type specimen; 3 associated slides (1 with FW, 1 with 3 legs, 1 with last 4 abdominal segments/female genitalia). **GUATEMALA:** Zapote, G.C. Champion [BMNH].

Leptohyphes ferruginus Allen and Brusca

Leptohyphes ferruginus Allen and Brusca, 1973:88; Allen, 1978; Lugo-Ortiz and McCafferty, 1995a; Baumgardner and McCafferty, 2000 (syn of *L. zalope*)

Leptohyphes piraticus Allen, 1978:554; Baumgardner and McCafferty, 2000 (syn of *L. alope*) **new synonym**

Diagnosis: Mature *L. ferruginus* larvae are relatively small among species of *Leptohyphes* in North and Central America. Mature male larvae are 3.0 – 3.5 mm in length, and female larvae 4.0 – 4.5 mm in length. Most other species of mature *Leptohyphes* larvae are at least 5 mm in length. The red body coloration (best seen in freshly preserved material) will readily distinguish this species from others in the genus in North and Central America. Some individuals have limited black maculation at the sublateral margins of the abdominal terga. Other characters include scattered setae on the sublateral margins of the abdominal terga, claws with four to six marginal and one submarginal denticle, and the presence of elongate setae on the dorsal surface of the profemur. The vertex of the head is red and without complex maculation as in *L. zalope* or *L. apache*.

The first description of the adult stage is given below on the basis of one reared male and one reared female subimago, one reared female imago, and one reared, partly emerged male adult with most of its subimago cuticle shed. No attempt is made to distinguish the adults from other species of *Leptohyphes* in the adult stage due to the relatively few adult imago species known at this time.

Description: *Male Imago***.** Length. Body, 3.0mm; forewing, 4.0 mm; hind wings, 0.75 mm, cercus, 10.0 mm; median caudal filament, 12.0 mm. General coloration reddish-grey with black and grey shading. Head: gray, with extensive black shading between lateral ocelli and on vertex; lateral and median ocelli black at base, clear in distal one-third; antenna pale. Thorax: prothorax gray, with extensive overshadings of black dorsally and laterally; meso- and metanotum yellowish-brown, with diffuse overshadings of black shading mostly on pleuron. Legs: prolegs not shed from subimago skin; mid- and hind legs grey with black maculation on mid dorsal surface of femora. Forewings (female imago) (Fig.25A): translucent; C, Sc, and R_1 reddish brown for most of their length; vein CuP strongly curved towards A; vein iCu_2 attached to iCu_1 by basal cross vein; iCu_1 attached to CuA by cross veins; MP_2 united basally to veins CuA and iMP by cross veins. Hind wings: present on male, with an elongated costal process and two longitudinal veins. Abdomen: gray, with diffuse black shading dorsally and along lateral margins; sterna pale, with black stippling limited to margins. Genitalia: forceps three-segmented, penes with basal half fused, distal parts divergent, "Y" shaped; cerci and median caudal filament present, well-developed.

*Female subimago***.** Body length 4.0mm. Forewing length 5.0mm. Hind wing absent. Cerci and median caudal filament missing. Head colored generally as in male; compound eyes small, widely separated; diameter of one eye less than distance between eyes. Thorax colored as in male. Forewings as in male; hind wings absent. Abdomen generally as in male, except yellowish-brown, with extensive black shading on terga.

Larva: Length: Body 3.0 – 4.5 mm; caudal filaments 3.5 – 4.5 mm. General color dark red to reddish-brown with black markings. Head: red, with thin black line on frons between compound eyes and at base of antennae (Fig.25B), or restricted to vertex between lateral ocelli (Fig.25C); medioposterior margin of head with inverted "U" markings (Figs. 26B – C); some individuals with thin, black lines running from compound eyes posteriorly (Fig.25B). Thorax: dark red; pronotum with black sublateral maculae (Fig.25B); without anterolateral projections and median tubercle. Legs. Proleg (Fig. 5E): femur with transverse row of elongate setae along dorsal surface; anterior margin with few, scattered filiform and elongate setae distally; tibia with setae absent along outer margin; inner margin with regularly-spaced filiform setae; tarsi with filiform setae along inner and outer margin. Meso- and metalegs (Fig.22A): femora with robust and stout setae medially on dorsal surface; anterior margin with robust setae; posterior margin with elongate setae medially and distally; tibiae with numerous elongate setae present along most of anterior and posterior margins; tarsus with few, scattered filiform setae along anterior and posterior margins; claw (Fig.22F) with four to seven marginal and one submarginal denticle. Abdomen: red, with pale margins; sublateral margins of tergites seven and eight, with scattered, sparse setae (Fig.26A); operculate gill pale reddish-brown, margins pale; gill formula 2/5/5/5/2.

Distribution: *Leptohyphes ferruginus* is known from the southwestern United States (Arizona and New Mexico), Mexico (Allen, 1978), Guatemala (McCafferty et al., 2004), Honduras (Allen, 1978), and is newly documented in Costa Rica. Although apparently widely distributed in Central America, the species does not appear to be common.

Discussion: *Leptohyphes ferruginus* was described by Allen and Brusca (1973) based on three larvae from a single location in Vera Cruz, Mexico. *Leptohyphes ferruginus* was distinguished from all other known species of *Leptohyphes* on the basis of red body color, shape of the denticles on the tarsal claws, and arrangement and number of spines on the femora. *Leptohyphes piraticus* was described by Allen (1978) based on a single larval specimen from Honduras, and distinguished it from other *Leptohyphes* on the basis of red body coloration and a transverse band between the compound eyes. Baumgardner and McCafferty (2000) synonymized *L. ferruginus* and *L. piraticus* under *L. zalope*, because of the general similarity of the larvae of the two species, a lack of any additional specimens that appeared to match the concept of *L. ferruginus*, and the lack of red coloration on the larvae of the type series. Recent examinations, however, of mature larvae from several locations in Guatemala, Costa Rica, and Arizona readily match the description of *L. ferruginus* given by Allen and Brusca (1973) in terms of the red body coloration, size of the larvae, and features of the claws, femoral spines, and arrangement of setae on the abdominal terga. In addition, many larvae possess a thick, black band between the compound eyes, as was described for *L. piraticus*, although this does appear to be somewhat variable among individual specimens. Although coloration is often highly variable in species of *Leptohyphes* larvae, this particular species appears to have little to no variation of the body coloration. Because of this new material which maintains the concept of *L. ferruginus*, the species is revalidated.

The only distinguishing feature separating *L. ferruginus* from *L. piraticus* is the reported presence of a thick, transverse black band between the compound eyes of *L. piraticus*. Otherwise, the two species are identical in terms of their unique red body coloration. However, as discussed above, this band is also infrequently found in some individuals of *L. ferruginus*. In addition, the presence of a transverse band between the compound eyes is not uncommon to many species of *Leptohyphes*. Also, it is not unusual to find individuals of the same species at the same location to vary in terms of head patterns. Because of this interspecific variation, *L. piraticus* is considered synonym of *L. ferruginus*.

The holotype of *L. ferruginus* is mature and in good condition, but the red color of the body appears to have faded and is not readily apparent. The two paratypes examined from CAS are also faded and in fair condition. The original description of this species listed six paratype larvae, four at CAS and two at the University of Utah. Only two of the four larvae listed as being at CAS could be located. The two specimens from the University of Utah are now evidently in the collection of FAMU. Although these two larvae at FAMU possess a label indicating that they are the paratype larvae of *Leptohyphes ferruginus*, their associated locality label reads, "Vera Cruz, Mexico, Río Tecolapan, Santiago Toxla on Highway 80, 16-VII-1966, RKA", which is an incorrect locality for the paratypes. Either these two specimens are not the two associated paratypes or either they have an incorrect locality label, which appears to be the case, because the two larvae appear to readily match the original description of *L. ferruginus*. The holotype of *L. piraticus* is a pre-emergent female, in poor condition, partly torn and badly faded. The head has been removed, dissected, and mounted on slide with mouthparts.

Type Material Examined: *Leptohyphes ferruginus* HOLOTYPE: MEXICO, Vera Cruz, Rio San Marcos at Apapantilla, 3 miles southeast Villa A Camacho, 12-XI-68, R.K. Allen. [CAS Type #11974]. PARATYPES, same data as holotype, 2L, 4 slides,

[CAS]. *Leptohyphes piraticus* Allen, HOLOTYPE, larva, HONDURAS; Dept. Chotuteca, small stream, Choluteca, ca. 16 mi. E. Jicaro-Galan, Pan American Highway, 10-X-64, JS Packer, 3 slides [FAMU, #E2043, 1T].

Other Material Examined: COSTA RICA: Heredia: Río Isla Grande at Hwy. 4, ca. 5 Km. W. of Río Frio (N10˚23'31"; W83˚58'04", elev. 200 ft), 10.vi.2001, 1L, D.E. Baumgardner [TAMU]. Puntarenas: Río Jaba at Las Cruses Biological Station, ca. 14 Km. S. San Vito (elev. 4000 ft.), 23-24.vi.2001, 1 reared male subimago with cuticle partly shed and larval cast skin, D.E. Baumgardner [TAMU]. **GUATEMALA,** Alta Verapaz: Río Cahabon at Hwy. 7E, San Julian (N15˚19'09"; W90˚19'06", elev. 4700 ft), 14.vii.2001, 2 reared female subimagos with larval cast skins, D.E. Baumgardner [TAMU]; Río Stainkreec, .8 Km E. from jct. of Hwy. 9&10, Rio Hondo (N15˚02'23; W89˚35'14", elev. 600 ft), 15.vii.2001, 12L, D.E. Baumgardner [TAMU]. El Progreso: Quebrada Las Pericas at Hwy. 17, 11.1 Km W. from jct. with Hwy. CA 9 (N14˚54'54"; W90˚05'52", elev. 1040 ft), 12.vii.2001, 7L, 1 reared male subimago, D.E. Baumgardner [TAMU]. Zacapa: Río Cayo at CA Hwy. 9, 2.3 Km E. Santa Cruz (N15˚00'54"; W89˚39'09", elev. 830 ft), 14.vii.2001, 4L, D.E. Baumgardner [TAMU]. **HONDURAS:** Choluteca: approx. 16 mi. E. Jicaro-Galan on Pan-American Hwy., small stream, 10.x.1964, JS Packer, 1L [CAS]. **UNITED STATES:** Arizona: Gila Co., East Verde River on Road 406, 10 mi. E. Payson, 19.vii.1970, 3L [CAS]. New Mexico: Grant Co., Gila R. at Hwy. 15, ca. 7 mi. S GilaNat. Monument (N33°10'46";W108°12'21"; 5580 ft), 18.v.2004, 1L, D.E. Baumgardner [TAMU].

Leptohyphes lestes Allen and Brusca

Leptohyphes lestes Allen and Brusca, 1973:89; Allen, 1978.

Diagnosis: The presence of a thick black line between the lateral ocelli in addition to the almost uniformly pale yellowish-brown to light brown body with very diffuse black maculation will distinguish larvae of this species from others in the genus in North and Central America. In addition, the vertex of head lacks extensive black maculation (as in *L. apache* and *L. zalope*), and the head, thorax, and legs are without long hair-like setae (as in *L. pilosus*).

Description: *Male Imago:* Unknown. *Larva*: Length. Body, 3.5 – 4.5 mm; caudal filaments, 4.0 – 5.0 mm. General coloration yellow to light brown, with black markings. Head: pale to light brown, with black transverse band between compound eyes (Fig.26B); frons unmarked, or with thin black line located at extreme posterior margin of head capsule, and with or without thin black line in shape of oval located at medioposterior margin of head (Fig.26B); antennae pale. Thorax: yellow to light brown with diffuse black markings; without anterolateral projections or median tubercles. Legs. Proleg (Fig.26C): femur with transverse row of elongate setae along dorsal surface; anterior margin with elongate setae along distal half of margin; posterior margin with few stout setae mostly distally; tibia with regularly-spaced filiform and elongate setae along most of anterior margin; posterior margin with few, scattered filiform setae; tarsus with dense filiform and elongate setae along inner margin; posterior margin with a few filiform setae, mostly along distal margin. Meso- and metalegs (Fig. 5F): femora with scattered, robust setae present on dorsal surface; anterior margin with regularly-spaced, robust and stout setae along entire margin; posterior margin with elongate stage along distal half of margin; tibiae with sparse elongate setae along anterior margin, and filiform setae at distal margin; posterior margin with regularly-spaced elongate setae along most of margin; tarsus with few, scattered filiform and elongate setae along anterior margin, with setae absent from posterior margins. Claws of all legs with five to eight marginal and a single submarginal denticle (Fig. 13C). Abdomen: terga yellow to light brown, with diffuse black markings; sterna pale; sublateral margins of tergite seven and eight each with eight to twelve setae (Fig.26A); operculate gill pale light brown; gill formula 2/5/5/5/2.

Distribution: The known range of this species includes the southwestern United States (Arizona and New Mexico), northeastern and southwestern Mexico (Guerrero and Nuevo Leon) and Honduras (Allen, 1978).

Discussion: *Leptohyphes lestes* was described on the basis of two larvae from the Mexican state of Guerrero. Allen (1978) later reported it from Honduras.
This species was distinguished from all other known *Leptohyphes* by having a distinctive black band between the compound eyes in combination with a pale vertex. Other larvae have been discovered that match very well this concept and the types, supporting the validity of the species. *Leptohyphes ferruginus* and *L. lestes* are very similar in appearance, in particular each can have a thick, black band between the compound eyes. However, *L. ferruginus* has a body which is dark red to dark red brown in color, while *L. lestes* has a pale yellow to light brown body.

Type Material Examined: HOLOTYPE: larva: MEXICO: Guerrero, Trib. Rio Papagayo nr. Tierra Colorado (elev. 500 ft.), 16.xi.968, R.K. Allen [CAS Type #11976]. PARATYPES: same data as holotype, 1L [CAS].

Other Material Examined: MEXICO: Nuevo Leon, Rio Sabinas at Sabinas Victoria, (elev. 1800 ft.), 4.viii.1970, 1L, RKA [CAS]. **UNITED STATES:** Arizona: Yavapai Co., West Clear Creek at Clear Creek Campground, ca. 1 mi. from Hwy. 260, ca. 4 mi SE Camp Verde (N34˚30'55"; W111˚45'45", elev. 3270 ft.), 26.v.2004, D.E. Baumgardner, 4L, [TAMU]. Yavapai Co.; Verde R. @ Perkinsville bridge, ca. 16 mi. N. Jerome on FSR 318, Prescott Nat. Forest, 6.vi.1993, Moulton and Alexander, 1L [TAMU]. Greenlee Co.; San Francisco R. at FS Rd. 212, ca. 1 mi. N Clifton (N33˚04'29.6"; W109˚18'03.5, elev. 3700 ft.), 21.v.2004, D.E. Baumgardner, 7L [TAMU]. **New Mexico**: Grant Co; Gila R. at Hwy. 15, ca. 7 mi. S. Gila Nat. Monument (N33˚10'46"; W108˚12'11", elev. 5580 feet), 18.v.2004, D.E. Baumgardner, 3L [TAMU]. Grant Co; Gila R. at Hwy. 15, ca. 30 mi. N. Silver City (N33˚10'50"; W108˚12'19", elev. 5500 feet), 08.vi.2000, D.E. Baumgardner, 5L [TAMU].

Leptohyphes mandibulus Baumgardner

Leptohyphes mandibulus Baumgardner, 2007:417.

Diagnosis: The reduced number of outer incisor denticles on both the left and right mandibles will distinguish this species from others in the genus *Leptohyphes* in Central America. While the vast majority of species within the genus *Leptohyphes* have four denticles on the outer incisor of the left mandible and three on the right mandible, *L. mandibulus* has only two outer incisor denticles on each mandible. In addition, the coloration of the operculate gills (basal half dark, apical half pale), and the contrasting coloration of the body and legs is also distinct for this species.

Description: *Male Imago:* Unknown. *Larva*: Length. Body, 3.0 – 3.5 mm; caudal filaments, 2.0 – 2.5 mm. General coloration gray and black. Head: Dark reddish-brown to black; small genal projections present; tubercles absent; antenna light brown. Left mandible (Fig.27A): outer incisor two-lobed, teeth fused almost their entire distance; inner incisor two-lobed; prostheca arising at base of inner incisor, with highly-branched setae projecting towards molar region. Right mandible (Fig.27B): outer and inner incisors two-lobed, fused almost their entire distance; prostheca arising at base of inner incisor with highly-branched, elongate setae projecting towards molar region; molar region mostly fused. Thorax: dark reddish-brown to black; without anterolateral projections or median tubercles; hind wing pads present in males, absent in females. Legs. Proleg (Fig.21C): femur with transverse row of elongate setae on dorsal surface; anterior and posterior margins with few, scattered filiform and acuminate setae; tibia with evenly-spaced, elongate setae along anterior margin; posterior margin with few, scattered filiform setae; tarsus without setae on anterior or posterior margin; ventral surface with row of four to six robust setae. Meso- and metalegs (Fig.26D): femora without setae present on dorsal surface; anterior margin with few setae of none; posterior margin with elongate stage along distal half of margin; tibiae with sparse elongate setae along anterior margin; posterior margin with few, scattered filiform and elongate setae; tarsus with elongate setae along anterior margin, and few filiform setae along distal half of posterior margin. Claws (Fig.22G) with one submarginal denticle, and a single row of four to six marginal denticles, similar in shape and size with equal spacing.

Abdomen: Dark reddish-brown to black; terga 5-9 each with a pair of elongate setae located medially on posterior margin; tubercles absent; operculate gill with basal portion black, apical portion pale (Fig. 6H); scattered acuminate setae present along inner and apical margins; gill formula 2/6/6/6/2.

Distribution: This species is currently known only from the type locality in northwestern Costa Rica.

Discussion: Of interest for *L. mandibulus* are the changes associated with the mandibles on mature and pre-emergent larvae. Mandibular description in the above species description is based upon relatively mature larvae, but not pre-emergent larvae. In pre-emergent larvae, the outer incisors of the right mandible are reduced to a single, rounded structure, while the inner incisor is reduced to a single denticle [Fig. 10 (Baumgardner, 2007)]. For the left mandible, the outer incisors are fused into a single, large incisor, while the inner incisor is reduced to a single denticle [(Fig. 11 (Baumgardner, 2007)]. Reduction and fusion of incisors is very rare among leptohyphid mayflies and is usually a result of wear associated with feeding. However, numerous larval paratypes associated with *L. mandibulus* also displayed this condition, indicating it is probably a naturally-occurring condition resulting from maturation, and not necessarily a result of feeding.

Type Material Examined: HOLOTYPE: *Mature Male Larva* - **COSTA RICA**: Alajuela Province; NE of Bijagua, nr. Las Flores, Río Areuo (N10º21'06", W85º21'05"), 07.vi.2000, WDS Shepard [TAMU]. PARATYPES: Same data as holotype, 6 larvae [FAMU], 25 larvae [TAMU].

Leptohyphes murdochi Allen

Leptohyphes murdocki Allen, 1967:355.

Leptohyphes murdochi Allen, 1967; Edmunds *et al*., 1976:254 (name amended); Allen, 1978; Lugo-Ortiz and McCafferty, 1995a.

Diagnosis: Larvae of *L. murdochi* are distinguished from all other known *Leptohyphes* larvae in North and Central America by the presence of numerous, small pale depressions on the femora (see "Discussion" under *L. alleni* concerning these depressions), which are absent in all other species, except *L. alleni*. *Leptohyphes murdochi* larvae can be distinguished from *L. alleni* larvae due to the presence of a distinct apical concavity on the middle and hind femora, which are absent on *L. alleni* larvae.

Description: *Male Imago*: Unknown. *Larva*: Length. Body, 5.5– 6.5 mm; caudal filaments, 5.0 – 6.0 mm. General dark brown. <u>Head:</u> brown, with black band on frons between compound eyes (Fig.26B); antennae pale brown. <u>Thorax</u>: brown to dark brown, with irregular pale brown markings; without anterolateral projections and median tubercles. Legs. Proleg (Fig.21B): femur with transverse row of robust setae and numerous, small, shallow circular depressions on dorsal surface; anterior margin with elongate setae along distal half of margin; posterior margin without setae; tibia with a few, scattered filiform setae along distal half of anterior margin; posterior margin without setae; tarsus with row of elongate setae along anterior margin, and without setae on posterior margin. Meso- and metalegs (Fig.22B): femora densely-covered with numerous, small, shallow circular depressions on dorsal surface; setae absent from dorsal surface; anterior margin with few, scattered filiform setae; posterior margin with regularly-spaced elongate setae along most of margin; tibiae with filiform and elongate setae present along much of anterior margin; posterior margin with elongate setae along most of margin; tarsus with few, scattered filiform setae along anterior and posterior margins. Claws of all legs with three to four marginal denticles (Fig.27C); submarginal denticle absent. Abdomen: terga dark brown; sublateral margins of tergites seven and eight without setae; operculate gill brown, with pale margins; gill formula 2/5/5/5/2.

Distribution: This species was described from Darién Province in eastern Panama (Allen, 1967), and later documented in Costa Rica (Lugo-Ortiz and McCafferty, 1995a). Additional records of this species in Costa Rica are given below.

Discussion: This species was described based upon a single larva (Allen, 1967), with no associated paratype specimens. All legs and the head have been removed from the holotype, and it is unknown where these slides are located. Since the most distinctive features of this species are the concave shape of the leading edge of the meso- and metalegs, and the presence of small, pale depressions on the dorsal surface of the femora, there may be some doubt that this specimen is, indeed, the original holotype. However, features such as size and coloration of the larvae, collection records of additional specimens from near the type locality, and the fact that no other species of *Leptohyphes* have been described from the type locality of *L. murdochi*, it does appear reasonably safe to assume this specimen is , indeed, the holotype of *L. murdochi*.

Type Material Examined: *Leptohyphes murdocki* Allen, HOLOTYPE: female larva: PANAMA: Darién: Río Tocarcuna (elev. 1,900 m), 30.v.1963, W.P. Murdoch [FSCA (FAMU) E2019.1T].

Other Material Examined: COSTA RICA: Alajuela: N of Bijagua, Río Zapote (N10°44'45"; W85°05'29"), 6.vi.2000, WDS, 1L [TAMU]. **Guanacaste**: P.N. Guanacaste, Río San Josecito, .5 km S. of Est. Cacao, Volcan Cacao (elev. 700 m), 22.iii.1990, RW Flowers, 3L [TAMU]; 4 Km W. Arenal, unnamed spring run, 17.i.2000, WDS, 3L [TAMU].

Leptohyphes musseri Allen 1967

Leptohyphes musseri Allen, 1967:353; Allen, 1978; McCafferty et al., 2004.

Leptohyphes brunneus Allen and Brusca, 1973:353 **new synonym**

Diagnosis: The following combination of characters will distinguish *L. musseri* larvae from other species in North and Central America: (1) abdominal terga yellow to pale yellowish-brown, with distinct sublateral, submedian and median black macula; (2) frons often with large median brown (usually black) macula between compound eyes; (3) middle and hind femora usually with distinctive black maculation distally, contrasting with the yellow to yellowish-brown coloration of the leg.

Description: *Male Imago*: Unknown. *Larva*: Length. Body, 5.0 – 7.0 mm; caudal filaments, 6.0 – 7.0 mm. General coloration yellow to light brown with reddish-brown and black maculation. Head: yellow to light brown; often with large brown or black macula between lateral ocelli (Fig.27D), or think black line between compound eyes (Fig.25C); antennae pale to yellowish-brown. Thorax: yellow to light brown; pronotum with extensive black maculation laterally and anterolaterally (Fig.27E); mesonotum with longitudinal black maculation medially, and scattered black maculation laterally; pro- and mesonota without anterolateral projections or median tubercles. Legs. Proleg (Fig.21E): femur with transverse row of elongate setae along dorsal surface; large, black macula present distally; anterior margin with scattered robust setae, mostly along basally margin; posterior margin with robust setae along distal margin; tibia with filiform and elongate setae along anterior margin, and row of robust setae along anterioventral surface; posterior margin with few, scattered, filiform setae; tarsus with row of elongate setae along anterior margin, and few, scattered, filiform setae along posterior margin. Meso- and metalegs (Fig.22C): femora with few robust setae on dorsal surface or none; large, black macula present distally; anterior margin with stout setae along most of margin; posterior margin with fairly regularly-spaced elongate setae along distal half of margin; tibiae with few elongate setae along anterior margin; posterior margin with elongate setae along most of margin; tarsus with elongate setae along anterior margins; posterior margin with few, scattered filiform setae, often in pairs. Claws of all legs with three to seven marginal, and a single submarginal denticle (Fig.27F). Abdomen: terga yellow to light brown, often with black maculation along posterior half of tergite, and on sublateral margins; operculate gill pale to light brown; gill formula 2/5/5/5/1.

Distribution: This species was previously known from Guatemala (Allen, 1978; McCafferty et al., 2004), Honduras (Allen, 1978), and Mexico (Allen and Brusca, 1973; Allen, 1978), and is newly-reported from Costa Rica.

Discussion: *Leptohyphes brunneus* was described by Allen and Brusca (1973) on the basis of a small series of larvae from several locations in southern Mexico. The presence of a "large brown to reddish-brown macula on the frons between the lateral ocelli" was considered distinctive for this species. It was also described as having abdominal terga that were light brown in color with reddish-brown markings, and numerous scattered spines. All specimens of the type series were examined and found to be badly faded to pale yellow, with none of the specimens having a brown maculation between the lateral ocelli. Other non-type material identified by Allen as *L. brunneus*, which is in excellent condition and unfaded, also does not possess the large median brown macula between the lateral ocelli.

Leptohyphes musseri was described from Guatemala based upon three larvae (Allen, 1967). In his key to the *Leptohyphes* larvae of North and Central America, Allen (1978) distinguished *L. musseri* from *L. brunneus* based upon differences in abdominal terga maculations and coloration as well as markings on the legs and head. Specifically, *L. musseri* possessed sublateral, submedian, and median black maculae on abdominal terga 6 -9, while *L. brunneus* lacked this maculation and had brown terga instead of yellow. The head of *L. musseri* was reported to have a thin black line between the lateral ocelli, and black maculation on the meso- and meta femora, while *L. brunneus* lacked the thin black line and black maculation on the femora. Recent collections of larvae from Guatemala show numerous individuals (from the same location) with both the black maculation leg characters of *L. musseri* and the large brown macula between the compound eyes characteristic of *L. brunneus*. It appears both these characters, in addition to the abdominal terga characteristics described previously, are highly variable, and often dependent on gender and maturity of individual larvae. In addition, some individual larvae possessed a variety of combinations of these characteristics. Since no other morphological features can be found that distinguish *L. brunneus* from *L. musseri*, *L. brunneus* is placed as a junior synonym of *Leptohyphes musseri*.

Type Material Examined: *Leptohyphes musseri* Allen, HOLOTYPE (larva): GUATEMALA: Soloa; Panajachel, 1500m, 21.viii.1962, G.G. Musser [FSCA (FAMU) E2020.1 T]. PARATYPES: GUATEMALA: Soloa; Panajachel, 1500m, 21.viii.1962, 16L, G.G. Musser [FAMU]; same but, 2L [CAS]. *Leptohyphes brunneus*: HOLOTYPE (larva): MEXICO: Oaxaca; stream 15 mi. N. Ayoquezco, Elev. 6,700', 20.x.68, RKA [CAS #11971]. PARATYPES: Same data as holotype, 8 larvae [CAS]; Jalisco; Rio La Pasion at Tizapan El Alto, 16.x.68, R.K. Allen, 3 larvae [CAS]; Chiapas; stream 7 mi. N. Arriaga on Hwy. 190, 23.x.68, elev. 1400', RKA, 1L [CAS]; Morelos; Amacuzuc at Huajintlan on hwy. 95, Elev 3,200', 29/30.vii.66, R.K. Allen, 6L [CAS].

Other Material Examined: COSTA RICA: Puntarenas; 1 Km S Coloradito Norte, Rio Coloradito at Hwy. 2, (N08°36’10:; W82°54’07”), 17.vi.2000, 4L, WDS [TAMU]. **San Jose**; Río Pedregoso at Hwy. 243, ca. 4 Km S. San Isidro de El General (N09°21’15”; W83°43’35”, elev. 2000 ft), 22.vi.2001, 6L, DEB [TAMU]; NE Dominical, unnamed stream (N09°16’48”; W83°49’22”, elev. 200 m), 19.vi.2000, 15L, WDS [TAMU]. **GUATEMALA**: Puerta Parada, 20.ii.1991, 1L, M. Esther Gonzalez [TAMU]; Río Latoma @ KM. 182 on Hwy. #2, Elev. 2300', Temp 82F, 24-x-68, R.K.A., 1 larva (CAS); Alta Verapaz; Río Cahabon at Hwy. 7E, San Julian (N15°19'09"; W90°19'06", elev. 1500 m), 14.vii.2001, 30L, DEB [TAMU]; Río Polochic, 2 Km W. Tucuru, 5.iv.1995, 4L, Bryan Yates [TAMU]; Baja Verapaz; Río San Jeronimo at San Jeronimo (N15°03'52"; W90°14'03", elev. 1050 m), 13.vii.2001, 4L, DEB [TAMU]. **HONDURAS:** Comayagua, 5 mi. So. Comayagua on Hwy. #1 at bridge, stream., 17.x.1964, 3L, J.S. Packer [CAS]. **El Paraiso**; 38 km. E. Zamorano on Hwy. #4, stream., 31.x.1964, 7L, J.S. Packer [CAS]. **Francisco**; Morazan, 10 mi. E. Guaimaca on Hwy. #3, Small stream, 6.xi.1964, 4L, J.S. Packer [FAMU]. **Olancho**; 6 mi. E. Juticalpa on Hwy. #3, Río Telica, 6.xi.1964, 1L, J.S. Packer [CAS]; 10 mi. W. Juticalpa, Río Juticalpa., 6.xi.1964, 1L, J.S. Packer [CAS]. **MEXICO: Queretaro**; MP10: Pinal de Amoles, Agua Fria (UTM 2338413), 28.viii.1997, 3L, R. Jones [TAMU]; Neblinas, Río Verdito (N21°15'56"; W99°03'25"), 13.vii.2000, 1L, WDS [TAMU].

Leptohyphes nigripunctus Traver

Leptohyphes nigripunctum Traver, 1943:82; Traver, 1958; McCafferty, 1985; Molineri, 2003b.

Leptohyphes nigripunctus Traver (spell).

Diagnosis: Very little is known concerning this species. The whitish pronotum, grayish head, dark gray mesosternum, and yellow femora evidently distinguishes it from other known adults in Central America (Traver, 1958).

Description: *Male Imago*: Length. Body, 4.0 mm; forewings, 4.0 mm; hind wings, 1.0 mm. General coloration: pronotum yellowish-white, meso- and metanotum reddish-brown; abdomen yellowish-white with reddish brown. Head: dorsally grey, ventrally white; antennae white. Thorax: pronotum yellowish-white, shaded with pale grey, lateral margins with blackish shading; meso- and metanotum bright reddish-brown, with grey shading medially and on pleura. Legs: femora yellowish; tibia and tarsus grayish-black. Forewing: membrane whitish; veins whitish, except C, Sc, and R grayish basally; no figure or description of the venation has been published. Hind wing: membrane pale; two longitudinal veins present. Abdomen. Segments two through six yellowish-white, basal and apical segments light reddish-brown; each nota with pale grey band medially. Genitalia: reported as the *peterseni* type (see "Discussion" below), which has forceps three-segmented, penes with basal half fused, distal parts divergent, "Y" shaped. *Larva*: Unknown.

Distribution: Known from Guerro, Mexico (McCafferty, 1985) and Antimano, Venezuela.

Discussion: Described by Traver (1943) from a single male subimago from Antimano, Venezuela (located near the capital, Caracas). The genitalia were described as the *peterseni* type ("Y" shaped, typical for all known male adults of the genus), but lost while being prepared for mounting. The sketch of the hind wing given by Traver (fig. 3, Traver, 1943) is also typical of male *Leptohyphes*. The whitish pronotum distinguished it from other known adults in Central America (Traver, 1958). McCafferty

(1985) reported it from Guerrero, Mexico, its only other documented record. Molineri (2003b) briefly mentioned this species in his revision of the South American *Leptohyphes*, but did not attempt to diagnosis it from other species. Despite attempts to located the type specimen, it cannot currently be found. The brief description given above is taken from Traver's (1943) original description.

Type Material Examined: None.

Other Material Examined: None.

Leptohyphes peterseni Ulmer 1920

Ulmer, 1920a:46; Needham and Murphy, 1924:32; Traver, 1958; McCafferty, 1985.

Diagnosis: Because of the limited descriptions published for this species and others in the adult stage, it is not possible to definitively diagnosis this species from other adult *Leptohyphes*. Traver (1958) stated that the yellowish-brown thoracic nota with several rows of dark blotches on the abdominal segments will separate it from others in the genus.

Description: Length. Body, 4 – 6 mm; forewings, 4.0 – 5.0 mm; hind wings, 1.0 – 1.5 mm. General coloration yellowish-brown. Head: light yellowish-gray with black shading. Thorax: yellowish-brown . Legs: light yellowish-gray with darker markings. Forewing: vein CuP not strongly curved towards A; vein iCu_2 united basally with iCu_1; iCu_1 attached basally to CuP and CuA by cross vein; MP_2 united basally to CuA and iMP by cross veins. Hind wing: present, with two longitudinal veins; costal process well-developed. Abdomen. yellowish-brown. Genitalia: forceps three-segmented, penes with basal half fused, distal parts divergent, "Y" shaped.

Larva: Unknown.

Distribution: *Leptohyphes peterseni* has been documented in Brazil, Bolivia, Argentina, El Salvador, and Guatemala (Ulmer, 1920a; McCafferty, 1985).

Discussion: The above description is based upon Ulmer's (1920a) original description, with additional comments from Traver (1958). The current location of the type specimens is unknown, despite attempts to locate them during this current study. Molineri (2003b) was not able to locate the type specimens in his study of the South American leptohyphids.

Leptohyphes ulmeri constitutes the first description of a male of *Leptohyphes*. Ulmer (1920a) assigned it to this genus because the wing venation was similar to that of the female of *L. eximius* (type species of the genus).

