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Generic Revision of the North and Central American Leptohyphidae (Ephemeroptera: Pannota)

N. A. WIERSEMA

14857 Briarbend Drive, Houston, TX 77035

W. P. MCCAFFERTY

Department of Entomology, Purdue University, West Lafayette, IN 47907
(to whom reprint requests should be sent).

ABSTRACT

The North and Central American Leptohyphidae (Leptohyphinae) consists of *Allenhyphes* Hofmann and Sartori, *Haplohyphes* Allen, *Leptohyphes* Eaton, and *Vacupernius*, n. gen. Leptohyphidae (Tricorythodinae, n. subfam.) of the same region consists of *Asioplax*, n. gen., *Epiphrades*, n. gen., *Homoleptohyphes* Allen and Murvosh, n. stat., *Tricoryhyphes* Allen and Murvosh, n. stat., *Tricorythodes* Ulmer, and *Tricorythopsis* Traver. *Asioplax* is from the Antilles, North, Central, and South America and includes *A. corpulenta* (Kilgore and Allen), n. comb., *A. curiosa* (Lugo-Ortiz and McCafferty), n. comb., *A. dolani* (Allen), n. comb., *A. edmundsi* (Allen), n. comb., *A. nicholsae* (Wang, Sites and McCafferty), n. comb., *A. sacchulobranchis* (Kluge and Naranjo), n. comb., *A. sierramaestrae* (Kluge and Naranjo), n. comb., and *A. texana* (Traver), n. comb. *Epiphrades* is from Central and South America and includes *E. bullus* (Allen), n. comb., *E. cristatus* (Allen), n. comb., and *E. undatus* (Lugo-Ortiz and McCafferty), n. comb. *Vacupernius* is from North and Central America and the Antilles and includes *V. packeri* (Allen), n. comb., *V. paraguttatus* (Allen), n. comb., and *V. rolstoni* (Allen), n. comb. Of species originally placed in *HomoLeptohyphes* only the type *H. dimorphus* (Allen), n. comb., is retained; *H. mirus* (Allen), n. comb. and *H. quercus* (Kilgore and Allen), n. comb., are added. *Tricoryhyphes* is also redefined and includes in North and Central America *T. condylus* (Allen), n. comb. and *T. mulaiki*, n. comb. *Allenhyphes* is revised to include an additional 10 species, including in North and Central America *A. michaeli* (Allen), n. comb., *A. nanus* (Allen), n. comb., and *A. vescus* (Allen), n. comb. Additional regional recombinations include *Tricorythodes costaricanus* (Ulmer), n. comb., *T. robacki* (Allen), n. comb., *Tricorythopsis dicinctus* (Allen and Brusca), n. comb., and *T. melanobranchus* (Allen and Brusca), n. comb. All higher taxa of the Leptohyphidae in North and Central America are reviewed, keyed, and illustrated.

INTRODUCTION

McCafferty and Wang (2000), in their phylogenetic systematics study of the pannote mayflies of the world, confirmed the integrity of the Western Hemisphere family Leptohyphidae, comparatively described it in detail, and showed it to be of Gondwanan origin, with its recent center

of radiation in the Neotropics. They also showed the Leptohyphidae to be the most apotypic family within the superfamily Ephemerelloidea, when viewed in terms of its cladistic position and the accumulated number of apomorphies represented in the lineage. McCafferty and Wang (2000) furthermore suggested that considerable additional study was required at the genus level in the family Leptohyphidae and that descriptions of new genera were imminent. No attempt to divide the family into subfamilies was made by McCafferty and Wang (2000), basically because of the inadequate base of knowledge at that time regarding intrafamilial diversity. Such a base is prerequisite to any hypotheses of relationships and groupings within such a diverse family of mayflies.

The family Leptohyphidae has historically been known primarily by two rather large and widespread genera, *Leptohyphes* and *Tricorythodes*. A few other, poorly known genera had also been described from South America. The broad concepts of *Leptohyphes* and *Tricorythodes* have been problematic, especially in North America and the Antilles, where they had been the only genera of Leptohyphidae recognized. Kluge and Naranjo (1990) went so far as to claim that descriptions of *Tricorythodes* and *Leptohyphes* species were all artificial and random, and proposed to lump species together under *Tricorythodes* by restricting *Leptohyphes* to its type species. We agree only that it has sometimes been difficult to accommodate interspecific variation consistently within the two ambiguous concepts. Unfortunately, as pointed out by McCafferty (1991), the circumvention of such perceived problems of delineation and diagnosis by the unequivocal synonymizing of genera in Ephemeroptera (e.g., as has been attempted in Baetidae and Heptageniidae) is usually not the answer. In fact, such actions have the effect of masking discrete evolutionary lineages and the ultimately important biological information associated with such lineages. Although we found the same symptoms of a systematic problem in the Leptohyphidae as Kluge and Naranjo, we have ascertained the root of the problem to be the lack of sufficient understanding of multiple evolutionary lineages in the family, rather than assuming that only one or few indivisible lineages are involved.

Only meager attempts at parceling or grouping species within the traditional *Leptohyphes* or *Tricorythodes* had been made prior to our study. Allen (1978), for example, included some 18 now valid species (see Baumgardner and McCafferty 2000) into what he called the apache group of species of *Leptohyphes*. It is now obvious that such a grouping was based on the common possession of either inconsequential or ancestral characteristics within the Leptohyphidae. As will be seen below, our present study has revealed that of those 18 species in Allen's apache group, nine not only do not belong to *Leptohyphes*, but actually represent five other genera, two of which are newly described herein.

Allen and Murvosh (1987) split *Tricorythodes* into three subgenera. Although those names, *Homoleptohyphes*, *Tricoryhyphes*, and *Tricorythodes* s.s., are usable for genera that we now recognize herein because of the fortuitous placement of types species, the concepts and species makeup of those taxa have had to be radically revised.

Lugo-Ortiz and McCafferty (1995) noted that their Costa Rican species

Tricorythodes undatus Lugo-Ortiz and McCafferty, along with two other species from Brazil, appeared to represent a finite grouping of species that could be separated easily from other traditional species of *Tricorythodes*. These authors, however, did not place these species in a separate genus at that time. This, however, has been done herein within the framework of the present revision.

Lugo-Ortiz and McCafferty (1995) also described *Leptohyphes curiosus* Lugo-Ortiz & McCafferty from Costa Rica, and noted that it was a unique species with a combination of characteristics that had been associated with either *Leptohyphes* or *Tricorythodes*. They suggested that it was a distinct lineage but took no action at that time to recognize it as a separate genus. Additional members of this lineage were subsequently discovered by Wang et al. (1998) in Ecuador, and by us in Texas. Our further study of this "curiosus" lineage indeed confirmed that it was distinct from other known genera of Leptohyphidae, and in fact was composed of some species originally placed in *Leptohyphes* and other species originally placed in *Tricorythodes*. Importantly, that investigation actually was the one that led to a more comprehensive study of the entire family, especially in North and Central American. This, in turn, not only revealed the presence of other apparently distinct lineages, including those associated with some of the groupings mentioned above as well as others, but also allowed us to redefine the traditional genera *Leptohyphes* and *Tricorythodes*, which we can now consistently diagnose from each other.

Hofmann et al. (1999), in the meantime, had independently placed the Antillean species *Leptohyphes flinti* Allen in a new genus *Allenhyphes*. Our analysis also confirms that generic lineage and allows a further definition of it, including the addition of several more species throughout the Western Hemisphere that require recombination with *Allenhyphes*.

Molineri (1999) gave a first description of the larval stage of *Tricorythopsis*. That discovery has allowed us to recognize that the genus *Tricorythopsis*, which has been known only from South America, is also represented in North and Central America by two species that were previously placed in the genus *Leptohyphes*.

Our generic level comparative study has revealed that Leptohyphidae genera characteristically fall into one of two large groupings within the family. Because we are able to associate synapomorphies with both of these groupings, we consider them as two monophyletic subfamilies herein. These subfamilies not only are established based on the criteria of a strict phylogenetic classification (McCafferty 1991) within the context of the infraorder Pannota and superfamily Ephemerelloidea (McCafferty and Wang 2000), but they are very convenient groupings with respect to the diagnosis of genera and species.

Below we describe the two subfamilies of Leptohyphidae and treat each of the genera within these subfamilies that occur in North and Central America. The speciose genera *Leptohyphes* and *Tricorythodes* occur throughout the Western Hemisphere and although we have studied considerable species from South America and the Antilles, we are not confident at this time in fully knowing the extent of variation in these groups outside North and Central America. Our preliminary analysis of

the South American fauna suggests that additional undescribed genera are perhaps represented by these groups in South America. Thus, herein we emphasize characteristics we have discovered to be of importance in the diagnoses of genera in North and Central America. We list only the North and Central American species under the treatments of previously named taxa, i.e., *Allenhyphes*, *Homoleptohyphes*, *Leptohyphes*, *Tricoryhyphes*, *Tricorythodes*, and *Tricorythopsis*, except we note any species that are newly recombined, including any from South America or the Antilles. Additionally, our larval and adult key to the genera is designed for the North and Central American representatives and we cannot guarantee its unqualified use for fauna outside these regions.

Material examined data in each of the generic treatments within this paper are given in short form to conserve space, except for new records, which are given in detail. Acronyms for the collections cited are BYU (Monte L. Bean Life Science Museum, Brigham Young University), CAS (California Academy of Sciences), CSU (C. P. Gillette Museum of Arthropod Diversity, Colorado State University), CU (Cornell University Insect Collection), FAMU (Florida A & M University), JRD (private collection of J. R. Davis), NAW (private collection of N. A. Wiersema), and PERC (Purdue Entomological Research Collection).

SYSTEMATICS

Subfamily Leptohyphinae, sensu stricto

The Leptohyphinae is distributed in South America, Central America, the Antilles, and North America. It presently includes the following genera: *Allenhyphes* Hofmann and Sartori, *Cotopaxi* Mayo, *Haplohyphes* Allen, *Leptohyphes* Eaton, *Leptohyphodes* Ulmer, and *Vacupernius*, n. gen. Of the currently established genera, only *Cotopaxi* and *Leptohyphodes* are confined to South America. The other four genera are represented in Central and North America and therefore are treated in some detail below. The existent material of *Cotopaxi* is fragmentary and remains enigmatic, but based on our examination of the shape of the forewing, the extent of crossvenation, venation within the cubital region, mesonotal and genitalic morphology, it would fall within the Leptohyphinae (see figures 1-7, Mayo 1968). There is at least one additional genus in this subfamily from South America, represented by *Leptohyphes indicator* Needham and Murphy from Argentina and Uruguay.

Members of this subfamily share the presence of posteromarginal tergal spines on abdominal segments 1-10 or 2-10 in the larvae (Figs. 24, 35), and the presence of hindwings (hindwingpads) in all males and some females (apparently independently lost in some genera). The mesonotum of the adults (Figs. 2, 3) is characterized by having the anterior parapsidal and posterior parapsidal sutures remaining independent of each other posteriorly to the level of the transverse interscutal suture, with the posterior parapsidal suture appearing to end at, or merge with, the interscutal suture. In addition, the pair of posterior scutal lobes (posterior of the transverse interscutal suture) are well developed and relatively

close to each other anteriorly, and there is a variously developed posterior transverse sulcus formed medially near the anterior margins of these lobes. The caudal filaments of female adults in the Leptohyphinae are similar to those of males in that cerci are not reduced relative to the median caudal filament. Adult tarsi (Figs. 11, 25, 39) are four segmented in both sexes, and the ventral side of segment 3 is distally extended. Forewings (Figs. 18, 37) in this subfamily are not highly sexually dimorphic, and species have relatively extensive crossvenation.

