CARLOS MOLINERI

Instituto Superior de Entomología "Dr. A. Willink"-CONICET, Argentina.

PHYLOGENY OF THE *ALLENHYPHES-TRAVERHYPHES* GROUP (EPHEMEROPTERA: LEPTOHYPHIDAE), WITH NEW SUBGENERA, SPECIES AND COMBINATIONS

Molineri, C., 2004. Phylogeny of the *Allenhyphes-Traverhyphes* group (Ephemeroptera: Leptohyphidae), with new subgenera, species and combinations. – Tijdschrift voor Entomologie 147: 197-220, figs. 1-135, table 1. [ISSN 0040-7496]. Published 1 December 2004.

A cladistic analysis of a group of 19 species is presented. These species are distributed in 4 closely related genera of Leptohyphidae (*Allenhyphes*, *Yaurina*, *Lumahyphes* and *Traverhyphes*), that belong to a highly supported monophyletic group. Three subgenera of *Traverhyphes* are proposed to accommodate some new species and combinations. *Traverhyphes (Traverhyphes)* is restricted to *T. (T.) indicator*, *T. (T.) pirai* and *T. (T.) chiquitano* sp. n. *Traverhyphes (Mocoihyphes)* subgen. n. is proposed for *T. (M.) edmundsi* comb. n. and *T. (M.) yuati* sp. n. *Traverhyphes (Byrsahyphes)* subgen. n. is proposed for *T. (B.) nanus* comb. n. and *T. (B.) yuqui* sp. n. Nymphs originally described as *Leptohyphes rallus* Allen are treated here as *Yaurina ralla* (Allen) comb. n. *Lumahyphes pijcha* sp. n. is described from adults and nymphs from Bolivia. A key and illustrations to distinguish all the treated taxa are given.

Correspondence: C. Molineri, Instituto Superior de Entomología "Dr. A. Willink", Facultad de Ciencias Naturales e Instituto M. Lillo, M. Lillo 205, S. M. de Tucumán, (4000), Tucumán, Argentina. E-mail: cmolineri@csnat.unt.edu.ar

Key words: *Leptohyphes*; cladistic analysis; phylogeny; taxonomy; Neotropics.

CONTENTS

INTRODUCTION

The taxonomy of the family Leptohyphidae suffered profound changes in the last few years. Numerous new genera or new combinations were proposed, mainly for a large number of species previously described in two genera, *Tricorythodes* Ulmer (1920) and

Table 1. Matrix of 21 taxa and 39 characters. Character state codes as in appendix 1.

	0 | 10 | 20 | 30
Leptohyphes cornutus	000000000001000000000001000000000020010
Leptohyphes eximius	100001000001000000000001000000000020010
Allenhyphes flinti	112011010012000101010101111111010112100
Allenhyphes vescus	112011010012000101010101111111010112100
Allenhyphes spinosus	----------100111101010-100
Allenhyphes asperulus	----------100111101010-100
Yaurina yapa	11101101101200010110000----------
Yaurina yuta	11101101101200010110000001111101011 3100
Yaurina mota	11101101101200010110000001111101011 3100
Yaurina ralla	----------0011111010113100
Lumahyphes pijcha	01101001000112110100100100111111011 1101
Lumahyphes guacra	01101011110110110100301100111111010 2101
Lumahyphes sp Mexico	0110101111011011010030----------
Lumahyphes yagua	01101011110110110100301100111111010 2101
T. (Traverhyphes) indicator	11111111010011000100200111111011101201
T. (Traverhyphes) pirai	1111111101011100010020----------
T. (Traverhyphes) chiquitano	11111111010111000100200111111011101201
T. (Mocoihyphes) yuati	11101111110111011100300101111011102201
T. (Mocoihyphes) edmundsi	11101111110111011100300111111011102201
T. (Byrsahyphes) nanus	11101211100011010100100111111010113101
T. (Byrsahyphes) yuqui	1110121110001101010010----------

Leptohyphes Eaton (1882). Some of these new genera conform a monophyletic group that includes (Molineri & Domínguez 2003): *Allenhyphes* Hofmann & Sartori (Hofmann et al. 1999), *Lumahyphes* Molineri (Molineri & Zuñiga 2004), *Traverhyphes* Molineri (2001b), *Vacupernius* Wiersema & McCafferty (2000) and *Yaurina* Molineri (2001a). The apomorphies that support this group are: presence of a pair of sublateral acute medial projections on posterior margin of styliger plate (between the forceps), long costal projections on hind wings (more than ½ the length of the wing), hind wings completely absent in females, nymphal gills II to VI with the following number of lamellae: 3/3-4/3-4/3/1-2, absence of a dorsal transverse row of setae at the base of femora II and III, and submentum enlarged.

All the South American species of these genera were cladistically analyzed to give a phylogenetic framework for the classification of the group. The Central American genus *Vacupernius* was not registered from South America and was not included in the analysis because specimens were not available for the study.

The aims of the present paper are: 1) to asses the phylogenetic relationships (at the species level) of a group of related genera; 2) to describe for the first time adults and eggs of *Leptohyphes edmundsi* Allen, and adults of *L. nanus* Allen; and 3) to describe four new species: *Traverhyphes (Traverhyphes) chiquitano*, *Traverhyphes (Mocoihyphes) yuati*, *Traverhyphes (Byrsahyphes) yuqui*, and *Lumahyphes pijcha*.

MATERIAL AND METHODS

Phylogenetic analysis

A matrix of 21 taxa and 39 morphological characters was constructed. The ingroup was composed of 20 species in the genera *Allenhyphes*, *Leptohyphes*, *Lumahyphes*, *Traverhyphes*, and *Yaurina* (see table 1). As seven species are only known from one of the major life stages (adult or nymph), those characters were coded as missing. Trees were rooted indistinctly in *Leptohyphes cornutus* or *L. eximius*. *Allenhyphes vescus* Allen, known from adults and nymphs from Mexico and Texas (Baumgardner 2003) was included to test the monophyly of *Allenhyphes*. Characters are from external morphology of adults (23 characters) and nymphs (16 characters). Multistate characters (10 characters) were treated as non-additive (unordered). The list of characters and states is shown in Appendix 1. The assignation of states to each taxon can be seen in the matrix (table 1).

The matrix was analyzed with the program TNT (Goloboff et al. 2004) conducting an implicit enumeration of the complete set of possible trees and retaining the shortest. This procedure guarantees the hit of all shortest trees, and was performed under two different criteria: common parsimony (i.e. un-weighted) and implied weightings (Goloboff 1993). During searches, trees were treated as non-collapsed, to obtain all possible resolutions.

Absolute and relative Bremer supports (Bremer 1988, 1994) were calculated for the most parsimo-

nious trees and 9000 suboptimal trees up to 10 steps longer. Suboptimal trees were gathered in nine consecutive stages, each stage saving 1000 trees and rising the length of suboptimal trees from 1 to 10 steps longer. In this way, the presence of suboptimal trees of varied lengths permits a more accurate estimation of Bremer supports.

Group supports were also calculated as Frequency Differences (Goloboff et al. 2003), that is the frequency of the group (obtained in the shortest trees) less the frequency of the contradictory more frequent group. Five hundreds (500) replicates of *jackknifing* (Farris et al. 1996) were conducted with symmetrical resampling of the original matrix (for each character the probability of being positively or negatively reweighted is the same, p=0.33, Goloboff et al. 2003). Ten (10) random addition sequences plus TBR (Tree Bisection and Reconnection) were analyzed for each replicate of *jackknifing*, saving ten trees per replicate, and collapsing the trees with TBR rearrangements that give the same fit.

Terminology

The term 'gill formula' is used to indicate the number of lamellae present in each abdominal gill. For example 'gill formula: 3/4/3/3/2' means that abdominal gill II is formed by 3 lamellae, gill III by 4, gill IV by 3, gill V by 3 and gill VI by 2. When interspecific variations occur, the minimum and maximum numbers of lamellae in the genus are given: '3/3-4/3-4/3/2' indicating that in gills III and IV the number of lamellae can be 3 or 4.

The terminology of Kluge (1992) was followed in the descriptions of thoracic structures.

The known distribution of the species is given in the key to facilitate the determination, but it should not be considered as part of the couplet.

Material and deposition

The material used in this study is preserved in 80% ethanol. The male genitalia and nymphal parts were dissected and mounted in Canada Balsam, wings were mounted dried on microscope slides. Glycerin Jelly was used as a temporary-mounting medium for studying male genitalia under different angles. Figures were drawn with a camera lucida mounted on a stereomicroscope. Eggs and male genitalia observed under scanning electron microscopy were dehydrated in a graded ethanol series, and dried by critical point-method using CO_2 in a Bomar apparatus. Then they were mounted with double-sided tape on SEM stubs and sputter coated with gold. They were observed and photographed with a JEOL 35CF Scanning electron microscope at 25 kV.

Institutions housing the material are abbreviated as follows: ANSP, Academy of Natural Sciences of Philadelphia (Philadelphia, USA); CAS, California Academy of Sciences (San Francisco, USA); FAMU, Florida Agricultural and Mechanical University (Tallahassee, USA); IFML, Instituto Fundación Miguel Lillo (Tucumán, Argentina); INTA, Instituto Nacional de Tecnología Agraria (Argentina), MEUV, Museo de Entomología de la Universidad del Valle (Cali, Colombia); MZUSP, Museu de Zoologia, Universidade de São Paulo (Brazil); NMNH, National Museum of Natural History (Washington, USA); UMSA, Universidad Mayor de San Andrés, Instituto de Limnología (La Paz, Bolivia) and SCWR, Stroud Center for Water Research (Philadelphia, USA).

Phylogenetic Analysis

Results

The analyses under both searching criteria (common parsimony and implied weightings) yielded the same 2025 shortest trees (length = 66 steps, fit = 3.70; Consistency Index = 0.742, Retention Index = 0.869). The strict consensus of the 2025 trees is shown in fig. 1. The synapomorphies of the nodes common to all trees are listed in Appendix 2.

Rooting the tree in *Leptohyphes cornutus* or *L. eximius* do not changed the results.

The consensus shows a high internal resolution with the exception of *Allenhyphes? spinosus* and *A.? asperulus*, only known from nymphs, which position is unresolved at the base of the ingroup (node A).

The genus *Allenhyphes* as conformed by Wiersema & McCafferty (2000) appears as polyphyletic. The type species of the genus (*A. flinti*) only is paired with *A. vescus*, relationship supported by four synapomorphies (node C).

Yaurina (node D), including four species, constitutes the sister group of *Allenhyphes*, because of similarities in penean structure of imago, 2-segmented maxillary palpi, and distal denticles of tarsal claws arranged in one row (see appendix 2, node B).

The remaining species (node E) are grouped together by the presence of two new structures in male genitalia: two pairs of apicomedial membranous lobes on penes (a. l. in figs. 130-131), and a dorsal structure associated with penes (a. d. s., figs. 128-129, 131); and one character in nymphs: operculate gills with a subapical lighter mark (depigmented zone, fig. 67). The genus *Lumahyphes* (node F), with four species constitutes the sister group of *Traverhyphes* (node H). This last genus is divided in three groups (nodes I, K and L), that are respectively treated here as subgenera: *Byrsahyphes*, *Mocoihyphes* and *Traverhyphes*.

Group support values can be seen in fig. 1. The best-supported groups under the three estimators calculated (frequency differences, absolute and relative Bremer support) are: node A (*Allenhyphes-Traverhy-*

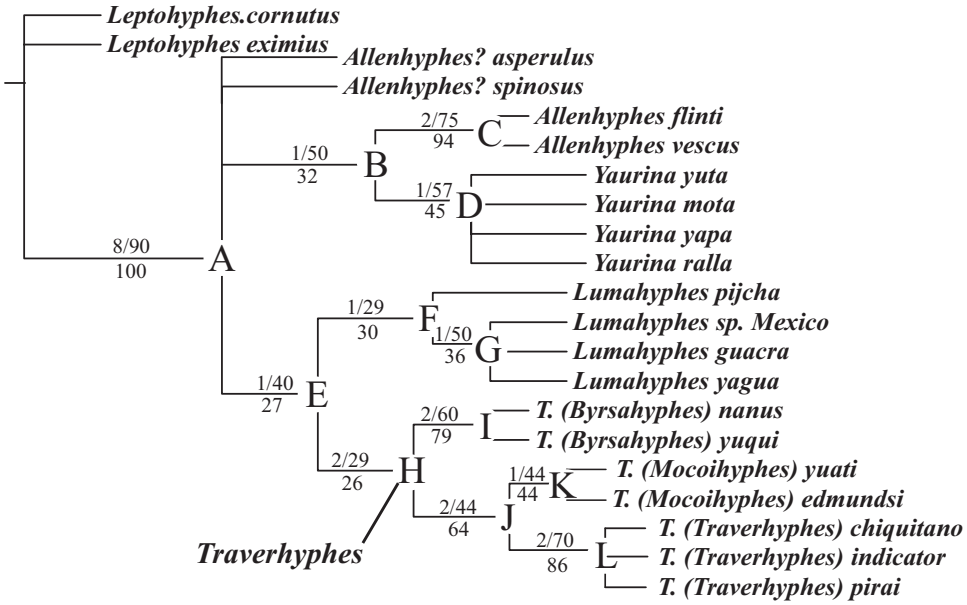


Fig. 1. Strict consensus of the 2025 shortest trees obtained. Numbers above nodes represent absolute and relative Bremer supports. Numbers below nodes represent the support as Frequency differences (see text for explanation).

phes group, 19 spp.), node C (*Allenhyphes flinti* + *A. vescus*), node I (subgenus *Byrsahyphes*, 2 spp.), and node L (subgenus *Traverhyphes*, 3 spp.). Other groups also show relatively high support at least under one of the estimators: node J (subgenera *Mocoihyphes* + *Traverhyphes*, 5 spp.) under frequency differences, and node D (*Yaurina*, 4 spp.) under relative Bremer supports.

Discussion

Wiersema & McCafferty (2000) included ten species in *Allenhyphes*, based on the following nymphal characters: 1) a dorsal mediolongitudinal row of branched setae on the mid- and hind tibiae, 2) fore femora dorsally with a transverse row of spatulate setae in the distal third, 3) absence of a basal beak-like process on the ventral outer lamella of the operculate gills; 4) operculate gills with ventral lamella of unequal size, and 5) greatly enlarged submentum. Only the first character was also given in *Allenhyphes* generic description (Hofmann et al. 1999). None of these features are informative for the analysis presented here since characters 1 to 4 are plesiomorphies and character 5 is a synapomorphy for the entire *Allenhyphes-Traverhyphes* group. Results of this study only recovered two species in the genus *Allenhyphes* (*A. flinti* and *A. vescus*) defined by one nymphal character: presence of distal seta in the maxillary palpi (a rather homoplastic, common state-change). Nevertheless, three adult characters (see appendix 2, node C) support this genus.