Molineri (2003b) noted that the type series of this species is represented by numerous male and female subimagos, probably representing more than one genus. Ulmer (1920a) described some males of the type series with penes not divergent at the tip, a situation not known to occur in the genus *Leptohyphes*, but known from other males in other leptohyphid genera. In addition, the divergent penes of *Leptohyphes* species are always well separated in the imagos, as well as the subimagos.

Traver (1958) noted the similarity between *L. peterseni* and *L. sabinas*, and stated that *sabinas* could be considered the northern counterpart of *peterseni*. Molineri (2003b) speculated that *L. plaumanni* might be a synonym of *L. peterseni*, based upon similarity between male genitalia. However, with numerous species of *Leptohyphes* not described as adults, a synonym would probably be premature.

Type Material Examined: None.

Other Material Examined: None.

Leptohyphes pilosus Allen and Brusca 1973

Leptohyphes pilosus Allen and Brusca, 1973:91; Allen, 1978.

Diagnosis: The larvae of *L. pilosus* possess long, hair-like setae on the head, thoracic nota, and legs, which distinguishes this species from others in North and Central America.

Description: *Male Imago*: Unknown. *Larva*: Length. Body, 4.5 mm; caudal filaments, 5.0 mm. General coloration light yellowish brown. Head: pale brown, with black markings; antennae pale. Thorax: pale light brown; without anterolateral projections or median tubercles; original description lists long seae along margin of nota, which are not present on the holotype (see "Discussion" below). Legs. Missing from specimen with no associated slide(s) (see "Discussion" below). The following brief description is based upon the original written description and figures (Allen and Brusca, 1973). Proleg (see fig. 10a, Allen and Brusca, 1973): femur with transverse row of elongate setae along dorsal surface; anterior margin with scattered robust and numerous filiform setae; posterior margin with elongate setae medially, and numerous filiform setae along entire margin; tibia with two rows of elongate setae along anterior margin, and numerous filiform setae; posterior margin with numerous filiform setae; tarsus row of elongate setae along anterior margin, and numerous filiform setae along anterior and posterior margin. Meso- and metalegs (see fig. 10b, Allen and Brusca, 1973): femora with scattered, stout setae on dorsal surface; anterior margin with numerous filiform setae; posterior margin with numerous filiform setae, and evenly spaced elongate setae along most of margin; tibia with numerous filiform and elongate setae along anterior and posterior margins; tarsus with elongate setae along anterior margin, and filiform setae along posterior margin. Claws of all legs with four to five marginal, and one submarginal denticle. Abdomen (see fig. 28, Allen and Brusca, 1973): terga light brown with black median macul on all tergites, and with black sublateral maculae on terga one through seven; numerous elongate setae present medially on terga; sublateral margins of terga with numerous elongate setae; operculate gill grey with pale markings; gill formula 2/?/?/?/? (most gills missing from body).

Distribution: This species is known only from the holotype larval specimen collected in Veracruz, Mexico.

Discussion: Examination of the holotype does not resemble the description given for this species in terms of long hair-like setae on the abdominal terga. The holotype specimen does not match figure 28 given by Allen and Brusca (1973), or figure 37 given by Allen (1978). Also, the holotype has faded to yellow, with no other markings or maculations as given in the original description. In addition, slides associated with the holotype specimen cannot be located, which evidently contained all the legs and mouthparts. The validity of this species will remain in doubt until additional specimens matching the description can be found or the holotype slides located.

Type Material Examined: HOLOTYPE (female larva): MEXICO: Vera Cruz: Río San Marcus at Apapantilla 3 mi. SE Villa A. Camacho (elev. 700 ft.), 12.xi.1968, RK Allen. [CAS Type #11979]

Other Material Examined: None

Leptohyphes priapus Traver 1958

Leptohyphes priapus Traver, 1958:86; Allen, 1978.

Diagnosis:*Leptohyphes priapus* was distinguished from other *Leptohyphes* adults on the basis of its reddish brown body and an abdomen which is much paler than the thorax. This description is very similar to other *Leptohyphes*, and does not allow for definitive diagnosis from other known species.

Description: *Male Imago*: Length. Body, 4.0 – 5.0 mm; forewings, 5.0 – 5.5 mm; hind wings, 1.5 – 2.0 mm. General coloration reddish-brown; abdomen yellowish with reddish-brown markings. Head. Yellowish to pale reddish-brown; antennae yellowish. Thorax. Overall reddish-brown, yellowish medially, with pale lateral areas; sterna yellowish with dark reddish-brown margins. Forewing: membrane pale brown; longitudinal veins light reddish-brown; costal vein reddish-brown; vein CuP not strongly curved towards A; vein iCu_2 united basally with iCu_1; iCu_1 attached basally with CuP by crossvein; MP_2 united basally to MP_1 and CuA by cross vein. Hind wing: with elongate costal process, and three longitudinal veins; hind margin of fore- and hind wings fringed with filiform setae. Legs: pale reddish-brown. Abdomen. Yellowish, banded with light reddish-brown. Genitalia: forceps three-segmented; first segment short, stout; second segment elongate; third segment small, globular. Penes with basal half fused, distal parts divergent, "Y" shaped, with small spine on apical margin of each lobe.

Distribution: Known only from the type locality in Costa Rica.

Discussion: Described by Traver (1958) based upon a long series of male imagos from the Río Pedregoso, a river which is evidently located in the Nicoya Complex of western Costa Rica (Savage *et al.*, 2005). No other collections of this species have been reported since its original description.

Type Material Examined: PARATYPES: COSTA RICA: Río Pedregoso, ii.1939, D.L. Rounds, 12♂ imagos [FAMU].

Other Material Examined: None

Leptohyphes sabinas Traver

Leptohyphes sabinas Traver 1958; Burks, 1953; Allen, 1978; McCafferty, 1985.

Leptohyphes castaneus Allen, 1967:354; Allen, 1978 **new synonym**

Leptohyphes consortis Allen and Brusca, 1973:87; Allen, 1978:554 (syn)

Leptohyphes tarsos Allen and Murvosh, 1987:36 **new synonym**

Diagnosis: *Leptohyphes sabinas* larvae can be distinguished from other species of *Leptohyphes* in North and Central America by the following combination of characters: (1) body coloration generally pale brown to brown (in freshly preserved specimens), with limited and diffuse black maculation; (2) abdominal terga with a limited number of setae present on the sublateral margins (terga 2 through 5 with zero to four setae each; terga 6 and 7 each with four to twelve setae; terga 8 through 10 with zero to ten setae each); (3) vertex of head with a complex pattern as in *L. zalope*, sometimes much reduced; and, (4) dorsal surface of meso- and metafemur generally with less than 10 stout setae present on the median elevated ridge. Adults are very similar to other described *Leptohyphes* adults from North and Central America. The presence of a pale yellowish abdomen with extensive grey maculation can help separate this species from other adults.

Description: *Male Imago*: Length. Body, 4.0 – 6.0 mm; forewings, 4.5 – 5.5 mm; hind wings, 1.0 – 1.5 mm. General coloration: head and thorax dark reddish-brown to black; abdomen translucent, pale yellowish with pale reddish brown. Head: blackish; antennae pale. Thorax: pronotum blackish with reddish coloration; meso- and metathorax dark red brown. Legs: reddish-brown, with black and purplish bands and streaks. Forewing: membrane pale brown, darker towards base; veins reddish-brown; vein CuP strongly curved towards A; vein iCu_2 united basally with iCu_1; iCu_1 attached basally to CuA; MP_2 united basally to CuA and iMP by cross veins. Hind wing: membrane very pale brown; two longitudinal and one cross vein present; costal process well-developed; hind margin of fore- and hind wings fringed with filiform setae. Abdomen. Pale yellowish to pale reddish-brown, with grey shading; some segments partially translucent; each tergite with wide transverse gray bands and pale sublateral margins. Genitalia pale reddish-brown, forceps three-segmented, penes with basal half fused, distal parts divergent, “Y” shaped; cerci and median caudal filament present, well-developed.

Larva: Length. Body, 4.5 – 5.5 mm; caudal filaments, 5.0 – 6.0 mm. General coloration light brown with darker brown markings. Head: light brown, with complex black pattern on vertex (Fig.24C); antennae pale. Thorax: light brown to brown, with darker brown markings; without anterolateral projections and median tubercle. Legs. Proleg (Fig.28A): femur with transverse row of stout and elongate setae along dorsal surface; anterior margin with robust setae along most of margin; posterior margin with elongate and robust setae distally; tibia with rows of elongate setae along anterior margin; posterior margin with few, scattered filiform setae or none; tarsus with elongate setae along anterior margin; posterior margin without setae. Meso- and metalegs (Fig.28B): femora with few (< 10) setae on dorsal surface; anterior margin with stout and robust setae along most of margin; posterior margin with elongate setae along all of margin; tibiae with elongate setae present along most of anterior and posterior margins; tarsus with few, scattered filiform setae along anterior margin; posterior margin without setae. Claws (Fig.28C) of all legs with four to seven marginal, and a single submarginal denticle. Abdomen: terga light brown to brown, often with irregular dark brown to black maculation along posterior and sublateral margins of tergites; few, scattered robust setae present at sublateral margins of tergites; operculate gill brown; gill formula 2/5/5/5/1.

Distribution: *Leptohyphes sabinas* is known from south-central Texas in the United States (Burks, 1953; Traver, 1958), throughout Mexico (Allen, 1967; Allen and Brusca, 1973; Allen, 1978), Guatemala (Allen, 1967) and Costa Rica (Lugo-Ortiz and McCafferty, 1995a). Larvae have been collected from a wide variety of streams at various elevations. Mature larvae have been found throughout much of the year, indicating an extended emergence for this species.

Discussion: *Leptohyphes sabinas* was described by Traver (1958) based upon a male "which has almost completely shed the submarginal cuticle", and male and female subimagos from Nuevo Leon, Mexico. Based upon this material, Traver considered the species to have dissimilar propretarsal claws, and unique based on this and color characters. In all known male adult imagos of *Leptohyphes*, however, the proclaws are similar, but dissimilar in the subimago. This was evidently unknown to Traver at the time, leading to her false conclusion.

The larval stage was described by Allen and Brusca (1973) as *L. consortis*. Allen (1978) noted that *L. consortis* was indistinguishable from larvae that were evidently part of the original type series of *L. sabinas*, but had not been previously published as such.

Leptohyphes consortis was described by Allen and Brusca (1973) on the basis of two larvae from Vera Cruz, Mexico. The holotype is in good condition, missing only the left proleg and right mesoleg. It has mostly faded, now pale yellow in color, and not matching any of the colors or patterns given in the original description. The single paratype specimen has the abdomen missing. It was apparently mounted on a slide, as indicated as such by a note in the vial. No associated slide, however, can be located. The figure used by Allen and Brusca (1973, fig. 30) to illustrate the arrangement of setae on the abdominal terga of *L. consortis* does not resemble the holotype. The abdominal terga of *L. consortis* is mostly glabrous, with a few, scattered setae on the sublateral margins of abdominal tergum 1-8. In addition, only a few elongate setae are present on the posterior margin of the abdominal terga, not as numerous as what was illustrated in the figure. Figure 30 from Allen and Brusca (1973) was also used by Allen (1978) to describe the new species *Leptohyphes zelus* (Allen, 1978), to which the figure is most appropriate. It is possible that Allen might have confused the undescribed *L. zelus* larvae (which had been collected by Allen in 1966, before the description of *L. consortis* was published) with *L. consortis* when he was originally describing the species and never corrected the figures in the literature.

Leptohyphes castaneus was described by Allen (1967) on the basis of larvae collected in southwestern Guatemala. There was no discussion on how this species differed from others in the genus. The types of *L. castaneus* are in excellent condition, undissected, and intact; however, the two paratype larvae are faded to a pale yellow. The holotype retains the brown coloration described for the species. All specimens of the type series have a few, scattered setae present on the lateral margins of the abdominal terga, as described by Allen (1967). Allen (1967) reported that the metafemur is 65% longer than the profemur; however, Allen (1973) reported the metafemur to be 35% longer than profemur. Re-examination of this character clearly shows that the metafemur is 65% longer than the profemur, as is typical of most larval *Leptohyphes.*

Allen (1978) distinguished *L. sabinas* from *L. castaneus* based upon darker brown markings and claws with five to seven marginal denticles, as opposed to four to six marginal denticles and unicolorous brown coloration on *L. castaneus*. Both these characters are variable for *L. sabinas*, with larvae possessing between four and six marginal denticles (with one submarginal denticle), and abdominal tergal coloration varying from yellowish brown to brown. Studies of extensive series has shown that colors and color patterns are variable, often changing with maturity, seasonality, and gender. Female larvae are typically much larger and more darkly colored than male larvae. Comparison of the types of these species clearly show them to be conspecific.

Leptohyphes tarsos Allen and Murvosh (1987) was described from Sonora, Mexico, on the basis of a small series of larvae. It was considered different from *L. sabinas*, and other species of *Leptohyphes* on the basis of markings around the compound eyes and brown median macula on the abdominal terga. Examination of the type series does not show any markings around the compound eyes that are not found in other *Leptohyphes*. In addition, characters such as body coloration and maculation, arrangement of setae on the abdominal terga, arrangement of denticles on the claws (four to six marginal and one submarginal denticle) are no different than that of *L. sabinas.* No features were found unique to *L. tarsos*, and no features, or combinations thereof, were found that could separate it from *L. sabinas*. Thus, *L. tarsos* is considered a junior synonym of *L. sabinas.*

Type Material Examined: *Leptohyphes brunneus* Allen and Brusca, HOLOTYPE: larva: Mexico, Oaxaca, stream 15 mi. N. Ayoquezco (6700 ft.), 20.x.1968, RKA [CAS Type #11971]. PARATYPES: MEXICO: Chiapas, stream 7 mi. N. Arriaga on Hwy. 190 (1400 ft. elevation), 23.x.1968, 1L [CAS], RKA; Jalisco, Rio La Pasion at Tizapan El Alto, 16.x.1968, 3L [CAS], RKA; Morelos, Rio Amacuzuc at Huajintlan on

Hwy. 95 (3200 ft. elevation), 29/30.vii.1966, 6L [CAS], RKA; Oaxaca, stream 15 mi. N. Ayoquezco, (6700 ft. elevation), 20.x.1968, 8L [CAS], RKA. *Leptohyphes castaneus* Allen, HOLOTYPE, larva: Guatemala, Solola, 1550m, Panjachel, G.G. Musser, 21-viii-1962, [FSCA (FAMU)E2013.1T] (also includes 4 paratype slides). PARATYPES: GUATEMALA, Solola, 1550m, Panjachel, 2L [CAS], 4L [PERC], G.G. Musser, 21-viii-1962. *Leptohyphes consortis* Allen and Brusca, HOLOTYPE, larva: Mexico, Vera Cruz, Rio San Marcos at Apapantilla 3 mi. SE Villa A. Camacho, Elev. 700’, Temp. 66F, 12-xi-1968, RKA, [CAS Type #11972]. PARATYPE, larva: MEXICO, Vera Cruz, Rio San Marcos at Apapantilla 3 mi. SE Villa A. Camacho, Elev. 700’, Temp. 66F, 12-xi-1968, RK Allen, CAS (originally labelled paratopotype). *Leptohyphes tarsos* Allen and Murvosh, HOLOTYPE, larva: Mexico, Sonora, Rio Cuchujaqui, 9.8 mi. SE Alamos, 16.i.1983, RKA and C.M. Murvosh [CAS Type #15893]. *Leptohyphes tarsos* Allen and Murvosh, PARATYPE: MEXICO, Sonora, Rio Cuchujaqui, 9.8 mi. SE Alamos, 8L, 16.i.1983, R.K. Allen and C.M. Murvosh [CAS].

Other Material Examined: COSTA RICA: Alajuela: N of Bijagua, Rio Zapote (N10°44’45”; W85°05’29”), 6.vi.2000, WDS, 1L [TAMU]. **Guanacaste**: Canas, Rio Canas (N10°26’; W85°06’), 23.i.2000, WDS, 4L [TAMU]. **Puntarenas**: 3 Km NE of Santa Elena, 25.i.2000, WDS, 8L [TAMU]; 5 km NE Santa Elena, 25.i.2000, WDS, 8L [TAMU]. **GUATEMALA:** Río Latoma at KM. 182 on Hwy. #2, (elev. 2300 ft.), 24.x.1968, RKA, 1L [CAS]. **Alta Verapaz**: Rio Cahabon at Hwy. 7E, San Julian (N15°19’09”; W90°19’06”, elev. 4700 ft.), 14.vii.2001, DEB, 10L [TAMU]; Rio Stainkreec, .8 Km E. from jct. of Hwy. 9&10, Rio Hondo (N15°02’23”; W89°35’14”, elev. 600 ft.), 15.vii.2001, DEB, 5L [TAMU]. **El Progreso**: Rio Hato at CA Hwy. 9, ca. 5.9 Km E. from jct. with Hwy. 17, Magdalena (N14°55'11"; W89°57'56", elev. 1040 ft.), 14.vii.2001, D.E. Baumgardner, 38L [TAMU]. **MEXICO: Jalisco**: Río Santa Maria at Cocouado, 15 km. E. Autlan on Hwy. 80 (elev. 3100 ft.), 26.viii.1977, RKA, 2L [CAS]. **Queretaro**: Las Adjuntas (N21°23'58"; W99°34'45"), 04.viii.1998, 5L [TAMU]; Rio Tanculin at Nevlians (N21°16'; W99°04', elev. 650 m), 07.i.2001, D.E. Baumgardner, 8L [TAMU]; Bucareli, Rio Estorax (N21°02'05"; W99°37'03"), 11.vii.2000, WDS, 3L [TAMU]; **Veracruz**: Coscomatepec, 23.xii.1979, P.W. Kovarik and D.S. Bogar, 3L [TAMU]. **UNITED STATES: Texas:** Bandera Co; Medina R. at TX. 16, 1 mi. N. Medina (N25°48'59.3"; W99°15'32.7"), 08.iii.1997, DEB & D.E. Bowles, 1L [TAMU]. Hays Co.; San Marcos R. at Co. Rd. 101 (Caners Crossing), 1 mi. below conf. with Blanco R., in San Marcos City Limits, at Hays/Caldwell Co. Line., Balconian, 21.ii.1997, DEB and DE Bowles, 5L, 1 male subimago (reared) [TAMU].

Leptohyphes zalope Traver

Leptohyphes zalope Traver 1958:85; Allen, 1978.

Leptohyphes zelus Allen 1978:557; Baumgardner and McCafferty, 2000 (syn).

Leptohyphes vulturnus Allen, 1978:557 **new synonym**

Diagnosis: *Leptohyphes zalope* larvae can be differentiated from other species of *Leptohyphes* in the larval stage in North and Central America by the following characters: (1) a pair of submedian elongate setae present on the posterior margin of abdominal terga 2-9; (2) the presence of numerous sublateral robust setae on the posterior margin of abdominal terga 2-9 (terga 2 and 3 each with four to six setae; terga

4 and 5 each with six to eight setae; tergum 6 with 8-14 setae; terga 7 with 10-20; tergum 8 with 12-18; tergum 9 with four to six setae; tergum 10 with zero to two) (Fig. 13H); (3) more than ten robust setae present on dorsal surface of meso- and metafemora (Fig. 12C); (4) vertex of head with a complex head pattern (Fig. 24C); (5) large body size of mature larvae (5 to 8 mm in length), and dark reddish-brown coloration of mature larvae (often fading in alcohol preserved material). In the adult stage, the dark reddish-brown body with grayish abdomen will tentatively distinguish this species from others in the genus in North and Central America.

Description: *Male Imago*: Length. Body, 3.0 – 5.5 mm; forewings, 4.0 – 6.0 mm; hind wings, 0.5 – 1.0 mm. General coloration highly variable from yellow or gray to light to dark reddish brown. Head: gray with extensive black maculation; antennae brownish. Thorax: pronotum gray with black shading; meso- and metathorax ranging from yellow-brown to light reddish-brown to dark brown. Legs: gray with black stippling. Forewing (Fig. 19J): membrane pale brown; veins pale reddish-brown; C, Sc, and R darker grayish-brown; vein CuP not strongly curved towards A; vein iCu_2 united basally with iCu_1; iCu_1 attached basally to CuA by cross vein; MP_2 united basally to CuA and iMP by cross veins. Hind wing: membrane pale brown; three longitudinal veins present; costal process well-developed; hind margin of fore- and hind wings fringed with filiform setae. Abdomen. Coloration variable; tergites with yellow to gray to reddish-brown background color, overshadowed by black stippling giving gray cast. Genitalia pale reddish-brown, forceps three-segmented, penes with basal half fused, distal parts divergent, "Y" shaped; each penal lobe with single posterolateral spine; cerci and median caudal filament present, well-developed.

Larva: Length. Body, 4.0 – 7.5 mm; caudal filaments, 3.5 – 7.0 mm. General coloration light brown to brown to dark reddish-brown, with dark brown markings. Head: dark reddish-brown, with complex black pattern on vertex (Fig. 24C); in pre-emergent larvae, vertex often entirely reddish-brown or black without complex pattern; antennae pale. Thorax: brown to reddish-brown, with irregular dark brown and black markings; without anterolateral projections and median tubercle. Legs. Proleg (Fig. 28D): femur with transverse row of elongate setae along dorsal surface; anterior margin with stout setae along basal half of margin; posterior margin with elongate and stout setae along distal half of margin; tibia with one row of elongate along anterior margin, and one row of setae along anterolateral margin; posterior margin with few, scattered filiform setae; tarsus with one row of elongate setae along anterior margin; scattered filiform setae along distal inner margin. Meso- and metalegs (Fig. 12C): femora with numerous (> 10) setae on dorsal surface; anterior margin with robust setae along most of margin; posterior margin with densely-spaced, elongate setae along most of margin; tibiae with elongate setae present along most of anterior and posterior margins; tarsus with elongate setae along anterior margin; posterior margin with few, scattered filiform setae. Claws of all legs with five to nine marginal and one submarginal denticle (Fig. 28E). Abdomen: coloration variable, often depending on larval instar; more mature larvae generally dark reddish-brown; less mature larvae pale yellow to pale reddish-brown; tergites two through nine with numerous robust setae on sublateral margins (terga two and three each with four to six setae; terga four and five each with six to eight setae; tergum six with eight to fourteen setae; terga seven with ten to twenty setae; tergum eight with twelve to eighteen setae; tergum nine with four to six setae; tergum ten with zero to two) (Fig. 13H); operculate gill brown to dark reddish-brown; gill formula 2/5/5/5/1.

Distribution: *Leptohyphes zalope* is very widely distributed, known from the southwestern United States (Arizona, New Mexico, Texas), Mexico, Guatemala, Honduras, and Costa Rica (Baumgardner and McCafferty, 2000). The adult was associated with the larval stage based upon reared specimens from Texas (Baumgardner and McCafferty, 2000).

Discussion: Both *L. vulturnus* and *L. zelus* were described by Allen (1978) on the basis of a larva from Honduras (*L. vulturnus*) and a long series of larvae from Guatemala and Honduras (*L. zelus*). Theses two species were distinguished from all other species of *Leptohyphes* based upon the presence of distinct submedian and sublateral setae on the posterior margin of abdominal terga 2-9 (see Fig. 39, Allen, 1978), and were distinguished from each other based upon minor color differences of the abdominal terga. Examination of extensive series of larvae from throughout Central America show the abdominal color patterns of both the species, and numerous intermediate forms support the synonymy of *L. vulturnus* with *L. zelus* under *L. zalope* (see Baumgardner and McCafferty, 2000 for the association of *L. zalope* with its larval stage). The presence of numerous submedian and sublateral setae on the abdominal terga distinguish the larvae from all other known *Leptohyphes* larvae in North and Central America.

Some of the confusion in determining the concept of *Leptohyphes zelus* involves the original figures describing this species. When Allen (1978) described *L. zelus*, he referred to fig. 39 (p. 548) to show the pattern of setae on the abdominal tergites. However, this exact same figure had been used to describe *Leptohyphes consortis* (fig. 30, page 93) by Allen and Brusca (1973), five years earlier. Figure 30 in Allen and Brusca (1973) does not resemble the holotype of *L. consortis*, but instead agrees with the description of *L. zelus*. The holotype of *L. zelus* was collected in 1964, and perhaps Allen confused the undescribed *L. zelus* with *L. consortis* when he was describing *L. consortis*.

Lugo-Ortiz and McCafferty (1995a) considered *L. zelus* a synonym of *Leptohyphes lumas* Allen and Brusca based upon overall morphological similarity of the larvae. Baumgardner and McCafferty (2000) considered *Leptohyphes zelus, L. apache, L. ferruginus, L. hispidus, L. lumas, L. piraticus,* and *L. succinus* synonyms of *Leptohyphes zalope*, based upon overall morphological similarity of each of the species in the larval stage. Examination of the types of *L. zelus* and *L. vulturnus*, a better understanding of original description errors, and extensive studies of numerous specimens of *Leptohyphes* have demonstrated that they are distinct from *L. apache* (= *L. hispidus, L. lumas*, and *L. succinus*, see discussion of *L. apache*) and *L. ferruginus* (=*L. piraticus*, see discussion of *L. ferruginus*), based upon the presence of numerous submedian and sublateral setae on the posterior margin of abdominal terga 2-9, which are absent, or greatly-reduced, in all other known species of *Leptohyphes* in North and Central America.

The holotype of *L. vulturnus* is faded and in overall poor condition. Its head has been removed, along with all the legs and gills on the right side of the body. There are, however, apparently no associated slides, or any indication of any associated slides. The abdominal color pattern of the terga is visible, along with the submedian and sublateral setae. The holotype of *L. zelus* is deposited at Florida A&M University and is in good condition.

Type Material Examined: *Leptohyphes vulturnus* Allen, 1978. HOLOTYPE, larva; HONDURAS: Dept. Cortes, 2 mi. N. Carcol @ Bridge on Hwy.#1, Rio Blance. 18-X-1964, J.S. Packer (FSCA/FAMU E2044.1). *Leptohyphes zalope* Traver. PARATYPES: MEXICO: 4 mi. S. of Rio Papagayo Bridge on Río Zalope, 4.i.1948, S. Mulaik, 12♂ imagos (in 4 vials, 1 associated slide) [FAMU]. *Leptohyphes zelus* Allen, 1978. HOLOTYPE: Honduras, Dept. Comayagua, 3 mi. N. Taulabe on Hwy. #1, large river, 20-X-64, JS Packer, 1L [FSCA (FAMU) #2045.1T]. PARATYPES: Honduras, Dept. Comayagua, 3 mi. N. Taulabe on Hwy. #1, large river, 20-X-1964, JS Packer, 5L [CAS] (2 associated slides); Honduras, Dept. Cortes, Chamelecon, Rio Chamelecon, 18-X-1964, JS Packer, 1L [FAMU]; Honduras, Dept. Francisco, Morazan, 10 mi. E. Guaimaca on Hwy. #3, small stream, 6-XI-1964, JS Packer, 4L [FSCA (FAMU) #2045.T]; Honduras, Dept. F. Morazan, stream 6.5 mi. From jct. Hwy. #3 and Hwy. #5 on hwy. #5, 7-XI-1964, JS Packer, 2L [CAS]; Honduras, Dept. Olancho, stream 1 mi. W. Campamento, Galera turn-off on Hwy. #3, 7-XI-1964, JS Packer, 1L [CAS];

Honduras, El Paraiso, small stream ca. 3 Km, E. Danli, 29-VIII-1964, JS Packer, 2L [CAS]; Honduras, Dept. Comayagua, stream 5 mi. S., on Hwy. 1 at bridge, 17-X-1964, JS Packer, 1L [CAS]; Dept. Comayagua, Rio Humuya 1 mi. N. Comayagua @ bridge, 17-X-1964, JS Packer, 1L [CAS]; Dept. Cortes, Rio Blanco 2 mi. N. Carcol @ bridge on Hwy. #1, 18-X-1964, JS Packer, 3L [CAS]; Honduras, Dept. Francisco Morazan, stream nr. La Venta @ Jct. Hwy. #3 and Rio Choluteca, 7-XI-1964, JS Packer, 1L [CAS]; Honduras, El Paraiso, stream ca. 8 Km E. Danli, 29-VIII-64, JS Packer, 1L [CAS], 4L [FSCA(FAMU) E2045.T; Honduras, Rio Clarrita @ San Morano on Hwy. To Escuela Agricola, 29-X-1968, RK Allen, 4L, Elev. 3000', Temp 78E F [CAS]; Guatemala, Rio Latoma @ Km. 182 on CA 2 (2,300'), 24-VII-1966, RK Allen, 44L [CAS]; Honduras, Dept. El Paraiso, 50 km E. Danli, Trib. Rio Guayambre @ Junct. Hwy. #4, 3-IX-64, JS Packer, 1L [FAMU].

Other Material Examined: COSTA RICA: Alajuela: Rio Negritos at Hwy. 140, 2 Km E. Agua Zarcas (N10°22’20”; W84°19’10”, elev. 1300 ft), 09.vi.2001, 2L [TAMU]; Chachagua, Rio Chachagua (N10°23’; W84°35’), 16.i.2000, WDS, 12L [TAMU]; Rio Guayabo at Hwy. 140, 1.8 Km E. Venicia (N10°40’45”; W84°15’13”, elev. 1400 ft), 9.vi.2001, DEB, 3L [TAMU]; N. of Bijagua, Río Bijagua (N10°43’35”; W85°04’58”), 06.vi.2000, WDS, 6L [TAMU]; 2.7 km S. La Fortuna, Río Burro (N10°27’; W84°38’), 16.i.2000, WDS, 12L [TAMU]; NE of Bijagua, nr. Las Flores, Rio Areuo (N10°21’06”; W85°21’05”), 07.vi.2000, WDS, 30L [TAMU]; 12 Km. E. Arenal, unnamed stream (N10°28’; W84°47’), 16.i.2000, WDS, 6L [TAMU]; La Fortuna, Quebrada Burio (N10°28’; W84°39’), 15.i.2000, WDS, 20L [TAMU]. **Cartago:** Rio

Kiri ca. 10 Km SE Orosi (N09°46’05”; W83°48’04”, elev. 3980 ft), 25-26.vi.2001, DEB, 5L [TAMU]; Rio Orosi, ca. 8 Km SE Orosi (N09°45’52”; W83°47’47”, elev. 3700 ft.), 26.vi.2001, DEB, 2L [TAMU]. **Guanacaste:** 4.5 km N. Bagaces, Rio Piedras, 17.vi.2000, WDS, 3L [TAMU]; Rincon de la Vieja Pk., trail, 18.i.2000, WDS, 7L [TAMU]; 6 km S San Miguel, Hwy. 1, Quebrada Culvert (N10°19’; W85°03’), 23.i.2000, WDS, 25L [TAMU]; 4.8 km N Canas, Hwy. 142, Rio Santa Rosa, 17.i.2000, WDS, 15L [TAMU]; Canas, Rio Canas (N10°26’; W85°06’), 23.i.2000, WDS, 20L [TAMU]; Rincon de la Vieja Lodge, unnamed stream (N10°45’; W85°21’), 19.i.2000, WDS, 20L [TAMU]; 4 Km W. Arenal, unnamed spring run, 17.i.2000, WDS, 4L [TAMU]. **Heredia:** La Selva Biological Station, SW Puerto Viejo, Sura Creek at Rio Puerto Viejo (N10°25’49”; W84°00’06”, elev. 100 ft.), 09.vi.2001, DEB, 7L [TAMU]; Rio Isla Grande at Hwy. 4, ca. 5 Km. W. of Rio Frio (N10°23’31”; W83°58’04”, elev. 200 ft.), 10.vi.2001, DEB, 3L [TAMU]. **Limon:** Unnamed creek at Hwy. 32, ca. 3 Km W. of Pocora (N10°10’38”; W83°37’03”, elev. 340 ft.), 10.vi.2001, DEB, 20L [TAMU]. **Puntarenas:** Rio Ceibo at CA Hwy. 2, SW Buenos Aries (N09°08’57”; W83°22’30”, elev. 800 ft.), 25.vi.2001, DEB, 4L [TAMU]; Río Jaba at Las Cruses Biological Station, ca. 14 Km. S. San Vito (elev. 4000 ft.), DEB, 23-24.vi.2001, 2 females (reared), 3 males (reared), 7L [TAMU]; Quebrada Culebra at Las Cruses Biological Station, ca. 14 Km S. San Vito, 24.vi.2001, DEB, 14L [TAMU]; Las Cruces Biological Station, Quebrada Culvert, 16.vi.2000, WDS, 7L [TAMU]; 5 Km SE Coloradito Norte, unnamed river (N08°34’41”; W82°52’28”), 17.vi.2000, WDS, 4L [TAMU]; 1 Km S Coloradito Norte, Rio Coloradito at Hwy. 2 (N08°36’10”; W82°54’07”), 17.vi.2000, WDS, 7L [TAMU];

unnamed ck at Hwy. 34, 11.9 Km SE Dominical (N09°11’48”; W83°46’57”, elev. 80 ft.), DEB, 22.vi.2001, 1L [TAMU]; 5.8 km S. Alturus, unnamed stream (N08°54’25”; W82°50’49”, elev. 1230 m), 18.vi.2000, WDS, 20L [TAMU]; 5.4 km NW San Gerado, 25.i.2000, WDS, 11L [TAMU]; 14.5 Km N. Ciudad Neily, unnamed stream (N08°42’44”; W82°56’05”, elev. 1069 m), WDS, 17.vi.2000, 2L [TAMU]; 4.1 Km N Dominical on Hwy. 243, unnamed river (N09°16’51”; W83°50’55”), 14.vi.2000, WDS, 6L [TAMU]. **San Jose:** Rio Pedregoso at Hwy. 243, ca. 4 Km S. San Isidro de El General (N09°21’15”; W83°43’35”, elev. 2000 ft.), 22.vi.2001, DEB, 7L [TAMU]. **GUATEMALA**: **Alta Verapaz**: Río Stainkreec, .8 Km E. from jct. of Hwy. 9&10, Río Hondo (N15°02’23”; W89°35’14”, elev. 600 ft), 15.vii.2001, DEB, 15L [TAMU]. Rio Cahabon at Hwy. 7E, San Julian (N15°19’09”; W90°19’06”, elev. 4700 ft), 14.vii.2001, DEB, 1L [TAMU]. **Baja Verapaz**: Rio San Jeronimo at San Jeronimo (N15°03’52”; W90°14’03”, elev. 3110 ft), 13.vii.2001, DEB, 3L [TAMU]. unnamed creek at CA Hwy. 14, ca. 2.6 Km S. Purulha (N15°13’34”; W90°13’80”, elev. 5100 ft), 14.vii.2001, DEB, 3L [TAMU]. **El Progreso**: Rio Hato at CA Hwy. 9, ca. 5.9 Km E. from jct. with Hwy. 17, Magdalena (N14°55’11”; W89°57’56”, elev. 1040 ft), 14.vii.2001, DEB, 41L [TAMU]. Quebrada Las Pericas at Hwy. 17, 11.1 Km W. from jct. with Hwy. CA 9, (N14°54’54”; W90°05’52”, elev. 1040 ft), 12.vii.2001, DEB, 28L [TAMU]. **Zacapa:** Rio Cayo at CA Hwy. 9, 2.3 Km E. Santa Cruz (N15°00’54”; W89°39’09”, Elev. 830 ft.), 14.vii.2001, DEB, 3L [TAMU]. **HONDURAS**: **Comayagua**: Taulabe, Rio Tamalito (N14°41’; W87°55’), 13.iii.2002, R. Caesar, A. Cognato, A. Harlin, J. Torres, 4L [TAMU]. **MEXICO:** **Nuevo Leon**: Cabazones R. at Hwy. 85, 15 mi. N. Linares, 16.v.1995, DEB, 8L [TAMU]. Pobillo R. @ St. Hwy. 115, near Linares, 15.v.1995, DEB, 12L [TAMU]. Queretaro: Bucareli, Rio Estorax (N21°02'05"; W99°37'03"), 11.vii.2000, WDS, 1L [TAMU]. San Louis Potosi: Naranjo R. at Hwy. 80, nr. Naranjo (town), 18.v.1995, DEB, 2L [TAMU]. Rio Moctezuma @ Tamazunchale on Hwy. 85 (elev. 400 ft), 18.viii.1977, RKA, 7L [CAS]. Tamaulipas: Rio Purification on Hwy. 85, (elev. 800 ft), 16.viii.1977, RKA, 1L [CAS]. R. Guayalejo (Tamasi), off Hwy 247 nr. San Ignacio, 26.v.1993, BC Henry, 30L [TAMU]. Branch of Chihue R. at Hwy. 101, ca. 12 mi. S. Juamave, nr. Kilo. Marker #91, (elev. 3575 ft), 17.v.1995, DEB, 2L [TAMU]. **UNITED STATES: Arizona:** Navajo Co.; North Fork White River at SR 55, Whitewater N33°49'47";W109°57'36", elev. 5170 ft.), 23.v.2004, DEB, 10L, [TAMU]. **Texas:** Bastrop Co.; McKinney Roughs, Colorado River at Wilbarger Bend about 8 mi. west of Bastrop, Balconian, 23.xi.1996, NA Wiersema, 3L [TAMU]. Bastrop Co.; Pedernales Falls State Park, Pedernales River, 5-6.IX.1997, NA Wiersema & CR Nelson, 1L [TAMU]. Hays Co.; San Marcos, pool below fall at University Drive, 25.iii.1978, P. Foerster, 2L [TAMU]. Hays Co.; San Marcos R. at Co. Rd. 101 (Caners Crossing), 1 mi. below conf. with Blanco R., in San Marcos City Limits, at Hays/Caldwell Co. Line, 21.ii.1997, DEB & DE Bowles, 2M (reared), 2F (reared), 6L [TAMU]. Hays Co.; San Marcos R. at Cheatum St. in San Marcos, 22.II.1997, DEB & DE Bowles, 20L, 1 male imago (reared) [TAMU]. Kerr Co.; Guadalupe R. just off Hwy. 27, nr. Center Point, 14.iii.2000, DEB, 5L [TAMU]. Kimble Co.; Llano R. at Texas Tech Field Station, Junction, 14.iii.2000, DEB, 25L, 1F (reared) [TAMU]. Kimble Co.; S. Llano River, nr. Junction, (N38°28'18"; W99°44'4"), 24.ii.1998, DE

Bowles, 6L [TAMU]. Kimble Co.; Junction South Llano Riverat Hwy. 456, 13.X.1996, R. Waugaman, 1L [TAMU].