When the characteristics associated with the Leptohyphinae are compared with those of the closely related pannote families (see McCafferty and Wang 2000), it becomes clear that of the two subfamilies established here within the Leptohyphidae, the Leptohyphinae is the most plesiotypic grouping in terms of total characteristics. Although most of the characteristics above can be safely regarded as plesiomorphic, given the entire Pannota outgroup, there are at least two features that provide synapomorphic evidence of the Leptohyphinae sharing a common ancestor and thus being monophyletic. The most compelling synapomorphic evidence is the independence of the anterior and posterior parapsidal sutures to the level of the transverse interscutal sutures (Figs. 2, 3). Although this feature in not unique among mayflies, the preponderance of mesonota that we have examined both within and without the Pannota show anteriorly merged parapsidal sutures, such as found in the Tricorythodinae n. subfam. (Figs. 4, 5), to be the rule. Within the Pannota, we have thus far detected a clear independence of these parasidal sutures to the level of the interscutal transverse suture elsewhere only in the genus *Teloganella* Ulmer (family Teloganellidae), which occurs in Southeast Asia. This is surely a convergence given the relative cladistic relationships of the two families involved, the latter being the most plesiotypic family of the holoptic eyed Ephemerelloidea and the Leptohyphinae representing the most apotypic of that same grouping (McCafferty and Wang 2000). In other Pannota, including the Tricorythidae, which is considered the sister group of the Leptohyphidae (McCafferty and Wang 2000), the mesonotum appears essentially like that of the Tricorythodinae with respect to the merging of the parapsidal sutures. Outside the Pannota, we have seen some homoplasy with respect to the anterior independence of the parapsidal sutures within the Baetidae and to some extent in Leptophlebiidae, both very large and highly diverse families.

The development of the posterior membranous extensions of the wings into relatively long, highly visible structures associated with the mesoscutellum (and which we refer to as "plumidia") might be considered a phenoclinal synapomorphy. Although these features are present in all Leptohyphidae they are only greatly developed in the Leptohyphinae as plumidia (long slender processes). They have secondarily become reduced, however, in *Haplohyphes* in the Leptohyphinae.

In the forewings of Leptohyphinae (Figs. 18, 37), there is a strong tendency for the ICuA1-CuP fork to be incomplete in that the two veins do not connect basally or the fork connection is attained only by a crossvein, or only by a strongly hooked basal curvature associated with ICuA1, the latter of which is probably homologous to the crossvein of

some. We interpret this compromising of the connection of these veins to be another possible synapormorphy for the subfamily Leptohyphinae, because the ICuA1-CuP fork is well formed in other closely related Ephemerelloidea as well as the subfamily Tricorythodinae (see below).

Leptohyphes and *Haplohyphes* (Fig. 18) have more than one crossvein connecting CuA to other longitudinal veins in the cubital area of the forewings. Based on our hypothesis that *Leptohyphes* may represent a basal lineage within the subfamily and that *Haplohyphes* is also a sister to that ancestral lineage (although it has a number of unique features associated with it), it appears that the addition of posterior crossveins distad of the basal crossvein on CuA may have been an initial synapomorphy also attributable to the most recent common ancestor of the Leptohyphinae. This trait is clearly apomorphic within the Ephemerelloidea (McCafferty and Wang 2000).

Genus **ALLENHYPHES**
Figs. 2, 6-14

Type species: *Leptohyphes flinti* Allen, 1973.

Hofmann et al. (1999) stated that the form of the male genitalia (see Fig. 13) provided the principle apomorphy allowing *Allenhyphes* to be distinguished from *Leptohyphes*. The reduction of wing venation, reduced maxillary palpi, and absence of a basal beak-like process on the outer ventral lamella of the operculate gills were used to further characterize the genus. Although the male genitalia can be considered an autapomorphic generic character state defining *Allenhyphes*, the lack of certain crossveins is apparently a species level rather than a generic level characteristic within Leptohyphinae. Also, the maxillary palpal morphology is subject to considerable specific variability and is often a variable trait within genera. The basal beak-like process on the outer ventral lamella of the operculate gills is absent in numerous species throughout the Leptohyphinae and all members of the Tricorythodinae. Its presence, rather than absence, must be considered apomorphic, and as such it appears to be restricted to *Leptohyphes* s. s.

Diagnosis.— In the larvae, the following combination of characteristics will distinguish *Allenhyphes* from other Leptohyphinae: a dorsal mediolongitudinal row of branched setae on the mid- and hindtibiae (Fig. 8); forefemora dorsally with a transverse row of spatulate setae in the distal third (Fig. 7); the absence of a basal beak-like process on the outer ventral lamella of the operculate gills (Fig. 10); operculate gills with ventral lamellae of unequal size (Fig. 10); and the possession of a greatly enlarged submentum (Fig. 6). Larvae of *Allenhyphes* usually also have tarsal claws (Fig. 9) with both a basal and distal set of denticles distinct from each other, although distal denticles are apparently secondarily lost in at least one species.

Adult characteristics associated with known *Allenhyphes* that will distinguish them from adults of other Leptohyphinae include the unique possession of a ventrally directed spike-like spine basally on the medial caudal filament in the males (Fig. 12); a complete lack of hindwing

vestiges in the females; a distally concave subanal plate (Fig. 14) in the females; and mid- and hindtarsi of both sexes that are approximately one-third the length of the respective tibiae.

Species included.— *A. asperlus* (Allen), n. comb.; *A. edmundsi* (Allen) [1973], n. comb.; *A. flinti* (Allen); *A. michaeli* (Allen), n. comb.; *A. minimus* (Allen), n. comb.; *A. nanus* (Allen), n. comb.; *A. rallus* (Allen), n. comb.; *A. spinosus* (Allen), n. comb.; *A. tinctus* (Allen), n. comb.; *A. vescus* (Allen), n. comb.; *A. viriosus* (Allen), n. comb.

Distribution.—South America; Central America; the Antilles; North America.

North and Central American composition.— *A. michaeli* (Mexico, USA); *A. nanus* (Honduras, Panama); *A. vescus* (Mexico, USA).

Material examined.— *A. asperlus*: holotype larva, Peru (PERC). *A. edmundsi*: holotype and paratype larvae, Brazil (PERC). *A. flinti*: paratype larva, Dominica (PERC). *A. minimus*: holotype larva, Brazil (PERC). *A. rallus*: paratype larvae, Peru (PERC). *A. tinctus*: holotype larva, Brazil (PERC). *A. vescus*: larvae, Texas (JRD); larvae, male and female adults (some reared), Texas (NAW); male adult, Texas (CAS). *A. viriosus*: holotype larvae, Brazil (PERC).

Genus **HAPLOHYPHES**
Figs. 15-20

Type species: *Haplohyphes huallaga* Allen, 1966.

This genus was originally described from Neotropical adults by Allen (1966). Descriptions of larvae by Domínguez (1984) and Lugo-Ortiz and McCafferty (1995) have confirmed the distinctiveness of this lineage among the Leptohyphidae. In particular among the Leptohyphinae, there are numerous differences in mouthpart structure between *Haplohyphes* and *Leptohyphes* s. s., for example, regarding the mentum and submentum of the labium (Fig. 15) and the galealaciniae of the maxillae (Fig. 16) [see also comparative figures in McCafferty and Wang (2000)].

Diagnosis.—Importantly, in distinguishing the genera of the Leptohyphinae, *Haplohyphes* is differentiated by the presence of hindwings (hingwingpads) in both male and females (Fig. 19). Additionally, the larvae have a maxilla (Fig. 16) with a well-developed crown, a labium (Fig. 15) with a long neck-like distal half of the submentum (possibly an extended mentum) with a fringe of long hairlike setae marginally on the basal half of the broad submentum proper . Furthermore, in the adults, the membranous outgrowths associated with the mesoscutellum are not developed into plumidia, and the male forceps (Fig. 20) are short and two segmented.

Distribution.—South America; Central America.

North and Central American composition.—*H. aquilonius* Lugo-Ortiz and McCafferty (Costa Rica); *H. mithras* (Traver) (Costa Rica).

Material examined.—*H. aquilonius*: larval holotype, Costa Rica (PERC); larvae, Colombia, Cundinamarca Prov., Río Barrablanco at Aquadita, IV-6-1968, W. P. McCafferty (PERC). *H. huallaga* adult holotype and allotype, Peru (PERC); larvae, Peru (PERC). *H.* sp. adults, Ecuador (PERC).

Genus **LEPTOHYPHES**
Figs. 3, 21-27

Type species: *Leptohyphes eximius* Eaton, 1882.

This genus was established by Eaton (1882). Navás (1920) erected the genus *Bruchella* (type species: *B. nigra* Navás), a name that was later synonymized with *Leptohyphes* by Edmunds et al. (1963). *Leptohyphes* is herein newly defined in North and Central America, resulting from the establishment of new genera along with our redefinition of the genus *Allenhyphes*. Besides certain species previously placed in *Leptohyphes* being moved to *Allenhyphes*, *Asioplax,* n. gen., *Homoleptohyphes,* n. stat., and *Vacupernius,* n. gen., herein, our research also shows that certain other formerly *Leptohyphes* species belong to *Tricorythodes* s. s. and *Tricorythopsis* (see below). In South America and possibly in the Antilles, the concept of *Leptohyphes* requires further refinement. Although we have examined certain materials from South America and the Antilles, additional research in these areas is necessary before our diagnoses and keys can with confidence be expanded to include the entire Western Hemisphere.

Diagnosis.—In North and Central America, *Leptohyphes* larvae are distinguished by the presence of a dorsal longitudinal ridge along the mid- and hindtibiae (Fig. 21), an outer ventral lamella of the operculate gills with a basal beak-like process (Fig. 23) (often difficult to detect), a single uniform row of marginal claw denticles as in Figure 22, and often the presence of hindwingpad vestiges in the females. The caudal filaments of examined species also possess whorls of setae on every other segmental joining and have a few darkened basal segments. We cannot be sure that these latter characteristics will be consistently reliable for distinguishing *Leptohyphes* larvae from other Leptohyphinae genera.

Leptohyphes adults from the region can be distinguished from other adults of the Leptohyphinae by their three-segmented forceps and typical Y-shaped penes (Fig. 26), the absence of a basal spike-like spine on the median caudal filament of males, foretibiae of males of at least some species heavily armored with stout sharp setae ventrally, forewings with ICuA1 basally detached from CuP, a somewhat convex subanal plate in females (Fig. 27), and often the presence of blunt, hindwing vestiges in the females.

Distribution.—South America; Central America; the Antilles; North America.

North and Central American composition.—*L. alleni* Brusca (Mexico); *L. berneri* Traver (Mexico); *L. brevissimus* Eaton (Guatemala); *L. brunneus* Allen and Brusca (Mexico, Guatemala); *L. castaneus* Allen (Costa Rica, Guatemala, Mexico, USA); *L. lestes* Allen and Brusca (Honduras, Mexico); *L. murdochi* Allen (Costa Rica, Panama); *L. musseri* Allen (Guatemala, Honduras); *L. nigripunctus* Traver (Mexico); *L. peterseni* Ulmer (Guatemala, El Salvador); *L. pilosus* Allen and Brusca (Mexico); *L. priapus* Traver (Costa Rica); *L. sabinus* Traver (Mexico, USA); *L. spiculatus* Allen and Brusca (Mexico); *L. tarsos* Allen and Murvosh (Mexico); *L. vulturnus* Allen (Honduras); *L. zalope* Traver (Mexico, Belize, El Salvador, Costa Rica,

Guatemala, Honduras, USA). A number of species of *Leptohyphes* were recently synonymized by Baumgardner and McCafferty (2000). We suspect that some of the above remaining species will also eventually fall to synonymy.

Material examined.—L. musseri: paratopotype larvae, Guatemala (PERC). *L. priapus*: paratype adults, Costa Rica (PERC). *L. sabinas*: larvae and adults, Texas (NAW). *L. zalope*: larvae and adults, Texas (NAW); larvae, Mexico (NAW). [see also extensive materials, including numerous types, examined by Baumgardner and McCafferty (2000)].

Genus **VACUPERNIUS**, new genus
Figs. 28-40

Type species: *Leptohyphes packeri* Allen, 1967.

