

Revision of the South American Species of *Leptohyphes* Eaton (Ephemeroptera: Leptohyphidae) with a Key to the Nymphs

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Abstract

The male imago of *Leptohyphes eximius* Eaton, 1882 (type species of the genus) and male and female adults of *L. cornutus* Allen (1967) and *L. plaumanni* Allen (1967) are described for the first time. The nymphs of these species are redescribed. A new generic definition is proposed to include all the stages. Characters for separating male, female, eggs and nymphs of this genus from the other genera of the family are discussed and illustrated. *Cotopaxi* Mayo (1968) is proposed to be a junior synonym of *Leptohyphes* Eaton; its type species *C. macuchae* is declared a Nomen Dubium. The type material of all the South American species of *Leptohyphes* described as nymphs was studied, and a key together with a diagnosis with illustrations are presented for them. The following new synonymies are proposed: *Leptohyphes eximius* Eaton (= *L. bruchi* Navás and *Bruchella nigra* Navás), *L. maculatus* Allen (= *L. comatus* Allen, *L. hirsutus* Allen & Roback and *L. myllonotus* Allen & Roback), *L. setosus* Allen (= *L. echinatus* Allen & Roback), *L. tacajalo* Mayo (= *L. albus* Mayo) and *L. plaumanni* Allen (= *L. pereirae* da Silva). After this revision the number of valid South American species of *Leptohyphes* is eighteen (18). Scanning microscope photographs of the eggs of two species: *L. eximius* and *L. cornutus* are presented.

Resumen

Se describen por primera vez el imago macho de *Leptohyphes eximius* Eaton, 1882 (especie tipo del género) y los imagos de ambos sexos de *L. cornutus* Allen (1967) y *L. plaumanni* Allen (1967). Las ninfas de estas especies son redescriptas. Se propone una nueva definición del género para incluir todos los estados. Se ilustran y discuten los caracteres para distinguir a los machos, hembras, ninfas y

huevos de *Leptohyphes*. Se propone a *Cotopaxi* Mayo (1968) como un nuevo sinónimo de *Leptohyphes* Eaton; y su especie tipo, *C. macuchae*, es declarada Nomen Dubium. Se estudió el material tipo de todas las especies sudamericanas de *Leptohyphes* descritas sobre la base de ninfas, y se presenta una clave, diagnosis e ilustraciones para distinguirlas. Se proponen los siguientes nuevos sinónimos: *Leptohyphes eximius* Eaton (= *L. bruchi* Navás y *Bruchella nigra* Navás), *L. maculatus* Allen (= *L. comatus* Allen, *L. hirsutus* Allen & Roback y *L. myllonotus* Allen & Roback), *L. setosus* Allen (= *L. echinatus* Allen & Roback), *L. tacajalo* Mayo (= *L. albus* Mayo) y *L. plaumanni* Allen (= *L. pereirae* da Silva). Después de esta revisión son dieciocho (18) las especies de *Leptohyphes* que permanecen válidas en Sudamérica. Se presentan fotografías de microscopio electrónico de barrido para los huevos de dos especies: *L. eximius* y *L. cornutus*.

Keywords: *Leptohyphes*, *Cotopaxi*, Neotropics, taxonomy, key.

Introduction

Since Eaton (1882) described *Leptohyphes* from a single female specimen, many species have been added in this genus. Surprisingly, almost all of them were described from nymphs without associated adults. This is the main reason for the large number of *Leptohyphes* species registered in South America, a lot of them actually representing different genera (Hofmann et al., 1999; Wiersema & McCafferty, 2000; Molineri, 2001a, b).

Leptohyphes eximius Eaton, the type species of the genus, is known from the female imago (Eaton, 1883), female

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subimago, nymph and egg (Kluge, 1992) but the males remained unknown until now. Nymphs and reared male and female adults of *L. eximius* Eaton are described or redescribed from material collected near the type locality. Male genitalia are shown to be of the 'peterseni' type (Traver, 1958a: 497), and the genus is restricted to the species with this type of genitalia, among other characters from females and nymphs.

In South America, only three species of *Leptohyphes* were known from adults and nymphs: *L. maculatus* Allen, *L. petersi* Allen and *L. setosus* Allen (1967). Five species were known only from male adults: *L. bruchi* Navás (1931), *L. mollipes* Needham & Murphy (1924), *L. niger* (= *Bruchella nigra* Navás) (1920), *L. nigripunctum* Traver (1943) and *L. peterseni* Ulmer (1919). The South American species originally described only from nymphs are numerous: *L. indicator* Needham and Murphy (1924); *L. asperulus* Allen, *L. comatus* Allen, *L. gibbus* Allen, *L. illiesi* Allen, *L. jodiannae* Allen, *L. rallus* Allen, *L. tuberculatus* Allen, *L. undulatus* Allen (1967); *L. echinatus* Allen and Roback, *L. hirsutus* Allen and Roback, *L. myllonotus* Allen and Roback, *L. spinosus* Allen and Roback (1969); *L. carinus* Allen, *L. edmundsi* Allen, *L. invictus* Allen, *L. minimus* Allen, *L. populus* Allen, *L. tinctus* Allen, *L. viriosus* Allen (1973); *L. albus* Mayo, *L. ecuador* Mayo, *L. tacajalo* Mayo (1968); *L. pereirae* Da Silva (1993); and *L. liniti* Wang et al. and *L. nicholsae* Wang et al. (1998). Some of them have recently been moved to other genera (see Table 1).