Discussion

The number of valid species of *Leptohyphes* now stands at thirty-six; fifteen from North and Central America, compared with twenty-one from South America (Molineri, 2003b; Molineri and Zúñiga, 2006). Of the fifteen species known from North and Central America, only three are known from both life stages (*L. ferruginus, L. sabinas*, and *L. zalope*), five from the adult life stage only (*L. berneri*, *L. brevissimus*, *L. nigripunctus*, *L. peterseni*, and *L. priapus*), and seven from the larval stage only (*L. alleni*, *L. apache*, *L. lestes*, *L. mandibulus*, *L. murdochi*, *L. musseri*, and *L. pilosus*). Of the twenty-one species known from South America , seven species are known from both life stages, three from only the adult stage, and eleven from only the larval stage. Association of life stages will need to continue so that many of the taxonomic problems within the genus can be solved.

Of the thirty-six known species of *Leptohyphes*, only two species are known from both Central and South America, although there remains the strong possibility that some species described from Central America are likely synonyms of South American species. No species are known from North, Central, and South America. These two species, *L. nigripunctum* Traver, and *L. peterseni* Ulmer, were both reported from Central America by McCafferty (1985). Both species are known only from the adult stage, and since adults of *Leptohyphes* are extremely difficult to distinguish, and most species unknown as adults, these records should be considered tentative. The number of valid species in North and Central America may decrease, because species such as *L. alleni* Brusca and *L. pilosus* Allen and Brusca remain highly suspect, and the larvae once known from species now known only as adults may prove synonymous with other species.

There does remain the strong possibility that several species of *Leptohyphes* known only from the larval stages could be the unassociated larval stage of at least one of five species of *Leptohyphes* reported from Mexico and Central America, which were described based upon only the adult stage. These species include *Leptohyphes berneri* Traver (1958) described from central Mexico; *Leptohyphes brevissimus* Eaton (1892) described from southern Guatemala based upon female subimagos; *Leptohyphes nigripunctum* Traver 1943 described from a male subimago from Venezuela and later reported from southern Mexico (McCafferty 1985); *Leptohyphes peterseni* Ulmer (1920) described from South America based upon male and female subimagos, and later reported from Central America (McCafferty 1985); or *Leptohyphes priapus* Traver (1958), which was described from Costa Rica. Extensive rearings of larvae throughout Central America will be necessary to solve these issues.

Many species of *Leptohyphes* in North and Central America are extremely similar as larvae and difficult to distinguish, in particular the species treated herein. Morphological differences are often few, subtle, and often prone to some variation, making limits difficult to define. The following key may be used to distinguish known larvae of North and Central species.

Key to *Leptohyphes* Eaton larvae of North and Central America

1a. Dorsal surface of legs densely covered with numerous small, pale depressions (Figs. 22A, D, F; 23B); submarginal denticles absent (Fig.22D; 28D) 2

1b. Dorsal surface of legs without with numerous small, pale depressions (Fig.21E); submarginal denticles present (Fig.22E, D) 3

2a. Meso- and metafemora with distinct apical concavity (Fig.22B); middle and hind tibiae without elongate inner marginal spines (Fig.22B) .... *murdocki*

2b. Meso- and metafemora without distinct apical concavity (Fig.21F); middle and hind tibiae with elongate inner marginal spines (Fig.21F) .... *alleni*

3a. Head, thorax, and legs covered with long hairlike setae (see figs. 37 and 38, Allen 1978) .... *pilosus*

3b. Head, thorax, and legs without long hairlike setae 4

4a. Sublateral margins of abdominal tergites seven and eight with stout setae (Fig. 13H, 27A).. 5

4b. Sublateral margins of abdominal tergites without stout setae (Fig.24D) .... *apache*

5. Body and appendages entirely pale to dark red; abdominal tergites with either no black maculation or limited black maculation confined to lateral margins ...... *ferruginus*

5b. Body and appendages yellow, yellowish-brown, reddish-brown, or gray; abdominal terga with or without sublateral black maculation 6

6a. Vertex of head extensively covered with black maculation/complex markings (Fig.24C); species dark reddish brown with extensive black maculation .... *zalope*

6b. Vertex of head without extensive black maculation or complex markings; thin black lines may be present on vertex of head between compound eyes (Figs. 26C – D; 27B; 28D); species pale yellow to dark brown 7

7a. Operculate gill with basal half black, distal half gray (Fig. 6H); two highly fused inner and two highly fused outer marginal denticles of both mandibles (Figs. 28A – B) .... *mandibulus*

7b. Operculate gill largely yellowish to yellowish-brown to brown; mandibles without highly fused denticles; inner denticles with two to four teeth (Figs. 21D – E) 8

8a. Body yellow with black maculation on thorax, abdomen; middle and hind femora with apical black macula (Fig.22C) .... *musseri*

8b. Body light to dark brown, with very limited black maculation on body; middle and hind femora with apical black macula (Fig. 5E) 9

9a. Thick black line present between compound eyes; femora lacking black mark (Fig.26B) .... *lestes*

9b. Vertex of head without dark markings (in particular the line running posteriorly from compound eyes); without a black line between lateral ocelli .... *sabinas*

CHAPTER V

BIOGEOGRAPHY OF THE LEPTOHYPHIDAE

Introduction

The family Leptohyphidae is found exclusively in the Western Hemisphere, including North, Central and South America, and the Caribbean region. There is no well-documented evidence or hypotheses explaining the distribution patterns of species in the family Leptohyphidae. McCafferty (1998) and McCafferty and Wang (2000) have hypothesized that the family Leptohyphidae evolved in South America, based on the known distribution of species, possible dispersal routes, and a proposed South American center of origin for the group.

The vast majority of leptohyphid species are known either exclusively from North and/or Central America or South America. Only five species are currently known to occur in both Central and South America, while none are known to occur in both North, Central and South America. One species is known from the Caribbean Region and North and Central America, while a second species is known from both South American and the Caribbean.

Biogeographic Hypotheses

Three alternative biogeographic hypotheses are discussed below, each of which proposes a different historical evolution that could explain the current distribution of leptohyphid mayflies in the New World.

1. *North American Origin Hypothesis*. The North American Origin Hypothesis assumes that the immediate ancestors of extant leptohyphids were distributed only in North America (not South America) prior to the formation of the Panamanian land bridge, and that leptohyphids reached South America by southward dispersal across that land bridge. This hypothesis predicts that an area cladogram of leptohyphid mayflies should possess basal clades that occur only in North America (representing early lineages of leptohyphid radiations that evolved prior to dispersal of the family into South America), with only more derived clades present in South America. The presence of basal clades in South America would tend to refute this hypothesis, as would the discovery of leptohyphid fossils in South America that predate the Panamanian land bridge.

2. *South American Origin Hypothesis*. The South American Origin Hypothesis assumes that the immediate ancestors of extant leptohyphids were found only in South America (not North America) prior to the formation of the Panamanian land bridge, and that leptohyphids subsequently invaded North America by dispersal across the land bridge. This hypothesis predicts that an area cladogram of leptohyphid mayflies should possess basal clades that occur only in South America (representing early lineages of leptohyphid radiations that evolved prior to the dispersal of the family into North America), with only relatively derived clades present in North America. The presence of basal leptohyphid clades in North America would tend to refute this hypothesis, as would the discovery of leptohyphid fossils in North America that predate the Panamanian land bridge.

3. *North and South American Origin Hypothesis*. This hypothesis assumes that leptohyphid mayflies were present in both North and South America before the formation of the Panamanian land bridge, and that dispersal has occurred across the land bridge since its formation around 3 mybp. The North and South American Origin Hypothesis assumes that leptohyphids evolved in Pangea (over 180 mybp), and that the family was distributed in at least the North and South American land masses. This hypothesis predicts that an area cladogram of leptohyphids should contain basal, or near basal, clades in both North and South America. The presence of basal clades on only one of the two continents would cast doubt on this hypothesis.

Biogeographic Methods

In order to test the biogeographic hypotheses discussed in the introduction, geographic distributions were overlaid onto the species cladograms with the goal of finding an area cladogram which matches one of the three predicted cladograms for a particular hypothesis. This technique, known as cladistic biogeography, examines area relationships based upon taxon relationships, and seeks to explain repeated patterns among taxons. This technique, known as cladistic biogeography, was formally developed by Platnick and Nelson (1978). Cladistic biogeography has been used by Brundin (1981) for chironomid midges and Ross (1974) for caddisflies. Platnick and Nelson (1978) and Rosen (1978) further refined cladistic techniques.

Results

Figure 29 shows the biogeographic distribution of leptohyphid genera and selected outgroup taxa, with major land masses overlaid onto the terminal clades. A comparison with the three proposed hypotheses (the North America Origin Hypothesis, the South American Origin Hypothesis, and the North/South American Origin Hypothesis) indicates that the South American origin hypothesis is best supported. This is because many of the basal clades within the family Leptohyphidae are distributed in South America, while the more derived clades are distributed largely in North America. The one exception is the genus *Tricorythopsis*. Although this genus is highly derived within the leptohyphids, all of its species are South American in distribution, which is the only genus which refutes the South American origin hypothesis and supports the North American origin hypothesis. However, since the trend within the family Leptohyphidae is clearly that of basal clades distributed in South America and derived clades in North America, the South American origin hypothesis is still the preferred hypothesis.

Discussion

The South American origin hypothesis is the best-supported hypothesis based upon the biogeographic results presented in Figure 29. This hypothesis assumes that the immediate ancestors of extant leptohyphids were found only in South America prior to the formation of the Panamanian land bridge, and that leptohyphids subsequently invaded North America by dispersal across the land bridge. This hypothesis predicts that an area cladogram of leptohyphid mayflies should possess basal clades that occur only in South America (representing early lineages of leptohyphid radiations that evolved prior to the dispersal of the family into North America), with only relatively-derived clades present in North America.

The three most basal leptohyphid clades, *Leptohyphdes*, *Amanahyphes*, and *Haplohyphes* contain a total of seven species, six of which are distributed only in South America, and one of which is distributed in South and Middle America, with its northern distribution in Nicaragua. This result clearly supports the South American hypothesis, in that all three basal leptohyphid clades are distributed almost entirely in South America.

The next most basal clade, *Leptohyphes*, contains 41 species, almost half of which (20 species) are distributed almost entirely in South America. Fifteen species are known only from Middle America, and four species from Middle America and the southwestern United States. This relatively-basal clade is likely of South American origin and was apparently able to successfully disperse into North America after the formation of the land bridge. Unfortunately, the phylogenetic resolution of species within this genus was very poor (Figs. 17 and 18), and no conclusions can be made concerning basal and derived relationships of species within the genus.

The *Traverhyphes* genera group (composed of four, closely-related genera) is almost entirely endemic to South America. Of the 19 species known in this genera group, 16 occur only in South America. Of the remaining three species, one occurs in South America and the Caribbean, one only in Middle America, and one in Middle America and the southwestern United States.

The relatively-derived genus *Vacupernius* contains a single species which is distributed throughout most of Middle America, and into the southwestern United States. Considering this is a relatively-derived genus within the Leptohyphidae, and its single species is distributed only in North America, this supports the South American origin hypothesis which predicts more derived taxa distributed in North America.

The genus *Tricorythopsis* contains nine species, all of which are distributed only in South America. Considering that this is one of the more derived genera and its species are distributed entirely in South America, this would support the North American origin hypothesis, and not the South American hypothesis. However, the South American origin hypothesis is still preferred, because the trend within the family Leptohyphidae is clearly one of basal clades in South America with more derived clades in North America. There are several explanations which could account for why this clade is apparently relatively derived, but with all of its species in South America, and still support the South American origin hypothesis. First, it is possible that the cladistic analysis failed to recognize the correct evolutionary history of this genus and placed it in an incorrect position within the cladogram. This conclusion could be supported by the fact that all males within this genus have only two-segmented forceps, whereas all the other more relatively-derived clades (*Vacupernius*, *Tricorythodes*) have males which possess three-segmented forceps. The most basal clades, *Leptohyphdes*, *Amanahyphes*, and *Haplohyphes*, all have males with two-segmented forceps, as do the sister families Tricorythidae and Coryphoridae. Second, the clade may indeed be highly-derived, but its species were never able to disperse northward across the Panamanian land bridge. There are several characters which place the genus in a derived position in the cladogram, mainly derived changes in wing venation.

The genus *Tricorythodes* is the most derived and specious genus in the family, with the majority of its species (30 out of 54) occurring north of the Panamanian land bridge. The fact that this is the most highly-derived genus, and its species are distributed largely in North America, supports the South American origin hypothesis which predicts the most derived clades with species in North America.

It appears that at least five independent invasions from South America to North and Central America have occurred in the evolution of Leptohyphidae. These invasions across the Panamanian land bridge occurred across the family, including the more basal genera *Haplohyphes* and *Leptohyphes*, and the most highly derived genus *Tricorythodes*. Within the *Traverhyphes* genera group, only two of the four genera have penetrated into Central America, and none of them into North America. Even the invasion of Central America by these two genera (*Allenhyphes* and *Traverhyphes*) was extremely limited with only three species having moved into Central America. It does appear that the Panamanian land bridge had a significant impact on the evolution and dispersal on the family into North and Central America.

CHAPTER VI

SUMMARY AND CONCLUSIONS

A cladistic analysis of the world genera of the mayfly family Leptohyphidae is presented. Analyses of a matrix of 59 ingroup and 9 outgroup species and 119 morphological characters strongly supports the monophyly of Leptohyphidae and its sister-group relationship with the Coryphoridae. Larval and adult taxonomic keys are provided to the 11 recognized extant genera. For each genus, a synonymical listing, differential diagnosis, list of proposed synapomorphies, diagnostic illustrations, and notes on distribution and included species are given. The following new synonyns of genus *Tricorythodes* are proposed: *Ableptemetes* **n. syn.,** *Cabecar* **n. syn.,** *Epiphrades* **n. syn.,** *Homoleptohyphes* **n. syn.,** *Macunahyphes* **n. syn.,** *Tricoryhyphes* **n. syn.** The former genus *Asioplax* is newly regarded as a subgenus of *Tricorythodes*. A species-level revision of North and Central American *Leptohyphes* is presented. A key to the 15 *Leptohyphes* species known as larvae is provided. In addition, detailed descriptions, diagnosis, and geographic distributions are given for all species of *Leptohyphes* known from North and Central America. Biogeographic analysis suggests that the family Leptohyphidae originated in South America, and that its North American species are the descendants of one or more ancestral species that crossed northward over the Panamanian land bridge.

LITERATURE CITED

Alba-Tercedor, J. and J. Flannagan. 1995. Two new Canadian species of the genus *Tricorythodes* Ulmer, with additional studies on other North American species (Insecta, Ephemeroptera: Leptohyphidae). Canadian Journal of Zoology 73:1588-1598.

Allen, R.K. 1966. *Haplohyphes*, a new genus of Leptohyphinae (Ephemeroptera: Tricorythidae). Journal of the Kansas Entomological Society 39:565-568.

Allen, R.K. 1967. New species of New World Leptohyphinae (Ephemeroptera: Tricorythidae). Canadian Entomologist 99:350-375.

Allen, R.K. 1973. New species of *Leptohyphes* Eaton (Ephemeroptera: Tricorythidae). Pan-Pacific Entomologist 49:363-372.

Allen, R.K. 1977. A new species of *Tricorythodes* with notes (Ephemeroptera: Tricorythidae). Journal of the Kansas Entomological Society 50:431-435.

Allen, R.K. 1978. The nymphs of North and Central American *Leptohyphes* (Ephemeroptera: Tricorythidae). Annals of the Entomological Society of America 71:537-558.

Allen, R.K. and R.C. Brusca. 1973. New species of Leptohyphinae from Mexico and Central America (Ephemeroptera: Tricorythidae). Canadian Entomologist 105:83-95.

Allen, R.K. and C.M. Murvosh. 1987. Mayflies (Ephemeroptera: Tricorythidae) of the southwestern United States and northern Mexico. Annals of the Entomological Society of America 80:35-40.

Allen, R.K. and S.S. Roback. 1969. New species and records of New World Leptohyphinae (Ephemeroptera: Tricorythidae). Journal of the Kansas Entomological Society 42:372-379.

Banks, N. 1903. Neuropteroid insects from Arizona. Proceedings of the Entomological Society of Washington 5:237-245.

Baumgardner, D.E. 2003. New synonyms and stage description for three species of Leptohyphidae (Ephemeroptera). Proceedings of the Entomological Society of Washington 105:203-208.

Baumgardner, D.E. 2007. New species of Leptohyphidae (Ephemeroptera) from Costa Rica. Proceedings of the Entomological Society of Washington 109:416-426.

Baumgardner, D.E. and S. Ávila. 2006. *Cabecar serratus*, a new genus and species of leptohyphid mayfly from Central America, and description of the imaginal stages of *Tricorythodes sordidus* Allen (Ephemeroptera: Leptohyphidae). Zootaxa 1187:47-59.

Baumgardner, D.E. and D.E. Bowles. 2005. Preliminary survey of the mayflies (Ephemeroptera) and caddisflies (Trichoptera) of Big Bend Ranch State Park and Big Bend National Park. Journal of Insect Science 5:28.

Baumgardner, D.E., S.K. Burian, and D. Bass. 2003. Life stage descriptions, taxonomic notes, and new records for the mayfly family Leptohyphidae (Ephemeroptera). Zootaxa 332:1-12.

Baumgardner, D.E., J.H. Kennedy, and B.C. Henry. 1997. New and additional records of Texas mayflies (Insecta: Ephemeroptera). Transactions of the American Entomological Society 123:55-69.

Baumgardner, D.E. and W.P. McCafferty. 2000. *Leptohyphes zalope*, a polytypic North American mayfly (Ephemeroptera: Leptohyphidae). Entomological News, 111:49-59.

Baumgardner, D.E., M.D. Meyer, and W.P. McCafferty. 2006. A new species of *Asioplax* (Ephemeroptera: Leptohyphidae) from Costa Rica and Nicaragua. Pan-Pacific Entomologist 82:346-350.

Berner, L. 1946. New species of Florida mayflies (Ephemeroptera). Florida Entomologist 28:60-82.

Berner, L. and M.L. Pescador. 1988. The mayflies of Florida: Revised Edition. University Presses of Florida, Gainesville. 415 pp.

Brundin, L. 1966. Transantartic relationships and their significance as evidenced by the chironomid midges, with a monograph of the subfamily Podonominae, Aphroteninae and the austral Heptagidae. Kungl. Svenska Vetenskapsakademiens Handlingar Fjärde Serien 11:1-472.

Brundin, L. 1981. Croizat's panbiogeography versus phylognetic biogeography. Pages 94 – 158. *In*: G. Nelson and E.E. Rosen, eds., Vicariance biogeography: a critique. Columbia University Press, New York.

Brusca, R.C. 1971. A new species of *Leptohyphes* from Mexico (Ephemeroptera: Tricorythidae). Pan-Pacific Entomologist 47:146-148.

Burks B.D. 1953. The mayflies, or Ephemeroptera, of Illinois. Bulletin of the Illinois Natural History Survey 26:1-216.

Bussing, W.A. 1985. Patterns of distribution of the Central American Ichthyofauna. Pages 427 – 453. *In:* F.G. Stehli and S.D. Webb, eds., The Great American Biotic Interchange. Plenum Press, New York.

Carpenter, F.M. 1992. Treatise on invertebrate paleontology, Arthropoda 4. The Geological Society of America., Inc., Boulder, Colorado, and The University of Kansas, Lawrence, Kansas. 277 pp.

Darlington, P.J. Jr. 1957. Zoogeography: the geographical distribution of animals. John Wiley & Sons, New York.

Darwin, C. 1859. On the origin of species by means of natural selection or the presevation of favored races in the struggle for life. John Murray, London.

Dias, L.G. and F.F. Salles. 2005. Three new species of *Tricorythopsis* (Ephemeroptera: Leptohyphidae) from southeastern Brazil. Aquatic Insects 27:235-241.

Dias, L.G., F.F. Salles, and C. Molineri. 2005. *Macunahyphes*: a new genus for *Tricorythodes australis* (Ephemeroptera: Leptohyphidae). Annales de Limnologie - International Journal of Limnology 41:195-201.

Domínguez, E. 1982. Una especie nueva de Tricorythidae de la Argentina (Insecta: Ephemeroptera). Revista de la Sociedad Entomologica Argentina 41:331-335.

Domínguez, E. 1984. Dos especies nuevas del genero *Haplohyphes* Allen (Ephemeroptera: Tricorythidae) Revista de la Sociedad Entomologica Argentina 43:l03-ll2.

Domínguez, E. 1999. Systematics, cladistics and biogeography of the American genus *Farrodes* (Ephemeroptera: Leptophlebiidae: Atalophlebiinae). Zoological Journal of the Linnean Society 126:155-189.

Domínguez, E., M.D. Hubbard, and W.L. Peters. 1992. Clave para ninfas y adultos de las familias y géneros de Ephemeroptera (Insecta) sudamericanos. Biologia Acuatica 16:1-32, fig. a-c, 1-39.

Domínguez, E., M.D. Hubbard, M.L. Pescador, and C. Molineri. 2001. Ephemeroptera. Pages 17 – 53. *In:* H.R. Fernández and E. Domínguez, eds., Guía para la determinación de los artrópods bentónicos sudamericanos. Secretaría de Ciencia y Ténica de la Universidad Nacional de Tucumán, Argentina.

Eaton, A.E. 1882. An announcement of new genera of the Ephemeridae. Entomol. Mon. Mag. 18:207-208.

Eaton AE. 1883-1888. A revisional monograph of recent Ephemeridae or mayflies. Transactions of the Linnean Society of London, Second Series, Zoology 3:1-352, 65 pl.

Eaton, A.E. 1892. Biologia Centrali-Americana, Insecta, neuroptera, Ephemeridae. Bernard Quaritch, London 38:1-16.

Edmunds, G.F., Jr. 1975. Phylogenetic biogeography of mayflies. Annals of the Missouri Botanical Garden 62:251-263.

Edmunds, G.F., Jr, R.K. Allen, and W.L. Peters. 1963. An annotated key to the nymphs of the families and subfamilies of mayflies (Ephemeroptera). University of Utah Biological Series 13:1-49.

Edmunds, G.F., Jr., S.L. Jensen, and L. Berner. 1976. The mayflies of North and Central America. University of Minnesota Press, Minneapolis.

Goloboff, P. 1996. Methods for faster parsimony analysis. Cladistics 12:199-220.

Goloboff, P. 1999. Analyzing large data sets in reasonable times: solutions for composite optima. Cladistics 15:415-428

Halffter, G. 1987. Biogeography of the Montane Entomofauna of Mexico and Central America. Annual Review of Entomology 32:95-114.

Hall, R.J., L. Berner, and E.F. Cook.1975. Observations on the biology of *Tricorythodes atratus* McDunnough (Ephemeroptera: Tricorythidae). Proceedings of the Entomological Society of Washington 77:34-49.

Henry, B.C., Jr. 1986. Mayflies (Ephemeroptera) of the Concho River, Texas. Southwestern Naturalists 31:15-21.

Hofmann C., M. Sartori, and A. Thomas. 1999. The mayflies (Ephemeroptera) of Guadeloupe (French West Indies). Mémoires de la Société Vaudoise des Sciences Naturelles 20:1-96.

Hubbard, M.D. 1982. Catalogo abreido de Ephemeroptera da América do Sul. Papeis Avulsos de Zoologia, San Paulo 94:257-282.

Hubbard, M.D. 2003. Obituary to William Lee Peters. Pages 15-20. *In*: Gain, E. Research Update on Ephemeroptera & Plecoptera. Università di Perugia, Perugia, Italy.

Illies, J. 1969. Biogeography and ecology of Neotropical Freshwater insects, esepically those from running waters. Pages 685 – 707. *In:* E.J. Fittkau, J. Illies, H. Klinge, G.H. Schwabe, and H. sioli, eds., Biogeography and ecology in South America. Dr. W. Junk, The Hague.

Jacobus, Luke M. and W.P. McCafferty. 2006. Reevaluation of the phylogeny of the Ephemeroptera Infraorder Pannota (Furcatergalia), with adjustments to higher classification. Transactions of the American Entomological Society 132:81-90.

Kilgore, J.I. and R.K. Allen. 1973. Mayflies of the Southwest: new species, descriptions, and records (Ephemeroptera). Annals of the Entomological Society of America 80:35-40.

Kimmins D.E. 1934. Notes on the Ephemeroptera of the Godman and Salvin collection, with descriptions of two new species. Annals and Magazine of Natural History (1)14:338-353.

Kluge, N. Ju. 1992. Redescription of *Leptohyphes eximis* Eaton and diagnoses of the genera *Leptohyphes* and *Tricorythodes* based on the structure of the pterothorax (Ephemeroptera: Tricorythidae, Leptohyphinae). Opuscula Zoologica Fluminensia 98:1-16.

Kluge, N. Ju. 2004. The phylogenetic system of Ephemeroptera. Kluwer Academic Publishers, Dordrecht.

Kluge, N. and J.C. Naranjo. 1990. Mayflies of the family Leptohyphidae (Ephemeroptera) of Cuba. Opuscula Zoologica Fluminensia 69:564-578.

Landa, V. and T. Soldon. 1985. Phylogeny and higher classification of the order Ephemeroptera: a discussion from the comparative anatomical point of view. Studie CSAV, Ceskoslovenska Akademie Vêd., Praha.

Lugo-Ortiz, C.R. and W.P. McCafferty. 1995a. Contribution to the taxonomy of the Leptohyphidae (Insecta: Ephemeroptera) of Central America. Studies on Neotropical Fauna and Environment 30:165-176.

Lugo-Ortiz, C.R. and W.P. McCafferty. 1995b. Annotated inventory of the mayflies of Arizona. Entomological News 106:131-140.

Lugo-Ortiz, C.R. and W.P. McCafferty. 1995c. The mayflies (Ephemeroptera) of Texas and their biogeograpic affinities. Pages 151 – 169. *In*: L. Corkum and J. Ciborowski, eds., Current directions in research on Ephemeroptera. Canadian Scholars' Press Inc., Toronto, Canada.

Marshall, L.G., S.D. Webb, J.J. Sepkoski, Jr., and D.M. Raup. 1982. Mammalian evolution and the great American interchange. Science 215:1351-1357.

Mayo, V.K. 1968. Some new mayflies of the subfamily Leptohyphinae (Ephemeroptera: Tricorythidae). Pan-Pacific Entomologist 44:301-308.

McCafferty, W.P. 1985. New records of Ephemeroptera from Middle America. International Quarterly of Entomology 1:9-11.

McCafferty, W.P. 1991. Toward a phylogenetic classification of the Ephemeroptera (Insecta): a commentary of systematics. Annals of the Entomological Society of America 84:343-360.

McCafferty, W.P. 1998. Ephemeroptera and the great American interchange. Journal of the North American Benthological Society 17:1-20.

McCafferty, W.P., D.E. Baumgardner, and J.L. Guenther. 2004. The Ephemeroptera of Central America. Part 1: Guatemala. Transactions of the American Entomological Society 130:201-219.

McCafferty, W.P., R.S. Durfee, and B.C. Kondratieff. 1993. Colorado mayflies (Ephemeroptera): an annotated inventory. Southwestern Naturalists 38:252-274.

McCafferty, W.P., C.R. Lugo-Ortiz, and G.Z. Jacobi. 1997. Mayfly fauna of New Mexico. Great Basin Naturalist 57:283-314.

McCafferty, W.P., R.W. Flowers, and R.D. Waltz. 1992. The biogeography of Mesoamerican mayflies. Pages 173 – 193. *In:* S.P. Darwin and L. Welden, eds., Biogeography of Mesoamerica: Proceedings of a Symposium. Tulane Studies in Zoology and Botany, Supplemental Publication 1, New Orleans.

McCafferty, W.P. and T.-Q. Wang. 2000. Phylogenetic systematics of the major lineages of Pannote mayflies (Ephemeroptera: Pannota) Transactions of the American Entomological Society 126:9-101.

McDunnough, J. 1931. New North American Caeninae with notes (Ephemeroptera). Canadian Entomologist 63:254-268.

Molineri, C. 1999a. Descripcion de una nueva especie de *Haplohyphes* Allen (Ephemeroptea: Leptohyphidae) y clave para separar los imagos machos del genero. Acta Zoologica Lilloana 45:29-32.

Molineri, C. 1999b. Revision of the genus *Tricorythopsis* (Ephemeroptera: Leptohyphidae) with the description of four new species. Aquatic Insects 21:285-300.

Molineri, C. 2001a. *Traverhyphes*: a new genus of Leptohyphidae for *Leptohyphes indicator* and related species. Spixiana 24:129-140.

Molineri, C. 2001b. A new genus of Leptohyphidae (Insecta: Ephemeroptera). Pages 337 – 345. *In:* E. Domínguez, ed., Trends in research in Ephemeroptera and Plecoptera. Kluwer Academic/Plenum Publishers, New York.

Molineri, C. 2001c. El género *Tricorythopsis* (Ephemeroptera: Leptohyphidae): nuevas combinaciones y descripción de nuevas especies y estadios. Revista de la Sociedad Entomologica Argentina 60:217-238.

Molineri, C. 2001d. A new species of *Tricorythodes* (Ephemeroptera: Leptohyphidae) from Argentina with biological notes. Revista de la Sociedad Entomologica Argentina 60:61-66.

Molineri, C. 2002. Cladistic analysis of the South American species of *Tricorythodes* (Ephemeroptera: Leptohyphidae) with the description of new species and stages. Aquatic Insects 24:273-308.

Molineri, C. 2003a. *Haplohyphes* (Ephemeroptera: Leptohyphidae), new species and stage descriptions with a key to separate the species of the genus. Zootaxa 263:1-11.

Molineri, C. 2003b. Revision of the South American species of *Leptohyphes* Eaton (Ephemeroptera: Leptohyphidae) with a key to nymphs. Studies on Neotropical Fauna and Environment 38:47-70.