Larva.—Body relatively elongate, not depressed, with abdomen longer than thorax (Fig. 2, Allen 1978). Head capsule nearly as wide as pronotum. Antennae more than twice as long as head capsule width. Labrum (Fig. 28) quadrate, with moderate anterior emargination in middle third. Mandibles (Figs. 29, 30) robust, with well-developed incisors. Maxillae (Fig. 31) with galealaciniae not narrowed in distal half, subequal to or slightly shorter than stipes, with short apical denticles pointed distomedially on poorly developed crown; palpi three segmented in known species, with second segment sometimes highly reduced resulting in apparently two-segmented palpi. Hypopharynx with lingua nearly truncate, with superlinguae broadly rounded apically. Labium (Fig. 32) with relatively well-developed glossae; submentum fringed with sparse, fine setae. Thorax with lateral margins of pronotum with weak to moderate constriction in posterior third. Hindwingpads present in males, absent in females. Legs relatively elongate; femora much shorter than tibiae and tarsi combined; forefemora (Fig. 33) robust, dorsally with transverse row of spatulate or apparently deeply forked setae medially; mid- and hindtibiae without dorsal longitudinal ridge and row of branched setae; mid- and hindtarsi approximately one-half as long as respective tibiae; claws (Fig. 34) approximately one-half length of respective tarsi, each claw with both basal and distal set (sometimes minute) of denticles, and with preapical setae (sometimes absent due to wear). Abdominal terga with small, sharp posteromarginal spines and long fine setae (Fig. 35); posterior abdominal segments with poorly developed posterolateral projections. Gills on abdominal segments 2-6. Operculate gills obovate (Fig. 36), with two ventral lamellae of subequal size; outer lamellae lacking basal beak-like process. Caudal filaments of North and Central American species with whorls of setae at each segmental joining in mid region of filaments.

Adult.—Head with occiptal tubercles apparently absent. Forewings (Fig. 37) with ICuA1 basally connected to CuP, usually by minute crossvein; field between Sc and MP1 with numerous crossveins. Hindwings (Fig. 38) present in males and absent in females. Legs with four-segmented tarsi (Fig. 39); hindtarsi approximately one-half length of hindtibiae. Mesoscutellum with plumidia. Cerci and median caudal filaments of

both sexes similar in length and diameter. Male forceps three segmented. Penes and subgenital plate of North and Central American species as in Figure 40. Distal margin of female subanal plate shallowly emarginate.

Etymology.— The generic name has a masculine arbitrary ending and is derived from the Latin vacans (unoccupied) and an allusion to perna (shank of leg).

Species included.—*V. packeri* (Allen), n. comb.; *V. paraguttatus* (Allen), n. comb.; *V. rolstoni* (Allen), n. comb.

Distribution.—Central America; Antilles; North America.

North and Central American composition.—*V. packeri* (Belize, Costa Rica, Guatemala, Honduras, Mexico, USA); *V. paraguttatus* (USA).

Material examined.—*V. packeri*: male adults, Texas (CAS); larvae, Texas (JRD, NAW); *V. rolstoni*: paratopotype larvae, Dominican Republic (PERC).

Remarks.—See key, below, for diagnosis.

Subfamily Tricorythodinae, new subfamily

The subfamily Tricorythodinae is distributed in South America, Central America, the Antilles, and North America. It presently includes the following genera: *Asioplax,* n. gen., *Coryphorus* Peters, *Epiphrades*, n. gen., *Homoleptohyphes*Allen and Murvosh, n. stat., *Tricoryhyphes* Allen and Murvosh, n. stat., *Tricorythodes* Ulmer, and *Tricorythopsis* Traver. *Coryphorus* is known only from South America, and the remaining six genera of the subfamily are treated herein.

Members of the subfamily Tricorythodinae are characterized by the absence of posteromarginal spines on at least the terga of gill-bearing abdominal segments of the larvae, and by the absence of hindwings (hindwingpads). Additionally, adults have five-segmented tarsi (Figs. 51, 80, 84, 90) rather than the four usually found in other Ephemerelloidea, including the sister subfamily Leptohyphinae. Both the ventral aspect of the tibiae and tarsal segment 4 are extended distally. In the adults, the anterior parapsidal suture of the mesonotum (Figs. 4, 5) merges with the posterior parapsidal suture just anterior to, or at, the transverse interscutal suture. The posterior scutal lobes are poorly developed or are well separated from each other anteromedially and thus there is usually no indication of a transverse sulcus in the vicinity of the transverse interscutal sutures (the exception being in the very small *Tricorythopsis*). Sexual dimorphism is highly developed in the forewings with respect to wing shape. The male wing is subtriangulate and usually widest in the basal third, whereas the female wing is generally subobovate and widest medially. Members of this subfamily also have forewings (Figs. 50, 91) in which the crossveins are relatively few in number and generally lack pigmentation (there is usually only one crossvein, or sometimes none, attaching CuA to any posterior longitudinal veins in the cubital region). The ICuA1-CuP attachment in the forewings is complete in that it involves a direct connection of these veins to form the ICuA1-CuP fork. The fork is usually 45-degree angle or less at the joining, except in some very small *Tricorythopsis* where it may be greater. The cerci of female adults are often reduced in length and width relative to the median caudal filament.

The paired posterior membranous outgrowths of the forewings in the posterolateral area of the mesoscutellum of adults of the subfamily Tricorythodinae have often been missed by workers, and their supposed absence in some genera has been given as a key or diagnostic characteristic (e.g., Traver 1958; Domínguez et al. 1992, 1994). Our research has shown that these structures are found in alate stages of all members of the Tricorythodinae. They are generally small and often tucked beneath the edge of the mesoscutellum of males, but are more obvious in females. In any case, however, these peculiar outgrowths are not well developed into plumidia in the subfamily Tricorythodinae, as they are in most genera of the Leptohyphinae (Figs. 2, 3) (not developed in *Haplohyphes*).

Although spines are not found on the posterior margins of abdominal terga of gill bearing segments in the known larvae of the Tricorythodinae, various types of setae may occur there. Abdominal terga 7-10 may or may not have small, sometimes irregular posteromarginal spines.

Of the characteristics associated with the subfamily Tricorythodinae and given above, the synapomorphies involving the larval armature, and adult tarsal segmentation, and dimorphic wing shapes are sufficient to define this subfamily cladistically. The mesonotum of Tricorythodinae is basically plesiomorphic in terms of the orientation of the parapsidal sutures compared with other Pannota and near relatives of the Pannota (see discussion under Leptohyphinae, above). The usually underdeveloped posterior scutal lobes and their relatively wide separation medially (Figs. 4, 5), and the usually associated absence of any posteromedial transverse sulcus might be interpreted as derived. However, this is essentially the situation that is found in many mayflies that lack hindwings. If associated with hindwing loss, then it is apomorphic but is obviously highly subject to homoplasy as seen by the plethora of independent hindwing loss in Ephemeroptera.

The strictly South American genera *Coryphorus* and *Cotopaxi* are known from only one of the major life stages: larvae and adult, respectively. Because of this, McCafferty and Wang (2000) suggested that eventually stage association could possibly prove them to be the same genus. However, their respective placement in the Tricorythodinae and Leptohyphinae, which has become evident in our study, precludes such a possibility.

Genus **ASIOPLAX**, new genus
Figs. 1, 41-52

Type species: *Tricorythodes edmundsi* Allen, 1967.

Larva.—Body (Fig. 1; Fig. 10, Lugo-Ortiz & McCafferty 1995) relatively short and depressed, with abdomen shorter than thorax. Head capsule nearly as wide as pronotum, fringed with fine setae. Antennae subequal to, or slightly longer than, head capsule width. Labrum (Fig. 41) with slight to moderate anterior emargination in middle third. Mandibles robust (Figs. 42, 43), with reduced molae. Maxillae (Fig. 44) with galealaciniae narrowed in distal one-half or more, with apical denticles pointing distally and no crown formed; palpi absent or one to three

segmented. Hypopharynx with lingua approaching truncate, and with superlinguae broadly rounded apically. Labium (Fig. 45) with small but well-defined glossae; submentum fringed with long, bristle-like setae. Thorax (Fig. 1) with lateral margins of pronotum nearly parallel and fringed with short, fine setae. Hindwingpads absent in both sexes. Legs (Fig. 1) short, with robust setae; femora subequal in length to tibiae and tarsi combined; femora and tibiae of some with dense row of long, well-demarcated setae along anterior and posterior margins; tibiae subequal in length to tarsi. Forefemora broadly expanded and bordered by setae, dorsally with transverse row of long dense or short spatulate setae in basal third (Fig. 1; Fig. 8, Allen and Murvosh 1987; Fig. 23, Allen 1978); claws (Fig. 46) about one-half length of respective tarsi, strongly curved, with ventral denticles, and with preapical setae (sometimes absent due to wear). Abdominal segments (Fig. 1) fringed with fine setae laterally; segments 2-6 reduced in length; segments 7-9 with well-developed posterolateral projections, posterolateral projections of terga 7-8 longer than medial length of terga 7-8. Dorsal abdominal tubercles present or absent. Gills on abdominal segments 2-6. Operculate gills (Figs. 1, 47-49) with rounded outer and inner margins, broadly subobovate, somewhat pointed apically in some, or somewhat pointed and falcate distolaterally in some; inner ventral lamellae of operculate gills absent or approximately one-third or less that of outer lamellae. Caudal filaments with whorls of setae at each segmental joining.

Adult.—Head with large occipital tubercles. Forewings (Fig. 50) 2.2-4.0 mm in length, with relatively few crossveins (venation of males pale, venation of females usually pigmented), in males, widest in basal third, in females, widest medially. Hindwings absent in male and females. Legs with five-segmented tarsi (Fig. 51). Mesoscutellum with short membranous processes in females; processes usually minute in males. Cerci of females shorter than body length and without setae; median caudal filament 2-3 times as long as body length and covered with numerous relatively long setae. Male genitalia (Fig. 52) with three-segmented forceps, and short, wedge-shaped penes; subgenital plate of males deeply emarginate medially (forcep bases extended posteriorly beyond midposterior margin of subgenital plate), and with moderate to well-developed distally projecting corners.

Etymology.—The generic name is feminine in gender and is derived from the Greek asio (muddy) and plax (flat plate or disk).

Species included.—*Asioplax corpulenta* (Kilgore and Allen), n. comb.; *A. curiosa* (Lugo-Ortiz and McCafferty), n. comb.; *A. dolani* (Allen), n. comb.; *A. edmundsi* (Allen) [1967], n. comb.; *A. nicholsae* (Wang, Sites and McCafferty), n. comb.; *A. sacculobranchis* (Kluge and Naranjo), n. comb.; *A. sierramaestrae* (Kluge and Naranjo), n. comb.; *A. texana* (Traver), n. comb.

Distribution.—South America; Central America; the Antilles; North America.

North and Central American composition.— *A. corpulenta* (USA); *A. curiosa* (Costa Rica); *A. dolani* (USA); *A. edmundsi* (USA); *A. texana* (Mexico, USA).

Material examined.— *A. corpulenta*: larvae, Utah (PERC). *A. curiosa*: holotype larva, Costa Rica (PERC). *A. dolani:* larvae, North Carolina (PERC); larvae and reared male adults, South Carolina (NAW). *A. edmundsi*: larval paratypes, larvae, adults, Utah (PERC). *A. texana*: paratype female adult, Texas (PERC); larvae, Texas (JRD, NAW, PERC); adults, Texas (NAW); larval paratypes misidentified as *Tricorythodes edmundsi*, Tamaulipas, Mexico (FAMU). *T.* sp.: adult, Texas (NAW).

Remarks.— *Asioplax* is a broad, short and stout, almost round appearing form as a larva. This is due to both the relative short abdomen and the very broad femora of the legs held against the side of the body. Convergences of this type of body shape and appearance may be found in the Tricorythidae (African Dicercomyzinae) and in one or two species of Ephemerellidae (North American Timpanoganinae). There also appears to be some South American Leptohyphinae that approach the *Asioplax* body plan.

Genus **EPIPHRADES**, new genus
Figs. 53-61

Type species: *Tricorythodes undatus* Lugo-Ortiz and McCafferty, 1995.