As is shown in the consensus (fig. 1), *Allenhyphes? spinosus* and *A.? asperulus* undoubtedly pertain to this group of genera (i.e. not to *Leptohyphes* as originally described by Allen) but their exact position is not resolved. As they show 3-segmented maxillary palpi (figs. 50-51), they could probably be members of *Lumahyphes*, *Byrsahyphes*, or *Vacupernius*. But because this feature is plesiomorphic, it seems better to maintain both species in *Allenhyphes* until the adults are known.

Apart from *Allenhyphes-Yaurina* group (node B), the other large division in the tree is formed by *Lumahyphes* and *Traverhyphes* species (node E). *Lumahyphes* is composed of four species, *Lumahyphes pijcha* (described here and appearing as the basal species of the genus) and *L. guacra*, *L. yagua* and *Lumahyphes* sp. from Mexico (Molineri & Zúñiga 2004).

The node H (genus *Traverhyphes*) includes three groups of species (nodes I, K, L), treated here as subgenera. In the phylogenetic hypothesis obtained, *T. (Byrsahyphes)* (node I) is the sister group of the remaining species of the genus (node J). Two groups form this last node: *Traverhyphes (Traverhyphes)* (node L) and *T. (Mocoihyphes)* (node K).

The description of numerous new taxa within this group of genera is expected. Their future inclusion (as well as the inclusion of *Vacupernius*) in the analysis, should provide a reasonable testing of the phylogenetic hypothesis and group supports presented here.

TAXONOMY

Traverhyphes
(figs. 2-31, 41-46, 48-49, 53-56, 61-84, 100-118, 128-135)

Traverhyphes Molineri, 2001b.

Type species: *Leptohyphes indicator* Needham & Murphy, original designation.

Imago. – Male genitalia: first forceps segments relatively short to very short (⅓-1/5 of the length of second forceps segments figs. 2, 9, 13, 15, 24). Penes relatively slender and with a similar width along their length (figs. 4, 11, 19, 27). Penean spines generally hidden by penes in ventral view, only the basal portion may be seen in some species. Dorsal membranous projections of penes double (d. l. in figs. 12, 18, 26, 131).

Nymph. – Maxillary palpi (figs. 53-56) with 2 or 3 segments reduced in size, with or without apical seta. Abdominal gills with a reduced number of lamellae, gill formula (figs. 61-84): 3/3-4/3-4/3/1-2. Operculate gills ovoid to subquadrate.

Diagnosis. – *Traverhyphes* can be separated from the other genera of the family by the following combination of characters. In the imago: 1) penes with a similar width along their length, with spines inserted dorsally or laterodorsally and hidden by penes in ventral view (figs. 4, 11, 19, 27); 2) vein CuP in fore wings without basal extensions (figs. 5, 8, 20-21, 29); 3) first forceps segments short to very short (figs. 2, 9, 13, 15, 24); 4) dorsal membranous projections of penes double (figs. 12, 18, 26, 131). In the nymphs: 1) maxillary palpi reduced in size, 2-3 segmented with or without apical seta (figs. 53-56); 2) spines on dorsum of fore femora spatulate and smooth apically (figs. 107, 112, 117); 3) gill formula 3/3-4/3-4/3/1-2 (figs. 61-84).

Traverhyphes (*Traverhyphes*)
(figs. 2-4, 53, 61-66, 100-103)

Traverhyphes Molineri, 2001b.

Type species: *Leptohyphes indicator* Needham & Murphy, original designation.

Species included: *T. (T.) indicator* (Needham & Murphy), *T. (T.) pirai* Molineri (2001b), and *T. (T.) chiquitano* sp. n.

Imago. – Male genitalia: styliger plate with a pair of large posterolateral projections (p.p. in figs. 2-3). Penes (fig. 4) with a deep (but inconspicuous) apical furrow. Penes with one pair of rounded membranous lobes on the apex. Lateral margins of penes sclerosed. Penean spines short and straight inserted dorsally or dorsolaterally. Accessory dorsal structure single, pyramidal. Female IX sternum slightly concave at the apex.

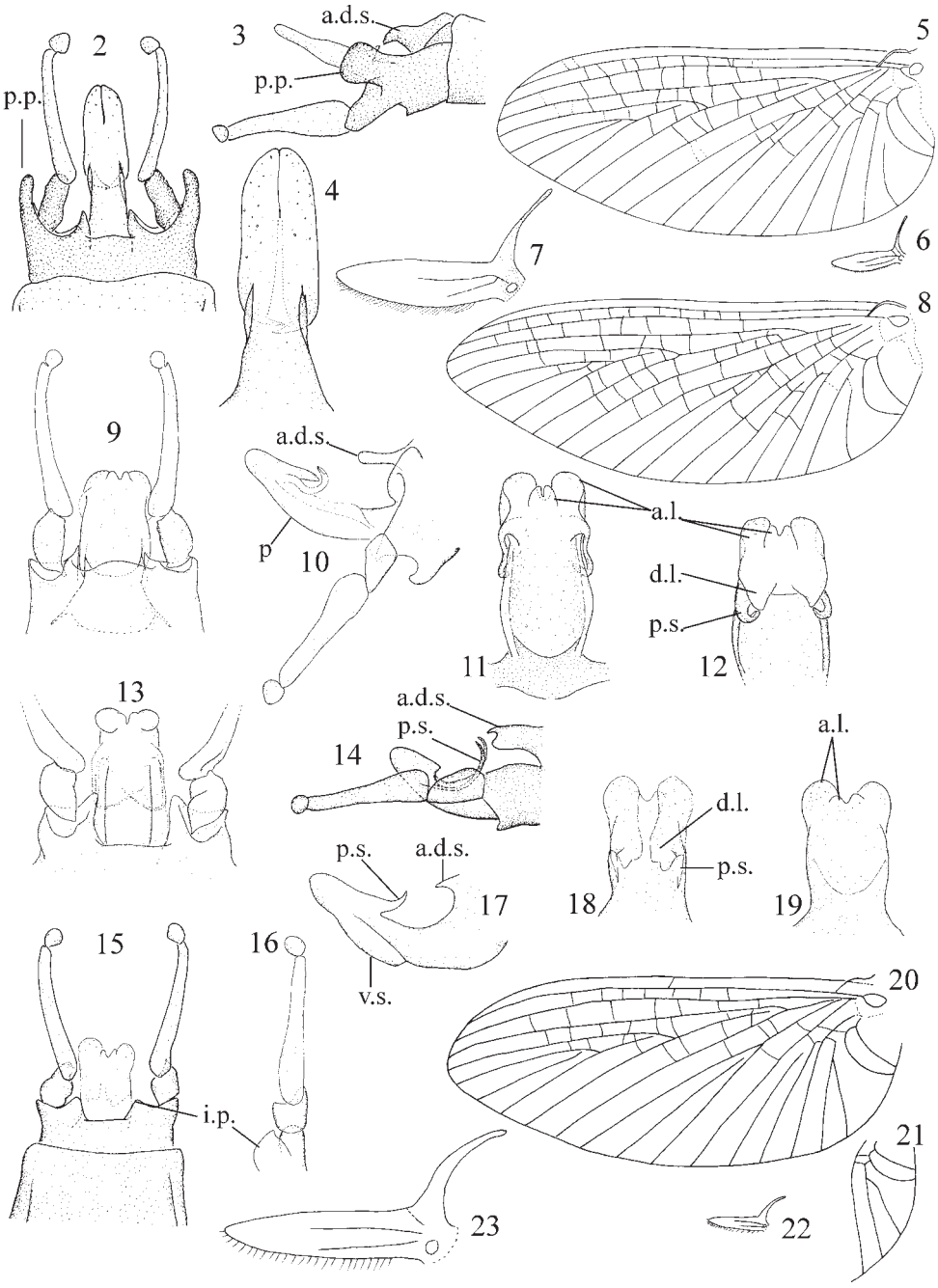
Nymph. – Maxillary palpi small 2-segmented with apical seta (fig. 53). Gill formula 3/4/3-4/3/2 (figs. 62-66). Operculate gills subquadrate (fig. 61).

Diagnosis. – This subgenus can be distinguished from the other by the following combination of characters: 1) posterolateral margins of styliger plate projected rearward (p.p. in figs. 2-3); 2) penes with a deep apical incision (fig. 4). In the nymphs: 1) operculate gills subquadrate (fig. 61); 2) gill formula: 3/4/3-4/3/2 (figs. 62-66); and 3) maxillary palpi small with 2 segments and apical seta (fig. 53).

Traverhyphes (Traverhyphes) chiquitano sp. n.
(figs. 2-4, 53, 61-66, 100-103)

Type material. – Holotype: male imago, BOLIVIA: Santa Cruz, río Marco Porvenir, near Ascension, S 16° 17' 10" -W 59° 30' 09", 190 m, 19.vi.2000, Domínguez col. (UMSA). – Paratypes: 8 male imagos, same data as holotype (IFML); 40 nymphs from BOLIVIA: Santa Cruz, río de las Petas, S 16° 22' 24"-W59° 10' 38", 120 m, 19.vi.2000, Domínguez col. (IFML); 13 nymphs from río Quizer, 10 km NE de San Ramón, S 16° 29' 10"-W 62° 28' 44", 290 m, 15.vi.2000, Domínguez col. (UMSA).

Male imago. – Length: body, 2.7-2.9 mm; fore wings, 3.1-3.5 mm; hind wings, 0.6-0.7 mm. General coloration yellowish light brown. Head yellowish shaded with gray, except on submedian circular sclerites of occipute, shaded stronger on hind margin of head. Antennae: scape and pedicel yellowish, flagellum hyaline. Thorax. Pronotum laterally yellowish, grayish black medially. Mesonotum yellowish brown, margins and carinae blackish, mesoscutellum slightly darker. Thoracic pleurae yellowish white, sterna yellowish. Wings. Membrane of wings tinged slightly with yellowish, longitudinal veins brownish yellow, cross veins yellowish translucent. Fore wing veins IMP and MP_2 of fore wings not joined by crossveins. Legs yellowish, except femora yellowish white shaded with gray on subapex. Abdomen. Translucent yellowish white shaded diffusely with gray, lateral margins darker. Genitalia (figs. 2-4): styliger plate yellowish turning whitish medially and posteriorly; posterolateral projections of styliger and first forceps segments yellowish, rest of forceps and penes whitish. Penes of a similar width along their length (fig. 4) with spines inserted laterally (fig. 4). Posterolateral projections of styliger relatively short and widely rounded distally (p.p. in fig. 3). Caudal filaments whitish shaded slight-



Figs. 2-23. *Traverhyphes* Adults. – *T. (T.) chiquitano*: 2, male genitalia, v.v.; 3, same, l.v.; 4, detail of penes, v.v. – *T. (Mocoihyphes) edmundsi*: 5, male fore wing; 6, male hind wing; 7, same, enlarged; 8, female hind wing; 9, male genitalia, v.v.; 10, same, l.v.; 11, detail of penes, v.v.; 12, same, d.v. –*T. (Mocoihyphes) yuati*: 13, male genitalia, v.v.; 14, same, l.v. – *T. (Byrsahyphes) nanus*: 15, male genitalia, v.v.; 16, detail of forceps and forceps base, l.v.; 17, detail of penes, l.v.; 18, same, d.v; 19, same, v.v.; 20, male fore wing; 21, variation in cubital venation; 22, male hind wing; 23, same, enlarged. Abbreviations: a.d.s.=accessory dorsal structure; a.l.=apical lobes; d.l.=dorsal lobes; i.p.=internal projections of styliger plate; p=penes; p.p.= posterolateral projection of styliger plate; p.s.=penean spines; v.s.= ventral swelling.

ly with gray at base.

Female imago. – Unknown.

Mature nymph. – Length of male: body, 2.8-3.2 mm; mesonotum, 1.0-1.2 mm; hind femora, 0.8 mm; terminal filament, 3.2-3.8 mm; cerci, 2.7-3.2 mm. Length of female: body, 3.8-4.0 mm; mesonotum, 1.4-1.5 mm; hind femora, 1.0 mm; terminal filament, 4.5 mm; cerci, 4.0 mm. General coloration brownish yellowish. Head. Yellowish white shaded with yellowish gray almost completely, except small marks before ocelli, and occipute shaded in reticular netting. Mouthparts yellowish; maxilla and maxillary palpi as in fig. 53. Antennae: scape and pedicel brownish yellow, flagellum translucent white. Thorax. Pro- and mesonotum brownish yellow, except wingbuds translucent yellow, shaded with blackish on costal margin and basal sclerites of fore wingbuds; mesoscutellum with a pair of submedian elongated grayish marks. Thoracic sterna whitish yellow shaded with light gray. Legs (figs. 100-102) yellowish white shaded with gray on a subapical mark; tarsal claws with marginal and submarginal denticles as in fig. 103. Abdomen. Yellowish light brown shaded diffusely with gray, stronger below gills. Abdominal sterna whitish yellow shaded stronger on lateral margins. Operculate gills (figs. 61-62) translucent yellowish brown, except posterolateral corners whitish translucent; shaded with gray on basal macula and transverse ridge (b.m. and t.r., respectively, in fig. 61); remaining gills (figs. 63-66) translucent whitish slightly shaded with gray. Caudal filaments yellowish white.

Life cycle associations. – Adults and nymphs are associated by a pharate male subimago (with partially developed genitalia) and by shared coloration.

Etymology

'Chiquitano', noun in apposition, in reference to the area of distribution of this species: the Chiquitania. This zone takes its name after the mountain-complex Chiquitos-Velasco, constituted by the oldest rocks in Bolivia (Rivera et al. 1996).

Diagnosis

Traverhyphes (Traverhyphes) chiquitano can be distinguished from the other species of the genus by the following combination of characters: 1) abdominal terga shaded with gray completely, stronger at lateral margins; 2) penes of a similar width along their length (fig. 4); 3) penean spines inserted laterally (fig. 4); 4) in lateral view the posterolateral projections of the styliger are relatively short and widely rounded distally (p.p. in fig. 3); 6) vein IMP and MP_2 of fore wings not joined by crossveins. In the nymph: 1) operculate gills shaded with blackish gray on a basal macula and transverse ridge (b.m. and t.r. in fig. 61); 2) gill formula 3/4/4/3/2 (figs. 62-66).

Traverhyphes (Mocoihyphes) subgen. n.
(figs. 5-14, 41-46, 48, 54-55, 67-78, 104-113, 128-135)

Type species: *Leptohyphes edmundsi* Allen, original designation.

Species included: *T. (Mocoihyphes) edmundsi* (Allen) comb. n., and *T.* (*Mocoihyphes*) *yuati* sp. n.

Imago. – Male genitalia: styliger without posterolateral projections (figs. 9-10, 13-14, 128-131). Penes completely fused, with a pair of small (figs. 12, 129) to long (figs. 13-14) spines arising dorsally near the apex. These spines are curved dorsally. Apex of penes with two pairs of membranous lobes (a.l. in figs. 11, 130-131). Lateral margins of penes with a subapical excavation (s.e. in figs. 129-130). Dorsal to penes and extending from their base, an accessory structure is present (a.d.s. in figs. 10, 14, 128-129, 131), the apex of which almost meet with the apex of penean spines (figs. 10, 14, 129). Female IX sternum slightly projected posteriorly with truncated apex.