Molineri, C. 2004. Phylogeny of the *Allenhyphes*-*Traverhyphes* group (Ephemeroptera: Leptohyphidae), with new subgenera, species and combinations. Tijdschrift voor Entomologie 147:197-220.

Molineri, C. 2005. *Leptohyphodes inanis* (Pictet) and *Tricorythodes ocellus* Allen and Roback (Ephemeroptera: Leptohyphidae): new stages and descriptions. Studies on Neotropical Fauna and Environment 40:247-254.

Molineri, C. 2006. Phylogeny of the mayfly family Leptohyphidae (Insecta: Ephemeroptera) in South America. Systematic Entomology 31:711-728.

Molineri, C. and E. Dominguez. 2003. Nymph and egg of *Melanemerella brasiliana* (Ephemeroptera: Ephemerelloidea: Melanemerellidae), with comments on its systematic position and the higher classification of Ephemerelloidea. Journal of the North American Benthological Society 22:263-275.

Molineri, C. and R.W. Flowers. 2001. Primera cita de *Allenhyphes* Hofmann Y Sartori, 1999 (Ephemeroptera: Leptohyphidae) para America continental. Entomotropica 16:61-62.

Molineri, C., J.G. Peters, and M.C. Zúñiga. 2001. A new family, Coryphoridae (Ephemeroptera: Ephemerelloidea), and description of the winged and egg stages of Coryphorus. Insecta Mundi 15:117-122.

Molineri, C. and M.C. Zúñiga. 2004. *Lumahyphes*, a new genus of Leptohyphidae (Ephemeroptera). Aquatic Insects 26:19-30.

Molineri, C. and M.C. Zúñiga. 2006. New species of Leptohyphidae (Insecta: Ephemeroptera) from Colombia with evidence of reproductive time segregation. Studies on the Neotropical Fauna 41:139-151.

Needham, J.G. and H.E. Murphy. 1924. Neotropical mayflies. Bulletin of the Lloyd Library Number 24, Entomological Series 4:1-79.

Needham, J.G., J.R. Traver, and Y.C. Hsu, eds. The biology of mayflies with a systematic account of North American species. Comstock Publishing Company, Ithaca, NY.

Newell, R.T. and G.W. Minshall. 1978. Life history of a multivoltine mayfly, *Tricorythodes minutus*: an example of the effect of temperature on the life cycle.Annals of the Entomological Society of America 71:876-881.

Pescador, M.L. and W.L. Peters. 1980. Phylogenetic relationships and zoogeography of cool-adapted Leptophlebiidae (Ephemeroptera) in Southern South America. Pages 43-56. *In*: J.F. Flannagan and K.E. Marshall (eds). Advances in Ephemeroptera biology. Plenum Press, NY.

Peters, W.L. 1981. *Coryphorus aquilus*, a new genus and species of Tricorythidae from the Amazon Basin (Ephemeroptera). Aquatic Insects 3:209-217.

Peters, W.L. and J.G. Peters. 1993. Status changes in Leptohyphidae and Tricorythidae (Ephemeroptera). Aquatic Insects 15:45-48.

Pictet FJ. 1843-1845. Histoire naturelle générale et particulière des insectes névroptères. Famille des éphémérines. Chez J. Kessmann et Ab. Cherbuliz, Geneva. 300 pp, xix + 47 pl.

Platnick, N.I. and Nelson, G. 1978. A method of analysis for historical biogeography. Systematic Zoology 27:1-16.

Randolph, R.P. and W.P. McCafferty. 1998. Diversity and distribution of the mayflies (Ephemeroptera) of Illinois, Indiana, Kentucky, Michigan, Ohio, and Wisconsin. Ohio Biological Survey Bulletin (new series) 13:1-188.

Randolph, R.P. and W.P. McCafferty. 2000. Mexican mayflies: inventory and additions (Ephemeroptera). Annales de Limnologie-International Journal of Limnology 36:113-121.

Raven, P. H. and D. I. Axelrod. 1974. Angiosperm biogeography and past continental movements. Ann. Missouri Bot. Gard. 61: 539-673.

Roback, S.S. 1966. The Catherwood Foundation Peruvian-Amazon Expedition. VI - Ephemeroptera nymphs. Monographs of the Academy of Natural Sciences of Philadelphia 14:129-199.

Rosen, D.E. 1978. Vicariant patterns and historical explanation in biogeography. Systematic Zoology 27:159-188.

Ross, H.H. 1974. Biological systematics. Addison-Wesley, Reading, PA.

Salles, F.F. and C. Molineri. 2006. *Amanahyphes saguassu*, a new genus and species of Leptohyphidae (Ephemeroptera: Ephemerelloidea) from northern Brazil. Aquatic Insects 28:1-12.

Savage, H.M. 1987. Biogeographic classification of the Neotropical Leptophlebiidae (Ephemeroptera) based upon geological centers of ancestral origin and ecology. Studies on Neotropical Fauna and Environment 22:199-222.

Savage, H.M., R.W. Flowers, and Porras-V W. 2005. Rediscovery of *Choroterpes atramentum* in Costa Rica, type species of *Tikuna* new genus (Ephemeroptera: Leptophlebiidae: Atalophlebiinae), and its role in the "Great American Interchange". Zootaxa 932:1-14.

Selander RB; Vaurie P. 1962. A gazetteer to accompany the "Insecta" volumes of the "Biologia Centrali-Americana". American Museum Novitates 2099:1-70.

Simpson, B.B. and J.L. Neff. 1985. Plants, their pollinating bees, and the Great American Interchange. Pages 427-453. *In:* F.G. Stehli and S.D. Webb, eds., The Great American Biotic Interchange. Plenum Press, NY.

Spieth, H.T. 1941. The North American Ephemeropteran types of the Rev. A. E. Eaton. Annals of the Entomological Society of America 34:87-98.

Swofford, D.L. 1990. PAUP: Phylogenetic analysis using parsimony, Version 3.0. Computer program distributed by the Illinois Natural History Survey, Champaign, IL.

Traver, J.R. 1943. New Venezuelan mayflies. Boletin de Entomologia Venezolan. 2:79-98.

Traver, J.R. 1944. Notes on Brazilian mayflies. Boletim do Museu Nacional (Rio de Janeiro), Nova Série, Zoologia 22:2-53

Traver, J.R. 1958. The subfamily Leptohyphinae (Ephemeroptera: Tricorythidae). Part I. Annals of the Entomological Society of America 51:491-503.

Traver, J.R. 1959. The subfamily Leptohyphinae. Part II: Five new species of *Tricorythodes* (Ephemeroptera, Tricorythidae). Proceedings of the Entomological Society of Washington 61:121-131.

Ulmer G. 1920a. Neue Ephemeropteren. Archiv füür Naturgeschichte (A)85(11):1-80.

Ulmer, G. 1920b. Über einige Ephemeropteren-Typen älterer Autoren. Archiv für Naturgeschichte 87:229-267.

Ulmer G. 1933. Aquatic insects of China. Article VI. Revised key to the genera of Ephemeroptera. Peking Natural History Bulletin 7:195-218.

Vanzolini, P.E. and W.R. Heyer. 1985. The American Herpetofauna and the Interchange. Pages 475-487. *In:* F.G. Stehli and S.D. Webb, eds., The Great American biotic interchange. Plenum Press, New York.

Vuilleumier, F. 1985. Fossil and recent Avifaunas and the Interamerican Interchange. Pages 287-401. *In:* F.G. Stehli and S.D. Webb, eds., The Great American biotic interchange. Plenum Press, New York.

Wallace, A.R. 1876. The geographic distribution of animals. 2 volumes, Macmillan, London.

Wang, T.Q., R.W. Sites, and W.P. McCafferty. 1998. Two new species of *Leptohyphes* (Ephemeroptera: Leptohyphidae) from Ecuador. Florida Entomologist 81:68-75.

Webb, S.D. 1997. The Great American Faunal Interchange. Pages 97-122. *In:* A.G. Coates, ed., Central America, a natural and cultural history. Edwards Brothers, Inc., Ann Arbor, MI.

Wiersema, N.A. and W.P. McCafferty. 2000. Generic revision of the North and Central American Leptohyphidae (Ephemeroptera: Pannota). Transactions of the American Entomological Society 126:337-371.

Wiersema, N.A., W.P. McCafferty, and D.E. Baumgardner. 2001. *Asioplax numinuh*, a new species of Ephemeroptera (Leptohyphidae) from Texas and Mexico. Entomological News 112:301-304.

Wiersema, N.A. and W.P. McCafferty. 2003. *Ableptemetes*: a new genus of Tricorythodinae (Ephemeroptera: Leptohyphidae) from Mexico and Central America. Entomological News 114:37-40.

Wiersema, N.A. and W.P. McCafferty. 2005. Contribution to the taxonomy of *Asioplax* (Ephemeroptera: Leptohyphidae: Tricorythodinae) in the New World. Entomological News 116:147-158.

APPENDIX A

FIGURES

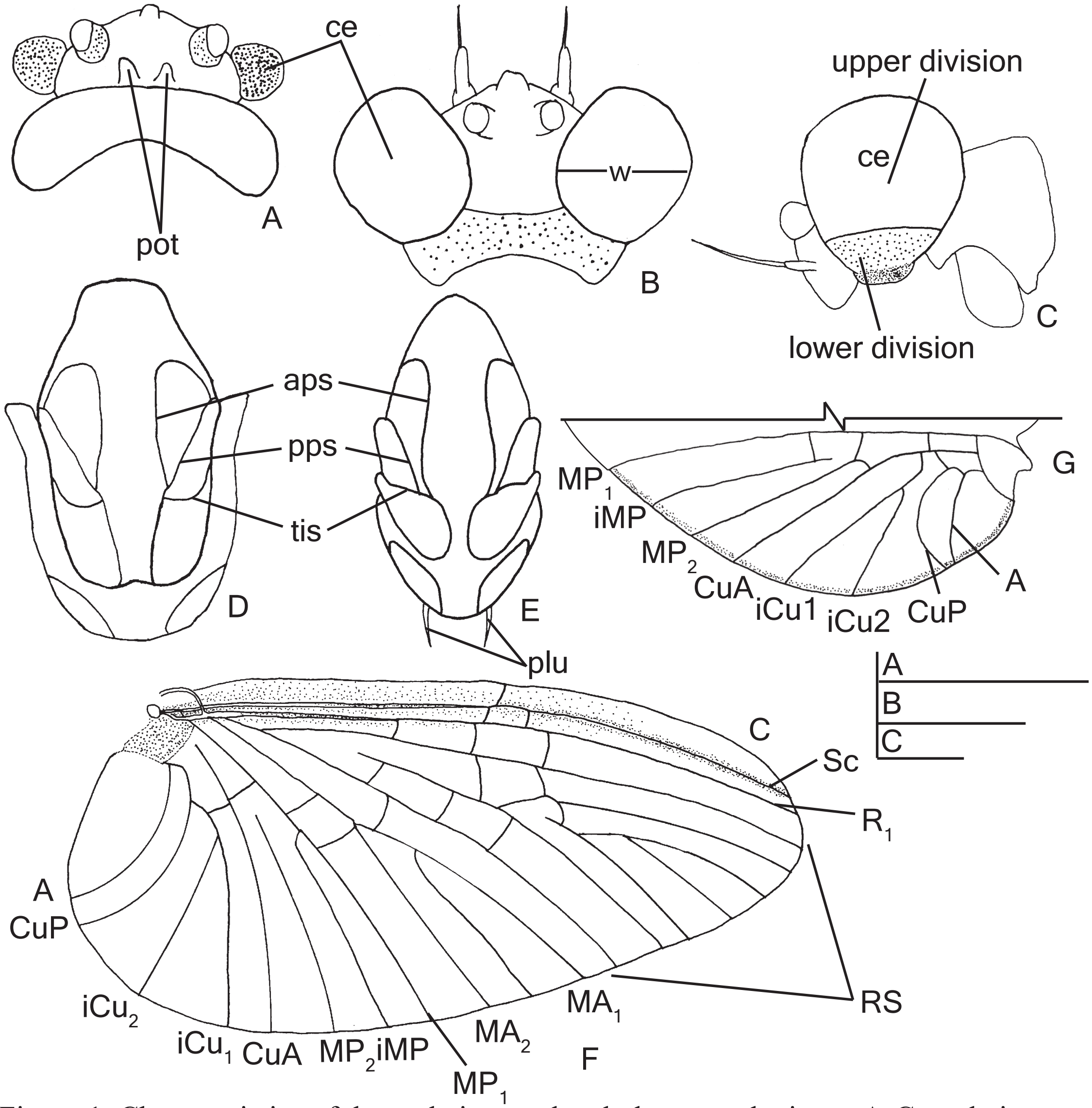


Figure 1. Characteristics of the male imago, head, thorax and wings. A-C, male imago head. A, *Tricorythodes* sp., compound eyes small, remote (dorsal) [scale bar B]. B, *Tricorythodes dimorphus,* compound eyes enlarged (dorsal) [B]. C, *Ephemerella* sp, compound eyes dioptic (lateral) [B]. D-E, male imago, mesonotum (dorsal). D, *Tricorythodes* sp. [B]. E, *Allenhyphes* sp. [B]. F, *Tricorythodes* sp., male imago, forewing [A]. G, *Haplohyphes mithras,* cubial - anal region, forewing [C]. aps = anterior parapsidal suture; ce = compound eye; cp = costal projection; plu = plumidium; pot = paired occipital tubercules; pps = posterior parapsidal suture; tis = transverse interscutal suture; w = width across eye. Abbreviations of veins: C = costa; Sc = subcosta; R_1 = radius 1; RS = radial sector; MA_1 = medius anterior 1; MA_2 = medius anterior 2; MP_1 = medius posterior 1; iMP = intercalary medius posterior; MP_2 = medius posterior 2; CuA = cubitus anterior; iCu_1 = cubital intercalary 1; iCu_2 = cubital intercalary 2; CuP = cubitus posterior; A = anal. Scale bars (mm): A, B = 1; C = 0.5.

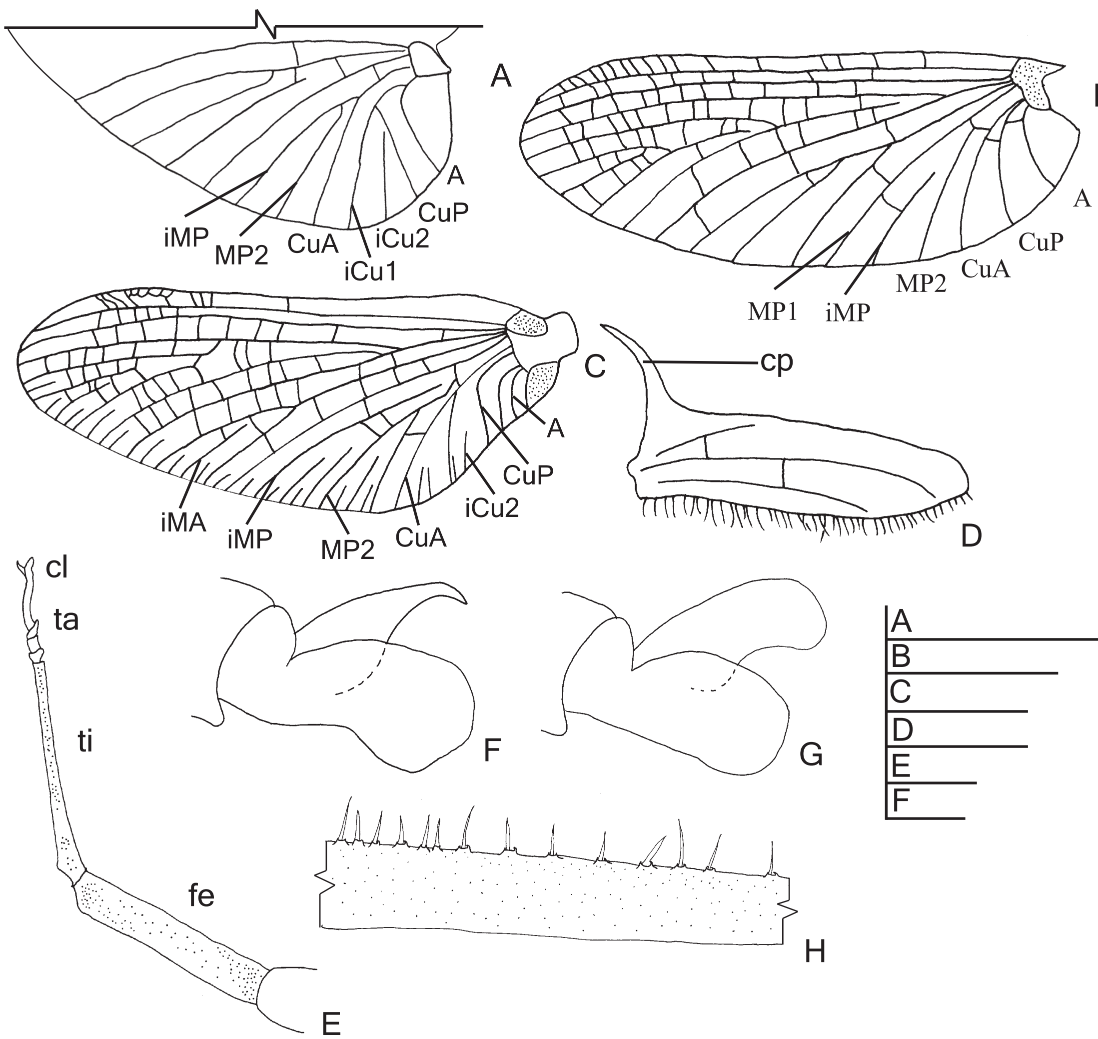


Figure 2. Characteristics of male imago, wings and legs. A, *Tricorythopsis undulatus,* cubital - anal region, forewing [scale bar E]. B - C, forewing. B, *Macunahyphes australis* [E]. C, *Drunella lata* [F]. D, composite leptohyphid hindwing [A]. E, *Leptohyphes* sp., male imago, mesoleg [C]. F-G, male imago, propretarsal claws. F, *Ephemerella* sp., claws dissimilar (one sharp, one blunt) [B]. G, *Leptohyphes* sp., claws similar (both blunt) [B]. H, *Letohyphes* sp., male imago protibia (ventrolateral) [D]. cl = claw; fe = femur; ta = tarsi; ti = tibia. Abbreviations of veins: MP_1 = medius posterior 1; iMP = intercalar medius posterior; MP_2 = medius posterior 2; CuA = cubitus anterior; iCu_1 = cubital intercalary 1; iCu_2 = cubital intercalary 2; CuP = cubitus posterior; A = anal. Scale bars (mm): A, C, G = 1.0; B, D = 0.1; E = 0.5; D = 1.0.

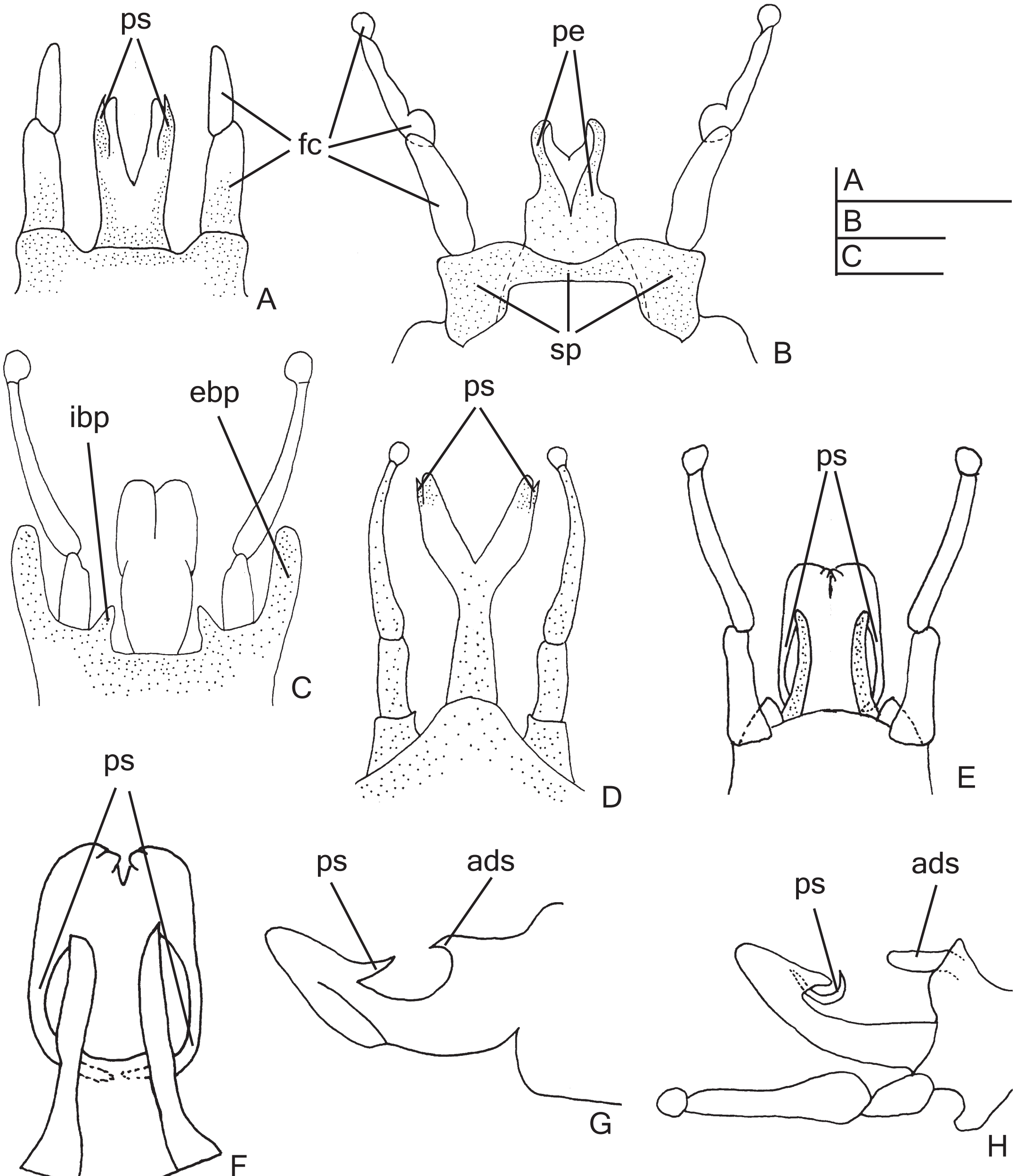
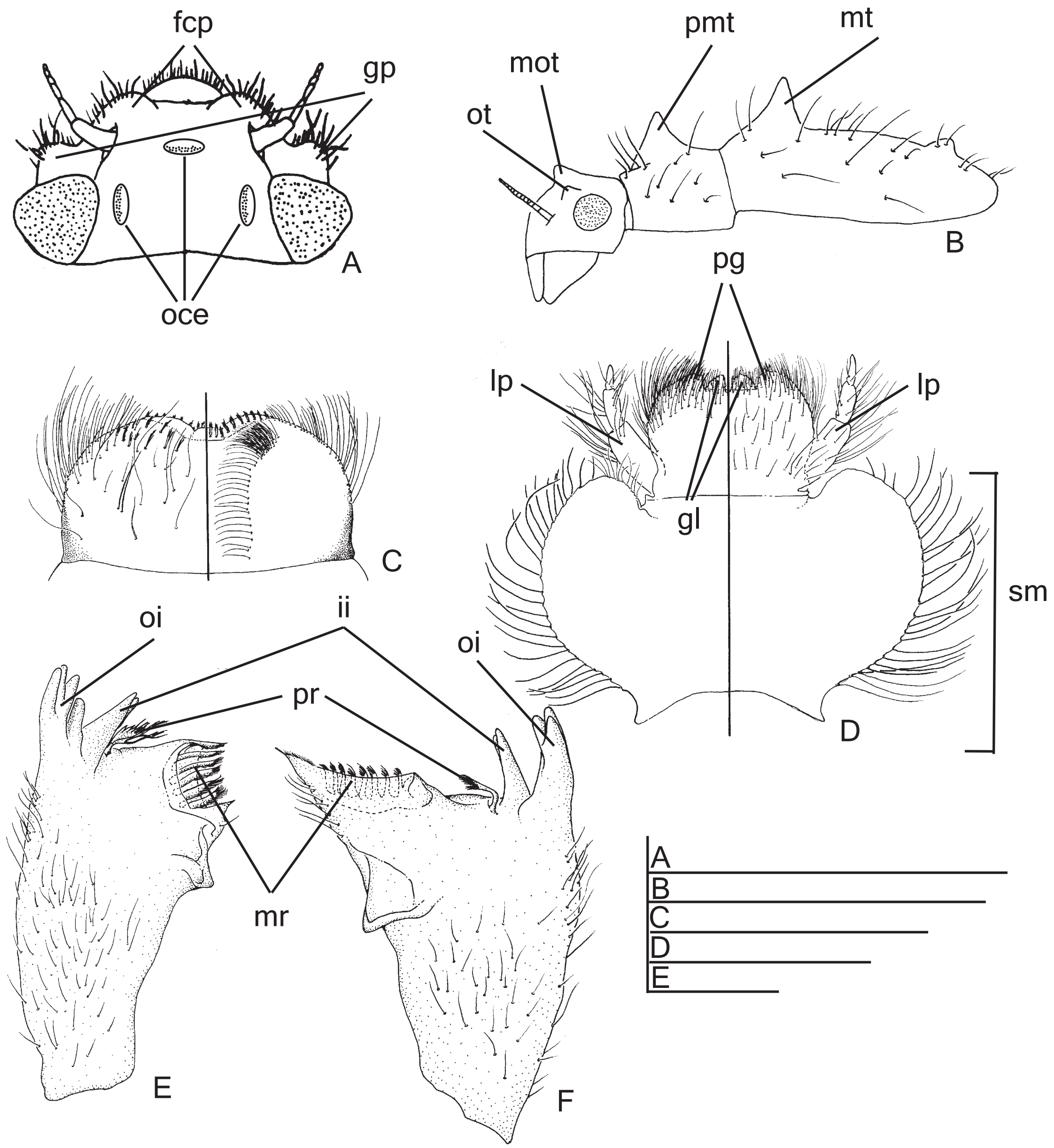


Figure 3. Male imago, genitalia and penes. A-E, male imago, genitalia (ventral). A, *Haplohyphes aquiloius* [scale bar B]. B, *Tricorythodes serratus* [C]. C, *Traverhyphes indicator* [C]. D, *Leptohyphes zalope* [B]. E, *Lumayphs guacra* [B]. F-H, male imago, penes. F, *Lumahyphes guacra* (ventral) [A]. G, *Traverhyphs nanus* (lateral) [A]. H, *Traverhyphes edmundsi* (lateral)[A]. ads = accessory dorsal structure; ebp = external basal projection; fc = forceps; ibp = internal basal projection; pe = penes; ps = penal spines; sp = styliger plate. Scale bars = 1 mm.



Figures 4. Characteristics of larval head, thorax, and mouthparts. A, *Tricorythodes primus*, larva, head casule (dorsal) [scale bar B]. B, *Tricorythodes bullus*, larva, head and thorax (lateral) [E]. C-F, *Tricorythodes* sp., larva, mouthparts. C, labrum (left: dorsal; right: ventral) [C]. D, labium (left: dorsal; right: ventral) [A]. E, left mandible (dorsal) [D]. F, right mandible (dorsal) [D]. fcp = frontoclypeal projections; g = glossae; gp = genial projections; ii = inner incisors; lp = labial palp; mt = mesonotal tubercle; mot = median occipital tubercle; mr = molar region; oce = ocelli; oi = outer incisors; ot = ocellular tubercles; sm = post mentum; pmt = pronotum medial tubercle; pg = paraglossae; pr = prostheca. Scale bars (mm): A = 0.25; B = 1.25; C = 0.25; D = 0.25; E = 1.0.

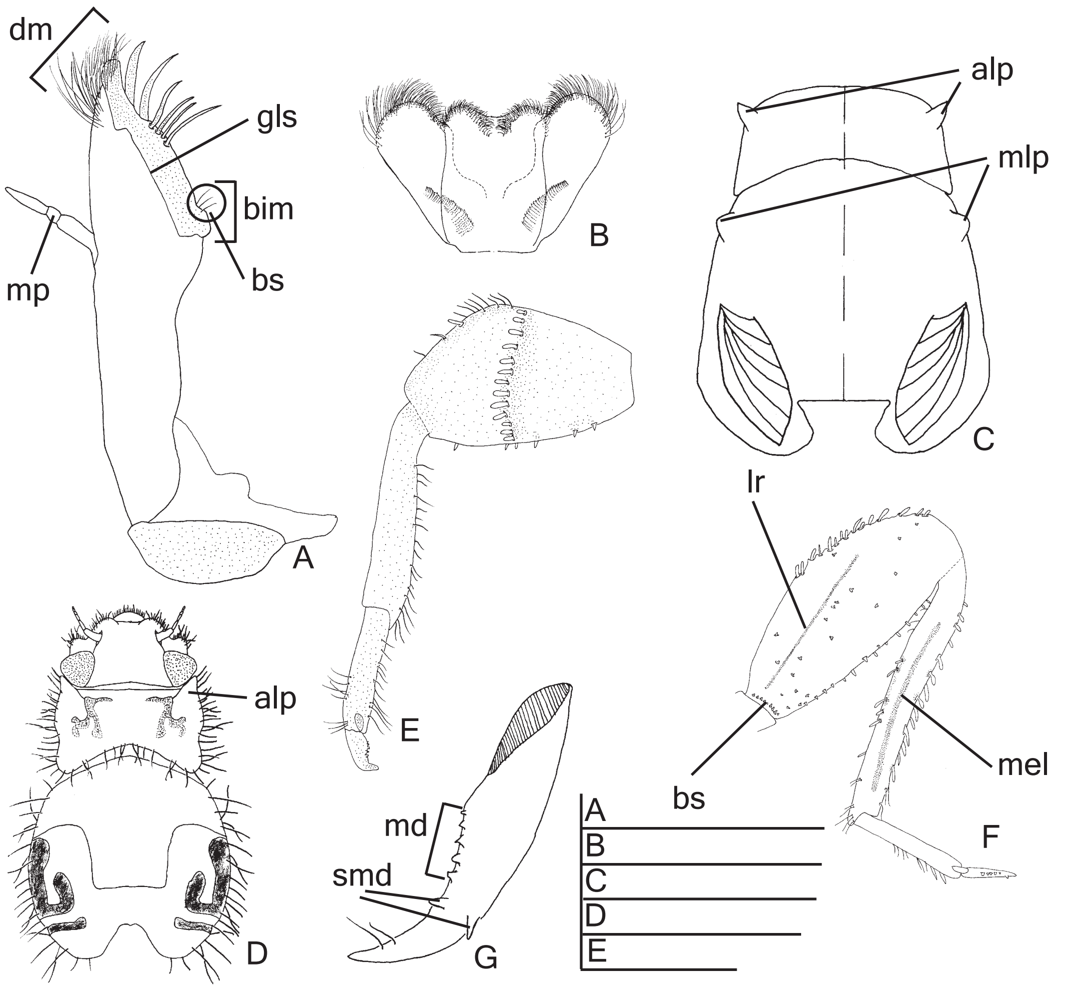


Figure 5. Characteristics of larval mouthparts, thorax, and legs. A, *Leptohyphes mandibulus*, maxilla (dorsal) [scale bar A]. B, *Tricorythodes* sp., hypopharynx (dorsal) [B]. C, *Tricorythodes serratus*, larva, pro- and mesonotum (dorsal) [C]. D, *Tricorythodes primus*, larva, head and thorax (dorsal) [C]. E, *Leptohyphes ferruginus*, larva, proleg (dorsal) [E]. F, *Leptohyphes lestes*, larva, metaleg (dorsal) [E]. G, *Tricorythodes isabelia*, larva, claw (dorsolateral) [D]. alp = anterolateral projections; bim = base of inner margin; bs = basal setae; dm = distal margin; gls = galea/lacinia suture; lr = longitudinal ridge; md = marginal denticles; mel = median elevated longitudinal ridge; mlp = meso-lateral projections; mp = maxillary palp; smd = submarginal denticles. Scale bars (mm): A = 0.5; B = 0.25; C = 1.0; D = 0.1; E = 0.5.