Larva.—Body relatively elongate, with thorax shorter than abdomen. Head capsule narrower than pronotum (Fig. 53). Small ocellar tubercles present (Fig. 53; Figs. 59, 63, Allen 1967); occipital tubercles present or absent. Antennae longer than head capsule width. Labrum (Fig. 54) width approximately twice that of length. Mandibles robust (Figs. 55, 56). Maxillae (Fig. 57) with galealaciniae with poorly developed crown, with apical denticles pointing mediodistally; palpi one to three segmented. Hypopharynx with lingua approaching truncate and with superlinguae broadly rounded apically. Labium (Fig. 58) with well-defined glossae; submentum long and relatively narrow, with lateral margins fringed with long, bristle-like setae. Thorax relatively long and narrow. Pronotum acute anterolaterally; lateral margins constricted medially; dorsal tubercle present or absent anteromedially. Mesonotum with paired anterolateral tubercles laterally directed (Fig. 53) or anteromedial tubercle dorsally directed (Figs. 59, 63, Allen 1967), and with well-developed posteromedial tubercle. Hindwingpads absent in both sexes. Legs relatively elongate. Femora narrow-elongate, shorter than tibiae and tarsi combined (Fig. 59), distally with slightly concave posterior margins. Tarsi (Fig. 59) approximately two-thirds length of respective tibiae. Claws (Fig. 59) approximately one-half length of respective tarsi, and with ventral marginal denticles and preapical setae. Abdominal segments fringed with setae laterally; segments 2-6 reduced in length; segments 7-9 narrowed and rounded, with well-developed, somewhat ventrally angled posterolateral projections. Gills on abdominal segments 2-6. Operculate gills (Fig. 60) subrectangulate to approximately triangulate and fringed with setae; inner ventral lamellae of operculate gills (Fig. 61) approximately two-thirds that of outer lamellae. Caudal filaments with whorls of setae at each segmental joining.

Adult.— Unknown.

Etymology.— *Epiphrades* is masculine in gender and derived from the Greek epi (on or after) and the Greek phrades (hints or understanding).

Species included.— *E. bullus* (Allen), n. comb.; *E. cristatus* (Allen) n. comb.; *E. undatus* (Lugo-Ortiz and McCafferty), n. comb.

Distribution.—Central and South America.

North and Central American composition.— *E. undatus* (Costa Rica).

Material examined.—*E. undatus*: larval holotype and paratypes, Costa Rica (PERC). *E. bullus*: paratype larvae, Brazil (FAMU). *E. cristatus*: paratype larval parts on slides, Brazil (FAMU).

Remarks.—Among the Tricorythodinae, *Epiphrades* larvae should be easily distinguished by their various dorsal tuberculation.

Genus **HOMOLEPTOHYPHES**, new status
Figs. 62-71

Type species: *Tricorythodes dimorphus* Allen, 1967.

This name was established originally by Allen and Murvosh (1987) for what they considered to be a subgenus of *Tricorythodes*. As such the taxon was defined to include species that had "obovate" operculate gills and a femoral band made up of "long and delicate" spines. Although the adult male of *T. dimorphus* had been described by Kilgore and Allen (1973), no reference was made to adult morphology by Allen and Murvosh (1987). Included originally in the subgenus were the species *T. corpulentus* Kilgore and Allen, *T. curvatus* Allen, and *T. edmundsi* Allen along with *T. dimorphus*. Based on our research, the Allen and Murvosh concept constituted a highly unnatural grouping of species, including elements of *Asioplax* (*A. corpulenta* and *A. edmundsi*, see above) and *Tricorythodes* s.s. (*T. curvatus*, see below). The type species, however, belongs to another group of leptohyphid species that is a natural grouping that includes the type species along with two species that Allen and Murvosh (1987) had continued to include in the genus *Leptohyphes* (see below). It therefore is only fortuitous that the name *Homoleptohyphes* is available for our generic grouping. The concept of the taxon is entirely different from that which was originally ascribed to the name. It is for this reason that it is necessary to provide a complete formal redescription of the genus herein.

Larva.—Body relative elongate, with abdomen slightly shorter to longer than thorax. Head (Fig. 62) with antennae longer than width of head capsule. Compound eyes (Fig. 62) sexually dimorphic, larger in males. Labrum (Fig. 63) narrow and with shallow anterior emargination in middle third. Mandibles (Figs. 64, 65) with well-developed incisors and well-developed molae. Maxillae (Fig. 66) with galealaciniae not narrowed in distal one-half and with partially developed crown with denticles pointing distomedially; palpi one segmented or may appear two segmented in known species. Hypopharnx with lingua shallowly emarginate, and with superlingua broadly rounded apically. Labium (Fig. 67) with submentum fringed with long, bristle-like setae. Thorax with hindwingpads absent in males and females. Tarsi length two-thirds to three-fourths that of respective tibiae. Femoral surfaces with short, spatulate setae, with apices usually bifurcate and serrate (Figs. 24, 25

Allen 1978; Fig. 7, Allen and Murvosh 1987). Forefemora dorsally with medial, transverse row of short, spatulate setae or long relatively robust bristle-like setae, with apices usually bifurcate and serrate. Abdomen and operculate gills (Fig. 68) with scattered bifurcate and simple setae dorsally and marginally (setae short and possibly appearing spatulate in some). Posterolateral projections of abdominal segments 7-9 well developed (Fig. 19, Allen 1978). Gills on abdominal segments 2-6. Operculate gills (Fig. 68) ranging from subobovate to subtriangulate, with inner ventral lamella of operculate gill (Fig. 69) approximately three-fourths or more that of outer lamella.

Adult.—Head with large, paired occipital tubercles. Compound eyes of males greatly enlarged and sexually dimorphic. Lateral ocelli of males separated by distances approximately equal to diameter of lateral ocelli; female lateral ocelli separated by distances approximately equal to diameter of compound eye (Fig. 70). Forewings 4.0-6.8 mm in length, with few crossveins (venation of males pale, venation of females usually pigmented); forewings of males, widest in basal third, in females, widest medially. Hindwings absent in male and females. Legs with five-segmented tarsi. Foretarsi approximately three-fourths length of foretibiae. Hindfemora less than three-fourths length of hindtibae and hindtarsi combined. Mesoscutellum with short membranous outgrowths in females and males. Caudal filaments of females slightly longer than body length and with sparse setation. Male genitalia (Fig. 71) with three-segmented forceps, and wedge-shaped penes; subgenital plate very narrow and shallowly emarginate (forcep bases extended posteriorly well beyond midposterior margin of subgenital plate), and without distally projecting corners.

Species included.—*H. dimorphus* (Allen), n. comb.; *H. mirus* (Allen), n. comb.; *H. quercus* (Kilgore and Allen), n. comb.

Distribution.—North America.

North and Central American composition.—*H. dimorphus* (Mexico, USA); *H. mirus* (Mexico, USA); *H. quercus* (USA).

Material examined.— *H. dimorphus*: adults and larvae, Arizona, New Mexico, Mexico (NAW, PERC). *H. mirus*: larvae, Texas (JRD, NAW, PERC). *H. quercus*: reared adult male and subimago, larvae, Arizona (PERC).

Genus **TRICORYHYPHES**, new status
Figs. 72-81

Type species: *Tricorythodes condylus* Allen, 1967.

This group was originally recognized as a monobasic subgenus by Allen and Murvosh (1987). None of the few characters as they had given and associated with this name can be unequivocally used to diagnose the group; they must be modified or taken in combination with some others. Larvae of *Tricoryhyphes*, as expanded on below, should be easily distinguished by mouthpart setation and morphology, leg setation and claw denticulation, along with the development of the frontal shelf and genal projections. Allen and Murvosh (1987) had emphasized the presence of a

frontal shelf and genal projections, but some *Tricorythodes* s.s. also have moderately developed genal projections and a moderately to well-developed frontal shelf. The triangular shape of the operculate gill used by Allen and Murvosh (1987) is not exclusive to *Tricoryhyphes*, and the "femoral band subapical spines long and delicate" requires elaboration.

Allen and Murvosh (1987) included in the subgenus *Tricoryhyphes* only *T. condylus*, a species that had been described as larvae and male adults (Allen 1967). The alate male paratypes of that species, which we examined, however, are subimagos, and the figure of the male genitalia given by Allen is obviously of a subimago. Nonetheless, examination of some alate material housed within the Purdue Entomological Research Collection revealed a single adult male and two male subimagos collected by W. P. McCafferty, A. V. Provonsha, and R. W. Koss from the Gila River in New Mexico. In addition, we were able to associate *T. mulaiki* (known from adults only) with the genus, allowing a meaningful redescription, which we give as follows.

Larva.—Body relatively elongate, with thorax shorter than abdomen. Head with frontal shelf and genal projections (Fig. 72); frontoclypeal projection present or absent. Compound eyes not sexually dimorphic. Labrum (Fig. 73) short and wide, with width well over twice length. Mandibles (Fig. 74, 75) with dorsal surface heavily armored with stout and fine setae of various lengths. Maxillae (Fig. 76) with crown of galealaciniae moderately developed, with palpi one, two, or three segmented. Hypopharynx with lingua slightly emarginate, and with superlinguae broadly rounded. Labium (Fig. 77) with well-defined, relatively long and narrow glossae; lateral margins of submentum rounded, fringed with long setae (very long basally). Thoracic nota (Fig. 72) without tubercles, fringed with setae. Hindwingpads absent in both sexes. Legs with anterior and posterior margins with long, fine setae. Forefemora dorsally with medial transverse row of fine setae. Hindfemora length subequal to that of hindtibiae and hindtarsi combined. Claws (Fig. 78) with or without minute basal denticles, and with at least single submarginal-subapical denticle, and sometimes with paired submarginal denticles. Abdominal terga with long, fine, marginal setae laterally and posterolaterally. Gills on abdominal segments 2-6. Operculate gills (Fig. 79) triangulate; inner ventral lamellae length approximately two-thirds that of outer lamellae. Caudal filaments with whorls of setae at each segmental joining.

Adult.—Head with small, paired occipital tubercles. Compound eyes not sexually dimorphic. Lateral ocelli widely separated. Forewings 4.5-7.0 mm in length, with relatively few crossveins (venation of males pale, venation of females usually pigmented). Hindwings absent. Legs with five-segmented tarsi (Fig. 80). Male foretarsi less than one-half length of foretibiae. Hindfemora approximately equal to, or longer than, hindtibiae and hindtarsi combined. Hindtarsi relatively short, approximately one-half to one-third length of hindtibiae. Mesoscutellum with short membranous outgrowths. Cerci of females apparently much shorter in length than median caudal filament. Male genitalia (Fig. 81) with three-segmented forceps and wedge shaped to nearly cylindrical penes; subgenital

plate produced distally beyond forcep bases and shallowly emarginate to more or less truncate, and with corners somewhat protruding in North and Central American species.

Species included.—*T. barbus* (Allen), n. comb.; *T. condylus* (Allen), n. comb.; *T. mulaiki* (Traver), n. comb.; *T. ocellus* (Allen and Roback), n. comb.; *T. popyanicus* (Domínguez), n. comb.

Distribution.—South America; North America.

North and Central American composition.—*T. condylus* (Mexico, USA); *T. mulaiki* (Mexico). Given the North and South American distribution of this genus, we expect that it eventually will also be found in Central America.

Material examined.—*T. condylus*: paratype subimagos and larvae, New Mexico (CAS); larvae, Arizona, New Mexico (PERC); male adult and subimagos, New Mexico (PERC). *T. mulaiki*: adult paratypes genitalia and legs, Mexico (PERC).

Genus **TRICORYTHODES** Ulmer
Figs. 4, 82-86

Type species: *Tricorythus explicatus* Eaton, 1892.

The genus *Tricorythodes* was described originally by Ulmer (1920). *Caenopsis* (type species: *C. fugitans* Needham) was described by Needham (1920), but that generic name was preoccupied and replaced by *Tricorythafer* Lestage (1942) and *Needhamocoenis* Lestage (1945), the latter of which was an unnecessary replacement. *Tricorythafer* was subsequently placed as a junior synonym of *Tricorythodes* by Peters and Peters (1993). We agree with that synonymy and that genital forceps segmentation had been misinterpreted by Traver (1958), and we further maintain that *T. fugitans* is a South American species of unknown locale rather than being from Africa, where it had been reportedly taken (Needham 1920). It is obvious to us that Needham confused locales of specimens at a time when he was also working on numerous collections from South America that had been collected primarily between 1918 and 1920 (see Needham and Murphy 1924).