Nymph. – Maxillary palpi small with 2 segments, apical seta present (fig. 54) or absent (fig. 55). Abdominal gills show a reduced number of membranous lamellae, gill formula 3/3/3/3/2 (figs. 68-72, 74-78). Operculate gills ovoid to subquadrate (figs. 67, 73).

Diagnosis. – *Traverhyphes* (*Mocoihyphes*) subgen. n. can be separated from the other subgenera by the following combination of characters. In the imago: 1) posterolateral projections of styliger plate absent; 2) penes almost completely fused with two pairs of apical lobes (figs. 11, 130-131); 3) penes with a pair of dorsal membranous lobes (d.l. in figs. 12 and 131); 4) penes with a pair of spines that arise at the base of these dorsal projections (figs. 12, 129-131); 5) penes with a lateral subapical excavation (figs. 129-130); 6) accessory dorsal structure associated with penes, double, blunt (figs. 10, 128-129, 131) or hooked (fig. 14). In the nymph: 1) operculate gills ovoid to subquadrate (figs. 67, 73); 2) gill formula: 3/3/3/3/2 (figs. 68-72 and 74-78); and 3) maxillary palpi small 2-segmented with or without apical seta (figs. 54-55).

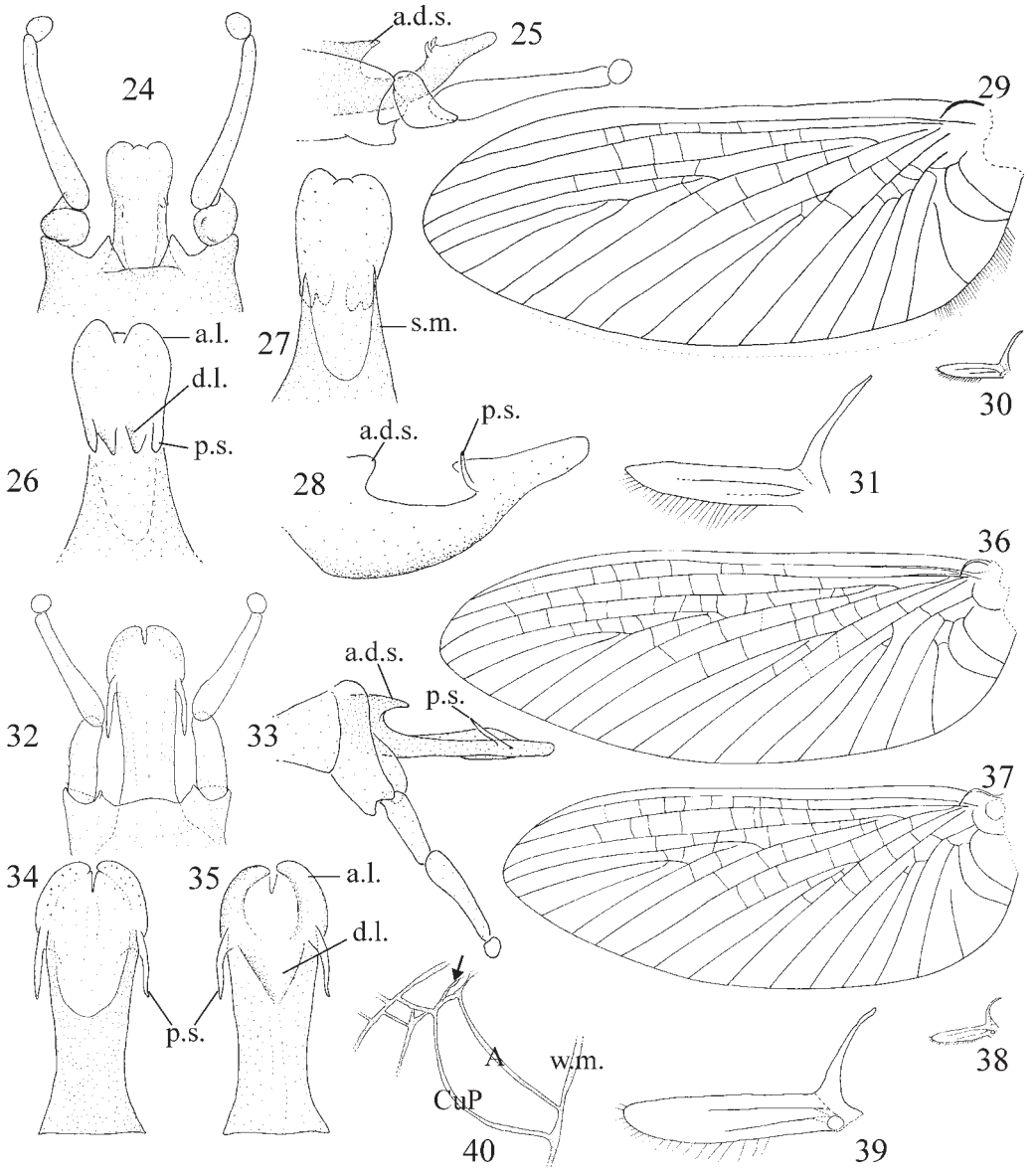
Etymology

'Mocoi', in Guarani language (ethnic group that inhabit the region where both species were collected) means 'two' (Ruiz de Montoya 1640), for the membranous lobes of the penes; and 'hyphes' (=net, suffix commonly used in generic names of the family).

Traverhyphes (Mocoihyphes) edmundsi (Allen) **comb. n.**
(figs. 5-12, 48, 54, 67-72, 104-108, 128-135)

Leptohyphes edmundsi Allen 1973, 49: 363; Hubbard 1982: 272; Molineri 2001b: 134.

Allenhyphes edmundsi; Wiersema & McCafferty 2000: 343; Molineri 2003: 48.



Figs. 24-40. Adults. – *Traverhyphes (Byrsahyphes) yuqui*: 24, male genitalia, v.v.; 25, same, l.v.; 26, detail of penes, d.v.; 27, same, v.v.; 28, same, l.v.; 29, male fore wing; 30, male hind wing; 31, same, enlarged. – *Lumahyphes pijcha*: 32, male genitalia, v.v.; 33, same, l.v.; 34, detail of penes, v.v.; 35, same, d.v.; 36, female fore wing; 37, male fore wing; 38, male hind wing; 39, same, enlarged; 40, detail of male cubital venation. Abbreviations: a.d.s.=accessory dorsal structure; a.l.=apical lobes; d.l.=dorsal lobes; p.s.=penean spines; s.m.=sclerosed margin; w.m.=wing margin.

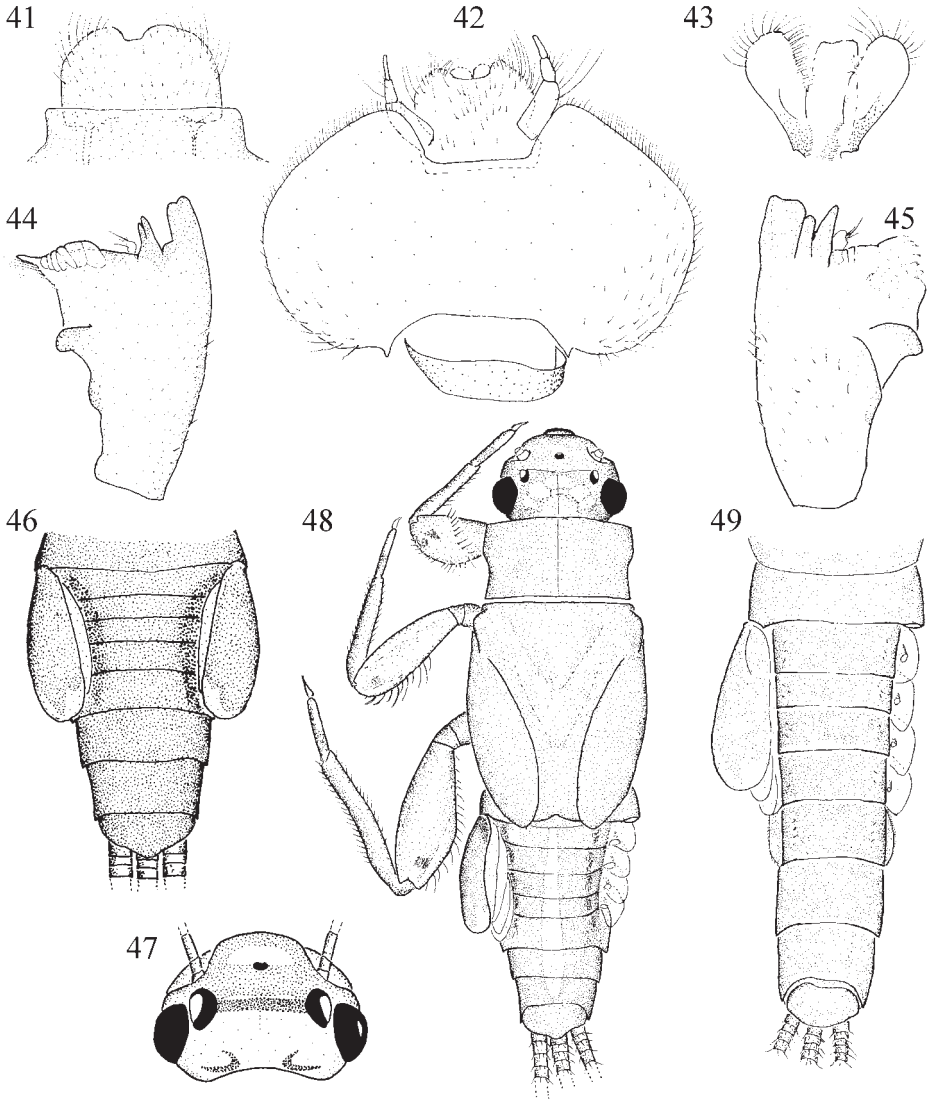
Type material. – 8 nymphs paratypes BRAZIL: Rio Grande do Sul, arroio Irapua, 30' 19º B 53' 13º L, 150 m, XI-1964, F. Plaumann; 19 nymphs paratypes idem except arroio do Hilario; 10 nymphs paratypes from BRAZIL, Parana, Morretes, rio Catiras, IV-1965, F. Plaumann; 2 nymphs paratypes from Brazil, Santa Catarina, rio Cubatao, XI-1965, F. Plaumann (FAMU, E2039).

Additional material. – ARGENTINA: Misiones, Domínguez, Molineri & Nieto Cols.: 1 nymph, 12 male imagos, 2 female imagos, 1 reared male from Aristóbulo del Valle, Río Cuñá Pirú, 19-20.xi.1998; 3 nymphs, 5 male imagos, 1 reared male from 10 Km NE of San Vicente, INTA Cuartel Victoria, 20.xi.1998; 5 nymphs, 7 male imagos, 5 female imagos from Alem, 5 Km W of Cerro Azul, arroyo Mártires, 17.xi.1998; 10 nymphs, 1 male imago, 10 female imagos, 2 reared female from San Pedro, Junction of rivers Alegría and Pirai-Guazú, 22-23.xi.1998; 70 male imagos, 2 female imagos, 5 reared female from Parque Provincial Urugua-í, arroyo Uruzú, 23-24.xi.1998; 2 reared male and 1 reared female from Brazo del Garupá, 17-18.xi.1998; 50 nymphs and 1 reared male from 25 Km S of El Soberbio, 21.xii.1998; 11 nymphs, 1 reared male from 3 Km W of María Magdalena, Puerto Mado, arroyo Yacutinga, 19-20.xi.1998; 4 nymphs from Candelaria, Camping 2 Km E of Bonpland, 18.xi.1998; 8 male subimagos from Parque Nacional Iguazú, Puerto Canoas, 26.xi. 1998. Sixty nymphs, 3 male imagos, 1 reared male from Misiones, Parque Provincial Urugua-í, arroyo Uruzú, 7-11.xii. 1999, Molineri Col.. Fourty male imagos from Misiones, INTA San Vicente, 1.xii.1986, Domínguez Col. All this material deposited in IFML. Also some subimagos of both sexes from BRAZIL: São Paulo, Intervales, córrego Agua Comprida, 18/II/2000, P. Bispo col. (MZSP); São Paulo, Campos do Jordão, Parque Estadual, córrego Galharada, luz, 6/III/1986, C. G. Froehlich et al. cols. (MZSP); BRAZIL: Parana, rio Passa una, 7 km W of Curituba, 26/II and 15/III/1969, W. L. & J. G. Peters (FAMU); Parana, rio Parana, Sete Quedas, 5 km S of Guairá, 650', 11/III/1969, W. L. & J. G. Peters (FAMU); rio dos Patos, 3 km E of Prudentópolis, 2300', 3/III/1969, W. L. & J. G. Peters (FAMU); Parana, rio Ipiranga, estrada do Itupaua, 2400', 21-23/II/1969, W. L. & J. G. Peters (FAMU).

Male imago. – Length: body, 3.2-3.5 mm; fore wings, 3.7-4.0 mm; hind wings, 0.62-0.65 mm. General coloration yellowish brown. Head yellowish brown shaded with black on occipute and with gray on front, ventrally whitish shaded with black on posterior margin. Antennae: scape and flagellum yellowish translucent, pedicel brownish translucent. Thorax. Pronotum yellowish, median region membranous widely shaded with grayish brown except at scattered whitish dots. Mesonotum yellowish brown shaded diffusely with gray, darker on carinae and margins; mesoscutellum translucent yellowish brown, membranous filaments whitish translucent shaded with gray. Metanotum yellowish light brown shaded with gray at margins. Thoracic pleurae and sterna yellowish white. Wings (figs. 5-7). Membrane of wing hyaline slightly tinged with yellowish light brown shaded with gray on basal half of C and Sc areas; longitudinal veins yellowish shaded with gray, cross veins yellowish. Legs. Yellowish except femora yellowish white with yellowish margins, with a small subapical blackish mark on dorsum. Abdomen translucent yellowish white except segments IX-X whitish yellow; terga shaded with gray completely except on whitish median band on terga II-IX, this band increasing in width toward rear segments, becoming widest on terga VII-IX; shaded more marked on margins of this translucent median band, sublateral regions of terga I-VII and median line of tergum X; lateral zones of terga III-VI near pleural folds without shading, whitish; pleural folds of segments VI-VII blackish. Abdominal sterna translucent yellowish white shaded diffusely with gray. Genitalia (figs. 9-12, 128-131): styliger plate whitish translucent except margins yellowish; forceps and penes whitish yellow translucent, tinged with light brown at apex of segment 1 of forceps and more diffusely on distal half of segment 2; lateral margins and spines of penes yellowish translucent. Cerci translucent yellowish white shaded very slightly with purplish gray, terminal filament whitish translucent.