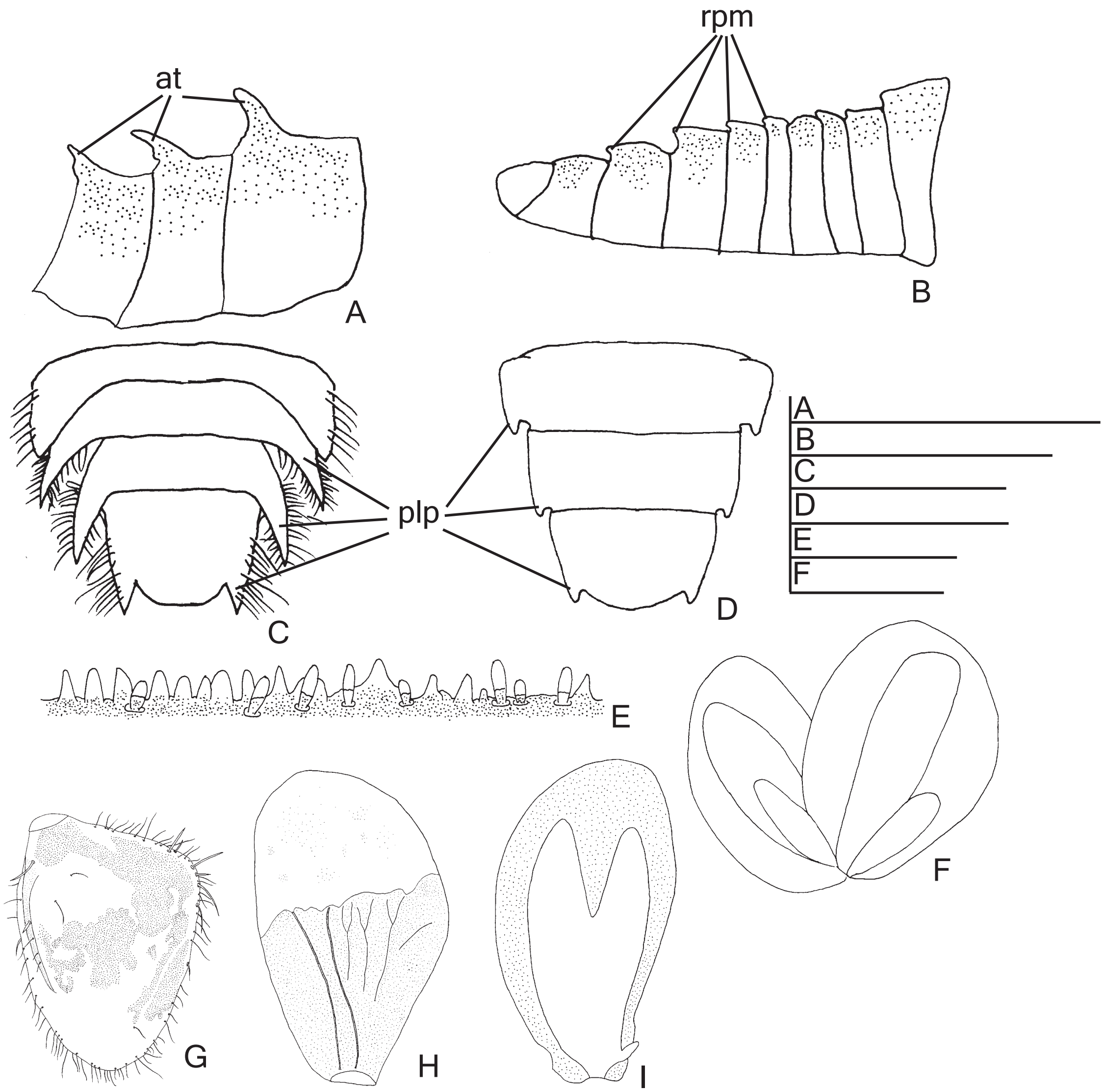


Figure 6. Abdominal characteristics of larvae. *Coryphorus aquilus*, pleurites 7-9 (lateral) [scale bar A]. B, T*ricorythodes melanobranchus*, plurites 1-10 (lateral) [C]. C, *Tricorythodes dolani*, tergites 6-9 (ventral) [F]. D - E, *Leptohyphes zalope*. D, abdominal tergites 7-9 (ventral) [F]. E, posterior margin abdominal terga 6 (dorsal) [B]. F, *Leptohyphes mandibulus*, abdominal gill 5 (dorsal) [E]. G, *Tricorythodes kirki*, abdominal gill 2 (dorsal) [E]. H, *Leptohyphes mandibulus*, gill 2 (dorsal) [D]. I, *Leptohyphes zalope*, gill 2 (ventral) [E]. at = abdominal tubercles; plp = posterior lateral projections; rpm = raised posterior margin. Scale bars (mm): A, C, E = 1.0; B = 0.05; D = 0.2; F = 0.5.

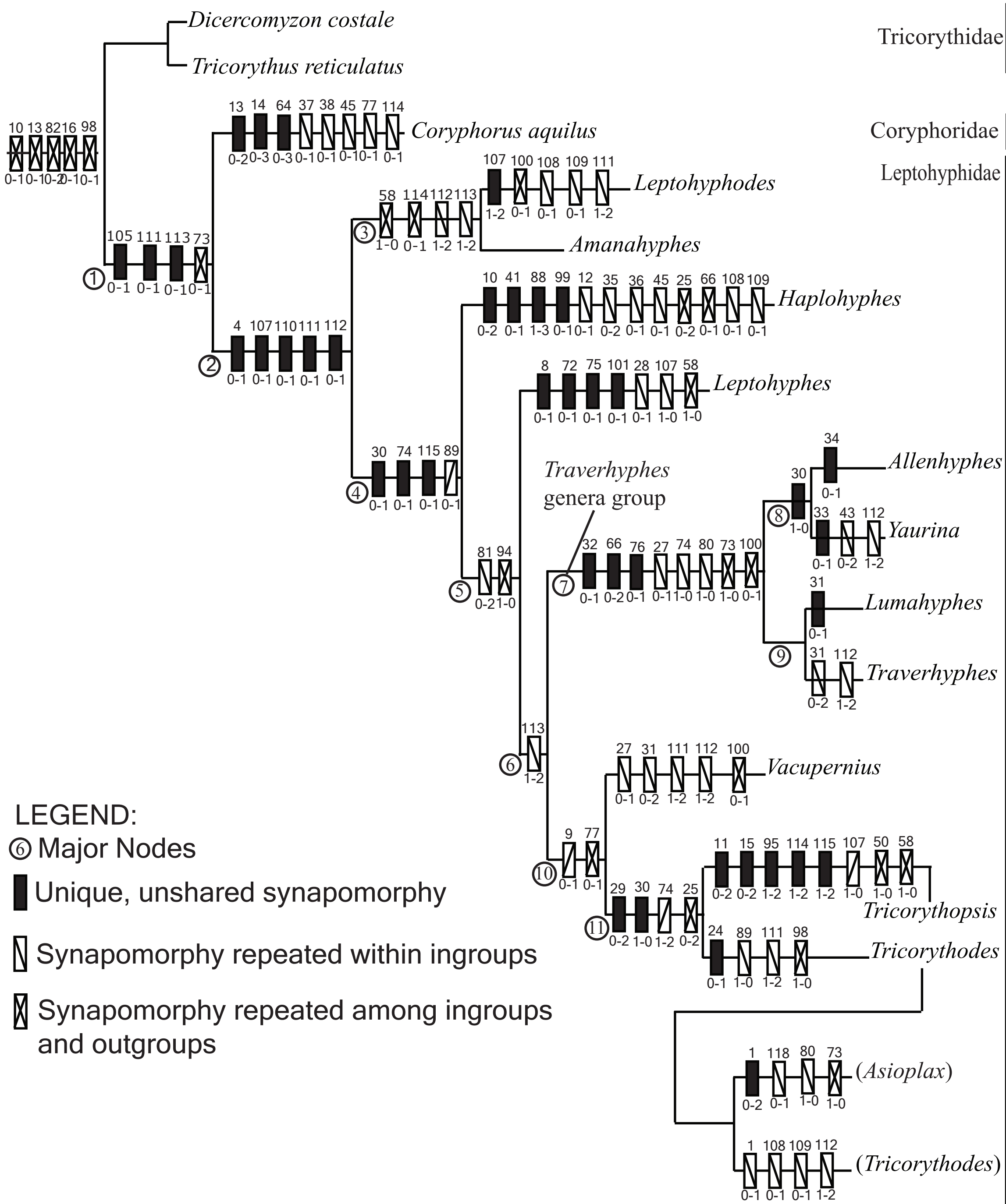


Figure 7. Final cladogram resulting from the parasomony analysis with species collapsed to monophyletic genera and subgenera. Numbers above boxes are character numbers. Only synapomorphic characters displayed. Numbers below boxes are character state transformations from the pleismorphic (left) to the derived (right) condition.

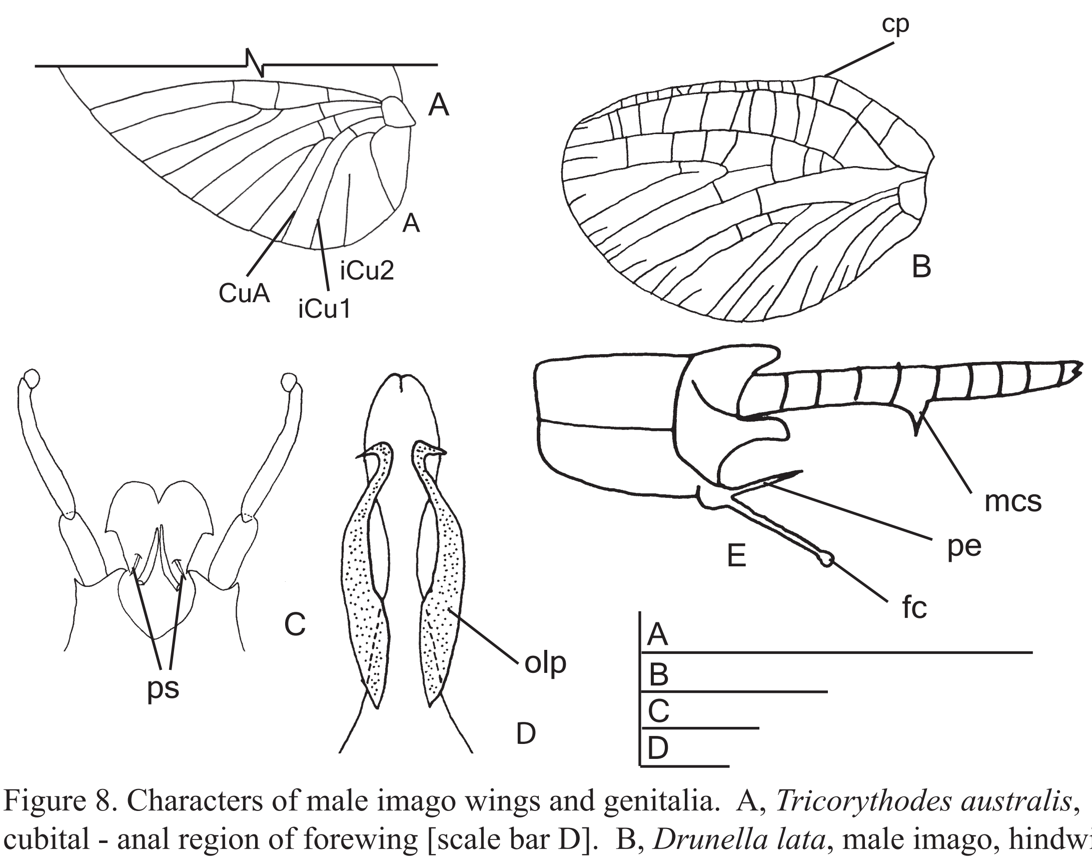


Figure 8. Characters of male imago wings and genitalia. A, *Tricorythodes australis*, cubital - anal region of forewing [scale bar D]. B, *Drunella lata*, male imago, hindwing [B]. C, *Vacuperinus packeri*, male imago, genitalia (ventral) [C]. D, *Yaurina yuta*, male imago, penes (dorsal) [B]. E, *Allenhyphes vescus*, male imago, abdominal segments 9-10 (lateral) [A]. Abbreviations of veins: CuA = cubitus anterior; iCu_1 = cubital intercalary 1; iCu_2 = cubital intercalary 2; CuP = cubitus posterior; A = anal. cp = costal process; fc = forceps; mcs = medial caudal spine; olp = outer longitudinal process; ps = penal spines. Scale bars (mm): A = 0.5;B = 1.0; C = 1.0; D = 0.5 mm.

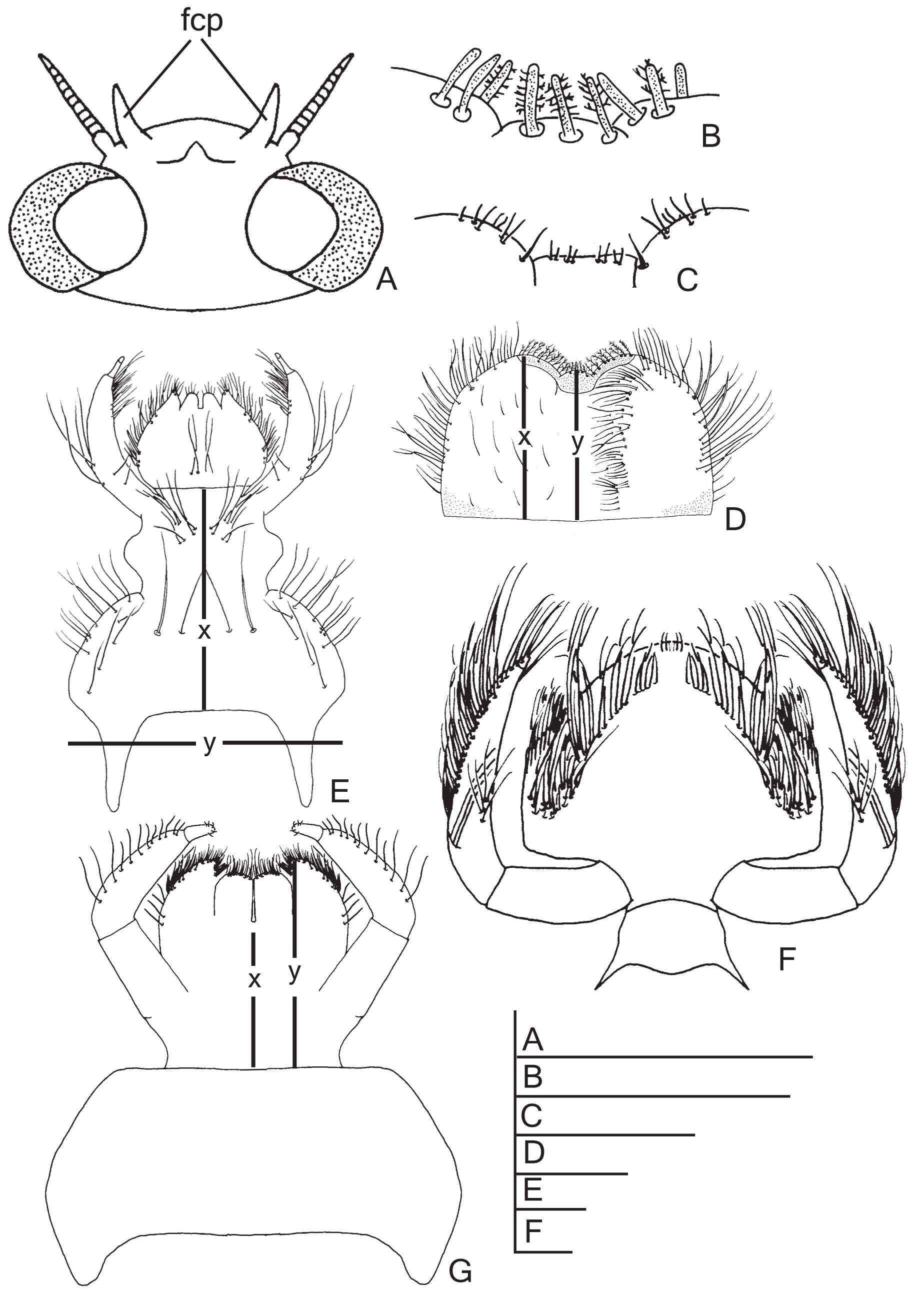


Figure 9. Larval head and mouthparts. A, *Drunella lata*, larval head (dorsal) [scale bar C]. B-C, labrum, anterior margin. B, *Tricorythodes fictus* (dorsal) [B]. C, *Leptohyphes ferruginus* (dorsal) [B]. D, *Tricorythodes kirki*, labrum (left ventral: right dorsal) [A]. E-G, labium (dorsal). E, *Haplohyphes aquilonius*. F, *Tricorythus reticulatus*. G, *Ephemerellina barnardi*. Scale bars (mm): A = 0.25; B = 0.1; C = 1.0; D = 0.5; E = 1.0; F = 0.1.

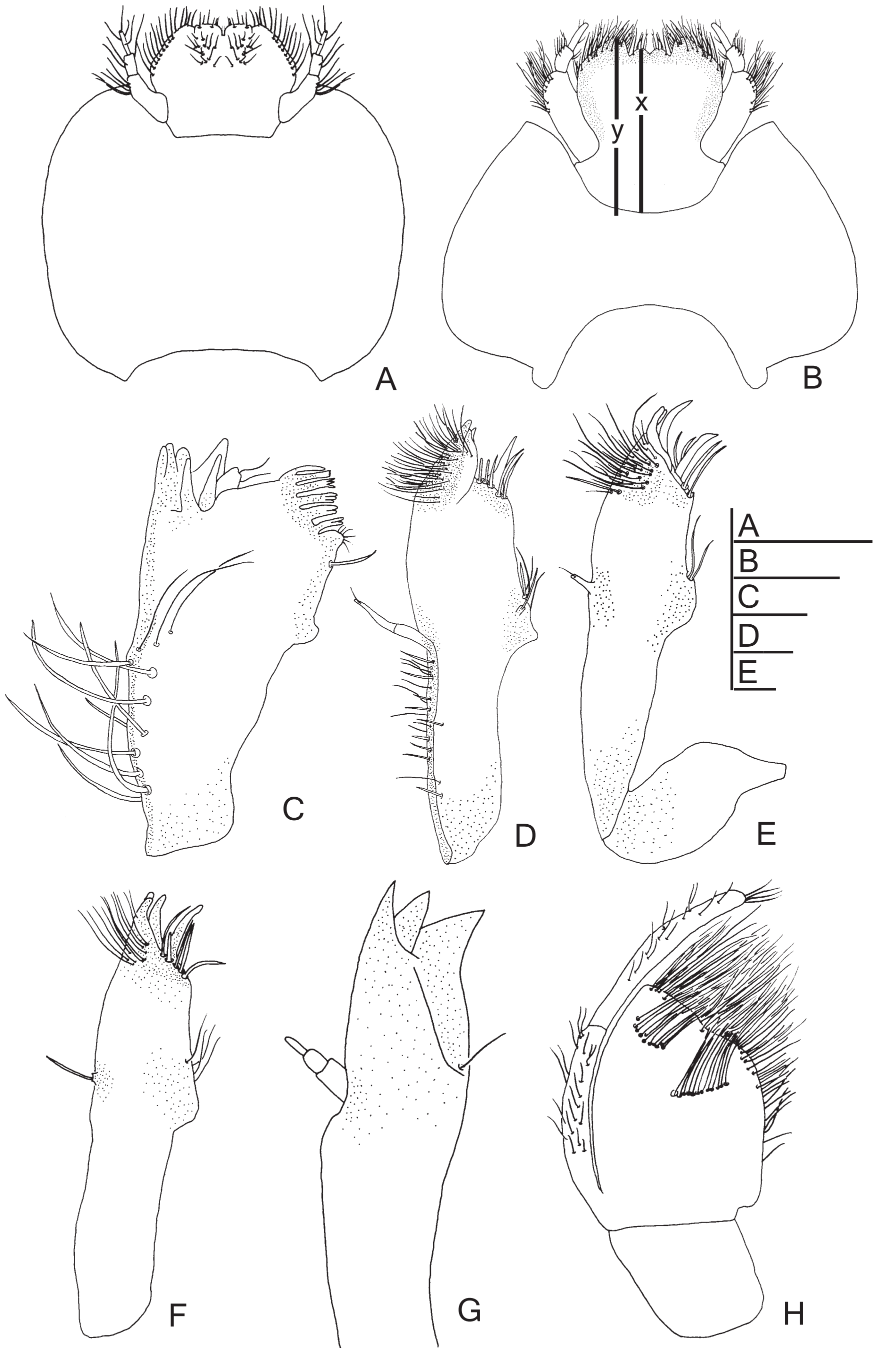


Figure 10. Larval mouthparts (dorsal view). A-B, labium. A, *Yaurina mota* [scale bar C]. B, *Leptohyphes cornutus* [D]. C, *Tricorythodes primus*, left mandible [A]. D-H, maxillae. D, *Tricorythodes explicatus* [C]. E, *Tricorythodes primus* [C]. F, *Tricorythodes numinuh* [B]. G, *Leptohyphes tuberculatus* [D]. H, *Tricorythus reticulatus* [E]. Scale bars (mm): A = 1.0; B, C, E = 0.1; D = 0.2.

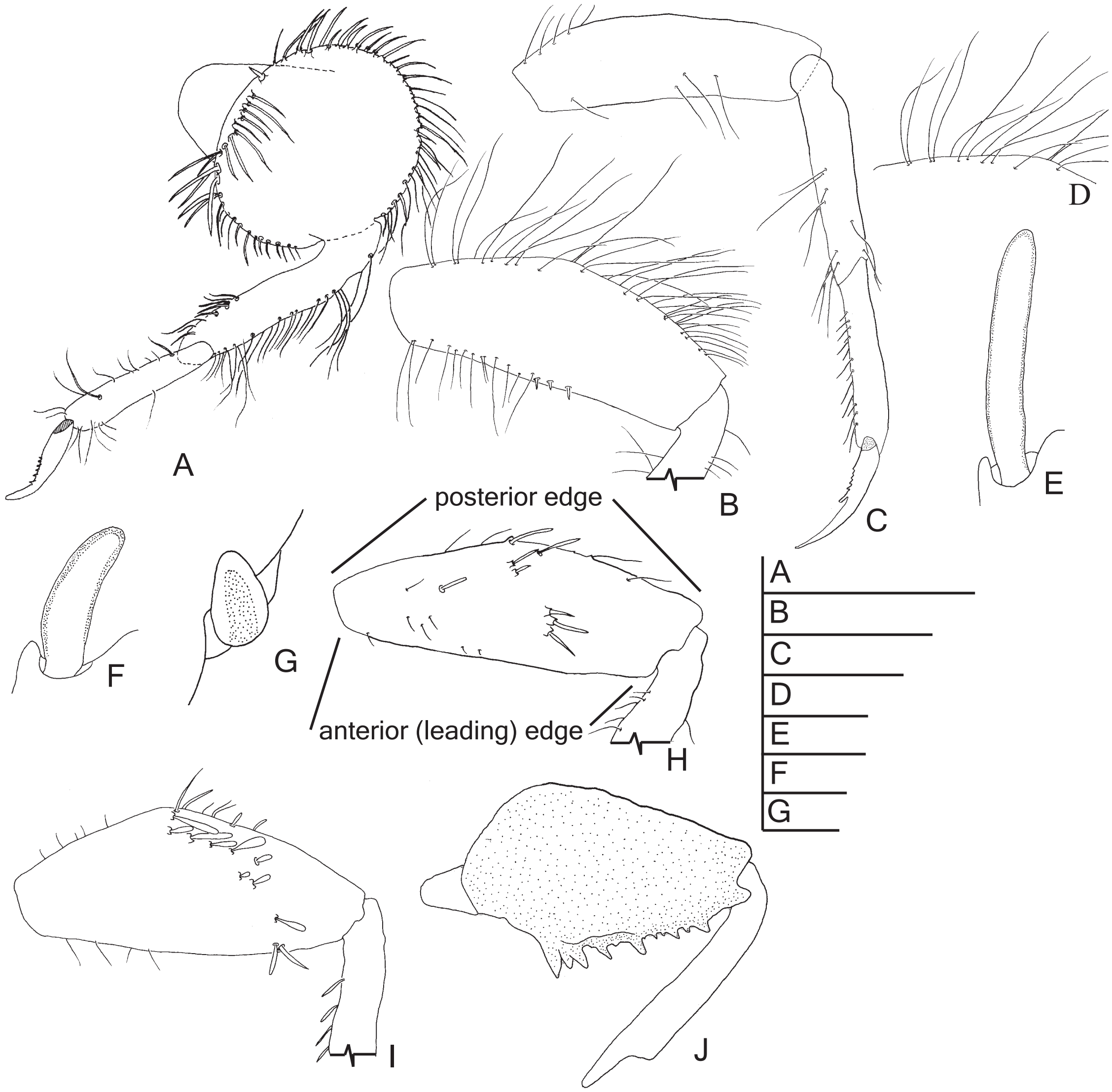


Figure 11. Characteristics of larval legs. A, *Asioplax isabelia,* proleg (dorsal) [D]. B, *Haplohyphes aquilonius,* profemur (dorsal) [G]. C, *Coryphorus aquilus*, proleg (dorsal) [E]. D-G, setal types. D, filiform [G]. E, elongate [C]. F, robust [C]. G, stout [A]. H-J, profemur (dorsal). H, *Tricorythodes undatus* [F]. I, *Traverhyphes nanus* [G]. J, *Drunella lata* [B]. Scale bars (mm): A = 0.05; B, D = 1.00; C = 0.05; E = 0.30; F = 0.20; G = 0.10.

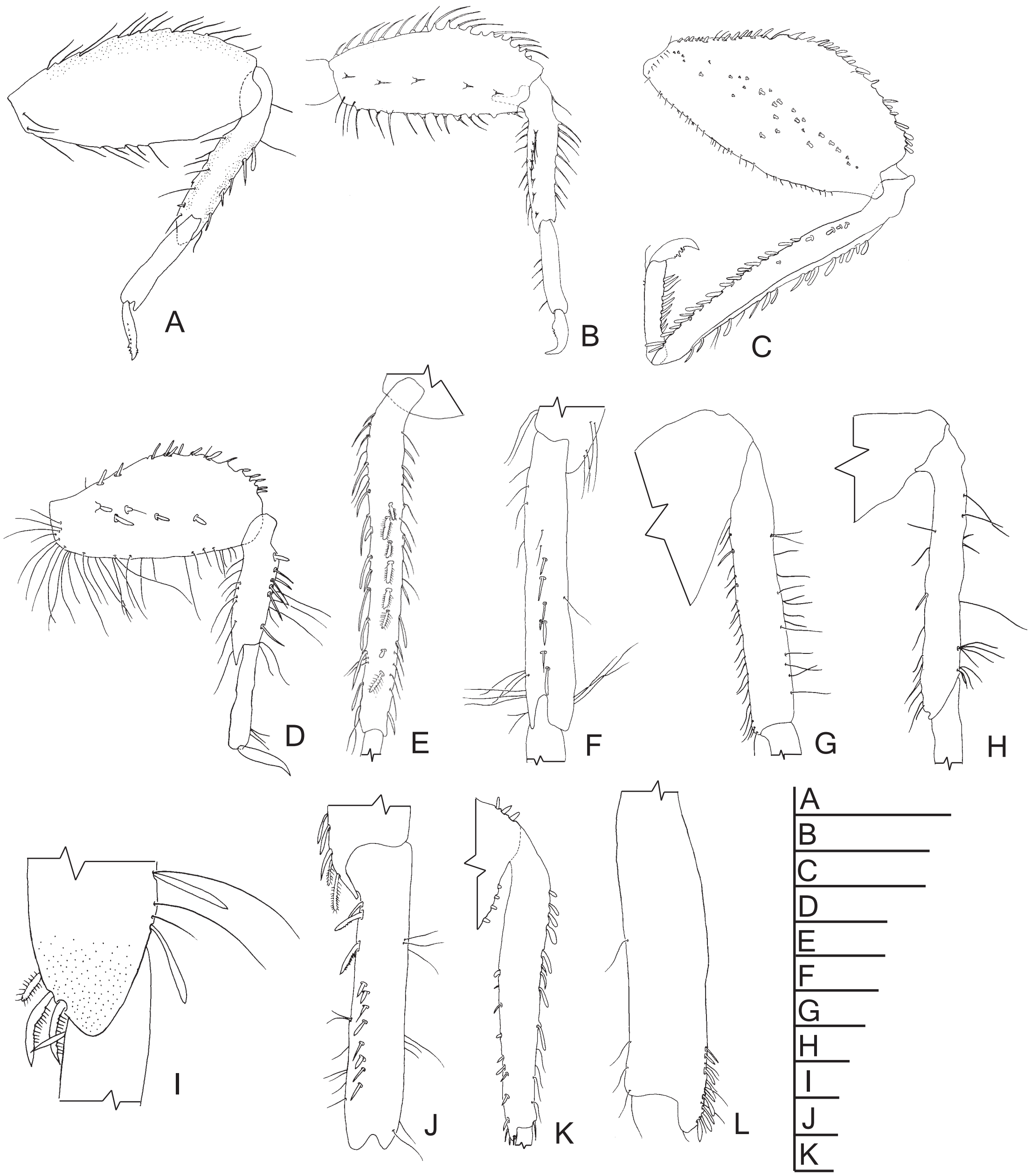


Figure 12. Larval legs. A - D, metalegs (dorsal). A, *Tricorythodes melanobranchus* [K]. B, *Tricorythodes serratus* [scale bar E]. C, *Leptohyphes zalope* [J]. D, *Tricorythodes dolani* [H]. E - F, metatibia (dorsal). E, *Allenhyphes vescus* [I]. F, *Traverhyphes edmundsi* [D]. G - I, protibia (dorsal). G, *Allenhyphes vescus* [I]. H, *Tricorythodes albilineatus* [B]. I, *Tricorythodes kirki,* distal end protibia [A]. J - K, metatarsi (dorsal). J, *Leptohyphes apache* [G]. K, *Leptohyphes plaumani* [C]. L, *Leptohyphes cornutus*, mesotibia (dorsal) [F]. Scale bars (mm): A, C, D, G, I, K = 0.1; B = 0.3; E = 0.4; F, H, J = 0.2.

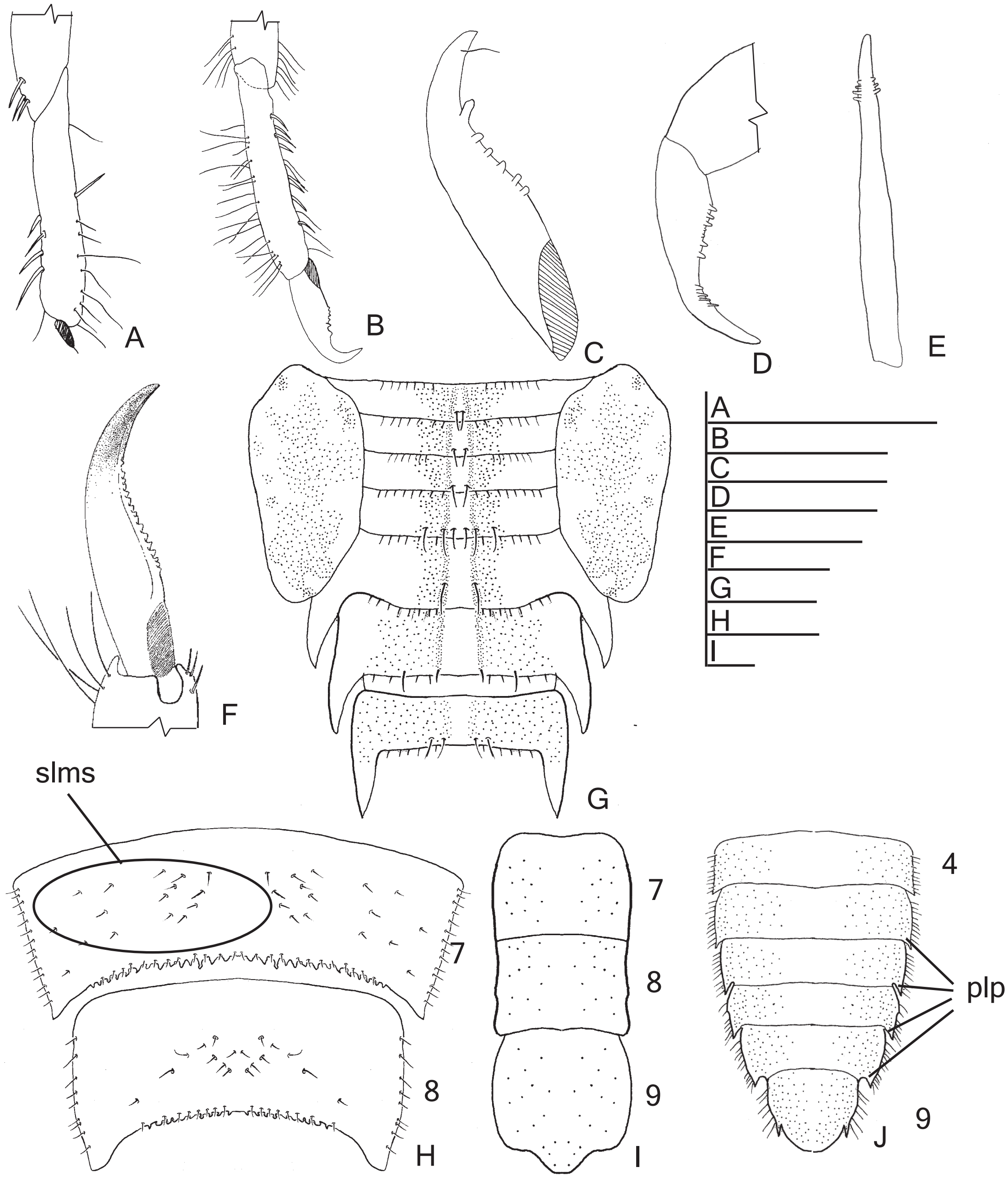


Figure 13. Features of larval legs, claws and abdomen. A-B, metatarsus (ventrolateral). A, *Tricorythodes kirki* [scale bar F]. B, *Tricorythosis undatus* [I]. C-F, proclaws. C, *Leptohyphes lestes* (ventrolateral) [E]. D, *Yaurina mota* (lateral) [B]. E, *Haplohyphes aquilonus* (ventral) [G]. F, *Tricorythodes fictus* (ventrolateral) [E]. G-J, abdomen. G, *Tricorythodes dolani*, abdominal tergites 3-9 (dorsal) [C]. H, *Leptohyphes zalope*, tergites 7-8 (dorsal) [A]. I, *Haplohyphes furtiva*, sternites 7-9 (ventral) [D]. J, *Drunella lata*, abdominal sternites 4-9 (dorsal) [H]. plp = posterolateral projections; slms = sublateral marginal setae. Scale bars (mm): A = 0.35; B, E, G, I = 0.1; C, H = 0.5; D = 1.0mm; F = 0.2.