There has been considerable confusion between this genus and *Leptohyphes* sensu lato, especially among species known only from the larval stage. Much of this confusion has resulted from the emphasis that was placed on superficial characteristics by R. K. Allen (see also comments in Introduction). *Leptohyphes* and *Tricorythodes* are only remotely related within the family Leptohyphidae, as is clear from their positions in different subfamilies herein. In North and Central America, *Tricorythodes* is distinct as larvae from other Tricorythodinae genera, which include species previously placed in both *Tricorythodes* or *Leptohyphes* (see elsewhere herein).

Diagnosis.—*Tricorythodes* larvae may be distinguished from larvae of other Tricorythodinae genera in North and Central America (*Asioplax*, *Epiphrades*, *Homoleptohyphes*, *Tricoryhyphes* and *Tricorythopsis*) by the combination of an abdomen that is longer than the thorax; a partially developed crown on the galealaciniae; a submentum that is evenly rounded

along the lateral margin and has long marginal setae in the apical third; a relatively well-developed inner ventral lamella of operculate gills (Figs. 82, 83) that is approximately two-thirds to three-fourths that of the outer lamella; a transverse row of simple setae on the forefemora; and the lack of dorsal thoracic tuberculation. The precise distribution of character states is clearly shown in the larval key to genera, included herein.

For adult diagnosis see distribution of characteristics outlined in the keys below. We do not yet know if the adults of *Tricorythodes* will be distinguishable at the generic level from those of *Epiphrades,* which remains unknown in the adult stage.

Distribution.—South America; Central America; the Antilles; North America.

North and Central American composition.— *T. albilineatus* Berner (USA); *T. allectus* (Needham) (Canada, USA); *T. cobbi* Alba-Tercedor and Flannagan (Canada); *T. comus* Traver (Mexico); *T. costaricanus* (Ulmer), n. comb. (Costa Rica); *T. curvatus* Allen (USA); *T. explicatus* (Eaton) (Mexico, USA); *T. fictus* Traver [= *T. angulatus* Traver, n. syn.] (Mexico, USA); *T. minutus* Traver (Canada, USA); *T. mosegus* Alba-Tercedor and Flannagan (Canada); *T. notatus* Allen and Brusca (Mexico); *T. robacki* (Allen), n. comb. (USA); *T. sordidus* Allen (Costa Rica); *T. stygiatus* McDunnough (Canada, USA); *T. ulmeri* Allen and Brusca (Mexico).

Material examined.— *T. albilineatus*: paratype adults, Florida (FAMU); larvae, Florida (FAMU); larvae and adults some reared, Texas (NAW); larvae, Texas (JRD, PERC); larvae and subimagos, Alabama, South Carolina (NAW); *T. allectus*: larvae, Arkansas, Michigan, Indiana (PERC); larvae, Nebraska, Holt Co, SF Elkhorn R, VI-26-1998, Kondratieff and Rhodes (NAW). *T. angulatus*: holotype and paratype male adults, Mexico (PERC); paratype adults, Mexico (FAMU). *T. cobbi*: paratype male and female adults, Manitoba (PERC). *T. curvatus*: larvae and reared adult and subimago males and females, Texas (NAW); larvae, Texas (JRD). *T. explicatus*: larvae, Arizona, New Mexico, Utah (PERC); larvae and adults, Texas (NAW). *T. fictus:* holotype, paratype, and allotype adults, Oklahoma (CU); paratype male adults, Oklahoma (PERC); reared larvae and adults, Texas, Kimble Co, South Llano R, IV-14-1998, N. A. Wiersema, and Comal Co, Guadalupe St Prk, Honey Cr, VII-16-1997, N. A. Wiersema (NAW). *T. minutus*: larvae, adults, Arizona, Arkansas, California, Colorado, Idaho, Indiana, New Mexico, South Dakota, Oregon, Washington, Wyoming (PERC); larvae, Colorado (NAW); adults, Wyoming (NAW). *T. mosegus*: paratype male and female adults, Manitoba (PERC). *T. mulaiki*: paratype male adult, Mexico (PERC). *T. notatus*: holotype and paratype larvae, Mexico (CAS). *T. sordidus*: larvae, Costa Rica (BYU, NAW). *T. stygiatus*: larvae, Indiana (PERC). *T. ulmeri:* holotype and paratype larvae, Mexico (CAS). *T.* sp.: larvae, Colorado (NAW). *T.* sp.: alates, Texas (NAW). *T.* sp.: larvae and adults, Mexico (NAW).

Genus **TRICORYTHOPSIS**
Figs. 5, 87-92

Type species: *Tricorythopsis artigas* Traver.

This genus was originally described by Traver (1958) based on male adults from Uruguay. Not much else was known of the genus until Molineri (1999) was able to describe the female adult and one larval exuviae from Argentina. That work has allowed us to add two distinctive species from Central America and Mexico to the genus *Tricorythopsis*. Although there are some differences between the distinctive species alluded to and the larval exuviae described from South America, we believe placement in *Tricorythopsis* is called for until the discovery of adults in Mexico or Central may or may not confirm recombination.

Diagnosis.—Larvae of *Tricorythopsis* may be distinguished from those of other genera of the *Tricorythodes* complex in North and Central America by the following combination of characteristics: mature larvae that are less than 3.4 mm in length and have a body that is not depressed and an abdomen that is longer than the thorax; a galealaciniae that lacks any development of a crown (denticles directed apically) (Fig. 4, Molineri 1999); lateral margins of submentum (Fig. 87) that are not evenly rounded or setate throughout, but have some constriction in the distal aspect, and lack marginal setae in the distal one-third; forefemora that have a more or less medial transverse row of spatulate or bristle-like setae (row sometimes interrupted); claws (Fig. 88) that have two parallel rows of submarginal denticles distally (possibly reduced to one denticle on one side), and marginal denticles that may or may not be present. Although the inner ventral lamella of the operculate gills (Fig. 89) is approximately one-half the size of the outer ventral lamella, these ventral lamella are particularly delicate in smaller larvae, such as those of *Tricorythopsis* and can be very difficult to see properly.

Male adults apparently may be distinguished from those of other known adults of Tricorythodinae by the presence of two-segmented forceps raised on distally elongated lateral aspects of the subgenital plate (forceps bases) and that lack any medial bulbous protuberances as typifies many other tricorythodine males. Female adults presumably may be distinguished by caudal filaments that are shorter than the distal three abdominal segments taken together (also see key below). Possibly of some comparative importance may be the consistently small size, the sexually non-dimorphic eyes, apparent absence of paired occipital tubercles, and presence of a posterior transverse sulcus on the mesonotum (Fig. 5).

Distribution.—South America; Central America; North America.

North and Central American composition.—*T. dicinctus* (Allen and Brusca), n. comb. (Belize, Mexico); *T. melanobranchus* (Allen and Brusca), n. comb. (Guatemala).

Material examined.—*T. dicinctus*: holotype larva, Mexico (CAS). *T. melanobranchus*: holotype larva, Guatemala (CAS). *T.* spp. adults, Brazil, Uruguay (PERC).

KEY TO THE NORTH AND CENTRAL AMERICAN GENERA OF LEPTOHYPHIDAE

Larvae

1 Posterior margins of abdominal terga 1-6 without spines, minute spines present or absent on 7-10. Hindtarsi more than one-half length of hindtibiae. Hindwingpads absent ....Tricorythodinae, **2**

1' Posterior margins of abdominal terga 1-10 or 2-10 with spines (Figs. 24, 35). Hindtarsi approximately one-half to much less than one-half length of hindtibiae. Hindwingpads present in males, present or absent in females..... Leptohyphinae, **7**

2 Head with small ocellular tubercles (Fig. 53), medial occipital tubercle present or absent. Mesonotum with paired, anterolateral tubercles (Fig. 53). Operculate gills subrectangulate (Figs. 60, 61) ..... ***Epiphrades***

2' Head without ocellular and occipital tubercles. Mesonotum without anterolateral tubercles. Operculate gills not as above, triangulate to approximately subobovate (Figs. 47-49, 68-69, 79, 82-83, 89) **3**

3 Body relatively dorsoventrally flattened (Fig. 1). Posterolateral projections of abdominal terga 7 and 8 longer than the medial length of respective terga (Fig. 1). Forefemora greatly expanded (width approximately three-fourths to subequal length), and bordered by setae (Fig. 1), and with dorsal setae transversing femora in basal one-third. Inner ventral lamellae of operculate gills absent, or present and ranging to nearly one-half length of outer lamellae (Figs. 47-49) ..... ***Asioplax***

3' Body not relatively dorsoventrally flattened. Posterolateral projections of abdominal terga 7 and 8 no more than subequal to medial length of respective terga. Forefemora not expanded (width no more than two-thirds of length, usually less than one-half as wide as long) not with armature as above, and with dorsal row of setae transversing femora at approximate medlength of femora. Inner ventral lamellae of operculate gills approximately one-half to three-fourths length of outer lamellae (Fig. 68-69, 79, 82-83, 89) **4**

4 Claws with two rows of apical denticles, (sometimes reduced to single denticle on one side) (Fig. 88). Submentum strongly constricted distally and without long bristle-like setae in apical one-third (Fig. 87). Crown of galealaciniae not developed, with apical denticles pointing distally ..... ***Tricorythopsis***

4' Claws without two rows of apical denticles, often with paired submarginal denticles present apically (Fig. 78). Submentum with rounded lateral margins and entirely fringed with long setae (Figs. 67, 77). Galealaciniae with partially developed crown, with apical denticles pointed distomedially (Figs. 66, 76) **5**

5 Head with large genal and frontoclypeal projections (Fig. 72). Claws with one to four minute, basally clustered denticles and with single or paired, subapical denticles (basal denticles sometimes absent due to wear) (Fig. 78). Hindfemora subequal in length to hindtibiae and hindtarsi combined ***Tricoryhyphes***

5 Head without frontoclypeal projections, and with or without small genal projections. Claws with numerous marginal denticles, and with or without subapical denticles. Hindfemora approximately one-half to three-fourths length of hindtibiae and hindtarsi combined **6**

6 Male eyes greatly enlarged, and head wider than pronotum (Fig. 62). Operculate gills approximately subobovate to subtriangulate (Figs. 68, 69). Dorsal femora surface with short spatulate setae (apices bifurcate and serrate). Operculate gills dorsal surface usually with bifurcate setae (Fig. 68) ..... ***Homoleptohyphes***

6' Male eyes not enlarged, and head narrower than pronotum. Operculate gills subtriangulate to triangulate (Figs. 82, 83). Dorsal femoral surface without short, spatulate setae. Operculate gills dorsal surface with only long, simple setae ..... ***Tricorythodes***

7 Forefemora dorsally without transverse row of spatulate setae (Fig. 17). Labium elongate and narrow; submentum with long narrow neck (Fig. 15). Operculate gills relatively elongate and subtriangulate, with fringe of long setae. Hindwingpads present in females ..... ***Haplohyphes***

7' Forefemora dorsally with transverse row of spatulate setae (Figs. 7, 33). Labium not as above; submentum neck very short (Figs. 6, 32). Operculate gills obovate, and usually without fringe of long setae (Figs. 10, 23, 36). Hindwingpads absent or reduced to minute vestiges in females **8**

8 Mid-, hind-, and usually foretibiae dorsally with elevated, mediolongitudinal ridge (Fig. 21). Ventral lamella of operculate gills (Fig. 23) distally constricted and narrowed, and subequal in length and width; outer lamella with basal beak-like process. Claws with only basal, marginal denticle row, with single submarginal denticle often present subapically (Fig. 22) ..... ***Leptohyphes***

8' Mid-, hind-, and foretibiae without elevated, mediolongitudinal ridge (Figs. 7, 8). Ventral lamellae of operculate gills (Figs. 10, 36) not distally constricted and narrowed; outer lamellae without basal beak-like process, and longer than inner lamellae. Claws with basal and apical rows of denticles (Figs. 9, 34) **9**

9 Mid- and hindtibiae dorsally with mediolongitudinal row of branched setae (Fig. 8). Hindtarsi approximately one-third length of respective tibiae. Spatulate setae traversing forefemora in distal one-third (Fig. 7) ..... ***Allenhyphes***