Female imago. – Length: body, 3.5-3.7 mm; fore wings (fig. 8), 4.0-4.1 mm. General coloration yellowish brown. Head. As in male except without shading with black on a circular mark before median ocellus. Thorax as male except shaded with gray between PSP. Legs and wings as male except common sexual dimorphism. Abdomen as in male. Egg mass whitish orange. Ninth sternum slightly excavated apically, whitish except lateral margins brownish translucent. Tails whitish relatively shorter than male.

Nymph (fig. 48). – Length of male: body, 3.1-3.5 mm; mesonotum, 1.1-1.3 mm; hind femora, 0.8-0.9 mm; tails, 2.3 mm. Length of female: body, 4.0-4.1 mm; mesonotum, 1.4 mm; hind femora, 0.9-1.1 mm; tails, 3.0-3.5 mm. General coloration varies from yellowish to brownish with grayish markings. Head yellowish brown tinged with black on a transverse band between lateral ocelli and irregular netting on occipute; tinged with brown anteriorly to ocelli except on a yellowish mark before median ocellus. Mouthparts translucent yellowish brown. Antennae: scape yellowish, pedicel and basal annuli of flagellum brownish, remaining portion of flagellum translucent yellowish. Thorax. Pronotum brownish diffusely shaded with black, stronger on lateral and anterior zones. Mesonotum brownish with blackish marks on anterolateral corners, base of wingpads and mesoscutellum; wingbuds brownish with blackish costal margins. Thoracic pleurae yellowish white, sterna yellowish diffusely shaded with gray. Legs yellowish with small blackish dorsal maculae on distal part of all femora; basal half of all tarsi brownish. Abdomen yellowish brown with whitish yellow median band on terga II-IX, this band wider on VII-IX; tergum X washed with black on median band; long spines present on dorsum of terga II-VI delineating gill borders, longer on VI. Sublateral zones of terga III-VII shaded more strongly with gray.



Figs. 41-49. Nymphs. – 41-46, *Traverhyphes (Mocoihyphes) yuati*: 41, labrum, d.v.; 42, labium, v.v.; 43, hypopharynx, v.v.; 44, right mandible, d.v.; 45, left mandible, d.v.; 46, abdominal color pattern. – 47, *Lumahyphes pijcha*: head color pattern, d.v.; 48, *Traverhyphes (Mocoihyphes) edmundsi*: general habit of nymph (left gills dissected); 49, *Traverhyphes (Byrsahyphes) nanus*: abdomen (right gills dissected).

Abdominal sterna I-VI yellowish, VII-IX yellowish brown. Lateral projections on sterna III-VI yellowish translucent, posterolateral spines present on VII-VIII. Gills (figs. 67-72): operculate lamellae translucent yellowish brown shaded with gray at base, with whitish translucent maculae at posterolateral inner corner; remaining gills whitish translucent shaded slightly with gray. Tails yellowish with whorls of brownish spines at articulations.

Eggs (figs. 132-135). – Length: 170-180 µm; maximum width: 75-85 µm. Polygonal and subcircular chorionic plates present on egg surface, except on the chorion surrounding the polar cap (fig. 132). Attachment structures: one subtriangular polar cap present, with blunt apex (fig. 133); few knob terminated coiled threads (KTC) present between chorionic plates and on the smooth chorion around the polar cap. KTC paddle-like as in fig. 135. Micropylar area subcircular and smooth surrounded by 5 chorionic plates (fig. 134). One small micropyle per egg located in the margin of the micropylar area.

Observations. – One male subimago showed the abdomen completely filled with eggs.

Life cycle associations. – Reared nymphs of both sexes associate nymphs and adult stages.

Diagnosis

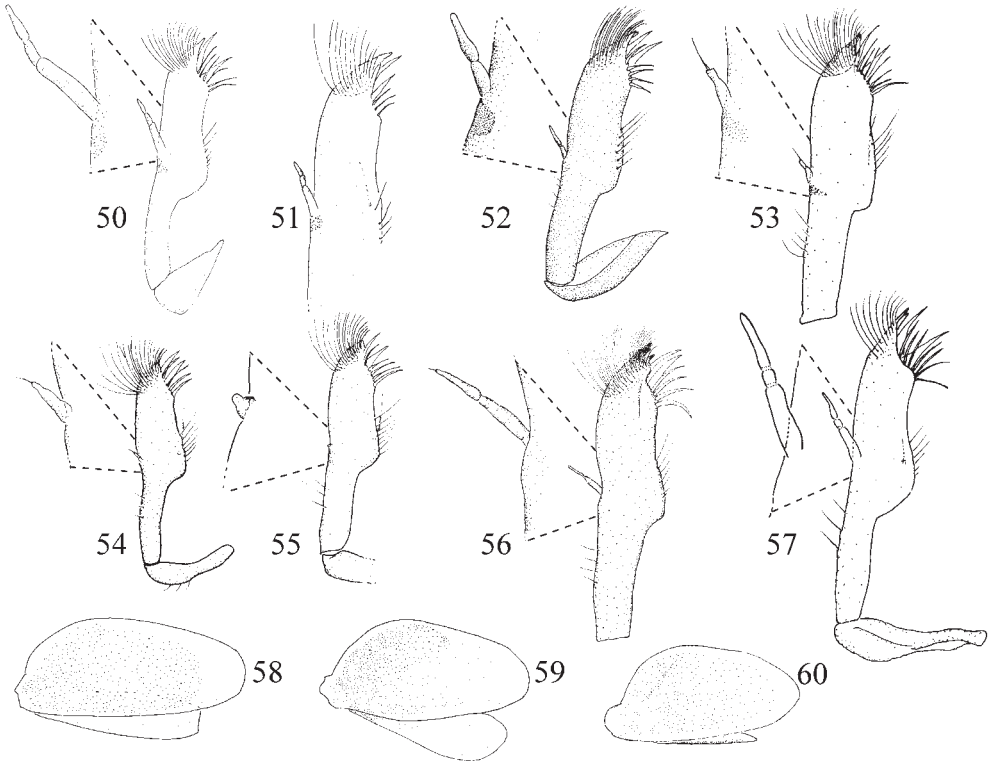
Leptohyphes edmundsi Allen was moved to *Allenhyphes* by Wiersema and McCafferty (2000), based on nymphal characters (adults were unknown at that moment). The adults of this species, described here for the first time, do not show the characteristics of *Allenhyphes* (form of penes and presence of a ventral spine on terminal filament). Instead, the results of the phylogenetic analysis indicate that *Leptohyphes edmundsi* belongs to *Traverhyphes* (fig. 1). *Traverhyphes* (*Mocoihyphes*) *edmundsi* (Allen) comb. n. can be distinguished from the other species of the subgenus by the following combination of characters. In the imago: 1) relatively small grayish marks present on subapex of femora; 2) abdominal terga with a lighter median band, widening in terga VII-IX; 3) spines of penes short, less than ¼ total length of penes (figs. 10, 12, 129); 4) fore wings veins yellowish translucent; 5) accessory dorsal structure of penes with relatively blunt apex (figs. 10, 128-129). In the nymphs: 1) grayish marks on subapex of femora relatively small (figs. 104-106); 2) abdominal terga with a lighter median band (fig. 48), as in adults; 3) operculate gills light yellowish brown; 4) general coloration without purplish glare; 5) maxillary palpi small, 2-segmented with apical seta (fig. 54).

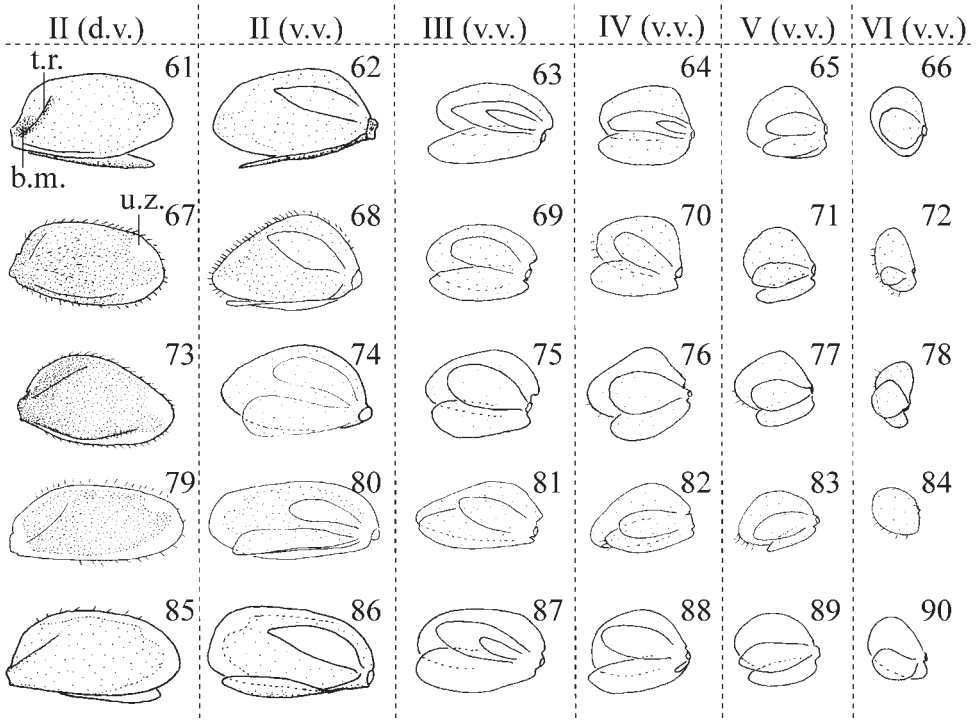
Among the species of the *Allenhyphes-Traverhyphes* group, only the eggs of *Traverhyphes (T.) indicator* and *Allenhyphes flinti* were known. The eggs of *Allenhyphes flinti* (in Hofmann et al. 1999) can be separated from those of *Traverhyphes* because they show semicircular chorionic plates covering the entire egg surface. Eggs of *Traverhyphes (T.) indicator* (Molineri, 2001b) and *T. (Mocoihyphes) edmundsi* (figs. 132-135) can be distinguished by the form of adhesive filaments (derived KTC, knob terminated coiled threads), showing long and thin peduncle in the first species, but with a short and stout peduncle in the second. Furthermore the knob of *T. (T.) indicator* show a radial disposition of fibers while in *T. (M.) edmundsi* fibers are placed along the main axis of the knob (fig. 135).

Traverhyphes* (*Mocoihyphes*) *yuati sp. n.
(figs. 13-14, 41-46, 55, 73-78, 109-113)

Type material. – Holotype: male imago, ARGENTINA: Misiones, Parque Provincial Urugua-í, arroyo Uruzú, 7-11.xii.1999, Molineri Col. (IFML). – Paratypes: 7 male imagos, 7 female adults (6 reared from nymph), and 33 nymphs, same data as holotype; 3 male adults (2 reared), 1 reared female and 12 nymphs, same data except date and collectors, 23-24.xi.1998, Domínguez, Molineri and Nieto cols. (=D M & N below); 1 male imago and 4 nymphs from Argentina, Misiones, Alem, 5 Km W Cerro Azul, arroyo Mártires, 17.xi.1998, D M & N; 1 male imago and 2 nymphs from Misiones, San Pedro, confluence rivers Alegría and Pirai-Guazú, 22-23.xi.1998, D M & N; 1 male and 3 female imagos from Misiones, Aristóbulo del Valle, río Cuñá Pirú, 19-20.xi.1998, D M & N; 1 male imago from 3 Km W of María Magdalena, Puerto Mado, arroyo Yacutinga, 19-20.xi.1998, D M & N (IFML). Additional material from BRAZIL: Rio de Janeiro, 950 m, Nova Friburgo, mun. Water supply, 20.iv.1977, C. M. & O. S. Flint, Jr. (NMNH); São Paulo, Campos do Jordão, Parque Estadual, córrego Casquilho, luz, 23.iv.1987, C. G. Froehlich (MZSP); São Paulo, Campos do Jordão, Parque Estadual, córrego Galharada, luz, 4.iii.1986, C. G. Froehlich et al. cols. (MZSP).

Male imago. – Length: body, 3.5-4.0 mm; fore wings, 4.1-4.3 mm; hind wings, 0.72-0.85 mm. General coloration grayish brown. Head brownish shaded completely with black, shaded less marked on a triangular mark behind median ocellus; frontal crest blackish. Antennae: scape yellowish white, pedicel brownish translucent, basal half of flagellum whitish translucent, distal part yellowish translucent. Thorax. Pronotum yellowish brown at lateral ⅓ with black markings, median ⅓ shaded completely with black; propleurae and prosternum lighter. Mesonotum brownish shaded widely with gray, shaded with black on margins, carinae and between PSP, mesoscutellum blackish brown with a pair of long grayish membranous filaments. Metanotum and pleural sclerites of meso- and metathorax light brownish, membranes


50
51
52
53
54
55
56
57
58
59
60


II (d.v.)
II (v.v.)
III (v.v.)
IV (v.v.)
V (v.v.)
VI (v.v.)
t.r.
b.m.
u.z.
61
62
63
64
65
66
67
68
69
70
71
72
73
74
75
76
77
78
79
80
81
82
83
84
85
86
87
88
89
90

yellowish white. Wings. Membrane of wing hyaline slightly tinged with yellowish, except costal margin tinged with brownish yellow, longitudinal veins brownish shaded with gray, cross veins yellowish translucent. Legs. Coxae and trochanters of all legs light brownish shaded with gray on coxae. Fore femora yellowish with brownish margins, tibiae and tarsi of fore legs translucent yellowish white shaded with purplish gray on tibiae and with gray on tarsi. Femora of all legs with a marked blackish band near apex. Middle and hind legs translucent yellowish. Abdomen translucent yellowish white shaded with gray dorsally and with yellow ventrally; tergum IX with yellowish lateral margins; tergum X with brownish median band and distal transverse mark. Genitalia (figs. 13-14): styliger plate whitish yellow with brownish lateral margins, hind margin yellowish; basal segment of forceps yellowish translucent, remaining segments translucent yellowish white; penes whitish except lateral margins, spines and dorsal paired hooks yellowish. Tails translucent yellowish white shaded with gray, darker near articulations.

Female imago. – Length: body, 4.2 mm; fore wings, 4.3-4.5 mm. Similar to male imago except membranous filaments of mesoscutellum very short (not extending beyond apical margin). Abdominal sternum IX slightly excavated apically.