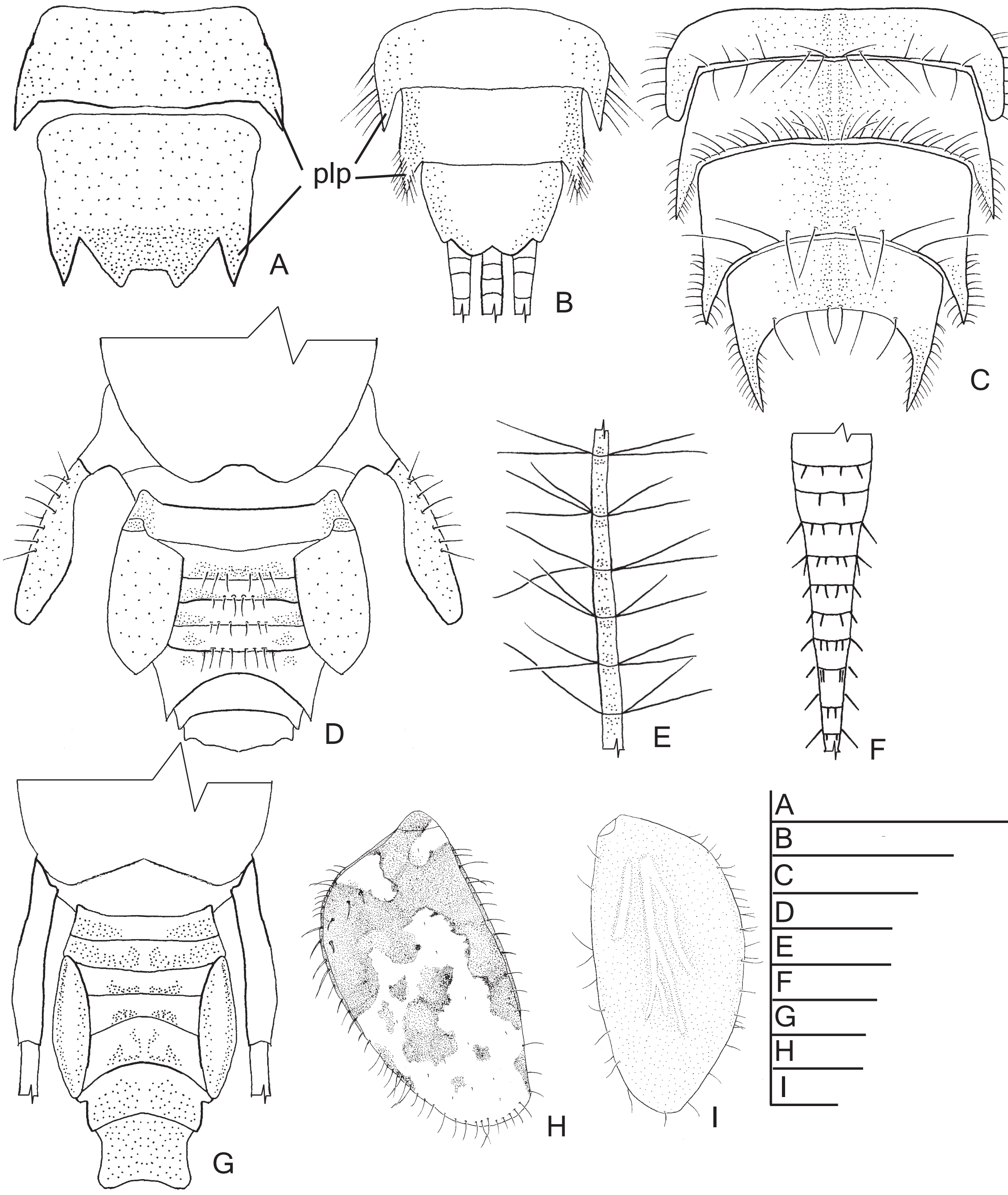


Figure 14. Characterisitcs of larval abdomens. A, *Tricorythopsis undulatus*, abdominal sternites 8-9 (ventral) [E]. B, *Tricorythodes notatus*, abdominal sternites 7-9 (ventral) [D]. C, *Tricorythodes fictus*, abdominal tergites 6-9 (dorsal) [C]. D, *Tricorythodes notatus*, abdominal tergites 1-9 (dorsal) [H]. E, *Tricorythodes undatus*, median caudal filament [G]. F, *Tricorythopsis undulatus*, right cercus [A]. G, *Haplohyphes furtiva*, abdominal tergites 1-7 (dorsal) [F]. H-I, abdominal gill 2 (dorsal). H, *Tricorythodes serratus* [B]. I, *Allenhyphes vescus* [I]. plp = posterolateral projections. Scale bars (mm): A, C, D, F, H = 0.5; B = 0.3; E, G = 0.25; I = 0.2.

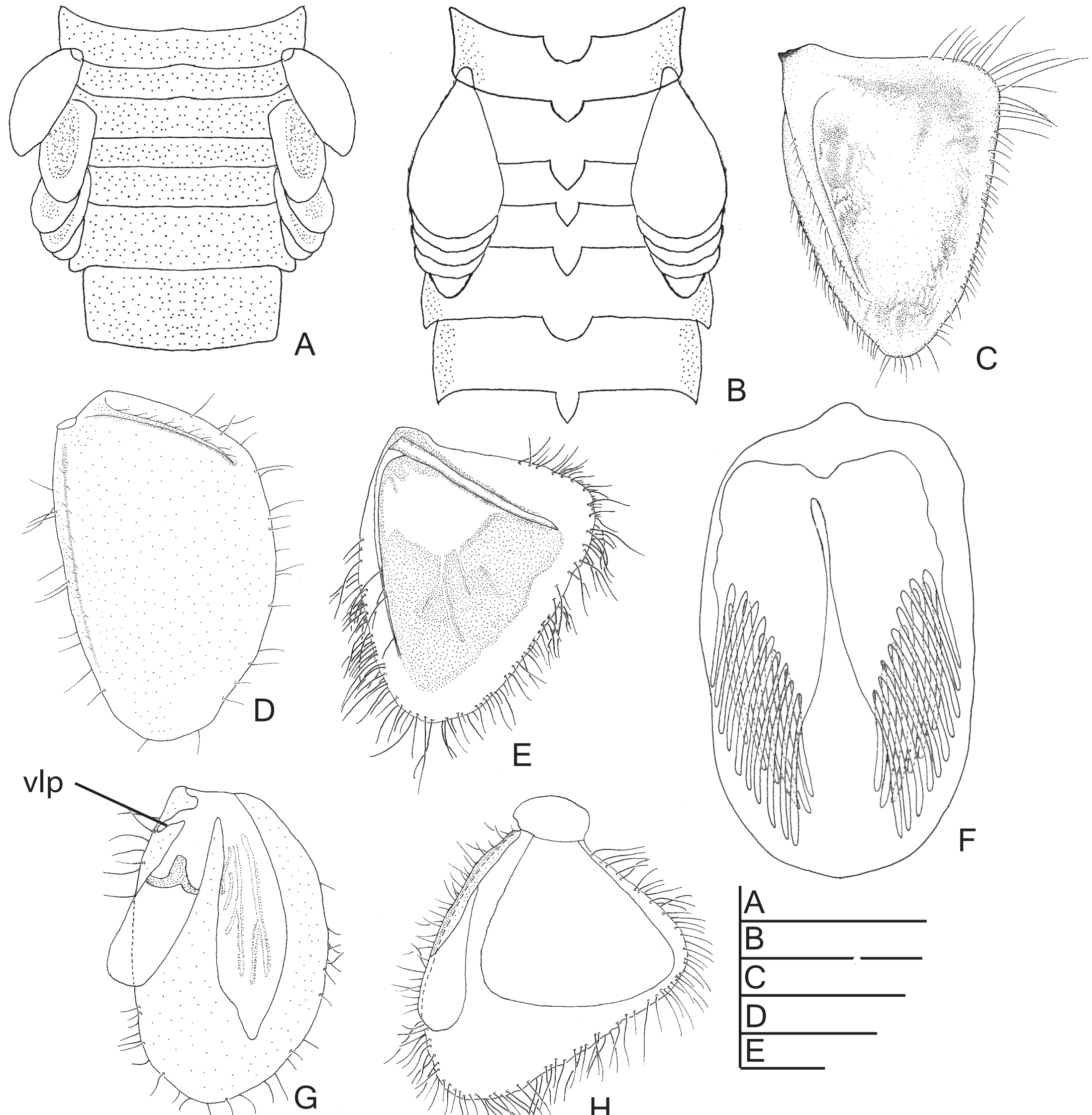


Figure 15. Characteristics of abdominal gills. A, *Tricorythus reticulatus*, abdominal tergites 2-8 (dorsal) [scale bar A]. B, *Ephemerellina barnardi*, abdominal tergites 2-7 (dorsal) [C]. C-H, abdominal gill 2. C, *Tricorythodes fictus* (dorsal) [D]. D, *Traverhyphes edmundsi* (dorsal) [E]. E, *Tricorythodes explicatus* (dorsal) [D]. F, *Tricorythus reticulatus* (ventral) [B]. G, *Leptohyphes apache* (ventral) [C]. H, *Tricorythodes explicatus* (ventral) [D]. vlp = ventrolateral projection. Scale bars (mm): A = 1.0; B, D = 0.3; C, E = 0.5; F = 0.2.

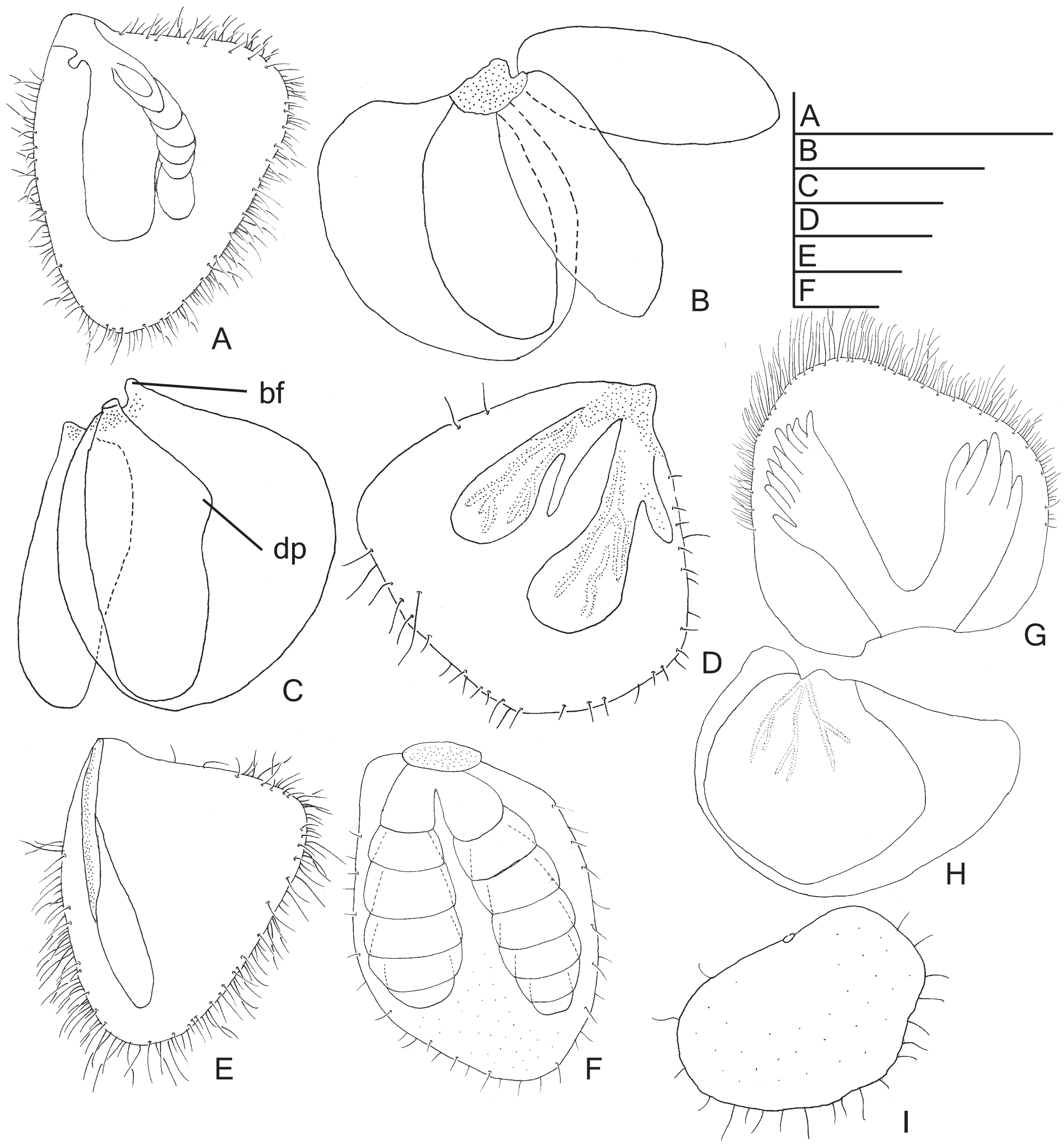


Figure 16. Abdominal gills. A, *Leptohyphodes inanis*, abdominal gill 2 (ventral) [scale bar C]. B - C, abdominal gill 3 (dorsal). B, *Leptohyphes zalope* [B]. C, *Tricorythodes explicatus* [B]. D - E, abdominal gill 2 (ventral). D, *Amanahyphes saguassu* [A]. E, *Tricorythodes bullus* [C]. F, *Ephemerella excrucians*, abdominal gill 3 (ventral) [B]. G, *Coryphorus aquilus*, abdominal gill 4 (ventral) [E]. H, *Tricorythodes explicatus*, abdominal gill 6 [F]. I, *Leptohyphes apache*, abdominal gill 6 [D]. bf = basal flap; dp = dorsal projection. Scale bars (mm): A - F = 0.5 mm; G - I = 0.2mm.

Figure 17. The preferred cladogram resulting from the cladistic analysis of the data. This cladogram includes all outgroup and ingroup species used in the analysis, and is the basis for the cladogram given in Figure 8.

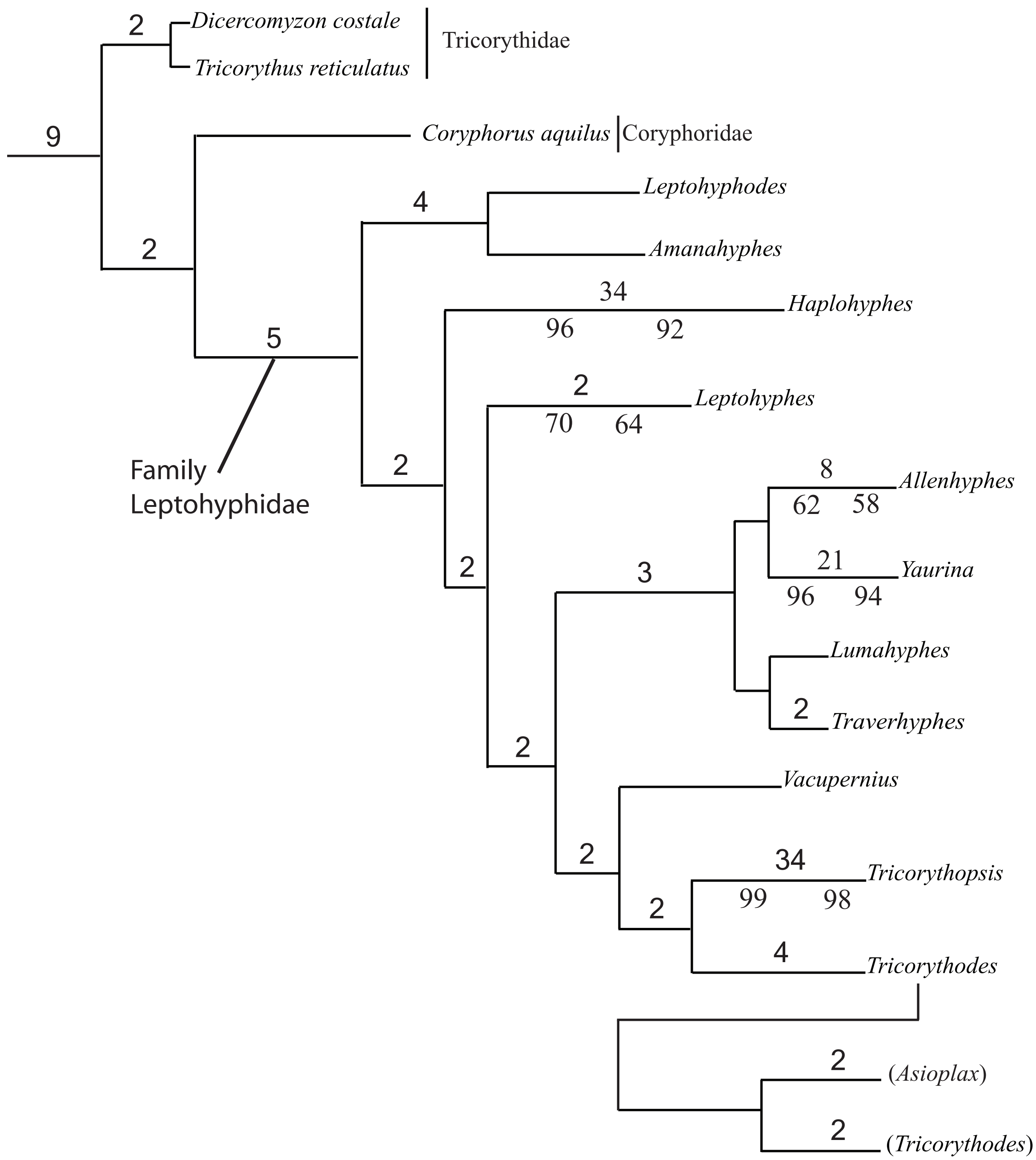


Figure 18. Bremer support, bootstrap, and jackknife values for selected nodes. Bremer support values are given above nodes. Only bootstrap (left) and jackknife (right) values greater than 50% are reported.

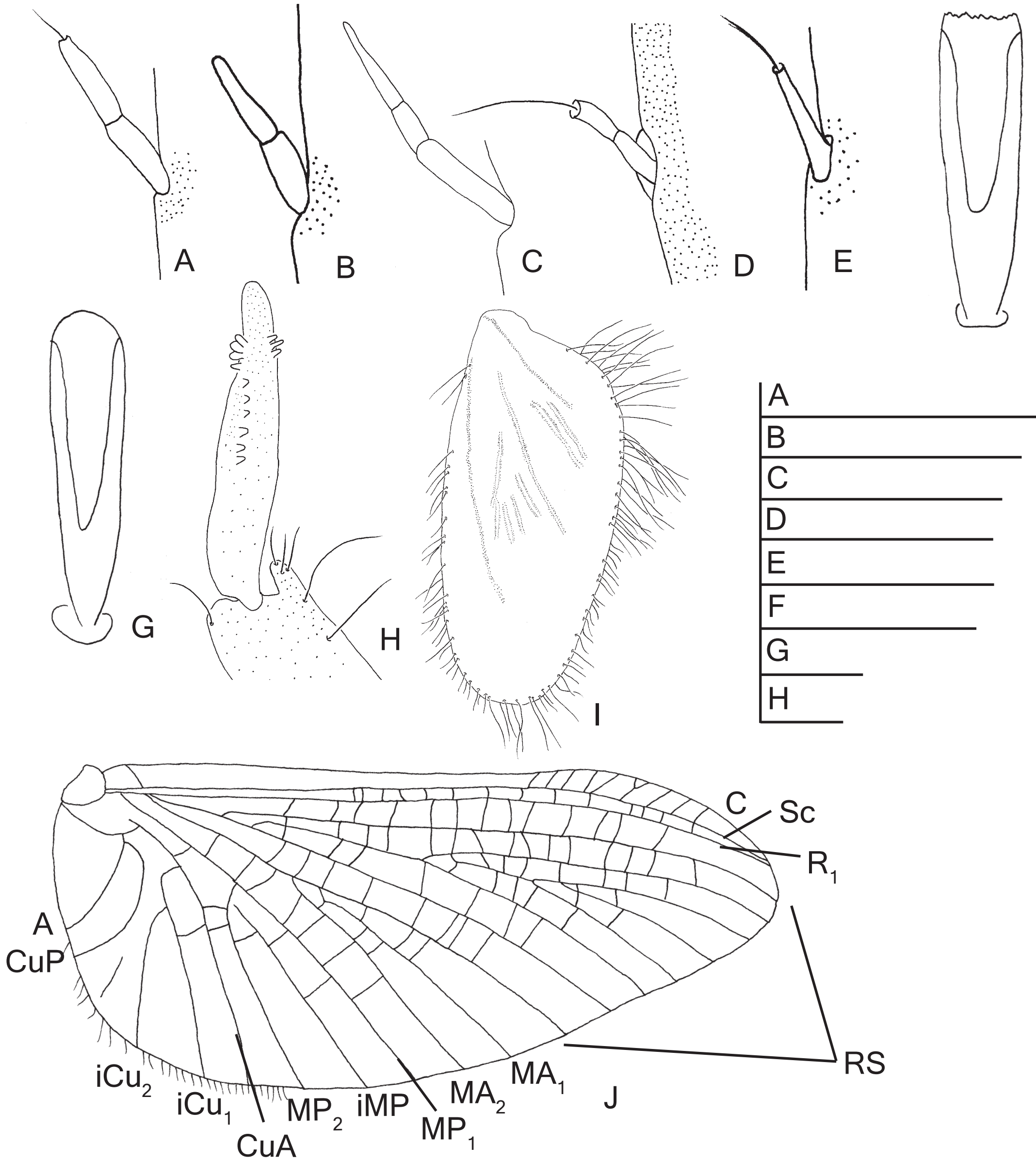


Figure 19. Features of maxillary palps, femora setae, gills, claw, and forewing. A - E, maxillary palp (dorsolateral). A, *Traverhyphes nanus* [scale bar A]. B, *Yaurina mota* [C]. C, *Vacupernius packeri* [G]. D, *Allenhyphes flinti* [C]. E, *Traverhyphes edmundsi* [E]. F-G, femoral spines. F, *Lumahyphes* sp. [D]. G, *Vacupernius packeri* [D]. H, *Tricorythodes* (*Asioplax*) *melanobranchus*, larva, proclaw [F].I, *Haplohyphes aquilonius*, operculate gill (dorsal) [H]. J, *Leptohyphes zalope*, male imago, forewing [B]. Abbreviations of veins: C = costa; Sc = subcosta; R_1 = radius 1; RS = radial sector; MA_1 = medius anterior 1; MA_2 = medius anterior 2; MP_1 = medius posterior 1; iMP = intercalar medius posterior; MP_2 = medius posterior 2; CuA = cubitus anterior; iCu_1 = cubital intercalary 1; iCu_2 = cubital intercalary 2; CuP = cubitus posterior. A = anal. Scale bars (mm): A, C, E, G = 0.05; B = 2.00; D = 0.50; F = 0.10; H = 0.30.

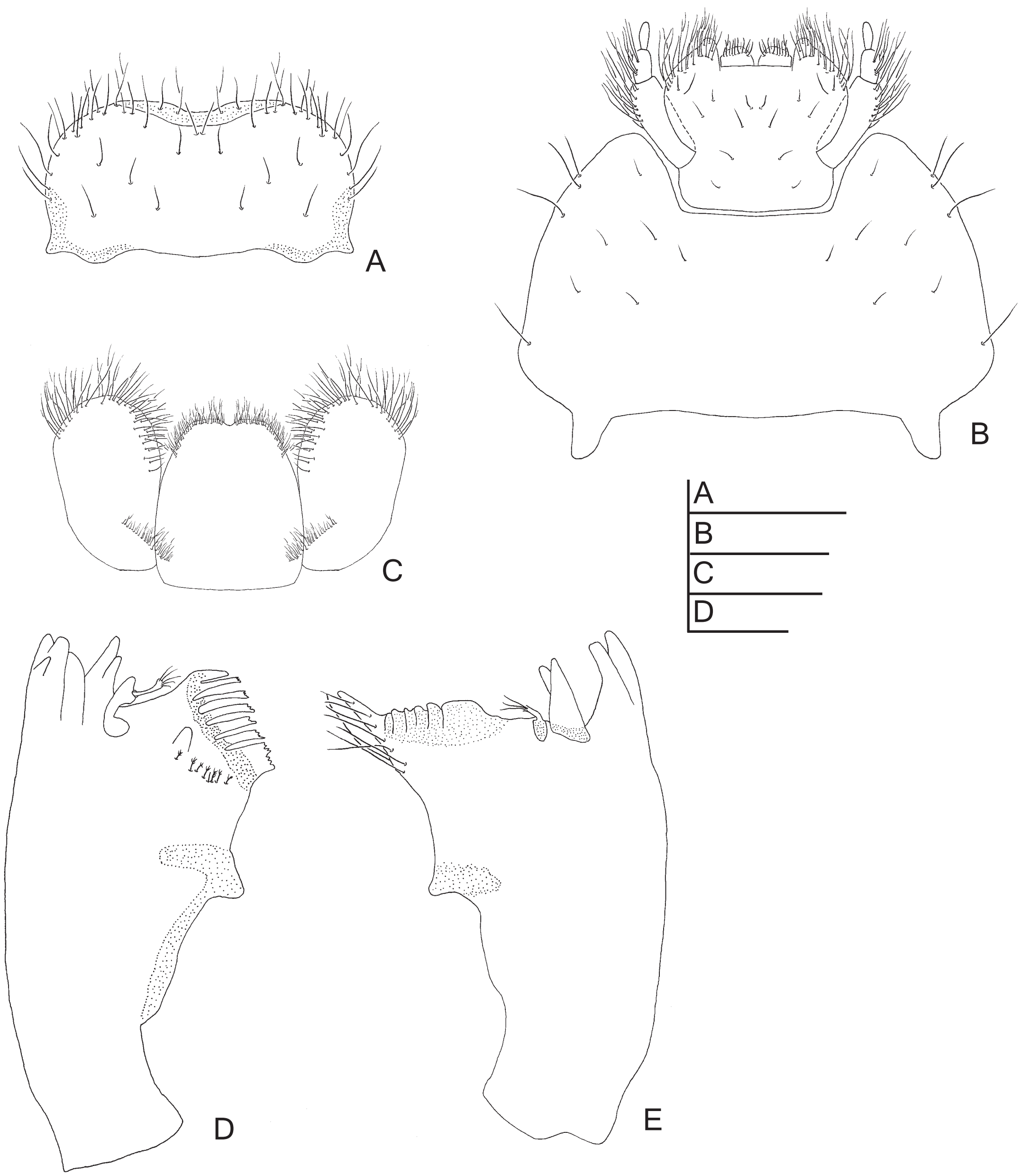


Figure 20. Characterisitcs of larval mouthparts of *Leptohyphes* (ventral). A, labrum [A]. B, labium [B]. C, hypopharynx [D]. D, left mandible [C]. E, right mandible [D]. Scale bars (mm): A = 0.15; B = 0.20; C, D = 0.10.

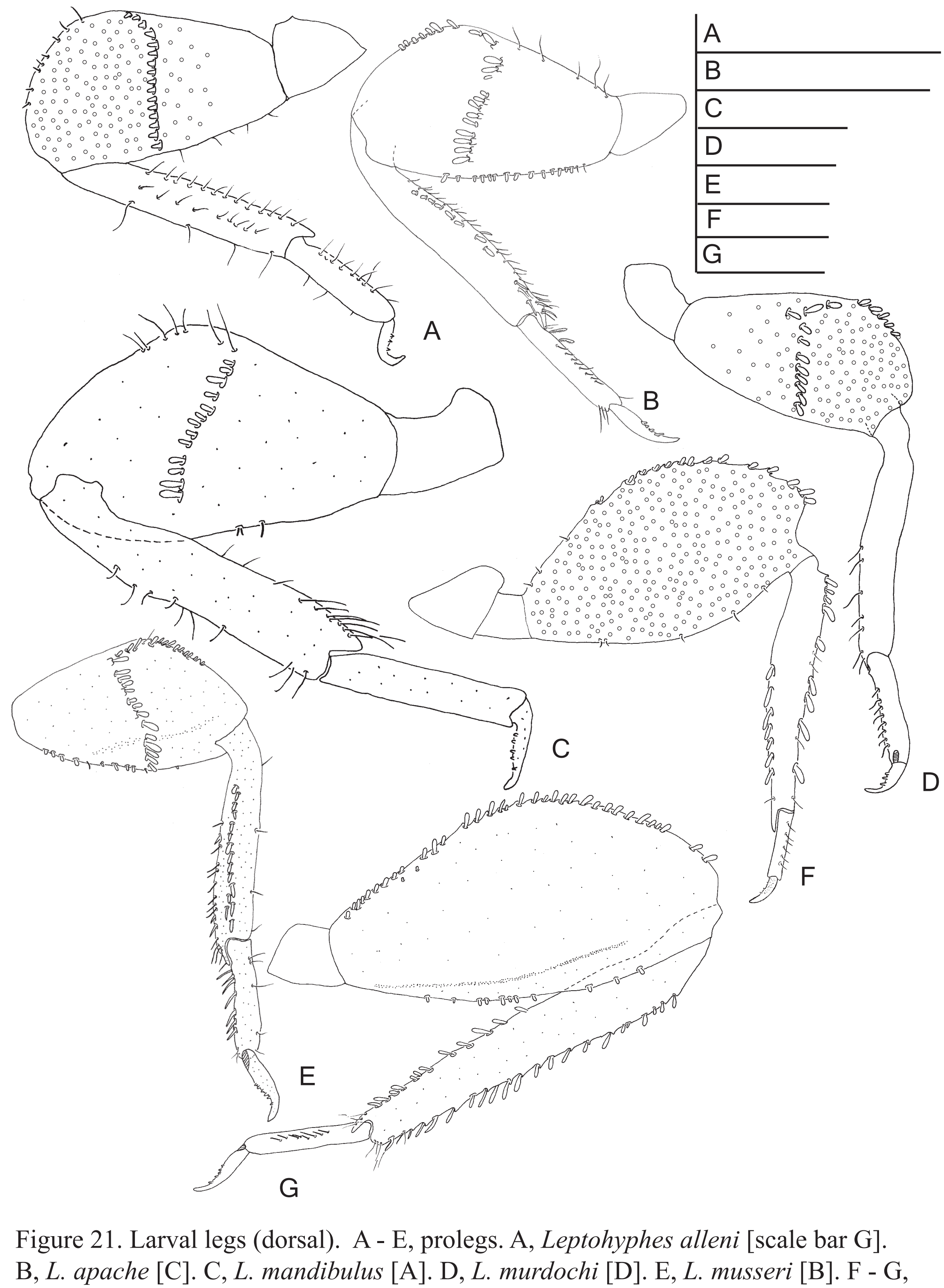


Figure 21. Larval legs (dorsal). A - E, prolegs. A, *Leptohyphes alleni* [scale bar G]. B, *L. apache* [C]. C, *L. mandibulus* [A]. D, *L. murdochi* [D]. E, *L. musseri* [B]. F - G, metalegs. F, *L. alleni* [f]. G, *L. apache* [E]. Scale bars (mm): A, B, D, E = 0.4; C, F, G = 0.05.

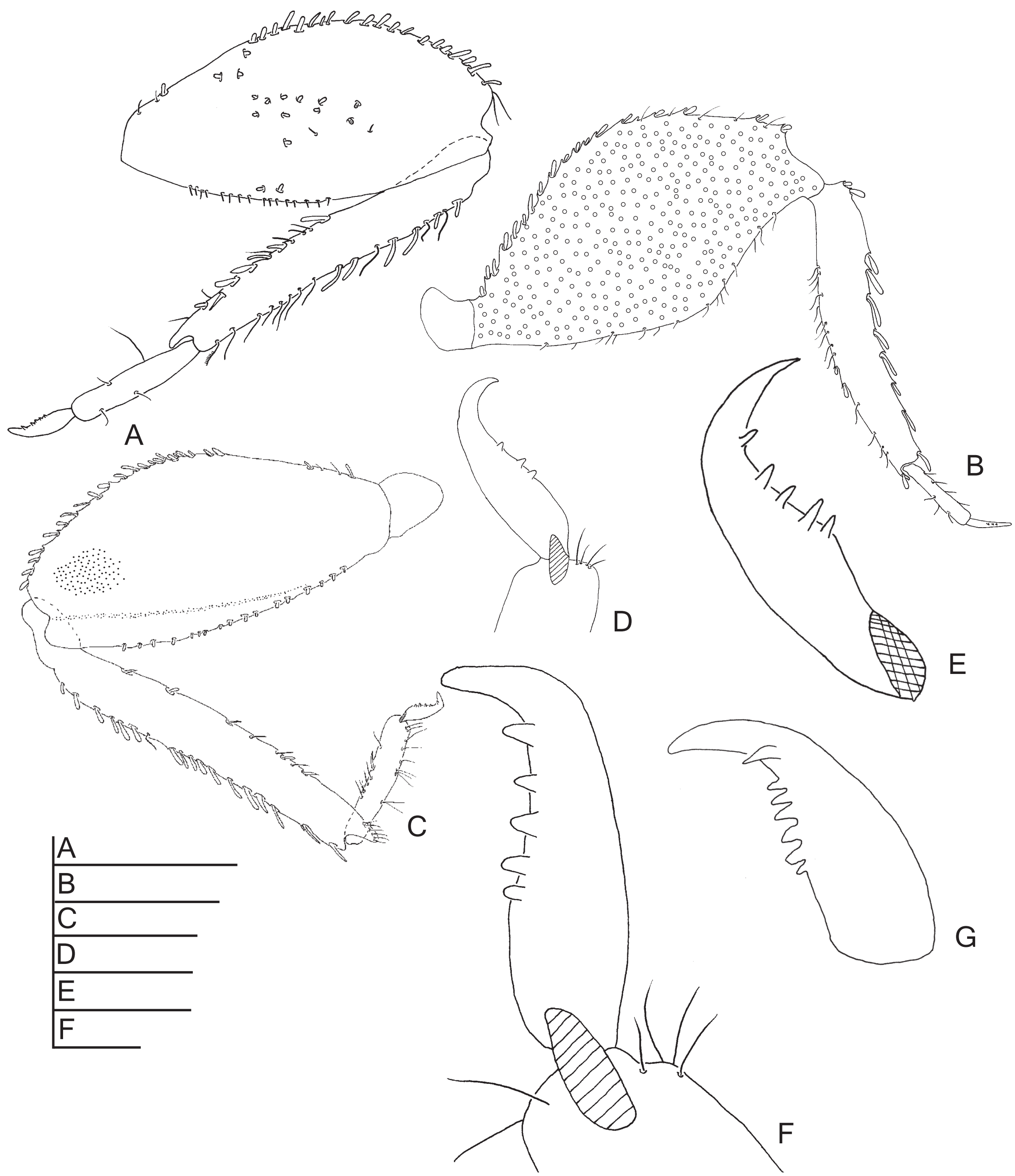


Figure 22. Larval metalegs and claws. A - C, metaleg (dorsal). A, *Leptohyphes ferruginus*, [A]. B, *L. murdochi* [E]. C, *L. musseri* [C]. D - G, metaclaw (ventrolateral). D, *L. alleni* [F]. E, *L. apache* [B]. F, *L. ferruginus* [D]. G, *L. mandibulus* [B]. Scale bars (mm): A, C, E = 0.5; B, F = 0.1; D = 0.05.