9' Mid- and hindtibiae dorsally without medial longitudinal row of branched setae. Hindtarsi approximately half as long as respective tibiae. Spatulate setae transversing forefemora at midlength (Fig. 33) ..... ***Vacupernius***

Adults

1 Hindwings absent. Tarsi five segmented (Figs. 51, 80, 85, 90). Mid- and hindtibiae of males and all tibiae of females distally extended in ventral aspect (Figs. 51, 80, 85, 90). Mesonotum (Figs. 4, 5) with posterior and anterior parapsidal sutures merged anterior to, or at level of, transverse interscutal suture; posterior scutal lobes well separated at least anteriorly, usually not well

developed; posterior transverse sulcus usually not formed (Fig. 4). Forewings with relatively few crossveins; forewings of males usually widest in basal third (Figs. 50, 91), but those of females widest medially ..... Tricorythodinae, **2**

1' Hindwings present in males (Figs. 19, 38), present or absent in females. Tarsi four segmented (Figs. 11, 25, 39). Mid- and hindtibiae of males and all tibiae of females not distally extended ventrally (Figs. 11, 25, 39). Mesonotum (Figs. 2, 3) with posterior parapsidal sutures ending in transverse interscutal suture (not merging with anterior parapsidal sutures anterior to, or at, interscutal suture); posterior scutal lobes well developed and approximate anteromedially; short posterior transverse sulcus formed; forewings of both sexes widest in basal half and with relatively numerous crossveins (Figs. 18, 37) ..... Leptohyphinae, **6**

2 Forceps two segmented (Fig. 92). Vein IMP longer than MP2 and usually united basally to CuA (Fig. 91). Head without paired occipital tubercles ..... ***Tricorythopsis***

2' Forceps three segmented (Figs. 52, 71, 81, 85, 86). Vein IMP shorter than, or subequal to, MP2 and not united basally to CuA (Fig. 50). Head with paired occipital tubercles adjacent to lateral ocelli (Fig. 70) **3**

3 Male eyes greatly enlarged. Lateral ocelli narrowly separated: in females separated by distance subequal to diameter of eye (Fig. 70), in males separated by distance subequal to diameter of lateral ocellus. Subgenital plate (Fig. 71) slightly concave for entire margin, without distally projecting corners ..... ***Homoleptohyphes***

3' Male eyes not greatly enlarged. Lateral ocelli widely separated: in both sexes separated by distance greater than diameter of eye. Subgenital plate (Figs. 52, 81, 85, 86) not as above, with distally projecting corners **4**

4 Male foretarsi less than one-half length of foretibiae. Hindfemora equal in length to, or longer than, hindtibiae and hindtarsi combined. Subgenital plate (Fig. 81) produced distally beyond forcep bases and shallowly emarginate to approximately truncate medially ..... ***Tricoryhyphes***

4' Male foretarsi greater than one-half (usually two-thirds to three-fourths) length of foretibiae. Posteromedial margin of subgenital plate either produced distally beyond forcep bases (Fig. 85) or not (Figs. 52, 86), if produced beyond forcep bases, then hindfemora less than three-fourths as long as hindtibiae and hindtarsi combined **5**

5 Hindfemora greater than three-fourths to equal length of hindtibiae and hindtarsi combined. Small forms, forewings 2.4-4.0 mm, usually 2.8-3.8 mm ..... ***Asioplax***

5' Hindfemora usually less than three-fourths length of hindtibiae and hindtarsi combined. Larger forms, forewings 3.0-9.0 mm, usually 4.5-6.5 mm ..... ***Tricorythodes***

6 Genital forceps short, robust, and two segmented (Fig. 20). Females with hindwings (Fig. 19). Mesoscutellum without plumidia ..... ***Haplohyphes***

6' Genital forceps three segmented (Figs. 13, 26, 40). Females without hindwings, but some females with minute, blunt, hindwing vestiges. Mesoscutellum with well-developed plumidia **7**

7 Penes Y-shaped, with long well-separated lobes, each lobe with apical incision (Fig. 26). Forewings with ICuA1 not basally connected to CuP (Fig. 19). Foretibiae of known males heavily armored ventrally with sharp, robust setae. Distal margin of female subanal plate broadly convex (Fig. 27) ..... ***Leptohyphes***

7' Penes not as above (Figs. 13, 40). Forewings with ICuA1 basally connected to CuP, usually by a short crossvein (Fig. 37). Foretibiae without sharp, robust setae ventrally. Posterior margin of female subanal plate concave (Fig. 14) **8**

8 Male median caudal filament with large, ventrally directed basal spine (Fig. 12). Male genitalia as in Figure 13. Mid- and hindtarsi less than one-third length of respective tibiae ..... ***Allenhyphes***

8' Medial caudal filament of males without basal spine. Male genitalia as in Figure 40. Mid- and hindtarsi slighty less than one-half length of respective tibiae ..... ***Vacupernius***

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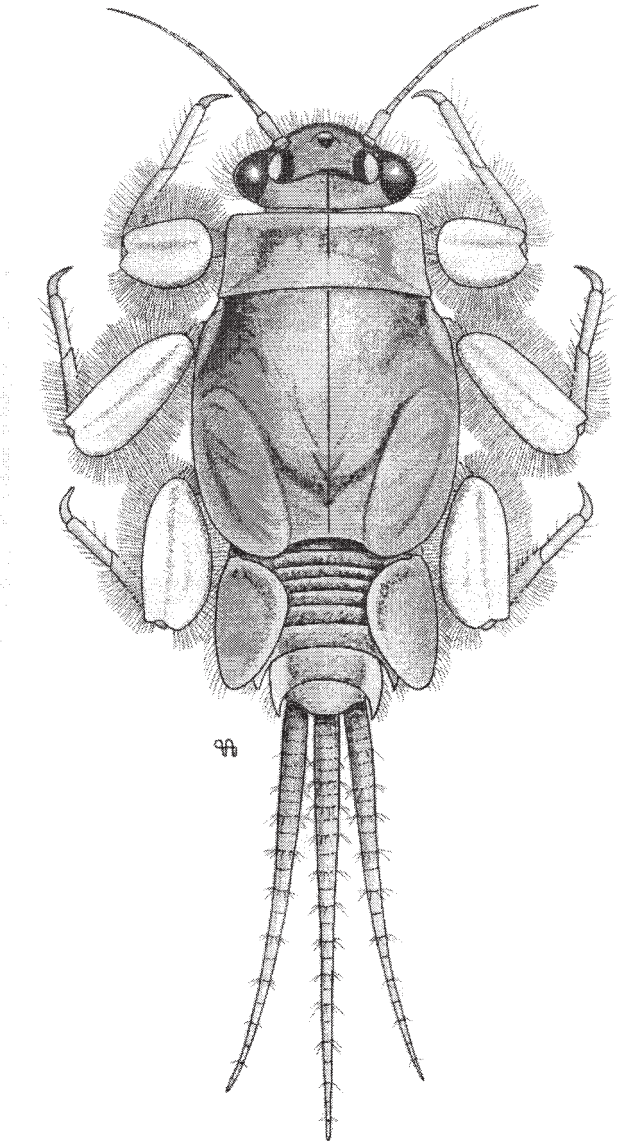
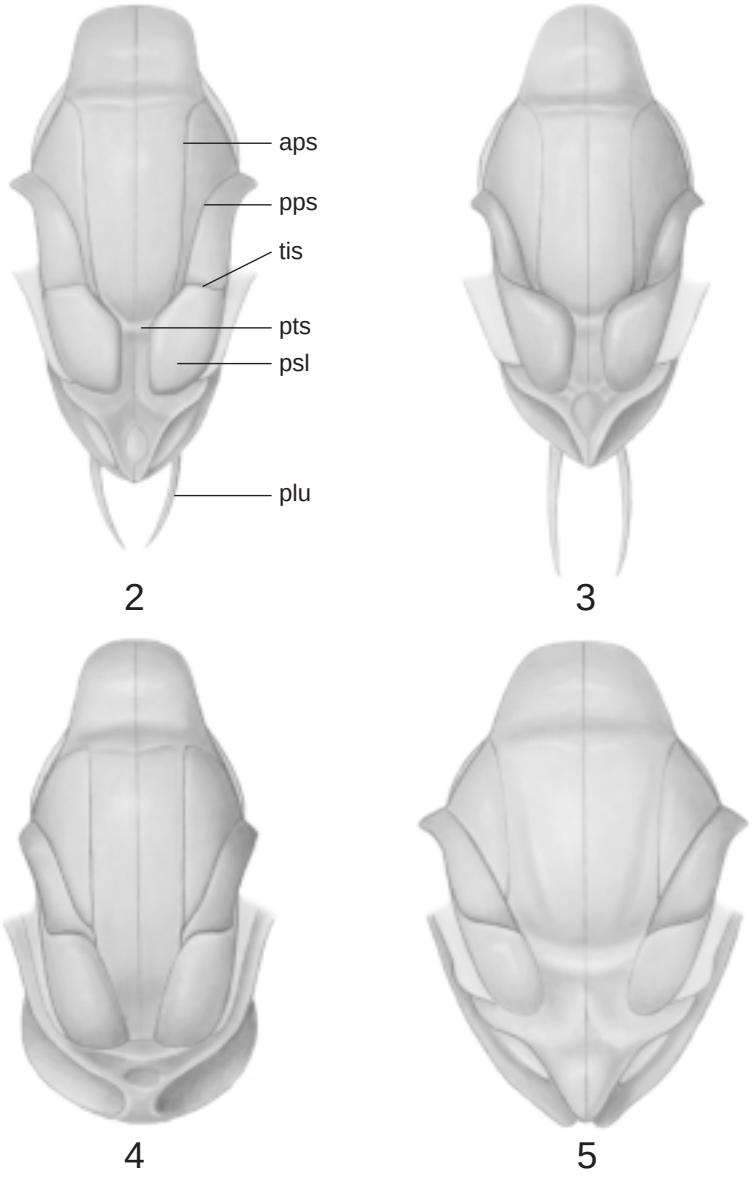
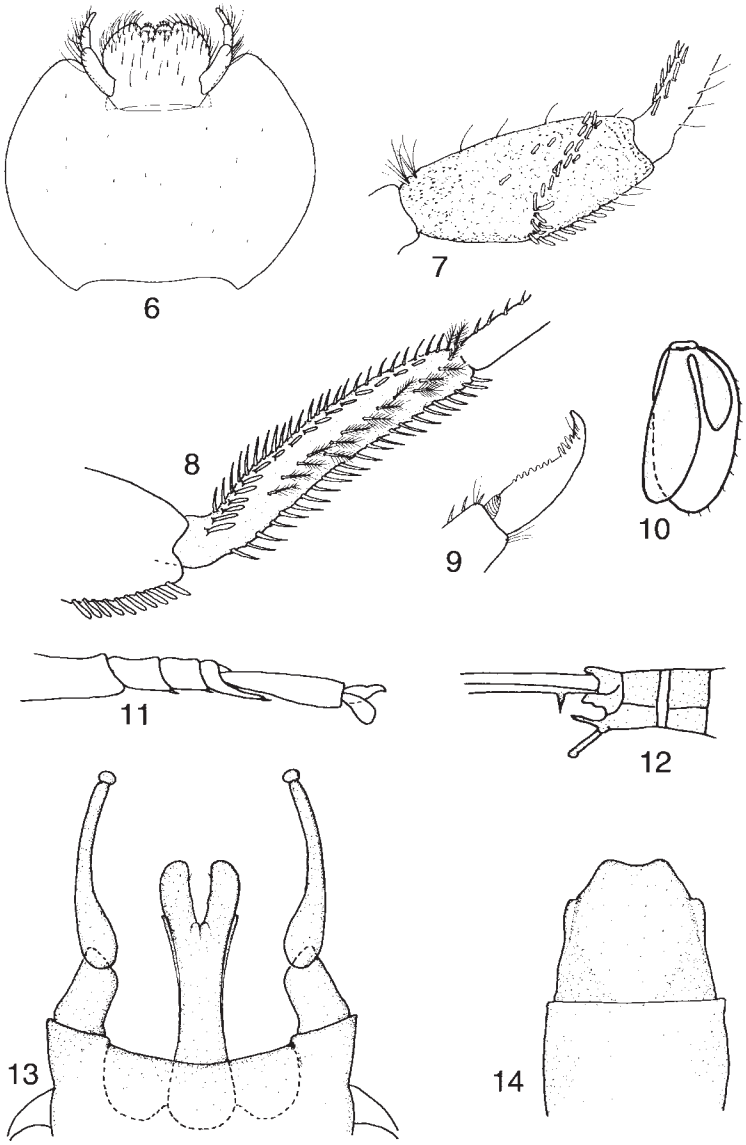