Mature nymph. – Length of male: body, 3.3-3.5 mm; mesonotum, 1.4-1.5 mm; hind femora, 1.0 mm; tails, 3.2 mm. Length of female: body, 4.2-4.7; mesonotum, 1.5 mm; hind femora, 1.1 mm; tails, 3.0 mm. General coloration yellowish light brown shaded with purplish gray. Head yellowish brown shaded with purplish gray on a band among ocelli, around antennae, on clypeus, and irregular net of lines on occipute. Antennae: scape and pedicel brownish translucent, flagellum translucent yellowish white. Mouthparts (figs. 41-45, 55) yellowish white shaded with purplish gray. Thorax. Thoracic nota yellowish brown shaded with purplish gray almost completely, shaded more marked on anterolateral corners of mesonotum and between developing wings, wings whitish with blackish costal margin. Thoracic pleurae and sterna yellowish shaded slightly with purplish gray. Legs (figs. 109-111) yellowish white shaded slightly with purplish gray on coxae; femora of all legs with marked subapical blackish macula on dorsum; basal ½ of tarsi brownish. Abdomen yellowish light brown shaded completely with purplish gray, shaded more marked on sublateral regions of terga I-VII, heavier on III-VI; terga III-VII with few small brownish spines along gill limits, increasing in number toward rear segments. Gills (figs. 73-78): operculate gills brownish with blackish fore margin, distally depigmented as in fig. 73, remaining gills whitish translucent slightly shaded with purplish gray at base; small posterolateral spines present on segments VII-IX, decreasing toward rear segments. Tails yellowish translucent with brownish spines at articulations.

Life cycle associations. – Reared nymphs of both sexes associate nymphs, male and female adults.

Observations. – Some paratypes have a pair of submedian blackish lines on abdominal terga II-V. General coloration of nymphs varies from whitish shaded widely with purple to yellowish light brown shaded with purplish gray.

Etymology

'Yuati' noun in apposition, in Guarani language means 'spine' for the long spine-like structure of the penes.

Diagnosis

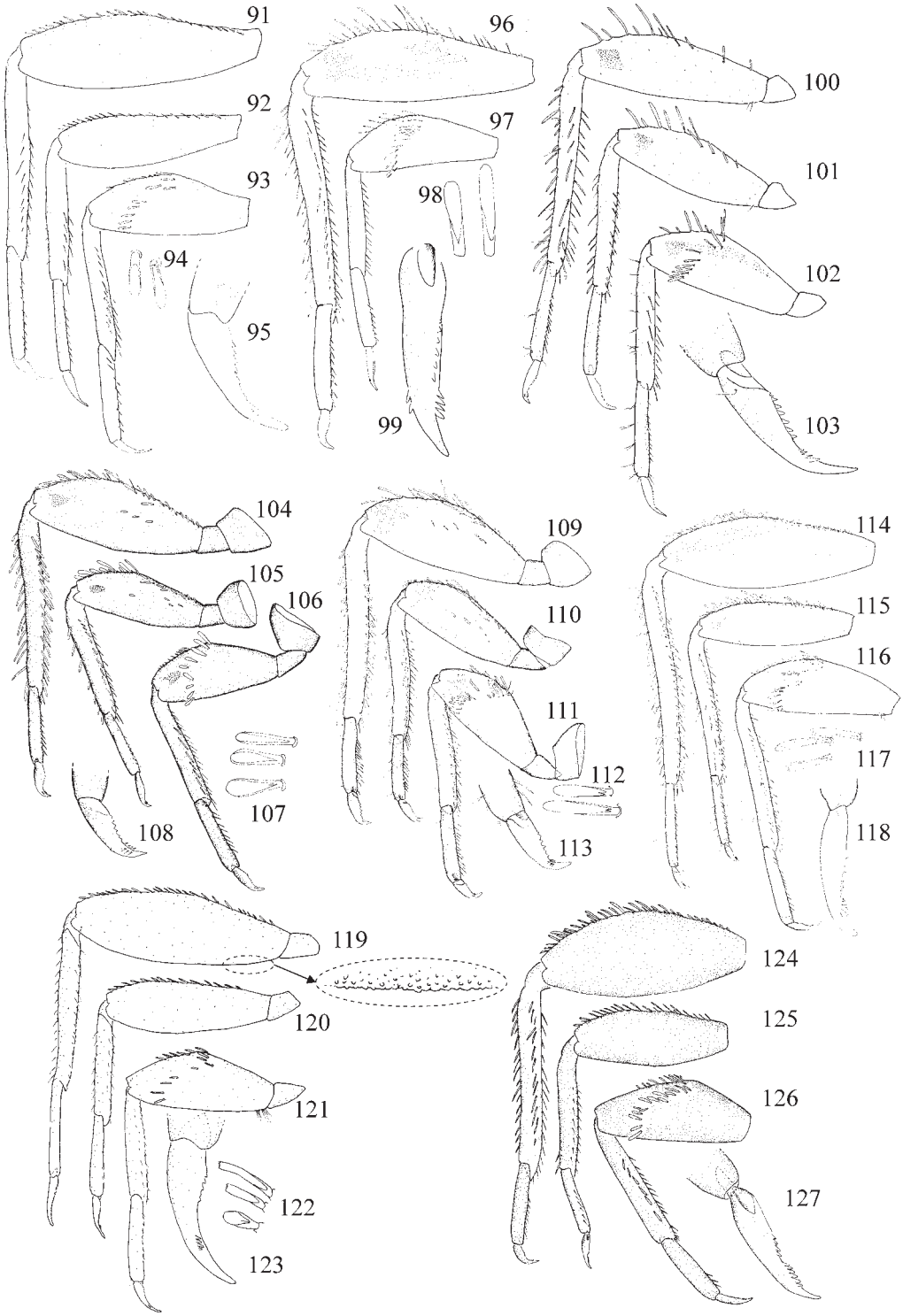
T. (*Mocoihyphes*) *yuati* can be distinguished from the other species of the subgenus by the following combination of characters. In the imago: 1) larger grayish marks present on subapex of femora; 2) abdominal terga uniformly shaded with purplish gray, rarely with a median lighter band but never widening on hind terga; 3) spines of penes long, more than ½ total length of penes (figs. 13-14); 4) veins of fore wings brownish; 5) accessory dorsal structure of penes with hook-like apex (fig. 14). In the nymphs: 1) grayish marks on subapex of femora relatively large (figs. 109-111); 2) abdominal terga uniformly shaded with purplish gray (fig. 46), some times with a median lighter band but never widening on hind terga; 3) operculate gills brownish; 4) general coloration with purplish glare; 5) maxillary palpi very small, 2-segmented and without apical seta (fig. 55).

Traverhyphes (Byrsahyphes) subgen. n.
(figs. 15-31, 49, 56, 79-84, 114-118)

Type species: *Leptohyphes nanus* Allen, original designation.
Species included: *T. (Byrsahyphes) nanus* (Allen) comb. n., and *T. (Byrsahyphes) yuqui* sp. n.

Imago. – Male genitalia: styliger plate without pos-

Figs. 50-90. Nymph. Maxillae. – 50, *Allenhyphes? asperulus*; 51, *A.? spinosus*; 52, *Yaurina ralla*; 53, *Traverhyphes (T.) chiquitano*; 54, *T. (Mocoihyphes) edmundsi*; 55, *T. (M.) yuati*; 56, *T. (Byrsahyphes) nanus*; 57, *Lumahyphes pijcha.* Gills II: 58, *A.? asperulus*, d.v.; 59, *A.? spinosus*; 60, *Yaurina ralla.* – Gills II-VI. – 61-66, *T. (T.) chiquitano*; 67-72, *Traverhyphes (Mocoihyphes) edmundsi*; 73-78, *T. (M.) yuati*; 79-84, *T. (Byrsahyphes) nanus*; 85-90, *Lumahyphes pijcha.* Abbreviations: b.m.=basal macula; t.r.=transverse ridge; u.z.=depigmented zone.


91
92
93
94
95
96
97
98
99
100
101
102
103
104
105
106
107
108
109
110
111
112
113
114
115
116
117
118
119
120
121
122
123
124
125
126
127

terolateral projections. Penes (figs. 17-19, 26-28) almost completely fused, dorsally curved. Penes with a pair of short spines inserted dorsally on apical ⅓ of penes; spines curved dorsally and arising from a pair of dorsal membranous lobes. Dorsal to penes and extending from their base, an acute structure is present, with its apex directed towards the apex of penean spines (a.d.s. in figs. 17, 28). First forceps segments very short, almost globular. Ninth female sternum slightly concave at apex.

Nymph. – Maxillary palpi small 3-segmented with apical seta (fig. 56). Abdominal gills show a reduced number of membranous lamellae, gill formula: 3/3/3/3/1 (figs. 80-84). Operculate gills elongated-ovoid (fig. 79).

Etymology

'Byrsahyphes', from Greek 'byrsa' (=pouch, for the ventral swelling of penes) and 'hyphes' (=net, suffix commonly used in generic names of the family).

Diagnosis

Traverhyphes (Byrsahyphes) subgen. n. can be distinguished from the other subgenera of the genus by the following combination of characters. In the imago: 1) posterolateral projections of styliger plate absent (fig. 15, 24-25); 2) penes almost completely fused with two pairs of apical lobes (fig. 19, 27); 3) penes with a pair of dorsal membranous projections (fig. 18, 26); 4) penes with a pair of spines that arise at the base of these dorsal projections; 5) accessory dorsal structure associated with penes, single (figs. 17, 28). In the nymph: 1) operculate gills elongated-ovoid (fig. 79); 2) gill formula: 3/3/3/3/1 (figs. 80-84); 3) maxillary palpi small with 3 segments and apical seta (fig. 56).

Traverhyphes (Byrsahyphes) nanus (Allen) **comb. n.**
(figs. 15-23, 49, 56, 79-84, 114-118)

Leptohyphes nanus Allen, 1967: 355; Allen 1978: 550.
Allenhyphes nanus: Wiersema & McCafferty 2000: 343; Molineri 2003: 48.

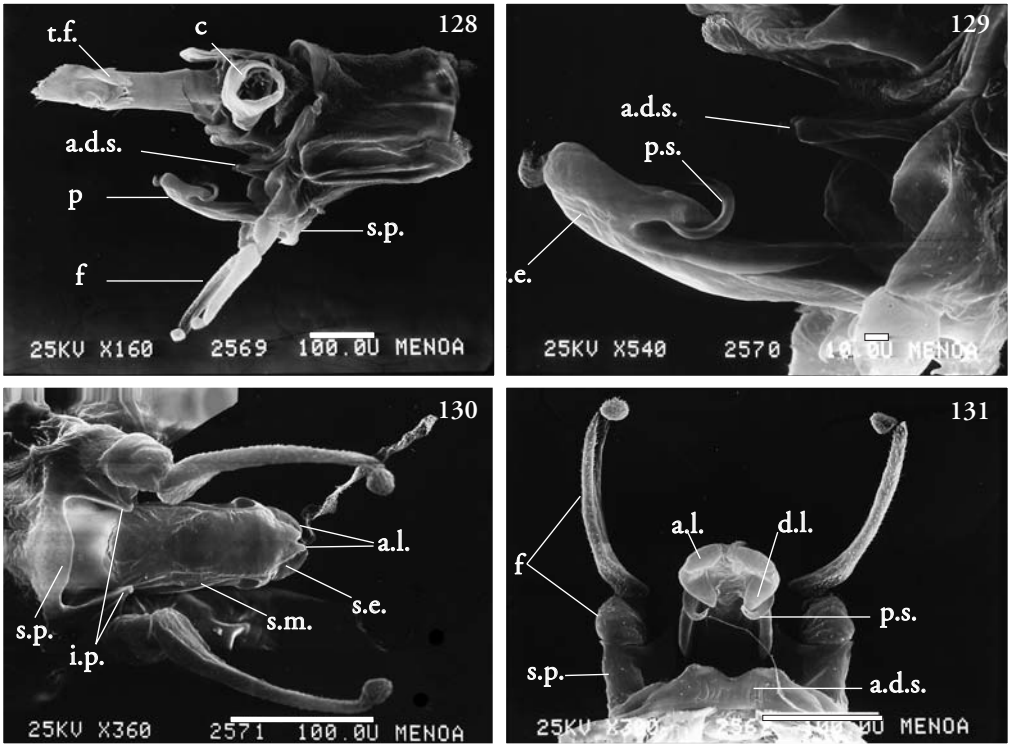
Material. – 3 nymphs and 2 reared males from COSTA RICA, Prov. Guanacaste, Est. Maritza, Queb. Marilin, 600 m, N 10º 57' 04"-W 85º 29' 24", reared from egg at SCWR, tray 93, mother 194-61, set up 18.ii.1994, emerged 3.v.1994; 4 male and 3 female imagos same data except collected at light 6-8 AM, 19.vi.1992; 1 nymph from Costa Rica, Prov. Guanacaste, Est. Maritza, Río Tempisquito, reared from egg at SCWR, tray 96, CR-1043, 1047, sample date 11.v.1993 (deposited in SCWR). Two male imagos from COLOMBIA, Chocó, Acandí, quebrada Coquital, Borojó, 19.vii.1999, E. Domínguez (MEUV).

Male imago. – Length: body, 3.0-3.1 mm; fore wings, 3.0 mm; hind wings, 0.45 mm. General coloration: thorax yellowish, abdomen whitish. Head whitish slightly tinged with yellowish around antennae and rest of mouthparts. Thorax. Prothorax yellowish white shaded with gray dorsally and ventrally. Meso- and metathorax yellowish shaded slightly with gray, shaded more marked on anterior half of mesopleurae and on mesosterna. Mesoscutellum yellowish translucent with grayish white membranous filaments. Wings (figs. 20-23). Membrane of wing hyaline very slightly tinged with yellowish; veins yellowish brown turning lighter toward margin. Legs. Coxae and trochanters of all legs yellowish shaded with gray, rest of all legs whitish except margins of femora yellowish, light subapical gray mark present on femora. Abdomen whitish completely but very slightly shaded with yellowish gray. Genitalia whitish; accessory dorsal structure apically acute (fig. 17); penes with a subdistal ventral swelling (fig. 17). Cerci whitish translucent.

Female imago. – Length: body (without eggs), 2.5 mm; fore wings, 3.0 mm. As in male except dorsum of head, pronotum and abdomen shaded with grayish black; hind femora shaded with gray almost completely.

Nymph. – Length: body, 4.5-4.7 mm; mesonotum, 1.3 mm; hind femora, 1.0 mm; tails, 3.0-3.7 mm. General coloration yellowish light brown. Head yellowish light brown with small whitish marks anteriorly to median ocellus and compound eyes; shaded slightly with gray between lateral ocelli and around antennae; ventrally paler. Thorax yellowish to yellowish brown shaded with gray slightly but extensively, more marked on anterior margin of pronotum, costal margin of wingbuds and mesoscutellum; thorax ventrally paler. Legs yellowish white with a small light grayish mark on subapex of femora. Abdomen cylindrical and long (fig. 49). Terga yellowish to yellowish white com-

Figs. 91-121. Nymph. – *Allenhyphes? asperulus*: 91, leg III; 92, leg II; 93, leg I; 94, detail of femoral spines; 95, detail of fore tarsal claw. *Allenhyphes? spinosus*: 96, leg III; 97, leg I; 98, detail of femoral spines; 99, detail of fore tarsal claw. *Traverhyphes (Traverhyphes) chiquitano*: 100, leg III; 101, leg II; 102, leg I; 103, detail of fore tarsal claw. *Traverhyphes (Mocoihyphes) edmundsi*: 104, leg III; 105, leg II; 106, leg I; 107, detail of femoral spines; 108, detail of fore tarsal claw. *T. (M.) yuati*: 109, leg III; 110, leg II; 111, leg I; 112, detail of femoral spine; 113, detail of tarsal claw. *T. (Byrsahyphes) nanus*: 114, leg III; 115, leg II; 116, leg I; 117, detail of femoral spines; 118, detail of fore tarsal claw. *Lumahyphes pijcha*: 119, leg III with detail of margin; 120, leg II; 121, leg I; 122, detail of femoral spines; 123, detail of fore tarsal claw. *Yaurina ralla*: 124, leg III; 125, leg II; 126, leg I; 127, detail of fore tarsal claw.