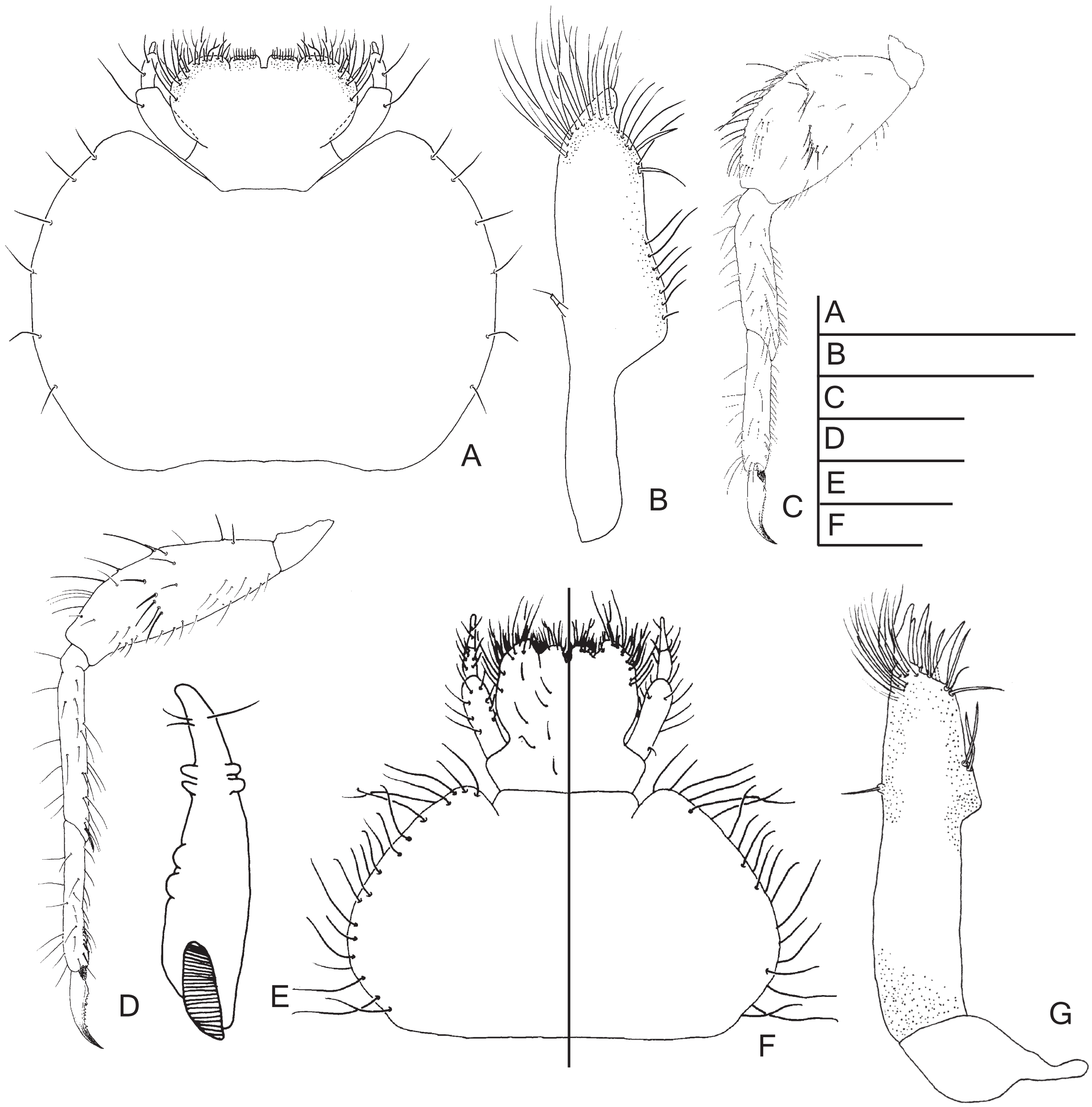


Figure 23. Larval mouthparts, legs, and claw. A - B, *Allenhyphes vescus*. A, labium (dorsal) [E]. B, maxilla (dorsolateral) [F]. C - D, larva, proleg (dorsal). C, *Tricorythodes* (*Tricorythodes*) *fictus* [C]. D, *T.* (*T.*) *cobbi* [C]. E, *T.* (*T.*) *primus*, larva, claw (ventrolateral) [D]. F - G, *Tricorythodes* (*Asioplax*) *isabelia*. F, labium (left ventral: right dorsal) [B]. G, maxilla [A]. Scale bars (mm): A, E = 0.20; B = 0.15; C = 0.60 mm; D = 0.05; , F = 0.1 mm.

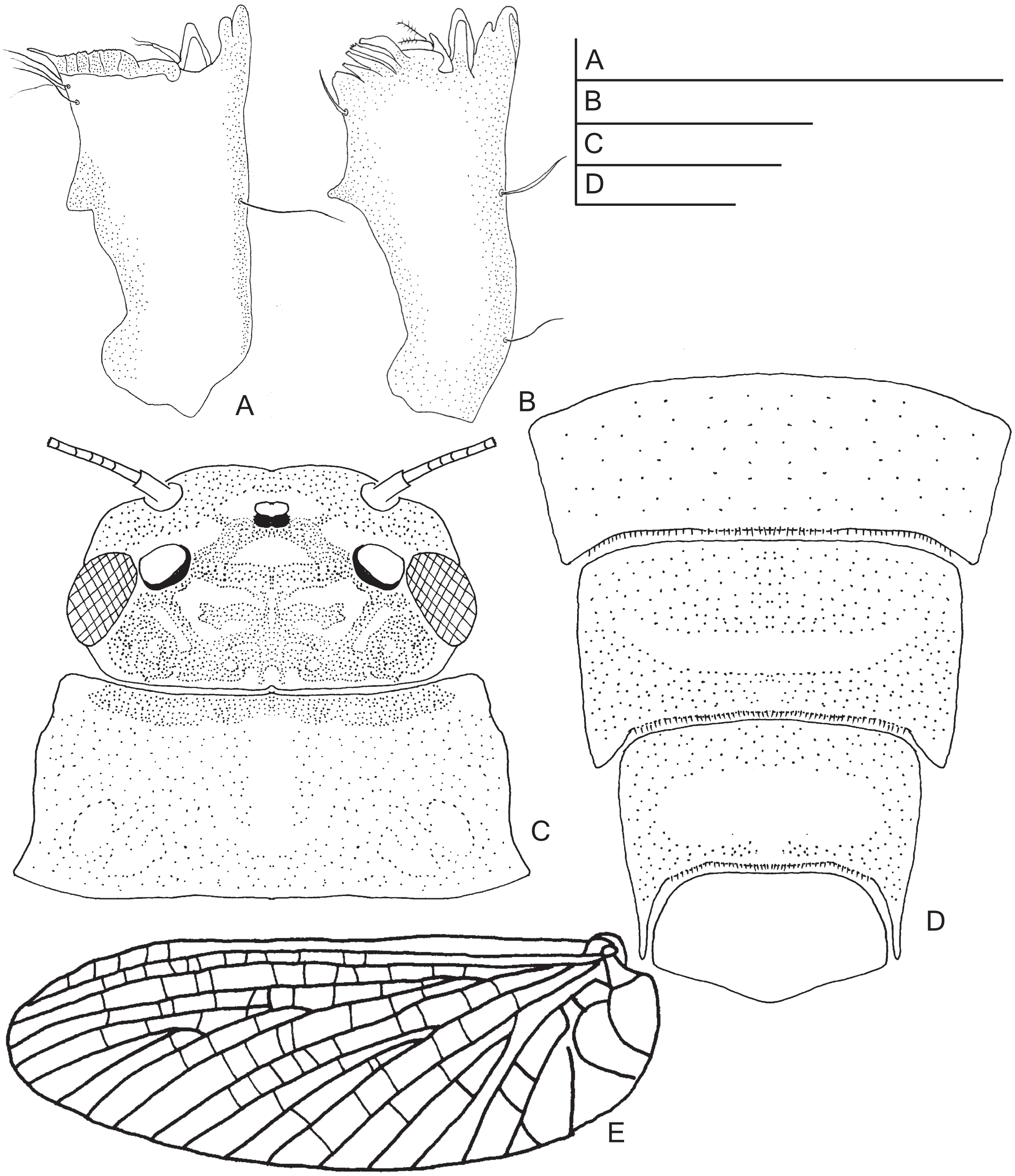


Figure 24. Features of *Tricorythodes* mouthparts and *Leptohyphes* larvae and adults. A - B, *Tricorythodes* (*Asioplax*) *isabelia,* larva. A, right mandible [A]. B, left mandible [A]. C - D, *Leptohyphes apache*, larva. C, head and prothorax [D]. D, abdominal tergites 7-10 [B]. E, *L. brevissimus*, female imago forewing [C].Scale bar (mm): A = 0.35; B, D = 0.05; C = 0.02.

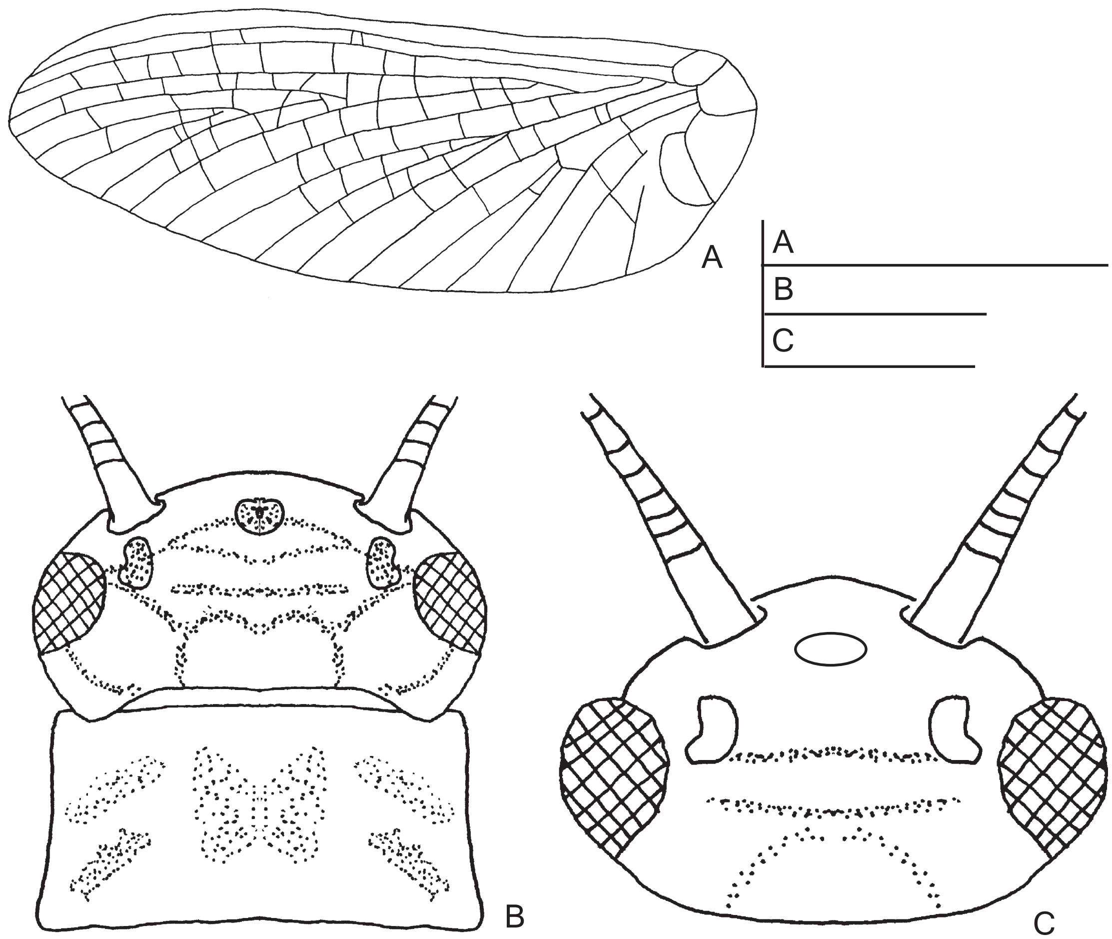


Figure 25. Characters of the adult and larval stages of *Leptohyphes ferruginus*. A, female subimago, forewing [scale bar A]. B, head and thorax (dorsal), dark form [B]. C, head (dorsal), pale form [C]. Scale bars (mm): A = 1.5; B = 0.025; C = 0.05.

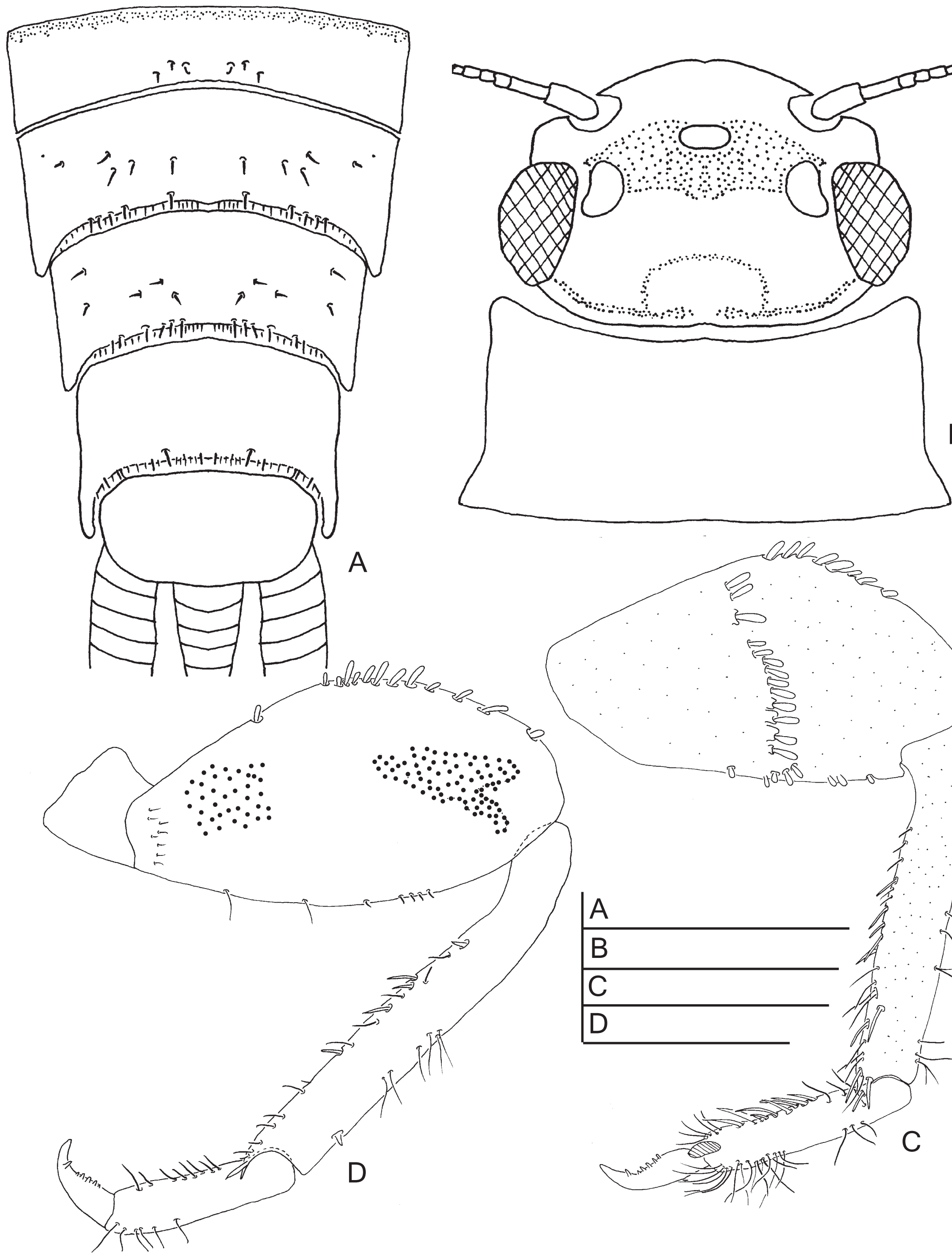


Figure 26. Characteristics of larval structures of *Leptohyphes ferruginus, L. lestes* and *L. mandibulus*. A, *L. ferruginus* (dorsal). Abdominal tergites 6 - 10 [scale bar A]. B - C, *L. lestes* (dorsal). B, head and prothorax [D]. C, proleg [C]. D, *L. mandibulus*, metaleg [B]. Scale bars (mm): A, B = 0.05; C, D = 0.50.

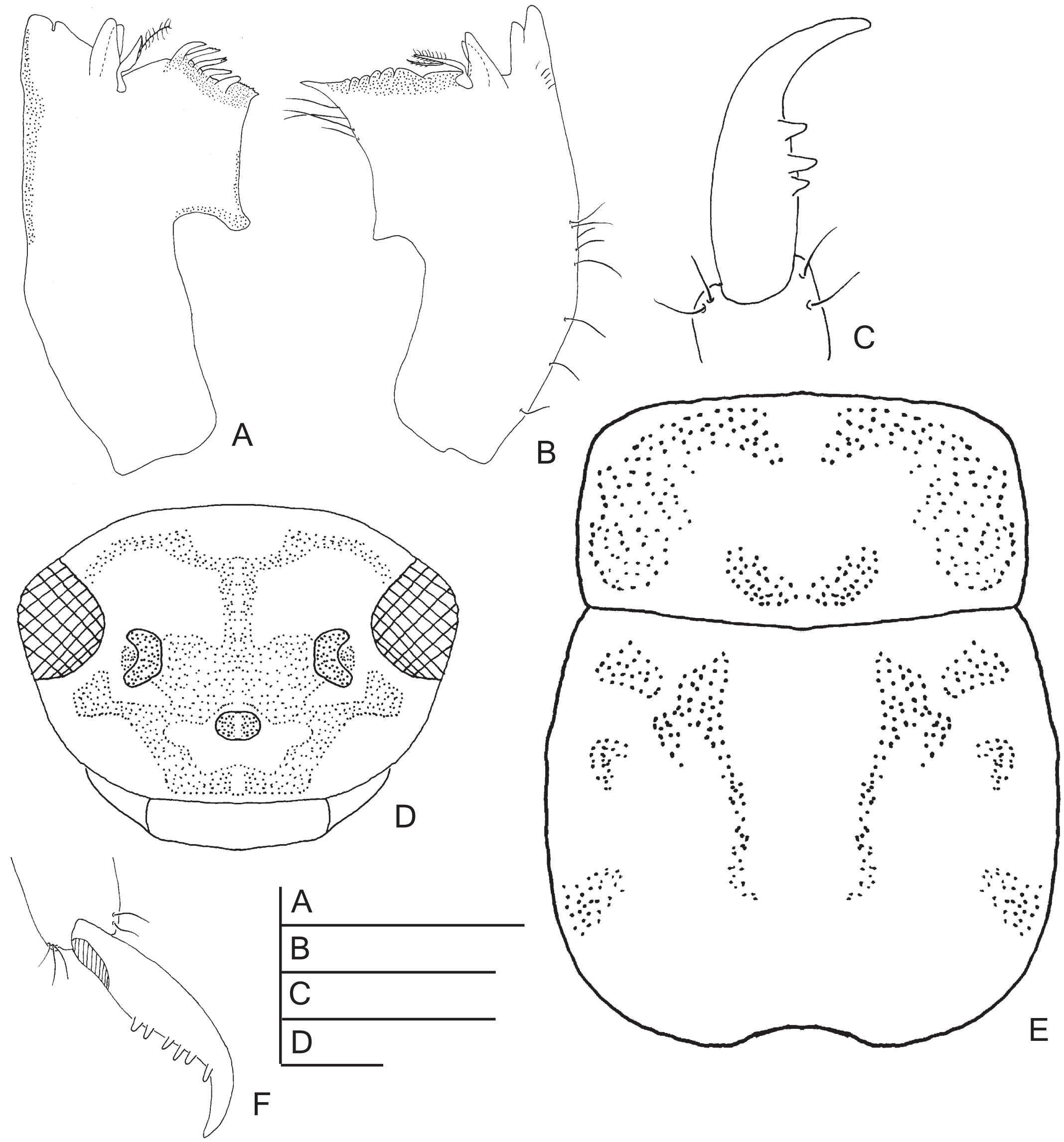


Figure 27. Characteristics of larval structures of *Leptohyphes mandibulus* and *L. musseri*. A - B, *L. mandibulus* (dorsal). A, left mandible [scale bar A]. B, right mandible [A]. C-F, *L. musseri*. C, proclaw (ventrolateral) [C]. D, larval head (anterior) [B]. E, pro- and mesothorax (dorsal) [B]. F, proclaw (ventrolateral) [D]. Scale bars (mm): A = 0.20; B = 0.05; C, D = 0.10.

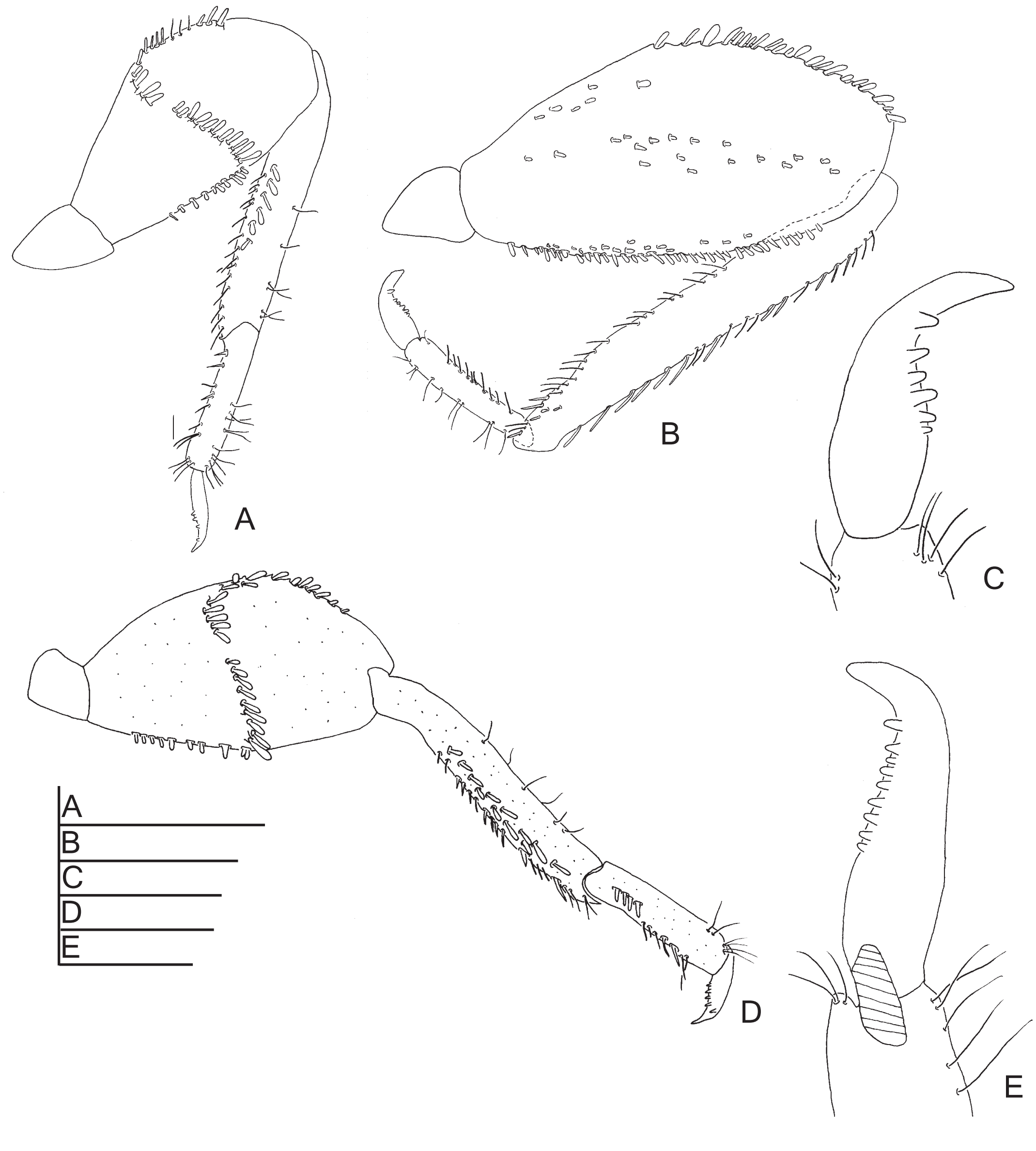


Figure 28. Characteristics of the larval stage of *Leptohyphes sabinas* and *L. zalope.* A - C, *L. sabinas.* A, proleg (dorsal) [scale bar B]. B, metaleg (dorsal) [C]. C, metaclaw (ventrolateral) [D]. D - E, *L. zalope*. D, proleg (dorsal) [A]. E, metaclaw (ventralateral) [E]. Scale bars (mm): A - C = 0.5; D = 0.1; E = 0.2.

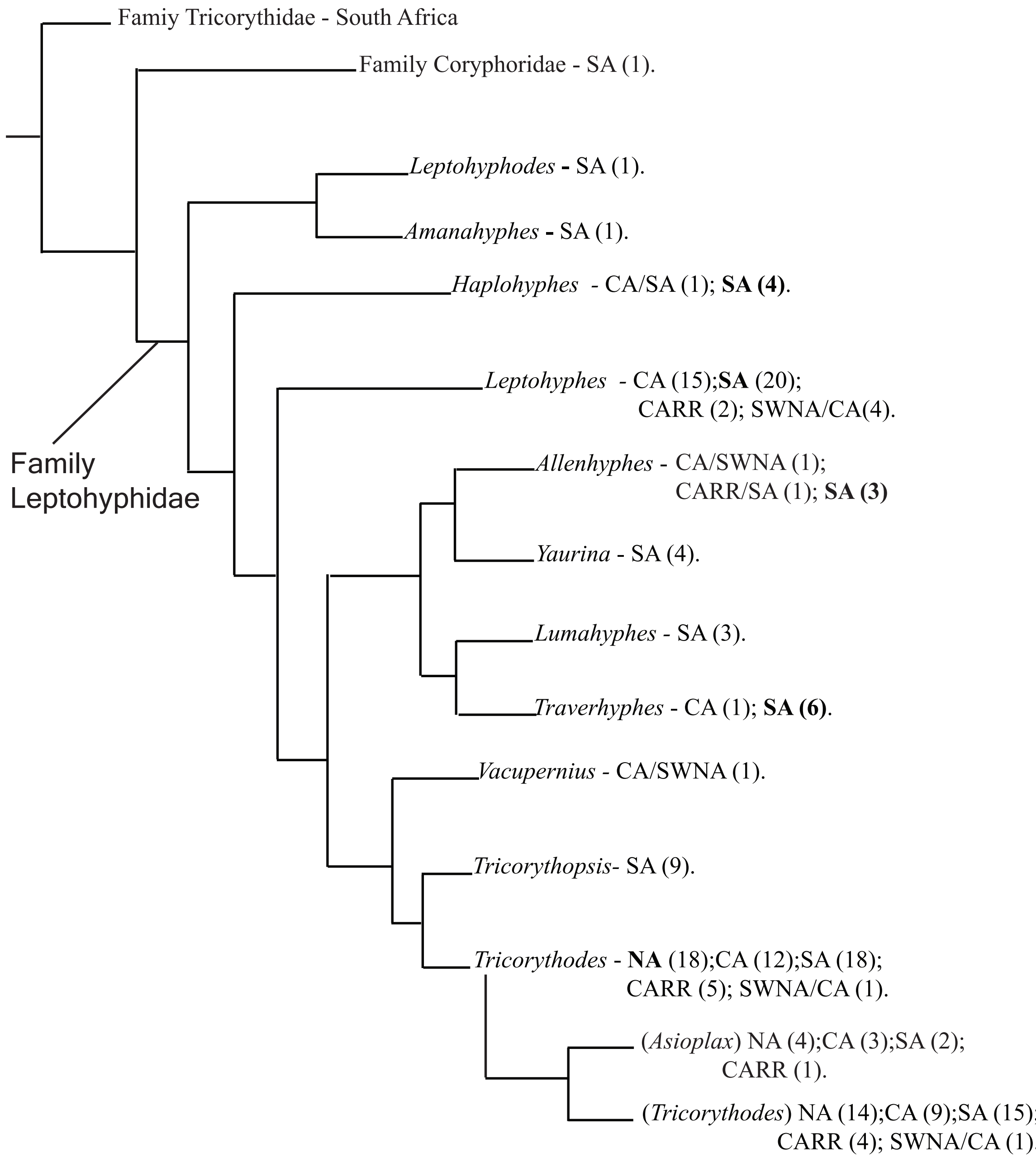


Figure 29. Biogeographic distribution of leptohyphid genera and subgenera. Following each genus or subgenus, the known distribution of its collective species is given. Those in bold indicate that the majority of species within the taxon are distributed in that region. The number of species of each genus is given in parenthases after each biogeographic region. Abbrevations: NA = North America; CA = Central America; SA = South America; SWNA = Southwestern North America;CARR = Carribean Islands.

APPENDIX B

TABLES

Table 1. Character matrix used in the phylogenetic analysis of the Leptohyphidae.

Species	0	10	20	30	40
OUTGROUPS					
Coryphorus aquilus	1000012101	10023011?1	???1000000	0?00010110	0003?13101
Dicercomyzon costale	100101?000	10012111?1	???1001001	0?00010002	0013?02113
Tricorythus reticulatus	2??00?????	10011011?1	???1000003	0?00010001	0203?02103
Ephemerellina barnardi	0????0???0	000000000?	0000022003	0?00010001	1001000203
Lestagella penicillata	0?????????	0001000?0	??????????	????010001	0000003103
Teloganodes sp. 1	0?????????	000?2000?0	001???????	???0?10001	0001001002
Vietnamella thani	0000001000	0000000020	1000010000	??00000001	0000003111
Ephemerella excrucians	0000010101	0000000000	0000000000	0?00010001	0000000000
Drunella lata	0000010000	0000000000	0000000000	0?00000000	0001000000
INGROUPS					
Allenhyphes flinti	2001112100	1001211011	11?0002110	0?00110000	1000000203
Allenhyphes vescus	2001112100	1011101011	1010001003	0?00110001	1000000200
Amanahyphes saguassu	0001??????	11012011?1	???1001003	0?00010001	0000000101
Haplohyphes aquilonius	20?011??0?	10012011?1	???0101002	0?00010000	0000000000
Haplohyphes furtiva	200011210?	10012011?1	???0101002	0?00010000	0000000000
Haplohyphes mithrus	2000112100	?????????1	??????????	?????10000	000000?000
Leptohyphes cornutus	2101112110	1001101010	1020000010	1000011101	1000101101
L. eximius	2???11????	1001201011	1000000010	1000010001	0000000000
L. ferruginus	210111????	10001?1011	10?000?010	1000010001	0000000000
L. guadeloupensis	2??111????	1000101011	1010000010	1000010000	0000000000
L. petersi	2101112110	1000101011	1020000010	1000010002	0000000000
L. plaumani	2101112110	1001101011	1020000010	1000010001	0000000000
L. sabinas	2??11?????	???????011	?0?0000010	1000010001	0000001101
L. setosus	2??1?1????	100?101011	10?00??01?	1000010001	0000001000
L. zalope	2101112110	1000111011	1010000010	1000010001	0000000000
Leptohyphodes inanis	0?0110????	10012011?1	???1002002	0?00010001	1000001101
Lumahyphes guacra	2101112100	1111201011	1010000101	11100??00?	?00000????
Macunahyphes australis	211010?101	10212011?1	???000?002	0?00010001	1002001000
Traverhyphes edmundsi	2001112100	1000201011	1020000103	1210010001	0000000000
T. indicator	2001112100	1001101011	1020001203	1210010001	1000000000
T. nanus	20?1112100	1010111011	1010001200	1210010001	1000000000
Tricorythodes albilineatus	2110101?0?	10010011?1	???0121002	0?00010000	0000000000
T. allectus	2110101101	10011011?1	???0121002	0?00010000	1000000000
T. arequita	2210101101	10011011?1	???0121002	0?0001000?	??????????
T. bullus	2110102101	10211011?1	???0121002	0?00010110	1010100000
T. condylus	2???10????	???????1?1	???0121002	0?00021001	1000000000
T. cubensis	2110102001	10011011?1	???0101002	0?00010000	1000001001
T. curiosus	21????????	???????1?1	???01?1002	0?00010000	0000001001
T. curvatus	2110102001	10011011?1	???0121002	0?00010000	0000000000
T. dimorphus	111010?001	10012011?1	???0101002	0?00010000	0000000000
T. dolani	2211?0?001	10?11011?1	??????????	????010001	00?0000000
T. edmundsi	2???10????	??????11?1	???0121002	0?00010000	0000001001
T. explicatus	2?101?????	10011011?1	???0121002	0?00010000	1000000000
T. fictus	2110102001	10010011?1	???0101002	0?00010000	0000000000
T. isabelia	2?????????	???????1?1	??????????	????10000	0000001001
T. kirki	2?????????	???????1?11	??????????	????10000	1000000000

Table 1. Continued.