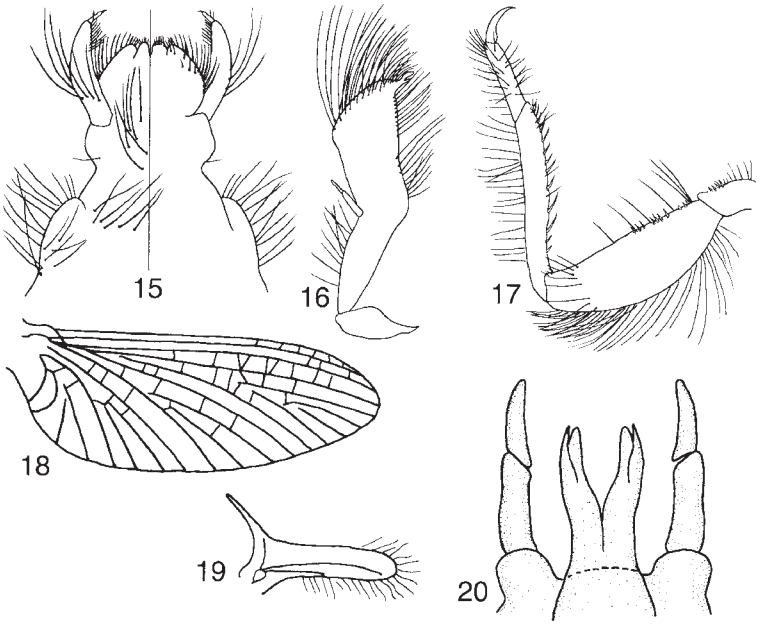
Fig. 1. *Asioplax edmundsi* (Allen) larval habitus.



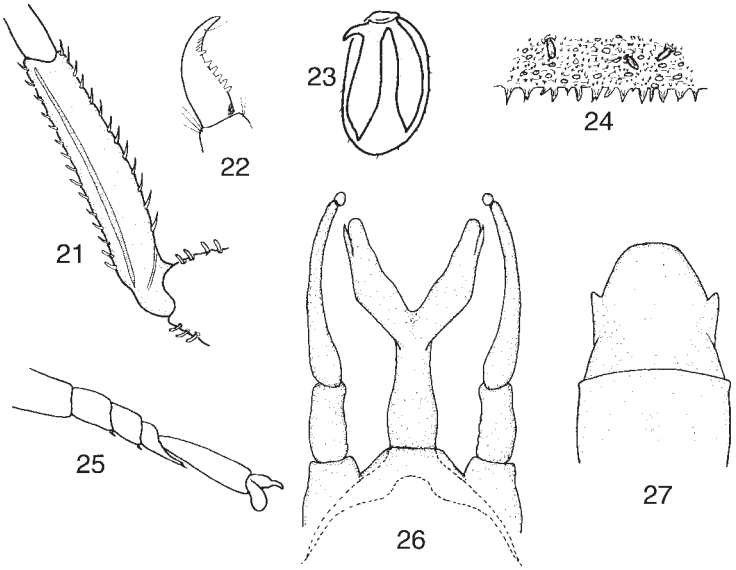
Figs. 2-5. Mesonotum. 2-3: Leptohyphinae. 2, *Allenhyphes* sp. (aps = anterior parapsidal suture, plu = plumidium, pps = posterior parapsidal suture, psl = posterior scutal lobe, pts = posterior transverse sulcus, tis = transverse interscutal suture). 3, *Leptohyphes* sp. 4-5: Tricoythodinae. 4, *Tricorythodes* sp. 5, *Tricorythopsis* sp.



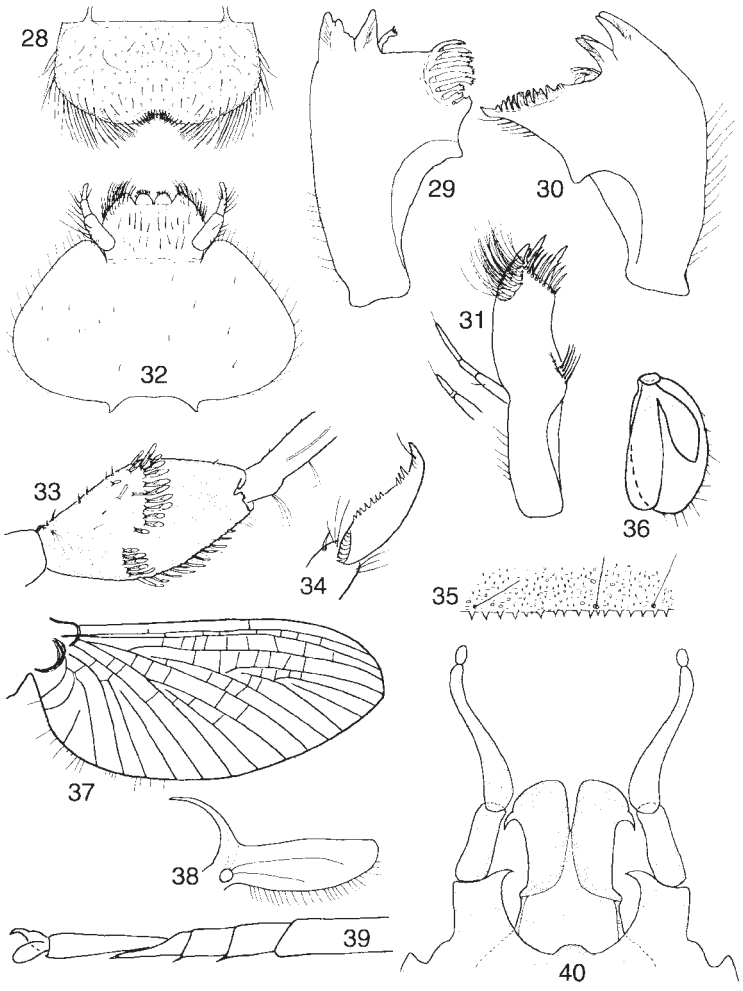
Figs. 6-14. *Allenhyphes vescus* (Allen). 6-10: Larva. 6, Labium (dorsal). 7, Forefemur (dorsal). 8, Midtibia (dorsal). 9, Claw (lateral). 10, Gill 2 (ventral). 11-14: Adult. 11, Hindtarsus and apex of tibia (lateral). 12, Male abdominal terminalia (lateral). 13, Male genitalia (ventral). 14, Female subanal plate.



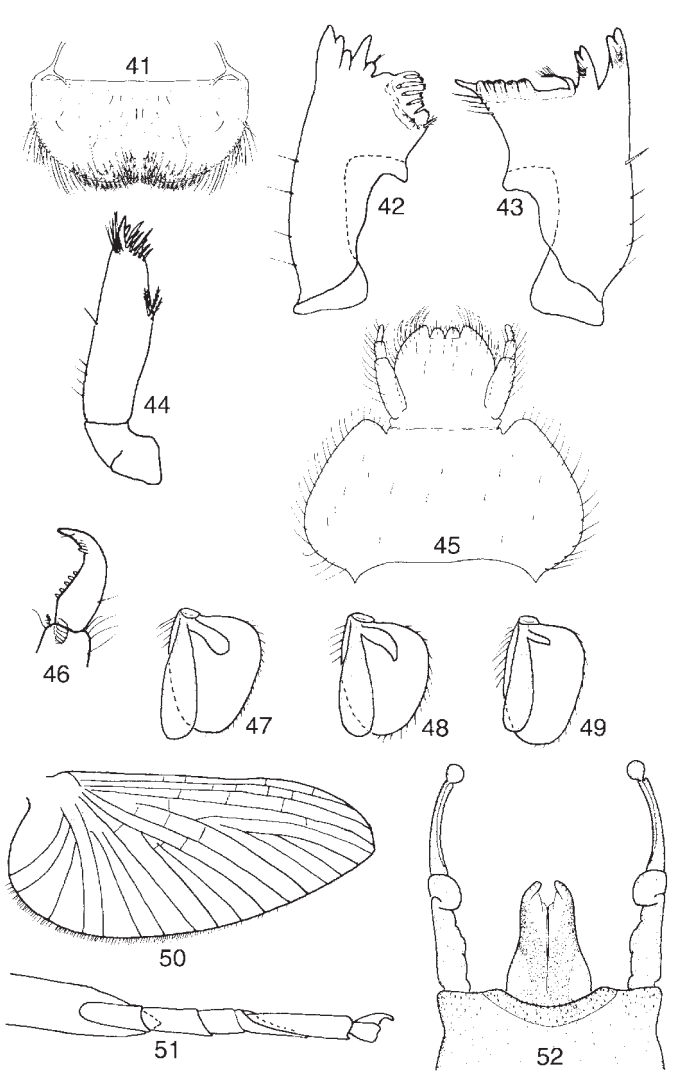
Figs. 15-20. *Haplohyphes*. 15-17, *H. aquilonius* Lugo-Ortiz and McCafferty larva (after Lugo-Ortiz and McCafferty 1995). 15, labium (left-dorsal, right-ventral). 16, Maxilla. 17, Foreleg (dorsal). 18-20: *H. mithras* (Traver) adult (after Allen 1966). 18, Forewing. 19, Hindwing. 20, Male genitalia (dorsal).



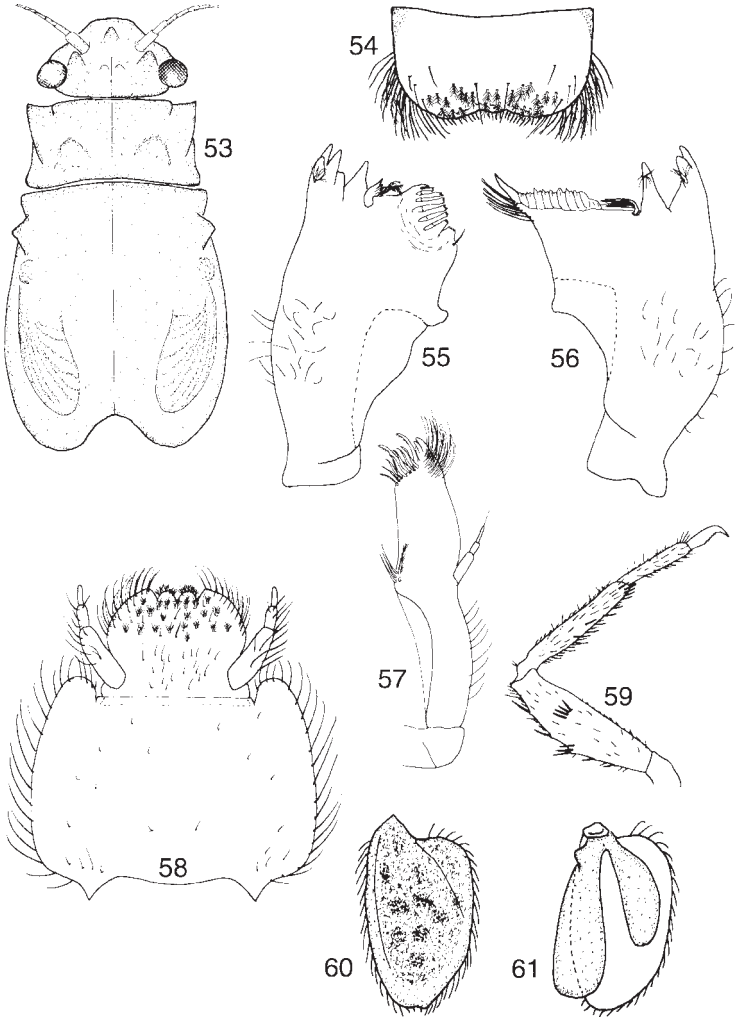
Figs. 21-27. *Leptohyphes zalope* Traver. 21-24: Larva. 21, Midtibia (dorsal). 22, Claw (lateral). 23, Gill 2 (ventral). 24, Abdominal tergum 5 posterior margin. 25-27: Adult. 25, Hindtarsus and apex of tibia (lateral). 26, Male genitalia (ventral). 27, Female subanal plate.