Figs. 128-131. SEM photographs, male genitalia, *Traverhyphes (Mocoihyphes) edmundsi*. – 128, Male terminalia, l.v.; 129, detail of penes, l.v.; 130, male genitalia, v.v.; 131, same, d.v. Abbreviations: a.d.s.=accessory dorsal structure; a.l.=apical lobes; c=cerci; d.l.=dorsal lobes; f=forceps; i.p.=internal projections of styliger; p=penes; p.p.=posterolateral projection of styliger plate; p.s.=penean spines; s.e.=subapical excavation; s.m.=sclerosed margin; s.p.=styliger plate; t.f.=terminal filament.

pletely shaded with gray except intersegmental membranes. Operculate gills (fig. 79-80) shaded almost completely with yellowish gray, remaining gills translucent (figs. 81-84). Lateral flanges of abdominal segments III-VI hyaline (fig. 49). Abdominal sterna paler. Tails yellowish white.

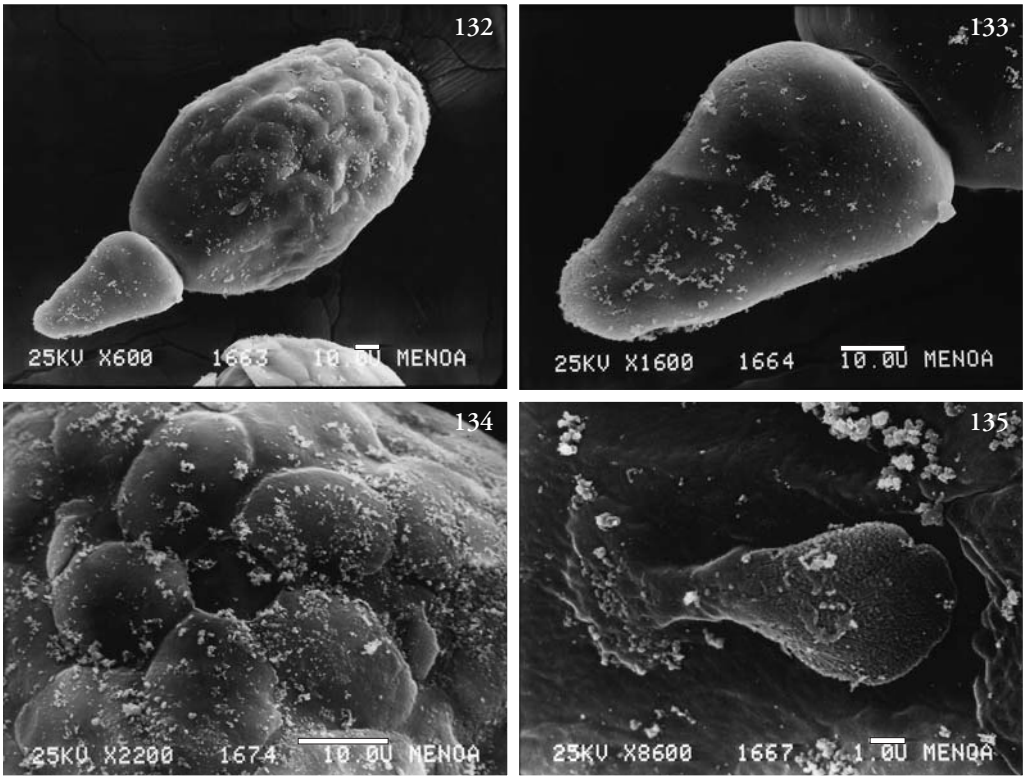
Life cycle associations. – Adults and nymphs are associated by reared nymphs of both sexes.

Diagnosis

Traverhyphes (Byrsahyphes) nanus comb. n. was included in *Allenhyphes* by Wiersema and McCafferty (2000), because the adults were not known at that time. As is shown here male imagos do not show the characteristics of *Allenhyphes*, and represent a different group more nearly related to *Traverhyphes* species group (fig. 1). *Traverhyphes (Byrsahyphes) nanus* can be distinguished from the other species of the subgenus by the following combination of characters. In the imago: 1) abdominal terga uniformly but slightly shaded with gray; 2) spines of penes very short, less than ¼ total length of penes (fig. 18); 3) penes with a ventral swelling (v.s. in fig. 17), and notched apically (figs. 18-19); 4) veins of fore wings yellowish brown; 5) accessory dorsal structure associated with penes single and acute (fig. 17). In the nymphs: 1) grayish marks on subapex of femora absent or very slightly marked (figs. 114-116); 2) abdominal terga uniformly shaded with gray, without whitish mediolongitudinal band (fig. 49); 3) opercular gills yellowish gray; 4) general coloration without purplish glare; 5) maxillary palpi 3-segmented with apical seta (fig. 56).

Traverhyphes (Byrsahyphes) yuqui sp. n.
(figs. 24-31)

Type material. – Holotype: male imago, BOLIVIA: Depto. La Paz, Reserva Carrasco, road to Caranavi-Alto Beni, S 15º 43' 09"-W 67º 31' 06", 940 m, light 4-6 AM, 28.xi.2000, Domínguez, Molineri & Nieto cols. (UMSA). – Paratypes: 8 male imagos and 3 female imagos (1 male and 1 female imagos deposited in



Figs. 132-135. SEM photographs, eggs, *Traverhyphes (Mocoihyphes) edmundsi*. – 132, General aspect of egg; 133, detail of polar cap; 134, micropylar area; 135, detail of adhesive filament (KTC).

UMSA; 7 male and 2 female imagos in IFML).

Additional material. – 11 male imagos from PANAMA: Bocas del Toro, río Teribe at Zegla, 23/IV/1985, light AM, R. W. Flowers (FAMU).

Male imago. – Length: body, 2.8-3.1 mm; fore wing, 2.8-3.0 mm; hind wing, 0.40 mm. General coloration yellowish white. Head whitish shaded with gray dorsally and with yellowish around antennae. Antennae whitish translucent. Thorax. Pronotum and propleurae translucent shaded with gray dorsally, prosternum whitish. Mesonotum yellowish turning yellowish white toward pleurae and sterna; FMI orangish; mesonotum shaded with gray on a medial line just before mesoscutellum (between PSP); mesoscutellum and membranous filaments yellowish translucent. Metathorax yellowish white. Wings (figs. 29-31). Membrane hyaline very slightly tinged with yellowish, longitudinal veins yellowish brown, cross veins yellowish. Coxae, trochanters and femora of all legs whitish yellow shaded with gray, tibiae and tarsi whitish shaded with gray only on fore legs. Abdomen whitish translucent shaded completely with yellowish gray, except on a mediolongitudinal lighter line of terga I-V; shaded more markedly on lateral margins of this lighter line. Genitalia (figs. 24-28) whitish translucent, except lateral margins of penes light yellowish; accessory dorsal structure apically blunt (fig. 28); apical notch of penes almost absent (fig. 27). Tails whitish translucent.

Female imago. – Length: body, 3.2-3.3 mm; fore wings, 3.4-3.5 mm. Similar to male imago, except mesonotal mark between PSP larger and darker; membranous filaments of mesoscutellum shaded with gray. Egg mass yellowish orange. Ninth sternum with a broad apical excavation.

Nymph. – Unknown.

Life cycle association. – Association between male and female imagos made by color pattern on body and wing venation.

Etymology

'Yuquí', noun in apposition, for one of the ethnic groups inhabiting the region where the types were collected.

Diagnosis

Traverhyphes (Byrsahyphes) yuqui sp. n. can be distinguished from the other species of the subgenus by the following combination of characters. In the imago: 1) abdominal terga uniformly but slightly shaded with gray, medial lighter line on terga I-V; 2) spines of penes very short, less than 1/6 total length of penes (fig. 28); 3) penes without ventral swelling, and without deep apicomedial notch (figs. 26-28); 4) veins of fore wings yellowish brown; and 5) accessory dorsal structure associated with penes single and relatively blunt (a. d. s. in fig. 28).

Allenhyphes Hofmann & Sartori
(figs. 50-51, 58-59, 91-99)

Allenhyphes Hofmann & Sartori in: Hofmann et al., 1999: 67; Wiersema & McCafferty 2000: 342; Molineri & Flowers 2001: 61; Baumgardner 2003: 203.
Type species: *Leptohyphes flinti* Allen, original designation.
Species included: *A.*? *asperulus* (Allen), *A. flinti* (Allen), *A.*? *spinosus* (Allen), and *A. vescus* (Allen).

Diagnosis. – *Allenhyphes* was erected (Hofmann et al., 1999) to accommodate *Leptohyphes flinti* Allen, because of some unique structures on male genitalia. Posteriorly Wiersema & McCafferty (2000) added 10 species described from nymphs by Allen. Three of them (*A. minimus*, *A. tinctus* and *A. viriosus*) were proven to be *Tricorythopsis* species (Molineri, 2001c). *Allenhyphes michaeli* was recently synonymized with *A. vescus* (Baumgardner, 2003). The remaining species were cladistically analyzed here and only *A. vescus* is grouped together with the type species (*A. flinti*, the only species registered from adults in South America). *Allenhyphes*? *asperulus* and *A.*? *spinosus* do not show a resolved position, but are temporarily maintained in *Allenhyphes* until their adult stage could be known. *Allenhyphes* can be distinguished from the other genera of the family by the following combination of characters: 1) male terminal filament with a large ventrobasal spine; 2) penes with a pair of large and elongated apical lobes; 3) median cleft of penes deep and well marked; 4) penes with a pair of basal sclerosed filaments attached ventrally. In the nymphs: 1) maxillary palpi very small, two-segmented with apical seta (similar to fig. 54), inserted in a straight or slightly concave margin; 2) abdominal gill VI formed by 2 lamellae (similar to fig. 90).

Allenhyphes*? *asperulus (Allen)
(figs. 50, 58, 91-95)

Leptohyphes asperulus Allen, 1967:366; Hubbard 1982: 273.
Allenhyphes asperlus (sic): Wiersema & McCafferty 2000: 343.
Allenhyphes asperulus: Molineri 2003: 48.

Type material. – nymph holotype in microscope slides (N° 17371) PERU: Tulumayo Valley, río Pendescia, 14-18.vi.1963, W. L. Peters (CAS).

Diagnosis. – *Allenhyphes*? *asperulus* (Allen) was described from a single nymph. Wiersema & McCafferty (2000) transferred it to *Allenhyphes*, but this is not supported in the present study. Nevertheless, and as discussed before, it seems better to keep this generic assignation until the adult stage could be known. *Allenhyphes*? *asperulus* can be separated from the other species of this group of genera by the following combination of characters: 1) maxillary palpi 3-segmented, without apical seta (fig. 50); 2) femoral spines relatively short and with smooth apex (fig. 94); 3) female gonopore, in mature nymphs, without black macula; 4) operculate gills widely shaded with gray (fig. 58); 5) legs and tarsal claw as in figs. 91-93 and 95 respectively.

Allenhyphes*? *spinosus (Allen & Roback)
(figs. 51, 59, 96-99)

Leptohyphes sp. 1 Roback, 1966:150.
Leptohyphes spinosus Allen & Roback 1969:372; Hubbard 1982:274.
Allenhyphes spinosus: Wiersema & McCafferty 2000: 366; Molineri 2003: 48.

Type material. – Nymph holotype (whole nymph in slide) PERU: río Rondos, 29.ix.1955, S. S. Roback (ANSP). – Paratype (whole nymph in slide, N° 20.55) PERU: río Tulumayo, Porto Nuevo, near Tingo María, 25.ix.1955 (ANSP).

Diagnosis. – As discussed in the previous species, *Allenhyphes*? *spinosus* was described first in *Leptohyphes* (Allen & Roback 1969) and later transferred to *Allenhyphes* (Wiersema & McCafferty 2000). It is known from two nymphs collected near to the type locality of *A.*? *asperulus*. Both species are similar and as explained above the generic placement of *A.*? *spinosus* will also remain uncertain until the discovery of male adults. The nymphs of *A.*? *spinosus* can be distinguished from the other of the group by the following combination of characters: 1) maxillary palpi 3-segmented, without apical seta (fig. 51); 2) femoral spines relatively long and with smooth apex (fig. 98); 3) female gonopore, in mature nymphs, without black macula; 4) operculate gills and hind femora with blackish marks as in figs. 59 and 96-97; 5) tarsal claws as in fig. 99.

***Lumahyphes* Molineri**

Lumahyphes Molineri, in Molineri & Zúñiga, 2004.
Type species: *Lumahyphes guacra* Molineri, original designation.
Species included: *Lumahyphes guacra* Molineri, *L. yagua* Molineri & Zúñiga, *Lumahyphes* sp. from Mexico, and *L. pijcha* sp. n.

Diagnosis. – *Lumahyphes* Molineri (Molineri & Zuñiga 2004) was recently described for three species, distributed from Mexico to central Argentina. *Lumahyphes guacra* Molineri was cited from Bolivia and Argentina. *Lumahyphes pijcha* sp. n. is the second species of the genus known to occur in Bolivia. This species belongs to *Lumahyphes*, because it presents the following characters, in the adults: 1) penes widening slightly toward the apex (fig. 34) with spines inserted laterally and not hidden by the penes in ventral view (figs. 32-35); 2) vein CuP in fore wings with remnants of a basal extension (arrow in fig. 40); 3) first forceps segments relatively long (fig. 32). And in the nymphs: 1) maxillary palpi relatively large and three-segmented (fig. 57); 2) spines on dorsum of fore femora with spiculate apical margin (fig. 122); and 3) gill formula 3/4/4/3/2 (figs. 86-90).

Lumahyphes pijcha sp. n.
(figs. 32-40, 47, 57, 85-90, 119-123)

Type material. – Holotype: male imago, BOLIVIA: Depto. La Paz, Reserva Carrasco, road to Caranavi-Alto Beni, S 15º 43' 09"-W 67º 31' 06", 940 m, light 4-6 AM, 28.xi.2000, Domínguez, Molineri & Nieto cols. (UMSA). – Paratypes: 44 male imagos, 28 female imagos, and 5 nymphs same data as holotype; and 4 male imagos from BOLIVIA: Depto. La Paz, Stream between Caranavi and Guanai, S 15º 40' 18"-W 67º 42' 04", 500 m, light 4-6 AM, 27.xi.2000, Domínguez, Molineri & Nieto cols. (5 male and 5 female imagos and 1 nymph deposited in UMSA; 43 male and 23 female imagos, and 4 nymphs in IFML).