Species	50	60	70	80	90
OUTGROUPS					
Coryphoru aquilus	00003??010	110034?4?1	1100000112	1022010010	001101?010
Dicercomyzon costale	01?0200312	000014?002	0100000001	00??00112?	?0101010?0
Tricorythus reticulatus	0002003312	00000104?1	0102002010	0220000300	001001?010
Ephemerellina barnardi	00003??200	0000010102	0103000010	0001012421	0011001010
Lestagella penicillata	00003??100	0000010002	0100200000	0000000110	1000001000
Teloganodes sp.	0100210110	0000010301	0100000010	0001011001	0011001000
Vietnamella thani	0000000110	0100110??2	0000000001	0000000000	0001001000
Ephemerella excrucians	0000002100	0000021002	0100001010	0200011021	0110000002
Drunella lata	0000003200	000004?001	1000002000	0000000000	1010000002
INGROUPS					
Allenhyphes flinti	2000110211	00000124?2	0100001011	0220011411	0010001010
Allenhyphes vescus	0000110211	00000124?2	0100001011	0220011411	0010003010
Amanahyphes saguassu	1000310201	0000211311	0104000010	1000010410	001001?010
Haplohyphes aquilonius	0000110211	0000201301	0100300010	1020000431	001001?011
Haplohyphes furtiva	0110110211	0100001301	0100300110	1020000431	001001?011
Haplohyphes mithrus	??????????	??????????	??????????	??????????	??????????
Leptohyphes cornutus	0010001201	1012130211	1112110010	0021110111	0010001010
L. eximius	0000000201	0000010103	0113212011	1220000111	1010001010
L. ferruginus	0000000201	0000010112	0113112011	1222122101	1210001010
L. guadeloupensis	2000000201	0000010212	0113112011	1220000101	1110001010
L. petersi	0000000200	00100104?2	1111112011	1220012101	0010001010
L. plaumani	0000000201	0000020102	1113111011	1220022101	1110001010
L. sabinas	2000000200	0000010102	0113110011	1220022111	1110001010
L. setosus	0000000100	0000020301	0110210011	0220000201	00100010?0
L. zalope	0000000201	0000010102	0112112011	0210010111	1110001010
Leptohyphodes inanis	0000200201	0000210011	0100002011	00?001141?	?01001?2?0
Lumahyphes guacra	????000211	????0124?2	010??0?010	0??101041?	?????????0
Macunahyphes australis	1002210211	0000010102	0102102110	1220011420	00100012?0
Traverhyphes edmundsi	0000110211	00000124?2	0100001011	0220002411	0010001010
T. indicator	0000110211	00000124?2	0100002010	0220010421	2010001010
T. nanus	0000110111	00002124?2	0100001011	0220012411	0010003010
Tricorythodes albilineatus	0000110211	0000201311	0100302110	1220000120	0010001100
T. allectus	0000110111	0000000311	0100302110	1220000120	0010003100
T. arequita	????000211	0000000311	010030?111	2??0000320	0010011?0
Tricorythodes bullus	0000210111	10012114?2	0100302110	1020201020	0010001200
T. condylus	0001001211	0100000301	0100302010	1220100100	0010001100
T. cubensis	0000100211	0000010102	0100302010	1210000310	0010001100
T. curiosus	000031?110	0000010301	0100300110	0000000310	0010021000
T. curvatus	0000210111	0000000311	0100302110	1220000010	0010003100
T. dimorphus	0000210211	0000000001	0100302110	1220001320	0010001210
T. dolani	00?0100110	0000110301	1104300110	1000000000	3010021100
T. edmundsi	0000310110	0000100301	0100302110	0020001310	0010021210
T. explicatus	0002110211	0000010011	0100302110	1120100120	0010001200
T. fictus	0000210111	0000210312	0100302111	1120011020	0010001100
T. isabelia	2000200110	0000110002	1100301100	0210000310	2010021000
T. kirki	0000210110	0000010012	0100302112	1122101310	0010001200

Table 1. Continued.

Species	100	110
OUTGROUPS		
Coryphoru aquilus	0100000120	1 0 1 1 1 ? 1 2 0
Dicercomyzon costale	?0?00?0?0?	0 0 0 0 0 0 1 1 1
Tricorythus reticulatus	01000?0?0?	0 0 2 2 0 1 1 0 0
Ephemerellina barnardi	1100030010	0 0 1 1 0 3 1 0 0
Lestagella penicillata	1100020121	1 0 2 3 1 ? 1 0 0
Teloganodes sp. 1	0100000020	0 0 2 3 1 ? 1 2 1
Vietnamella thani	01000?000?	? 0 ? ? 0 2 0 0 0
Ephemerella excrucians	01000???0?	? 0 0 0 0 0 0 0 0
Drunella lata	01000???0?	? 0 0 0 0 0 0 0 0
INGROUPS		
Allenhyphes flinti	1022011100	1 1 1 1 0 3 1 2 0
Allenhyphes vescus	1022011100	1 1 1 1 0 3 1 2 0
Amanahyphes saguassu	0022011100	0 2 1 1 1 ? 1 1 0
Haplohyphes aquilonius	0012111111	1 2 2 2 0 2 1 0 0
Haplohyphes furtiva	0012111111	1 2 2 1 0 2 1 0 0
Haplohyphes mithrus	??????????	? ? ? ? ? ? ? ? ?
L. cornutus	0102011000	1 2 2 2 0 1 1 2 0
L. eximius	0122011000	1 2 2 2 0 2 1 2 0
L. ferruginus	0122011000	1 2 2 2 0 3 1 0 0
L. guadeloupensis	0122011000	1 ? ? ? 0 ? 1 2 0
L. petersi	0122011000	1 2 2 1 0 3 1 2 0
L. plaumani	0122011000	1 2 2 2 0 3 1 2 0
L. sabinas	0102011000	1 2 2 2 0 3 1 2 0
L. setosus	0102011000	1 2 2 2 0 2 1 2 0
L. zalope	0122011000	1 2 2 2 0 3 1 1 0
Leptohyphodes inanis	1012111000	2 1 1 1 1 ? 1 2 0
Lumahyphes guacra	1022011000	1 2 1 1 0 2 1 ? 0
Macunahyphes australis	0012111000	1 1 1 1 0 2 1 ? 0
Traverhyphes edmundsi	1022211000	1 1 1 1 0 2 1 2 0
T. indicator	1012211000	1 2 1 1 0 2 1 2 0
T. nanus	1022111000	1 1 1 1 0 3 1 2 0
Tricorythodes albilineatus	2012111111	1 1 1 1 0 2 1 0 0
T. allectus	2012111111	1 1 1 1 0 2 1 2 0
T. arequita	2012211111	1 1 1 1 0 2 1 ? 0
Tricorythodes bullus	2012111111	2 1 1 1 0 1 1 0 0
T. condylus	2012111111	1 1 1 1 0 2 1 0 0
T. cubensis	0012111111	2 1 1 1 0 2 1 2 0
T. curiosus	0012011110	1 1 1 1 0 2 1 2 1
T. curvatus	0012111111	1 1 1 1 0 2 1 2 0
T. dimorphus	0012111111	1 1 1 1 0 2 1 2 0
T. dolani	0012011111	2 1 1 1 0 3 1 1 1
T. edmundsi	0012011111	1 1 1 1 0 3 1 2 1
T. explicatus	2012211111	1 1 1 1 0 2 1 2 0
T. fictus	2012111111	1 1 1 1 0 2 1 1 0
T. isabelia	0012011111	2 1 1 1 0 2 1 2 1
T. kirki	0022111111	1 1 1 1 0 2 1 2 0

Table 1. Continued.

Species	0	10	20	30	40
T. melanobrancus	2?????????	???????1?1	??????????	???0?10000	0000001000
T. minutus	2110101100	10011011?1	???0121002	0?00010000	1000000000
T. mirus	1110103001	10012011?1	???0101002	0?00010000	0000000000
T. montanus	2110102000	10001011?1	???0121002	0?00010000	1000001000
T. notatus	2??0??????	???????1?1	??????????	?????10000	0000000000
T. numinuh	2211101001	10011011?1	???0121002	0?00010000	0000001001
T. popayanicus	2110101001	10011011?1	???0121002	0?00021000	1000000000
T. primus	??????????	???????1?1	??????????	?????2100?	1000000000
T. quercus	??????????	?????????1	??????????	?????10000	000000?000
T. robacki	2?????????	???????1?1	??????????	?????10000	1000000000
T. sacculobranchis	221110?001	10011011?1	???01??002	0?00010000	0000000000
T. serratus	2110101001	10011011?1	???0111002	0?00010001	0000000000
T. sierramaestrae	211?10?0?0	10011011?1	???01??002	0?00010000	0000000000
T. sordidus	2110102001	10012111?1	???0121002	0?00010000	1000000000
T. ulmeri	2?????????	???????1?1	??????????	?????10000	1000000000
T. undatus	2?????????	?????????1	??????????	???0?10001	0000001001
Tricorythopsis artigas	2001111101	12012211?1	???1022002	0?00010001	00000010?0
T. chiriguano	2001112101	12012211?1	???1020002	0?00010001	0000001000
T. minimus	2???11????	12012211?1	???1020002	0?00010001	0000001000
T. undulatus	2001111101	12012211?1	???1020012	0?00010001	0000001000
Vacupernius packeri	2011112001	1101111011	1020003100	1200010001	0000001000
Yaurina mota	2001112100	1001101011	1020002103	0?01010001	1002001000
Y. yuta	2001112100	1001201011	1020002102	0?01010001	1002001001

Table 1. Continued.

Species	50	60	70	80	90
T. melanobranchus	0000210111	0000110002	1100300110	0100020411	0010101200
T. minutus	0002010211	0000010301	0100302110	0120000020	0010001100
T. mirus	0000210210	0000010103	1100302110	1220000320	1010001210
T. montanus	0000100111	0000010301	0100302010	1230000100	3010001200
T. notatus	0000210210	0000010311	0100302110	1220010120	0010003200
T. numinuh	0000310110	0000100301	0100302100	0020011010	0010021210
T. popayanicus	0001210210	0000000301	0100302110	1220001400	0010001100
T. primus	0001210210	0100000301	0100302000	1120000400	0010001200
T. quercus	0000210210	0100010002	0102300110	0021000320	0010011200
T. robacki	0000210110	0000010401	1100302110	1220010010	0010001200
T. sacculobranchis	0000000110	0000010102	0100302110	0220001320	0010001000
T. serratus	0000110211	0110010002	1101202110	1220000010	0010021000
T. sierramaestrae	0000010210	0000010102	0000302010	1220111410	3010001000
T. sordidus	0000110111	0000211312	0100302010	1220010320	0010001100
T. ulmeri	0000210111	0000010012	0100302110	1122100320	0010001200
T. undatus	0000110111	01122104?2	0100202110	0020010010	1010101000
Tricorythopsis artigas	0000110100	00000104?2	0100202110	1200002411	0010002010
T. chiriguano	0000210100	00000104?2	0100202110	1200000411	0010002010
T. minimus	0?00110100	0000010122	0104202110	1200002411	0010002010
T. undulatus	0000210100	00000104?3	0100202110	1200202411	0010002010
Vacupernius packeri	0000010211	0000010112	0100102110	1221010221	2010001010
Yaurina mota	0000100211	00000124?1	0100001011	0100000211	0210001010
Y. yuta	0000100211	00000124?1	010000?011	0100000211	0?10001010

Table 1. Continued.

Species	100	110
T. melanobranchus	0022011110	111103121
T. minutus	2012211111	111102120
T. mirus	0012111111	211102120
T. montanus	0012211111	111102120
T. notatus	2012011111	211102120
T. numinuh	0012011111	111103121
T. popayanicus	2012111111	111102120
T. primus	2012111111	211102100
T. quercus	0012111111	111102110
T. robacki	0012111111	111102120
T. sacculobranchis	0012011111	111102120
T. serratus	1012111111	111102100
T. sierramaestrae	0012011111	111102120
T. sordidus	2012111111	111102110
T. ulmeri	2012111111	211102120
T. undatus	1022111111	111102100
Tricorythopsis artigas	0002011000	122103110
T. chiriguano	0002011000	122103110
T. minimus	0002011000	022103120
T.sundulatus	0002011000	122103110
Vacupernius packeri	1012011100	111102100
Yaurina mota	1022011100	111102120
Y. yuta	1022111100	111103120

Table 2. Listing of ingroup and outgroup taxa used in the current study with depository information (see Materials and Methods for Museum abbrevitations). Symbols Used: * indicates holotype/primary type housing; ~ indicates paratypes housing. L = larvae, A = adults (males and females).

Genus	**Species**	**Depository**	**Number Examined**
Allenhyphes	*A. flinti*	FAMU~, TAMU	A=165; L=24
	A. vescus	CAS*; TAMU	A=41; L=59
Amanahyphes	*A. saguassu*	FAMU	L=4
Haplohyphes	*H. aquilonius*	FAMU~	L=2
	H. furtiva	TAMU	A=6; L=6
	H. mithrus	CAS~; TAMU	A=51
Leptohyphes	*L. cornutus*	IFML; TAMU	A=5; L=2
	L. eximius	TAMU	L=7
	L. ferruginus	CAS*~; TAMU	A=4; L=25
	L. guadeloupensis	TAMU	L=2
	L. petersi	FAMU~	A=55; L=4
	L. plaumani	CAS~; TAMU	A=3; L=10
	L. sabinas	TAMU	A=5; L>100
	L. setosus	FAMU~	A=4; L=4
	L. zalope	TAMU	A=35; L=300+
Leptohyphodes	*L. inanis*	NA	None
Lumahyphes	*L. guacra*	TAMU	A=6
Macunahyphes	*M. australis*	FAMU	A=11
Traverhyphes	*T. edmundsi*	TAMU	A=4; L=4
	T. indicator	TAMU	A=9; L=9
	T. nanus	CAS~; TAMU; IFML	A=1; L=35
Tricorythodes	*T. albilineatus*	TAMU	A=6; L=24
	T. allectus	TAMU	A=85; L>150
	T. arequita	TAMU	A=2
	T. bullus	CAS~; IFML; TAMU	A=6; L=4
	T. condylus	TAMU	L=8
	T. cubensis	TAMU~	A=2; L=3
	T. curiosus	FAMU, TAMU	L=7
	T. curvatus	ANSP*~; TAMU	L=74
	T. dimorphus	CAS*~; TAMU	A=47; L=300+
	T. dolani	ANSP*~; TAMU; FAMU	A=2; L=23
	T. edmundsi	TAMU	L=21
	T. explicatus	BMNH*~	A=5
	T. fictus	CU*; TAMU	A=100+; L=300+
	T. isabelia	TAMU~	L=4
	T. kirki	TAMU*~; FAMU~	L=33

Table 2. Continued

Genus	**Species**	**Depository**	**Number Examined**
Tricorythodes	*T. melanobranchus*	CAS*; TAMU	L=32
	T. minutus	CU*~; TAMU	A=100+; L=200+
	T. mirus	TAMU*~; TAMU	A=10; L=200+
	T. montanus	TAMU~	A=2; L=3;
	T. notatus	CAS*~	L=30
	T. numinuh	TAMU~	A=12; L=41
	T. popayanicus	TAMU	A=5; L=5
	T. primus	TAMU*~	L=2
	T. quercus	CAS*; TAMU	L=3
	T. robacki	ANSP*~; TAMU	L=10
	T. sacculobranchis	TAMU~	A=2; L=4
	T. serratus	TAMU*~; FAMU~	A=10; L=21
	T. sierramaestrae	TAMU~	A=1; L=3
	T. sordidus	FAMU*~CAS~TAMU	A=9; L>100+
	T. ulmeri	CAS*~	L=40
Tricorythopsis	*T. artigas*	TAMU	A=18
	T. chiriguano	FAMU~; IFML~	A=6; L=13
	T. minimus	CAS~	L=2
	T. undulatus	TAMU	A=2; L=2
Vacupernius	*V. packeri*	TAMU	A=34; L>175+
Yaurina	*Y. mota*	IFML~	A=2; L=2
	Y.yuta	TAMU	A=10
OUTGROUPS			
Dicercomyzon	*D. costale*	FAMU	A=6
Tricorythus	*T. reticulatus*	TAMU	L=4
Ephemerellina	*E. barnardi*	FAMU	L=4
Lestagella	*L. penicillata*	TAMU	L=4
Teloganodes	*T.* sp. 1	FAMU	L=5
Vietnamella	*V. thani*	FAMU	A=3; L=1
Ephemerella	*E. excrucians*	TAMU	A=58; L=130
Drunella	*D. lata*	TAMU	A=2; L=191
Coryphorus	*C. aquilus*	FAMU~	L=3

Table 3. Detailed collection records of outgroup species used in the phylogenetic analysis of the family Leptohyphidae.

FAMILY CORYPHORIDAE

Coryphorus aquilus Peters: **Type Material Examined:** PARATYPE: BRASIL: Pará State, Rio Maró, nr. Mouth, 18.xi.1952, 2L, H. Sioli (coll) [FAMU]. **Other Material Examined:** BRASIL: Amazonas state; Presidente Figueiredo, Igarapé da Pantera, 10-13.xii.2001, 1♂ imago, J.L. Nessimian & N. Hamada [FAMU].

FAMILY TRICORYTHIDAE

Tricorythus reticulatus Barnard: **Type Material Examined:** None. **Other Material Examined:** SOUTH AFRICA: Selati River (S24°09'43"; E30°15'15"), 26.v.2003, Barner-James and F.C. de Moor, 4L (Slide #DB06i1605).

Dicercomyzon costale Kimmins: **Type Material Examined:** None. **Other Material Examined:** *Paratypes:* GOLD COAST: Afram River, Mankrong, 13.ix.1950, L. Berner, 3 males and 3 females (No. 3944.31).

FAMILY TELOGANODIDAE

Ephemerellina barnardi Lestage: **Type Material Examined:** None. **Material Examined:** SOUTH AFRICA: Upper Hex River, Western Cape, (S32°43'17"; E19°12'41"), 12.iv.2005, F.C. de Moor, 4L (Slide #DB06i1702).

Lestagella penicillata (Barnard): **Type Material Examined:** None. **Material Examined:** SOUTH AFRICA: Salta River at Canal Weir (S33°55'30"; E23°29'25"), 28.x.2005, F.C. de Moor, 4L (Slide #DB06i2601) [TAMU].

Table 3. Continued.

Teloganodes sp.: **Type Material Examined:** None. **Other Material Examined:** INDONESIA: N. Sulawesi, vicinity of Manado, Kali Village Site 1, Kali Strm at Kali village above bridge (N01.41412d; E124.84124d), 206m, 8.xii.2004, Coll. C. Geraci, M. Dien, F. Mirah, D. Lapasi, 5 larvae (1 slide, #DB05x0503) (FAMU).

FAMILY AUSTREMERELLIDAE

Vietnamella dabieshanensis You and Su: **Type Material Examined:** None. **Other Material Examined:** CHINA: Anhui Prov, Huoshan Co., Zhu-Fu-An Village, 14.vi.1983, D-U You and C-R Su, 1L, 3 males [FAMU].

FAMILY EPHEMERELLIDAE

Ephemerella excrucians Walsh: **Type Material Examined:** None. **Material Examined:** UNITED STATES: Arizona; Apache Co.; North Fork White River at SR 473 (N34°02'46"; W109°43'43"); 23.v.2004, DE Baumgardner, 19 larvae [TAMU]; Greenlee Co.; Blue River at FS Rd. 475 (Juan Miller Rd.) (N33°17'30"; W109°11'46"), 22.v.2004, DE Baumgardner, 25 larvae, 1♀ (reared) [TAMU]. New Mexico: Catron Co., San Francisco R., Hwy. 180, Head of the Ditch Camping Area (Apache Nat. Forest), ca. 1 mi. W. Luna, 25.v.2000, DE Baumgardner, 2 larvae, 1♂, 1♀ (reared) [TAMU]; San Francisco R. (at San Franciso Hot Spring), Gila National Forest, ca. 5 mi. S. Glenwood (N33º14'18"; W108º52'46"), 20.v.2004, DE Baumgardner, 1♂ (reared) [TAMU]; creek at FS Road 233, ca. 5 mi. NE Reserve, Gila National Forest

Table 3. Continued.

(N33°43'54"; W108°42'28"), 20.v.2004, DE Baumgardner, 30 larvae [TAMU]; Gila R. at Hwy. 15, Gila Nat. Monument (N33°13'17"; W108°14'33"), 18.v.2004, DE Baumgardner, 4 larvae, >50 adults [TAMU]; Grant Co.; Gila R., Gila Riparian Reserve, Gila Wilderness, ca. 6.7 mi. NE Cliff (N33°02'3"; W108°31'48"), 19.v.2004, DE Baumgardner, 18 larvae, 1♂, 1♀ (reared) [TAMU]; Gila R. at Hwy. 15, ca. 7 mi. S. Gila Nat. Monument (N33°10'46"; W108°12'11"), 18.v.2004, DE Baumgardner, 5 larvae, [TAMU]; Lincoln Co., Rio Ruidoso at Main St. in Ruidoso (N33º19'14"; W105º42'43"), 22.v.2000, DE Baumgardner, 7 larvae [TAMU]; Sandoval Co., Jemez R. at Vista Linda Camp Sight (Santa Fe Nat Forest), Hwy. 4, ca. 5 mi. N. Jemez Puebloa (N35º43'02"; W106º43'17"), 26-27.v.2000, DE Baumgardner, 1♀ (reared), 15 larvae [TAMU]; Rio Guadalupe at FS Rd. 376, ca. 5 mi. from jct. with Hwy. 4 (N35º44'14"; W106º45'50"), 26.v.2000, DE Baumgardner, 5 larvae [TAMU]; San Miguel Co.; Pecos R., Hwy. 63, Field Tract Camp Site, ca. 9 mi. N. Pecos, Santa Fe Nat. Forest (N35°41'13"; W105°41'35"), 13.vii.2004, DE Baumgardner, 1 larvae [TAMU].

Drunella lata (Morgan): **Type Material Examined:** None. **Other Material Examined:** UNITED STATES: Maryland: Harford Co.; Gunpowder River at Jerusalem Rd., Gunpowpowder Falls State Park, 24.v.1998, DE Baumgardner, 1 larva [TAMU]. North Carolina: Haywood Co.; Cataloochee Creek, ca. 2 mi. NE Cataloochee, GSMNP (N35 °39'03"; W83 °04'26"), 04.vii.2005, DE Baumgardner, 2♂ (reared), >100 larvae

Table 3. Continued.

[TAMU]; Rough Fork, ca. 2 mi. SW Cataloochee Ranger Station, GSMNP (N35 °37'02"; W83 °07'12"), 04.vii.20005, DE Baumgardner, 7 larvae [TAMU]; Cataloochee Creek at Mount Sterling Road, ca. 1 mi. N Cataloochee Ranger Station, Great Smoky Mountains Nat. Park (N35 °38'33"; W83 °04'42"), 04.vii.2005, DE Baumgardner, 15 larvae [TAMU]; Cataloochee Creek at Mount Sterling Road, ca. 3 mi. NE Cataloochee Ranger Station (N35 °40'02"; W83 °04'23"), 04.vii.20005, DE Baumgardner, 20 larvae [TAMU]; Swain Co.; Oconaluftee R. at Hwy. 441, ca. 11 mi. N. Cherokee, Great Smoky Mountains National Park (N35 °34'30"; W83 °20'24"), 06.vii.2005, DE Baumgardner, 22 larvae [TAMU]; Blount Co.; Mill Creek at Parson Branch Road, ca. 1/4 mi. from Cable Mill Historic Area, GSMNP (N35 °34'07"; W83 °50'49"), 05.vii.2005, DE Baumgardner, 3 larvae [TAMU]; Forge Ck. at Parson Branch Rd., ca. 2 mi. S. Cable Mill Historic Area, Great Smoky Mountains National Park (N35 °34'07"; W83 °50'49"), 05.vii.2005, DE Baumgardner, 2 larvae [TAMU]; Cocke Co.; Rocky Ck. at Crosby Ranger Station, Great Smoky Mnts. Nat. Park (N35 °46'41"; W83 °12'45"), 06.vii.2005, DE Baumgardner, 1 larva [TAMU]; Sevier Co.; Little River at Elkmont Rd., N. of Campground, Great Smoky Mountain National Park (N35 °39'54"; W83 °35'28"), 03.vii.2005, DE Baumgardner, 20 larvae [TAMU].

Table 4. Summary of characters used in cladistic analysis.

Character Number	# States/ Steps	Character Description
ADULT		
Head		
0	3/5	Compound eyes of male (Figs. 1A – 1C).
1	3/6	Paired occipital tubercles (Fig. 1A).
Thorax		
2	2/2	Fusion of anterior and posterior parapsidal sutures (Fig. 1D – 1E).
3	2/4	Plumidium. (Fig. 1D – 1E).
Legs		
4	2/1	Male imago propretarsal claw (Fig. 2F – 2G).
5	2/4	Tarsal segmentation (Fig. 2E).
6	3/7	Male protarsus/protibia ratio (ppt).
7	2/7	Male metafemur/(metatibia plus metatarsus) ratio (mmm).
8	2/1	Male, protibia, setae (Fig. 2H).
9	2/6	Male metatarsus/metatibia ratio (mmr).
Forewings		
10	3/2	Imago, hind margin fringe. (Fig. 2D).
11	3/4	iMP/MP_2 ratio (Figs. 1F, 2A).
12	3/6	Male, configuration of CuP and A (Figs. 1F – G; 8A).
13	3/7	Vein iCu_1 (Figs. 1F – G; 2B).
14	4/14	Vein iCu_2 (Figs. 1F; 2A, C; 7D; 8A).
15	3/7	Vein iMP (Figs. 1F; 2A – B).
16	2/1	Marginal intercalaries (Figs. 1F, 2C).
Hind wing		
17	2/3	Male, presence/absence.
18	3/2	Male, costal projection (2D, 8B).
19	2/3	Female, presence/absence.
20	2/1	Posterior margin (imago).
21	2/1	Longitudinal veins (Fig. 2D).
22	3/8	Number of longitudinal veins.
Male Genitalia		
23	2/3	Number of forceps segments (Figs. 3A – E).
24	2/2	Basal swelling of second forceps segment (Fig. 3A – E).
25	3/8	First forceps segment.
26	4/13	Shape of posterior margin of styliger plate (Figs. 3A – B, D; 8A).
27	3/5	Internal basal projection of styliger plate (Figs. 3B – C, E).
28	2/4	Fusion of penis (Figs. 3B – D).
29	4/13	Penes width (Figs. 3B, D; 8C).
30	2/3	Penal spines (Figs. 2B – C; 3A, D – E).
31	3/2	Penal spines position (Figs. 3A, D – E, G; 8C).
32	2/2	Accessory dorsal structure (Figs. 3G – H).
33	2/1	Outer longitudinal processes of penes (Fig. 8D).
34	2/1	Median caudal filament spine (Fig. 8E).
LARVA		
Head		
35	3/4	Frontoclypeal projections (Figs. 4A; 9A).
36	2/3	Genal projections (Fig. 4A).

Table 4. Continued.

Character Number	# States/ Steps	Character Description
LARVA		
37	2/3	Ocellar tubercles (Fig. 4B).
38	2/2	Median occipital tubercle (Fig. 4B).
Mouthparts		
39	3/11	Setae along dorsal margin of labrum (Fig. 9B – C).
40	2/12	Anteromedian emargination of labrum (ael), length to width ratio (4C; 9D).
41	3/2	Postmentum, length to width ratio (plw) (Figs. 4D; 9E – F).
42	2/2	Branched setae along lateral margin of postmentum.
43	4/6	Glossae and paraglossae, fusion ratio (gpf) (Figs. 4D; 9F – G; 10A)
44	2/2	Paraglossa and glossa, length ratio (pgr) (Figs. 4D; 10B).
45	2/2	Labial palps, ratio of segment one to segments two and three (lpr) (Figs. 4D; 9E).
46	4/17	Left mandible, number of outer incisor denticles (Fig. 4E).
47	3/8	Left mandible, number of inner incisor denticles (Fig. 4E).
48	2/2	Left mandible, prostheca (Fig. 4E).
49	4/15	Right mandible, number of outer incisor denticles (Fig. 4F).
50	3/6	Right mandible, number of inner incisor denticles (Fig. 4F).
51	2/3	Right mandible, prostheca.
52	2/2	Right mandible, setae of prostheca.
53	3/4	Mandibles, setae along outer margin (Fig. 4E – F; 10C – D).
54	4/20	Maxillary palp segmentation (Figs. 5A; 10D – F).
55	2/12	Maxillary palp, terminal seta (Figs. 5A; 10E – F).
56	4/5	Maxillary palp, lateral palp setae.
57	4/14	Galea, number of long, curved filiform setae on distal margin (Figs. 5A; 10F – H).
58	2/6	Fusion between galea and lacinia (Figs. 5A; 10E – F).
59	3/15	Maxilla, setae at base of inner margin (Figs. 5A; 10E).
Thorax		
60	2/3	Pronotum, medial tubercles (Fig. 4B, pmt).
61	2/6	Pronotum, antero-lateral projections (Fig. 5C, D, alp).
62	2/3	Mesonotum, anterolateral tubercles (Fig. 5C, mlp).
63	3/3	Mesonoum, median tubercle (Fig. 4B, mmt).
Legs		
64	4/12	Proleg, femoral length/width ratio (5E; 11A – C).
65	5/14	Profemur, form of setae in fore femoral band (dorsal surface) (Fig. 11D – G).
66	3/7	Profemur, number and arrangement of femoral band of setae (Fig. 5E; 11H – I).
67	5/25	Profemur, form of setae along anterior (leading) margin (Fig. 11D – H).
68	2/9	Profemur, number of setae along anterior (leading) margin (Fig. 10H; 11A, I).
69	4/15	Profemur, form of setae along posterior margin (Fig. 11D – F, H).
70	2/8	Femora (all legs), outline of posterior margin.
71	2/3	Profemur, tubercles of anterior margin (Fig. 11J);
72	2/1	Meso- and metafemora, longitudinal ridge (Fig. 5F).
73	5/12	Meso- and metafemora, dorsal surface row of setae (Fig. 5F; 12A – D).
74	3/10	Meso- and metafemora, basal setae (Fig. 11D, F).
75	2/1	Meso- and metatibiae, mediolongitudinal ridge. (Fig. 5F, mel).
76	3/10	Meso- and metatibiae, median longitudinal row of setae (Fig. 12E – F);
77	2/7	Metaleg, metatarsus/metatibia ratio (mmr).
78	2/5	Metaleg, femur/(tibia + tarsus) ratio (fttr).

Table 4. Continued.

Character Number	# States/ Steps	Character Description
LARVA		
79	3/9	Proleg and metaleg, profemur/metafemur ration (pmt).
80	3/12	Protibia, setae of anterior margin (Figs. 12G – H).
81	3/15	Protibia, highly branched setae at distal end (Fig. 12I)
82	3/9	Protarsus, setae of mid-line/anterior margin (Fig. 11A; 12J).
83	3/8	Meso- and metatibia, setae of anterior margin (Figs. 12L – K).
84	3/8	Meso- and metatibia, setae of posterior margin (Figs. 12L – K).
85	3/18	Meso- and metatarsus, setae of anterior margin (Figs. 13A – B).
86	3/18	Meso- and metatarsus, setae of posterior margin (Figs. 13A – B).
87	5/24	Pretarsal claw, submarginal denticles (Figs. 5D, G; 13C – E).
88	4/18	Pretarsal claws, number of marginal denticles (Figs. 5G, 13C, E – F).
Abdomen		
89	2/4	Abdominal terga 1 – 6, posterior margin (Fig. 6E).
90	4/12	Abdominal terga, setae at posterior submargin (Fig. 6E; 13G).
91	3/5	Abdominal terga, setae of sublateral margins (Fig. 13H, slms).
92	2/2	Abdominal sternites five through nine, tubercles (Fig. 6A).
93	2/3	Abdominal terga, raised posterior margins (Fig. 6B, rpm).
94	3/3	Abdominal sternites 7 – 9, relative length of posterolateral projections (Fig. 6C – D, plp Fig. 13I)
95	4/6	Abdominal sternites, posterolateral projections (plp) (Figs. 6C – D; 14A – B; 12J).
96	3/8	Abdominal tergum 7, row of elongate setae on anterior margin (Figs. 14C – D).
97	2/11	Cercus, cercomere joint setae (Figs. 14E – F).
98	2/5	Abdominal segment one, gill.
99	3/3	Abdominal somite 2, gill insertion (Figs. 14D, G).
100	3/8	Abdominal somite 2, operculate gill shape (Figs. 6G – H; 14H).
101	2/2	Abdominal somite 2, operculate gill, beak-like basal process of first lamellae (Fig. 6I).
102	3/11	Operculate gill, arrangement of setae along margin (Figs. 6G – H; 14I).
103	3/4	Abdominal somite 2, gill (Figs. 13G; 14D; 15A – B)
104	3/11	Abdominal somite 2, operculate gill, dorsal ridges (Figs. 6G – H; 15C – E).
105	2/2	Gills 3 – 6, ventral lamellae (Figs. 6F; 15F).
106	2/1	Gills, lamellar structure.
107	3/4	Gill 2, ventral inferior lamella (Figs. 6I; 15G – H; 16A).
108	2/6	Gills 3 – 5, basal flap of dorsal lamellae (Figs. 16B – C).
109	2/3	Gills 3 – 5, dorsal projection of ventral lamella (Figs. 16B – C).
110	3/4	Gill 2, number of lamellae (Figs. 6I; 15F – H; 16D – E).
111	3/5	Gill 3, number of lamellae (Figs. 16B – C, F).
112	3/9	Gill 4, number of lamellae (Figs. 16B – C, F – G).
113	3/4	Gill 5, number of lamellae (Figs. 6F; 16B – C; 16F – G).
114	2/4	Gill 6, presence/absence.
115	3/2	Gill 6, number of lamellae (Figs. 16F – I).
116	2/2	Gill 7, presence/absence.
Body Shape		
117	3/16	Abdomen / thorax, length ratio (atlr).
118	2/3	Body shape.

Table 5. Proposed generic taxonomy for Leptohyphidae.

Family Leptohyphidae Landa and Soldan
Genus *Leptohyphodes* Ulmer, 1920
Genus *Amanahyphes* Salles and Molineri, 2006
Genus *Haplohyphes* Allen, 1966
Genus *Leptohyphes* Eaton, 1882
Genus *Allenhyphes* Hofmann and Sartori, 1999
Genus *Yaurina* Molineri, 2001
Genus *Traverhyphes* Molineri, 2001
Genus *Lumayphes* Molineri, 2004
Genus *Vacupernius* Wiersema and McCafferty, 2000
Genus *Tricorythopsis* Traver, 1958
Genus *Tricorythodes* Ulmer, 1920 (= *Ableptemetes* **n. syn.**, *Cabecar* **n. syn.**, *Epiphrades* **n. syn.**, *Homoleptohyphes* **n. syn.**, *Macunahyphes* **n. syn.**, *Tricoryhyphes* **n. syn.**).
Subgenus *Asioplax* Wiersema and McCafferty, 2000 (**new status**)
Subgenus *Tricorythodes*

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