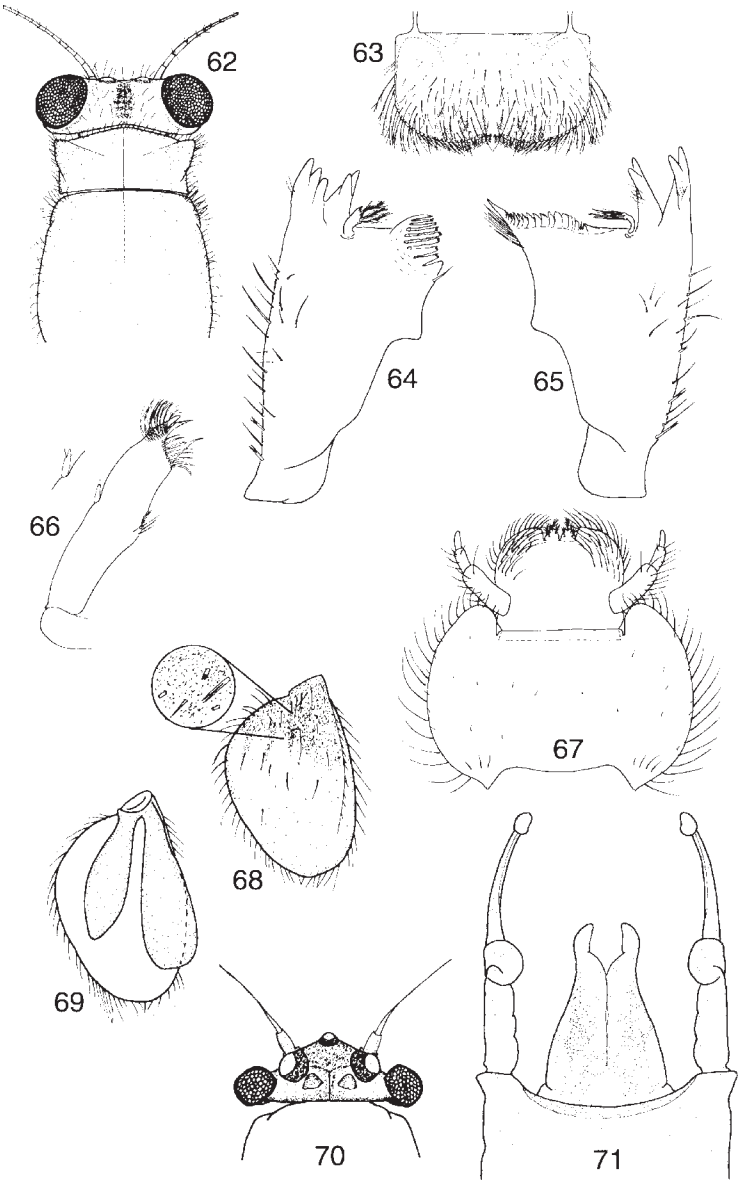
Figs. 28-40. *Vacupernius packeri* (Allen). 28-36: Larva. 28, Labrum (dorsal). 29, Left mandible. 30, Right mandible. 31, Maxilla + palp variant. 32, Labium (dorsal). 33, Forefemur (dorsal). 34, Foreclaw (lateral). 35, Abdominal tergum 5 posterior margin. 36, Gill 2 (ventral). 37-40: Adult. 37, Forewing. 38, Hindwing. 39, Hindtarsus and apex of tibia (lateral). 40, Male genitalia (ventral).



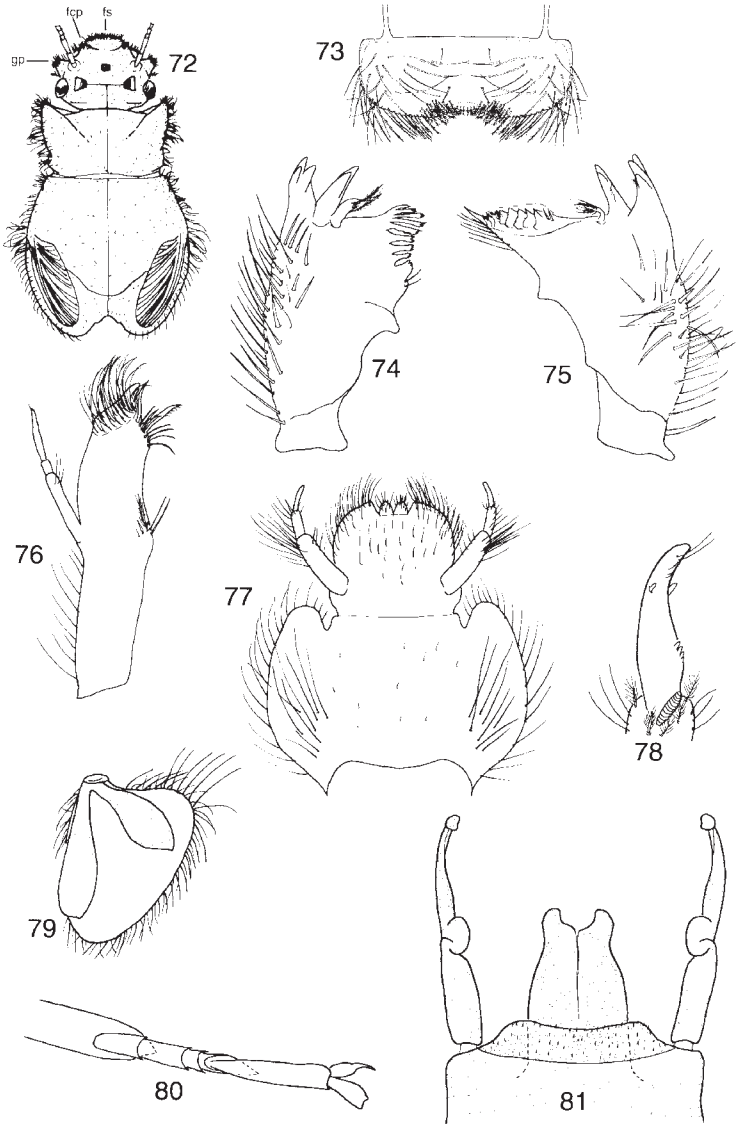
Figs. 41-52. *Asioplax* . 41-46: *A. edmundsi* (Allen) larva. 41, Labrum (dorsal). 42, Left mandible. 43, Right mandible. 44, Maxilla. 45, Labium (dorsal). 46, Claw (lateral). 47-49: Gill 2 (ventral). 47, *A. edmundsi*. 48, *A. texana* (Traver). 49, *A. dolani* (Allen). 50-52: *A. edmundsi* adult. 50, Forewing. 51, Hindtarsus and apex of tibia (dorsal). 52, Male genitalia (ventral).



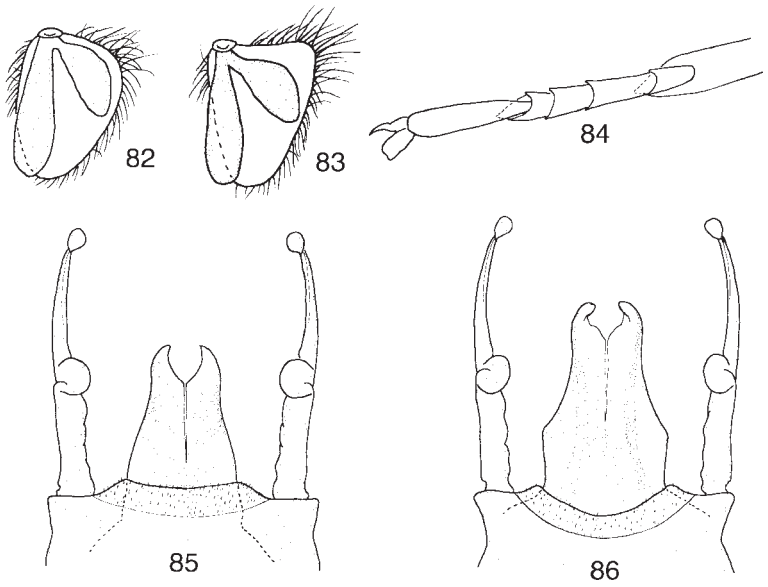
Figs. 53-61. *Epiphrades undatus* (Lugo-Ortiz and McCafferty) larva. 53, Head and thorax (dorsal). 54, Labrum (dorsal). 55, Left mandible. 56, Right mandible. 57, Maxilla. 58, Labium (dorsal). 59, Foreleg (dorsal). 60, Gill 2 (dorsal). 61, Gill 2 (ventral).



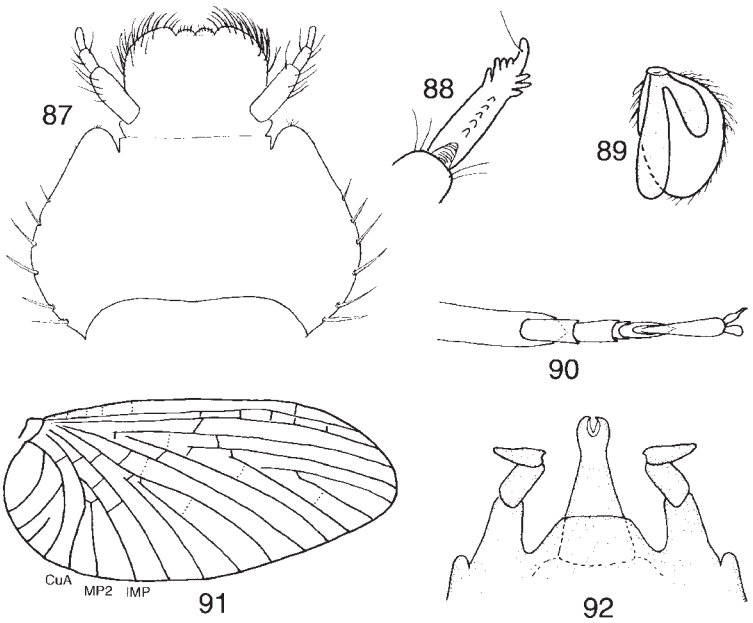
Figs. 62-71. *Homoleptohyphesdimorphus* (Allen). 62-69: Larva. 62, Head and thorax (dorsal). 63, Labrum (dorsal). 64, Left mandible. 65, Right mandible. 66, Maxilla + palp variant. 67, Labium (dorsal). 68, Gill 2 (dorsal). 69, Gill 2 (ventral). 70-71: Adult. 70, Female head (dorsal). 71, Male genitalia (ventral).



Figs. 72-81. *Tricoryhyphes condylus* (Allen). 72-79: Larva. 72, Head and thorax (dorsal) (gp= genal projection, fcp= frontal-clypeal projection, fs= frontal shelf). 73, Labrum (dorsal). 74, Left mandible. 75, Right mandible. 76, Maxilla. 77, Labium (dorsal). 78, Claw (lateral). 79, Gill 2 (ventral). 80-81: Adult. 80, Hindtarsus and apex of tibia (dorsal). 81, Male genitalia (ventral).



Figs. 82-86. *Tricorythodes*. 82-83: Gill 2 (ventral). 82, *T*. sp. 83, T. sp. 84, *T*. sp. adult hindtarsus and apex of tibia (dorsal). 85-86: Male genitalia (ventral). 85, *T*. sp. 86, *T. fictus* Traver.



Figs. 87-92. *Tricorythopsis*. 87-89: Larva. 87, *T. dicintus* (Allen and Brusca) labium (dorsal). 88, *T. dicintus* claw (ventral). 89, *T. melanobranchus* (Allen and Brusca) gill 2 (ventral). 90-92: *T. artigas* Traver adult. 90, Hindtarsus and apex of tibia (dorsal). 91, Forewing (modified from Traver 1958). 92, Male genitalia (ventral).

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