Additional material. – 4 male and 1 female imagos from COLOMBIA, Parque Nac. Farallones de Cali, Peñas Blancas, rio Pichinde, N 03º 25' 45", W 76º 39' 27", 18.ii.1999, light 5-6 h AM, Zuñiga, Domínguez & Molineri cols. (2 male imagos in MEUV, 2 male and 1 female imagos in IFML).

Male imago. – Length: body, 3.2-3.5 mm; fore wings, 2.8-3.2 mm; hind wings, 0.45-0.50 mm. General coloration yellowish white. Head yellowish white shaded with gray around antennae and on dorsum, darker at posterolateral corners. Antennae yellowish translucent. Thorax. Pronotum yellowish translucent shaded with gray, prosternum whitish shaded with gray. Mesonotum yellowish, darker at carinae, mesopleurae and mesosternum lighter; mesoscutellum yellowish translucent. Wings (figs. 37-40). Membrane of both wings hyaline slightly tinged with yellow; longitudinal veins of fore wings yellowish brown, cross veins yellowish. Legs. Coxae and trochanters yellowish; femora yellowish white; tibiae and tarsi whitish shaded slightly with gray. Abdomen whitish translucent, except segments IX-X light yellowish white; all segments shaded with yellowish gray dorsally, except on a mediolongitudinal lighter line; sterna whitish translucent. Genitalia (figs. 32-35) whitish except lateral margins of penes yellowish. Tails whitish translucent except first and second segments whitish.

Female imago. – Length: body, 3.5-3.7 mm; fore wings (fig. 36), 3.4-3.5 mm. As in male except grayish shading of body more marked. Ninth sternum with slightly concave hind margin. Egg mass light yellowish.

Mature nymph. – Length: body, 3.5-3.7 mm; mesonotum, 1.0-1.1 mm; cerci 2.5-3.0 mm; terminal filament, 3.0-3.5 mm. General coloration yellowish. Head (fig. 47) yellowish shaded with gray around antennae and on a band between ocelli; occipute with a pair of small submedian marks on hind margin. Mouthparts yellowish, maxillary palpi 3-segmented without apical seta (fig. 57). Antennae yellowish translucent, 4 times length of head. Thorax. Pro- and mesonotum yellowish with irregular gray markings. Mesoscutellum slightly darker than the rest. Legs (figs. 119-121) yellowish white; femoral spines spatulate with the apex slightly concave and with tiny spiculae (fig. 122); fore margin of all femora spiculate as in fig. 119; tarsal claws relatively long and slender, with 5-7 marginal denticles and a subdistal row of 4-5 submarginal denticles (fig. 123). Abdomen yellowish completely shaded with light gray on terga, except below gills; sterna paler. Operculate gills (figs. 85-86) yellowish translucent, shaded with gray, becoming lighter toward apex; remaining gills almost hyaline; gill formula 3/4/4/3/2 (figs. 86-90, gill IV presents a tiny ventral most lamellae, fig. 88). Small posterolateral spines present on segments VII-IX, lateral flanges present on segments III-VII (smaller on VII). Tails yellowish translucent.

Life cycle association. – Association between male and female imagos made by color pattern on body and wing venation. Nymphs were not reared, they are tentatively associated with adults by color markings and presence in the same locality.

Etymology

'Pijcha', action of chewing 'coca' leaves (*Erithroxylum coca*, Erithroxilaceas), ancestral tradition of the region where the species is distributed.

Diagnosis

Lumahyphes pijcha sp. n. can be distinguished from the other species of the genus by the following combi-

nation of characters. In the imago: 1) grayish marks on subapex of femora absent or very slightly marked; 2) abdominal terga shaded with yellowish gray dorsally, lighter on a mediolongitudinal line; 3) penes relatively long and slender (figs. 32-35); 4) spines of penes relatively short and straight, near ⅓ total length of penes (figs. 34-35); 5) veins of fore wings yellowish brown; 5) female gonopore without black macula. In the nymph: 1) color markings of head as in fig. 47; 2) abdominal terga shaded with light gray completely; 3) operculate gill shaded slightly with gray; 4) gill formula 3/4/4/3/2 (figs. 86-90), ventral most lamellae of gill IV very small (fig. 88); 5) fore margin of femora spiculate (fig. 119); 5) tarsal claws long and slender, with 5-7 marginal and 4-5 submarginal denticles (fig. 123).

Colombian specimens do not show considerable variations from this description except for a larger body size and wing length. Length of male: body, 3.90-4.00 mm; fore wings, 4.10-4.50 mm; hind wings, 0.50-0.57 mm. Length of female: body, 4.25 mm; fore wings, 5.00 mm. Also the costal projection of male hind wings is slightly larger. Two male imagos deposited in MEUV, 2 male and 1 female imagos deposited in IFML.

Yaurina Molineri
(figs. 52, 60, 124-127)

Yaurina Molineri, 2001a: 338.
Type species: *Y. yuta* Molineri, original designation.
Species included: *Y. mota* Molineri, *Y. ralla* (Allen) comb. n., *Y. yapa* Molineri, and *Y. yuta* Molineri.

Diagnosis. – *Yaurina* can be distinguished from the other genera of the family by the following combination of characters: 1) male terminal filament without large ventrobasal spine; 2) penes with a pair of long basal sclerosed filaments attached ventrally; 3) penes with a lateral furrow; 4) median cleft of penes slightly marked. In the nymphs: 1) maxillary palpi small, two-segmented without apical seta, second segment wider at base (fig. 52), inserted in a concave margin; 2) abdominal gill VI formed by 1 lamella (similar to fig. 84).

Yaurina ralla (Allen) comb. n.
(figs. 52, 60, 124-127)

Leptohyphes rallus Allen, 1967:363; Hubbard 1982:274.
Allenhyphes rallus (Allen), Wiersema & McCafferty 2000: 343; Molineri 2003: 48.

Type material. – 1 Female nymph holotype and 1 female nymph paratype (in alcohol), and paratype slide (FAMU Nº 2027.2) PERU: San Martín, Río Supte Grande, 10 km E Tingo María, 19.vii.1963, W. L. Peters.

Diagnosis. – This species was originally described in *Leptohyphes* (Allen, 1967), and later (Wiersema & McCafferty, 2000) transferred to *Allenhyphes*. As a result of the present cladistic analysis it is here transferred to *Yaurina*. The character supporting this new combination is from maxillary palpi (2-segmented, with the distal segment widening slightly toward its base, fig. 52). Other character shared with *Yaurina* is gill II (fig. 60) oval and with one slightly marked ridge. Legs are illustrated in figs. 124-126 and the tarsal claws show 4 marginal denticles and a single palisade of 6 submarginal denticles (fig. 127). In spite of *Yaurina* nymphs being perfectly distinguishable from nymphs of other genera, the nymphs of the three species known do not show reliable morphological characters to be separated. As *Yaurina yapa* Molineri (2001a) is only known from male adults from Ecuador, it could prove to be a junior synonym of *Y. ralla*.

Key for the species of the *Allenhyphes-Traverhyphes* Group

Note: distribution of the species should not be considered as part of the couplet.

Male imagos

1. Male terminal filament with a strong ventral spine at the base ..... *Allenhyphes*
– Male terminal filament not as above 2
2. Penes with a pair of long sclerosed filaments of ventrobasal insertion ..... *Yaurina* 3
– Penes with sclerosed spines (sometimes hyaline) but never forming ventrobasal filaments as above 5
3. Sclerosed filaments coiled distally and longer than penes (if unfolded) [Ecuador] ..... *Y. yapa*
– Sclerosed filaments shorter than penes, the apex may be curved outward or not 4
4. Sclerosed filaments curved outward, apex acute [Argentina, Bolivia] ..... *Y. yuta*
– Sclerosed filaments relatively straight, apex blunt [Argentina] ..... *Y. mota*
5. Penes with a pair of strong spines inserted laterally (fig. 32); penes without dorsal extensions or with a single membranous dorsal extension (fig. 35) ... . *Lumahyphes* 6
– Penes with a pair of spines inserted dorsally or dorsolaterally (figs. 2, 12, 18, 28); penes with paired dorsal extensions (figs. 12, 18, 26). .... *Traverhyphes*, 9
6. Penes relatively long and slender (fig. 32), penean spines not strongly curved, directed dorsally (fig. 33) [Bolivia, Colombia] ..... *Lumahyphes pijcha*
– Penes relatively wider and more robust, penean spines curved medially 7
7. Penean spines short, near 0.5 total length of penes..... *Lumahyphes* sp. from Mexico

– Penean spines longer, at least 0.7 total length of penes 8
8. First forceps segment much darker than the rest [Argentina, Bolivia] ..... *Lumahyphes guacra*
– First forceps segment as dark as remaining segments [Colombia, Peru] ..... *Lumahyphes yagua*
9. Posterolateral margins of styliger projected posteriorly (figs. 2-3) ..... *T. (Traverhyphes)*, 10
– Posterolateral margins of styliger not projected as above (figs. 9-10, 13-15, 24) 12
10. Spine of penes inserted dorsally [Argentina, Brazil, Uruguay] ..... *T.(Traverhyphes) indicator*
– Spine of penes inserted dorsolaterally (fig. 2) 11
11. Penes long and slender, with a similar width along their length (figs. 2-4) [Bolivia] .... *T.(Traverhyphes) chiquitano*
– Penes wider on distal half [Brazil] .... *T.(Traverhyphes) pirai*
12. First forceps segment very short, almost globular (figs. 15, 24); lateral margins of penes entire (figs. 18-19, 26-28); accessory dorsal structure single (figs. 17, 28) ..... *T.(Byrsahyphes)*, 13
– First forceps segment longer and subrectangular (figs. 9, 13, 130); lateral margins of penes with a subapical excavation (figs. 130-131); accessory dorsal structure double (fig. 131) .... *T.(Mocoihyphes)*, 14
13. Penes notched apically (figs. 18-19) and with a subdistal ventral swelling (fig. 17) [Costa Rica, Panama, Colombia] ..... *T.(Byrsahyphes) nanus*
– Penes very slightly notched (fig. 27) and without subdistal ventral swelling (fig. 28) [Panama, Bolivia] ..... *T.(Byrsahyphes) yuqui*
14. Spines of penes long, about ½ total length of penes (figs. 13-14) [Argentina, Brazil] .... *T. (M.) yuati*
– Spines of penes short, less than ¼ total length of penes (figs. 10, 12, 129) [Argentina, Brazil] .... *T. (M.) edmundsi*

Nymphs

1. Body relatively stout; maxillary palpi 2-segmented; operculate gills ovoid and relatively small, not reaching posterior half of abdominal segment VII 2
– Body relatively elongated; maxillary palpi 2 or 3-segmented; operculate gills ovoid to subquadrate and relatively large, at least reaching posterior half of abdominal segment VII 3
2. Abdominal gill VI with 2 lamellae; maxillary palpi with apical seta, palpi inserted in a straight (or very slightly concave) margin ..... *Allenhyphes* .....[only 1 species recorded from South America (Venezuela) ..... *A. flinti*]
– Abdominal gill VI with 1 lamella; maxillary palpi without apical seta, palpi inserted in a concave margin ..... *Yaurina* [nymphs of *Yaurina* are indistinguishable at species level]
3. Maxillary palpi 3-segmented and relatively large (figs. 50-51, 56-57) 4
– Maxillary palpi 2-segmented and relatively small (figs. 53-55) 9
4. Femoral spines with fringed apex (fig. 122); female mature nymph generally with a median black macula between abdominal sterna VII and VIII. ..... *Lumahyphes* 5
– Femoral spines apically smooth (figs. 94, 98, 117); female mature nymph without median black macula between abdominal sterna VII and VIII 7
5. Color markings of head as in fig. 47; abdominal terga completely shaded with light gray [Bolivia, Colombia] ..... *Lumahyphes pijcha*
– Color markings of head not as above; abdominal terga completely shaded with light gray except on a mediolongitudinal line 6
6. Abdomen with a relatively wide mediolongitudinal lighter line on abdominal terga; tarsal claws with double row of 2-3 submarginal denticles near the apex [Argentina, Bolivia] .... *Lumahyphes guacra*
– Mediolongitudinal line narrower; tarsal claws with 1 pair of submarginal denticles near the apex [Colombia, Peru] ..... *Lumahyphes yagua*
7. Maxillary palpi with small apical seta (fig. 56) [Central America, Colombia]..... .....*Traverhyphes(Byrsahyphes) nanus*
– Maxillary palpi without small apical seta (figs. 50-51) 8
8. Hind femora with large blackish marks and with relatively long spines (figs. 96, 98); operculate gills shaded with black in a basal C-shaped asymmetric mark (fig. 59) [Peru] .... *Allenhyphes? spinosus*
– Hind femora without strong marks and with relatively shorter spines (figs. 91, 94); operculate gills completely shaded with black (fig. 58) [Peru] ..... *Allenhyphes? asperulus*
9. Abdominal gills III with 4 lamellae, abdominal gills IV with 3 or 4 lamellae (figs. 63-64)..... ..... *T. (Traverhyphes)*, 10
– Abdominal gills III and IV with 3 lamellae (figs. 69-70, 75-76) ..... *T. (Mocoihyphes)*, 11
10. Operculate gills shaded with black on anteromedian corner [Argentina, Brazil, Uruguay] .... *T. (T.) indicator*
– Operculate gills shaded with black on a basal macula and transverse ridge (fig. 61) [Bolivia] .... *T. (T.) chiquitano*
11. Body heavily shaded with purplish gray, large marks present on subapex of femora (figs. 109-

111); abdomen uniformly shaded, rarely with a mediolongitudinal lighter line (fig. 46); maxillary palpi 2-segmented without apical seta (fig. 55) [Argentina, Brazil] ..... *T. (M.) yuati*

– Body shaded slightly with gray, femoral marks smaller (figs. 104-106); abdomen with a mediolongitudinal lighter line, widening on terga VII-IX (fig. 48); maxillary palpi 2-segmented with apical seta (fig. 54) [Argentina, Brazil] .... *T.(M.) edmundsi*

Acknowledgments

The following persons and institutions are greatly acknowledged for loan of material: J. G. Peters and R. W. Flowers (FAMU), D. Funk (SCWR), W. J. Pulawski (CAS), Claire Hofmann, Michel Sartori (Musee de Zoologie, Palaice de Rumine, Suitzerland), P. Bispo (MZSP) and David Baumgardner (Texas A&M University, USA). Nymphs of *L. nanus* were reared from eggs by John Jackson (SCWR). For collecting trips arrangements I am indebted to M. C. Zúñiga (Universidad del Valle, Cali, Colombia), S. Duque (Instituto de Investigaciones Amazónicas, Universidad Nacional de Colombia), Instituto de Ecología (Universidad Mayor de San Andrés, La Paz, Bolivia), and C. G. Froehlich (Universidade de Sao Paulo, Brazil). For collecting permits issued in Argentina: Administración Nacional de Parques Nacionales, Ministerio de Ecología de la Provincia de Misiones, and Direcciones de Flora y Fauna (Provincias de Salta y Jujuy). Eduardo Domínguez and J. G. Peters provided useful comments and discussion during the course of this study.

The author is a postdoctoral student in CONICET (National Council of Scientific Research, Argentina), which support is greatly acknowledged. This research was partially supported by the following grants: CONICET PIA 8019/96, PIP 4973/97, and FONCyT 0100692/97 (ANPCyT).

References

Allen, R. K., 1967. New species of New World Leptohyphinae (Ephemeroptera: Tricorythidae). – Canadian Entomologist 99(4): 350-375.

Allen, R. K., 1973. New species of *Leptohyphes* Eaton (Ephemeroptera: Tricorythidae). – Pan-Pacific Entomologist 49(4): 363-372.

Allen, R. K., 1978. The nymph of North and Central American *Leptohyphes* (Ephemeroptera: Tricorythidae). – Annals of the Entomological Society of America 71(4): 537-558.

Allen, R. K. & S. S. Roback, 1969. New species and records of New World Leptohyphinae (Ephemeroptera: Tricorythidae). – Journal of the Kansas Entomological Society 42(4): 372-379.

Baumgardner, D. E., 2003. New synonyms and stage descriptions for three species of Leptohyphidae (Ephemeroptera). – Proceedings of the Entomological Society of Washington 105(1): 203-208.

Bremer, K., 1988. The limit of amino-acid sequence data in angiosperm phylogenetic reconstruction. – Evolution 42: 795-803.

Bremer, K., 1994. Branch support and tree stability. – Cladistics 10: 295-304.

Eaton, A. E., 1882. An announcement of new genera of the Ephemeridae. – Entomological Monthly Magazine 18: 207-208.

Farris, J. S., V. A. Albert, M. Källersjö, D. Lipscomb and A. G. Kluge, 1996. Parsimony jackknifing outperforms neighbor-joining. – Cladistics 12(2): 99-124.

Goloboff, P. A., 1993. Estimating character weights during tree search. – Cladistics 9: 83-91.

Goloboff, P. A., J. S. Farris, M. Källersjö, B. Oxelman, M. J. Ramírez and C. A. Szumik, 2003. Improvements to resampling measures of group support. – Cladistics 19(4): 324-332.

Goloboff, P. A., J. Farris & K. Nixon, 2004. T.N.T.: Tree Analysis Using New Technology. – Program and documentation available from the authors and at http://www.zmuc.dk/public/phylogeny

Hofmann, C.; M. Sartori & A. Thomas, 1999. Les Ephéméroptères (Ephemeroptera) de la Guadeloupe (petites Antilles françaises). – Mémoires de la Société Vaudoise des Sciences Naturelles 20(1):1-96.

Hubbard, M. D., 1982. Cat logo abreviado de Ephemeroptera da América do Sul. – Papeis Avulsos de Zoologia, Sao Paulo 94(24):257-282.

Kluge, N. Ju., 1992. Redescription of *Leptohyphes eximius* Eaton and diagnoses of the genera *Leptohyphes* and *Tricorythodes* based on the structure of pterothorax (Ephemeroptera: Tricorythidae, Leptohyphinae). – Opuscula zoologica fluminensia 98: 1-16.

Molineri, C., 2001a. A new genus of Leptohyphidae (Insecta: Ephemeroptera). – In: E. Domínguez (Ed.), Trends in research in Ephemeroptera and Plecoptera:. 337-345. Kluwer Academic/Plenum Publishers

Molineri, C., 2001b. A new genus of Leptohyphidae (Insecta: Ephemeroptera) for *Leptohyphes indicator* and related species. – Spixiana 24: 129-140.

Molineri, C., 2001c. El género *Tricorythopsis* (Ephemeroptera: Leptohyphidae): nuevas combinaciones y descripción de nuevas especies y estadios. – Revista de la Sociedad Entomológica Argentina 60(1-4): 217-238.

Molineri, C., 2003. Revision of the South American species of *Leptohyphes* Eaton (Ephemeroptera: Leptohyphidae) with a key to the nymphs. – Studies on Neotropical Fauna and Environment 38: 47-70.

Molineri, C. & E. Domínguez, 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(2): 263-275.

Molineri, C. & R. W. Flowers, 2001. Primera cita de *Allenhyphes* Hoffman y Sartori, 1999 (Ephemeroptera: Leptohyphidae) para América continental. – Entomotropica 16: 61-62.

Molineri, C. & M. C. Zuñiga, 2004. *Lumahyphes* a new genus of Leptohyphidae (Ephemeroptera). – Aquatic Insects 26(1): 19-30.

Rivera, M. O., M. Libermann, S. Beck & M. Moraes, 1996. Vegetación de Bolivia. – In: B. Kathy Mihotek B. Cimar (Ed.), Comunidades, territorios indígenas y biodiversidad

en Bolivia: 170-222. Universidad Autónoma Gabriel René Moreno, Centro de Investigación y Manejo de Recursos Naturales Renovables, Santa Cruz, Bolivia.
Roback, S. S., 1966. Catherwood Foundation Peruvian-Amazon Expedition. VI. Ephemeroptera Nymphs. – Monographs of the Academy of Natural Sciences of Philadelphia 14: 129-199.
Ruiz de Montoya, A., 1640. Arte y Bocabvlario de la Lengva Gvarani. – Edición facsimilar, Ediciones de Cultura Hisp nica (Agencia Española de Cooperación Internacional) y UNESCO, 1994, Madrid, España.
Ulmer, G., 1920. Neue Ephemeropteren. – Archiv für Naturgeschichte 85: 1-80.
Wiersema, N. A. & W. P. McCafferty, 2000. Generic revision of the North and Central American Leptohyphidae (Ephemeroptera: Pannota). – Transactions of the American Entomological Society 126 (3-4): 337-371.

Received: 8 September 2003
Revised version accepted: 1 October 2004

APPENDIX 1. LIST OF CHARACTERS AND STATES.

Adults

0 Base of CuP: 0=present 1=absent;
1 Ratio length costal projection/length of hind wing: 0=less than 0.46 total length of wing 1=at least 0.53 of total wing length;
2 Number of longitudinal veins on male hind wings: 0=three 1=two 2=one;
3 Posterolateral projection of styliger (external to forceps base): 0=absent 1=present;
4 Posterior projections of styliger plate (medial): 0=absent 1=present;
5 Ratio length of forceps segment 2+3/ forceps segment 1: 0=long (<2) 1=median-rectangular (2.3-3.3) 2=short-globular (>3.5);
6 Sclerosed ring of penes: 0=absent 1=present;
7 Male gonopore associated with hollow spine: 0=absent 1=present;
8 Penean spines curved ventrally: 0=no 1=yes;
9 Penean spines curved medially: 0=no 1=yes;
10 General location of penean spine: 0=apical or subapical 1=basal;
11 Location of bases of penean spines: 0=dorsal 1=lateral 2=ventral;
12 Median membranous lobes of penes: 0=absent 1=present;
13 Dorsal membranous projections of penes: 0=absent 1=double 2=single;
14 Penes width: 0=similar width along their length 1=markedly wider at apex;
15 Penes fusion: 0=partial 1=total;
16 Penes with lateral subapical excavation: 0=no 1=yes;
17 Penean arms divergence: 0=>45 1=<30º;
18 Lateral furrow of penes: 0=absent 1=present;
19 Penes: 0=other form 1= *Allenhyphes* kind (with a pair of large and elongated apical lobes, deep median cleft);
20 Dorsal structure associated with penes: 0=absent 1=single 2=bifid 3=double;
21 Male terminal filament: 0=normal 1=with a large ventral spine;
22 Black macula at female gonopore: 0=absent 1=present;

Nymphs

23 Distal segment of maxillary palpi: 0=with rounded base, markedly wider than the apex (fig. 52) 1=more or less cylindrical;
24 Apical seta of maxillary palpi: 0=absent 1=present;
25 Number of segments of maxillary palpi: 0=three 1=two;
26 Maxillae, setae at base of inner margin forming a group: 0=present 1=absent;
27 Maxillae, setae at base of inner margin forming a longitudinal row: 0=absent 1=present;
28 Furrow between galea and lacinia: 0=complete 1=incomplete 2=absent (galea-lacinia completely fused);
29 Length of femoral spines: 0=short (length less than 2 times width) 1=median (length more than 3 times width);
30 Femoral spines: 0=spatulate, apex smooth 1=bifid, apex spiculate;
31 Femora II and III with a mediolongitudinal ridge: 0=yes 1=no;
32 Femora with subapical blackish mark: 0=no 1=yes;
33 Femora II and III with a basal row of spines at dorsum: 0=yes 1=no;
34 Submarginal subapical denticles of tarsal claw: 0=double row 1=single row 2=1 asymmetric denticle;
35 Number of lamellae on abdominal gills: 0=3/6/6/4/2 or more 1=3/4/3-4/3/2 2=3/3/3/3/2 3=3/3/3/3/1;
36 Dorsal ridges on gill II: 0=absent 1=one 2=two;
37 Ventral inferior lamellae of gill II: 0=large, plate-like 1=reduced to a basal spine;
38 Pigmentation of gill II: 0=relatively uniform 1=with a subapical lighter mark.

APPENDIX 2.
SYNAPOMORPHIES COMMON TO THE 2025 SHORTEST TREES

Lettered nodes refer to nodes in consensus (fig. 1).

Lumahyphes pijcha:
All trees:
– Dorsal membranous projections of penes (13): 0=absent → 2=single
– Number of lamellae on abdominal gills (35): 2=3/3/3/3/2 → 1=3/4/3-4/3/2
Some trees:
– Submarginal subapical denticles of tarsal claw (34): 0=double row → 1=single row

T. (Traverhyphes) indicator:
All trees:
– Location of bases of penean spines (11): 1=lateral → 0=dorsal

T. (Mocoihyphes) yuati:
All trees:
– Apical seta of maxillary palpi (24): 1=present → 0=absent

Node A (entire *Allenhyphes-Traverhyphes* group, 19 spp.):
All trees:
– Maxillae, setae at base of inner margin forming a group (26): 0=present → 1=absent
– Maxillae, setae at base of inner margin forming a longitu-

dinal row (27): 0=absent → 1=present
– Furrow between galea and lacinia (28): 0=complete → 1=incomplete
– Length of femoral spines (29): 0=short → 1=median
– Femora II and III with a mediolongitudinal ridge (31): 0=yes → 1=no
– Femora II and III with a basal row of spines at dorsum (33): 0=yes → 1=no
– Dorsal ridges on gill II (36): 0=absent → 1=one
– Ventral inferior lamellae of gill II (37): 1=reduced to a basal spine → 0=large, plate-like

Some trees:
– Ratio length costal projection/length of hind wing (1): 0=less than 0.46 total length of wing → 1=at least 0.53 of total wing length
– Number of longitudinal veins on male hind wings (2): 0=three → 1=two
– Posterior projections of styliger plate (medial) (4): 0=absent → 1=present
– Male gonopore associated with hollow spine (7): 0=absent → 1=present
– Penes fusion (15): 0=partial → 1=total
– Penean arms divergence (17): 0=→45 → 1=<30º
– Submarginal subapical denticles of tarsal claw (34): 2=1 asymmetric denticle → 0=double row, or 1=single row
– Number of lamellae on abdominal gills (35): 0=3/6/6/4/2 or more → 2=3/3/3/3/2

Node B (*Allenhyphes* + *Yaurina*, 6 spp):
Some trees:
– General location of penean spine (10): 0=apical or subapical → 1=basal
– Location of bases of penean spines (11): 1=lateral → 2=ventral
– Number of segments of maxillary palpi (25): 0=three → 1=two
– Submarginal subapical denticles of tarsal claw (34): 0=double row → 1=single row

Node C (*Allenhyphes flinti* + *A. vescus*):
All trees:
– Number of longitudinal veins on male hind wings (2): 1=two → 2=one
– Penes (19): 0=other form → 1= Allenhyphes kind (with a pair of large and elongated apical lobes, deep median cleft)
– Male terminal filament (21): 0=normal → 1=with a large ventral spine
– Apical seta of maxillary palpi (24): 0=absent → 1=present

Node D (*Yaurina*, 4 spp.):
Some trees:
– Lateral furrow of penes (18): 0=absent → 1=present
– Distal segment of maxillary palpi (23): 1=more or less cylindrical → 0=with rounded base, markedly wider than the apex (fig. 52)
– Number of lamellae on abdominal gills (35): 2=3/3/3/3/2 → 3=3/3/3/3/1

Node E (*Lumahyphes* + *Traverhyphes*, 11 spp.):
All trees:
– Pigmentation of gill II (38): 0=relatively uniform → 1=with a subapical lighter mark

Some trees:
– Median membranous lobes of penes (12): 0=absent → 1=present
– Dorsal structure associated with penes (20): 0=absent → 1=single, or 3=double

Node F (*Lumahyphes*, 4 spp.):
All trees:
– Base of CuP (0): 1=absent → 0=present
– Ratio length of forceps segments 2+3/segment 1 (5): 1=2.3-3.3 (first segment median-rectangular) → 0=2.0 or less (first segment long)
– Penes width (14): 0=similar width along their length → 1=markedly wider at apex
– Femoral spines (30): 0=spatulate, apex smooth → 1=bifid, apex spiculate

Node G (*Lumahyphes* sp. Mexico + *L. guacra* + *L. yagua*):
All trees:
– Penean spines curved medially (9): 0=no → 1=yes

Some trees:
– Black macula at female gonopore (22): 0=absent → 1=present

Node H (genus *Traverhyphes*, 8 spp.):
All trees:
– Dorsal membranous projections of penes (13): 0=absent → 1=double
– Apical seta of maxillary palpi (24): 0=absent → 1=present

Some trees:
– Number of segments of maxillary palpi (25): 0=three → 1=two

Node I (subgenus *Byrsahyphes*, 2 spp.):
All trees:
– Ratio length of forceps segments 2+3/segment 1 (5): 1=2.3-3.3 (first segment median-rectangular)→ 2=→3.5 (first segment short-globular)
– Location of bases of penean spines (11): 1=lateral → 0=dorsal

Node J (subgenera *Traverhyphes* + *Mocoihyphes*, 5 spp.):
All trees:
– Penean spines curved medially (9): 0=no → 1=yes
– Femora with subapical blackish mark (32): 0=no → 1=yes
– Dorsal ridges on gill II (36): 1=one → 2=two

Node K (subgenus *Mocoihyphes*, 2 spp.):
All trees:
– Penes with lateral subapical excavation (16): 0=no → 1=yes

Node L (subgenus *Traverhyphes*, 3 spp.):
All trees:
– Posterolateral projection of styliger (external to forceps base) (3): 0=absent → 1=present
-Penes fusion (15): 1=total → 0=partial

Some trees:
– Number of lamellae on abdominal gills (35): 2=3/3/3/3/2 → 1=3/4/3-4/3/2