Baumgardner and McCafferty (2000) synonymized numerous species under *L. zalope* Traver (1958b) giving diagnostic characters of this species at all stages. The majority of the morphological characters used by them to distinguish *L. zalope* are used here at the generic level. This situation does not invalidate their work and, because of the

problems discussed by these authors, some synonymies also occur in South American species; the following are proposed in the present paper: *L. eximius* Eaton (= *L. bruchi* Navás and *L. niger* (Navás)), *L. maculatus* Allen (= *L. comatus* Allen, *L. hirsutus* Allen & Roback and *L. myllonotus* Allen & Roback), *L. setosus* Allen (= *L. echinatus* Allen & Roback), *L. tacajalo* Mayo (= *L. albus* Mayo) and *L. plaumanni* Allen (= *L. pereirae* Da Silva).

Besides *L. zalope*, the other Central and North American species congeneric with *Leptohyphes eximius* are: *L. bernerii* Traver, *L. sabinas* Traver and *L. priapus* Traver (1958b); *L. castaneus* Allen, *L. murdochi* Allen, *L. musseri* Allen (1967); *L. alleni* Brusca (1971); *L. brunneus* Allen and Brusca, *L. lestes* Allen and Brusca, *L. pilosus* Allen and Brusca, *L. spiculatus* Allen and Brusca (1973); *L. vulturinus* Allen (1978); *L. tarsos* Allen and Murvosh (1987); and *L. guadeloupensis* Hofmann and Sartori (Hofmann et al., 1999). *L. brevissimus* Eaton (1892) and *L. costaricanus* Ulmer (1919) were described from one female respectively and their placement in *Leptohyphes* remains uncertain.

The genus *Cotopaxi* Mayo (1968) is only known from the holotype and was never collected again in spite of the efforts conducted to find it. From the study of the holotype slides and original drawings *Cotopaxi* is proposed here to be a junior synonym of *Leptohyphes* Eaton. The type and only species of this genus, *C. macuchae* is proposed to be a *Nomen Dubium*.

As a result of the present paper the number of valid species of *Leptohyphes* in South America is 18:6 known from nymphs and adults, 3 known from adults and 9 known only as nymphs. A key to separate the 15 species known from nymphs is given. A key for the adults is not available at this time because the knowledge of this stage is too scarce.

Table 1. Actual or probable status of some species originally described as *Leptohyphes*.

Original designation	Author and year	Present status	Author and year
<i>Leptohyphes asperulus</i>	Allen (1967)	<i>Allenhyphes</i>	Wiersema & McCafferty, 2000
<i>Leptohyphes edmundsi</i>	Allen (1973)	<i>Allenhyphes</i>	Wiersema & McCafferty, 2000
<i>Leptohyphes nanus</i>	Allen (1973)	<i>Allenhyphes</i>	Wiersema & McCafferty, 2000
<i>Leptohyphes gibbus</i>	Allen (1967)	<i>Tricorythopsis</i>	Molineri, 2001b
<i>Leptohyphes flinti</i>	Allen (1973)	<i>Allenhyphes</i>	Hofmann et al., 1999
<i>Leptohyphes indicator</i>	Needham & Murphy (1924)	<i>Traverhyphes</i>	Molineri 2001a
<i>Leptohyphes minimus</i>	Allen (1973)	<i>Tricorythopsis</i>	Molineri, 2001b
<i>Leptohyphes viriosus</i>	Allen (1973)	<i>Tricorythopsis</i>	Molineri, 2001b
<i>Leptohyphes rallus</i>	Allen (1967)	<i>Allenhyphes</i>	Wiersema & McCafferty, 2000
<i>Leptohyphes jamaicanus</i>	Allen (1973)	<i>Tricorythodes?</i>	this publication
<i>Leptohyphes tinctus</i>	Allen (1973)	<i>Tricorythopsis</i>	Molineri, 2001b
<i>Leptohyphes spinosus</i>	Allen & Roback (1969)	<i>Allenhyphes</i>	Wiersema & McCafferty, 2000
<i>Leptohyphes undulatus</i>	Allen (1967)	<i>Tricorythopsis</i>	Molineri, 2001b
<i>Leptohyphes nicholsae</i>	Wang et al. (1998)	<i>Tricorythodes</i>	Molineri, in press
<i>Leptohyphes rolstoni</i>	Allen (1973)	<i>Tricorythodes?</i>	this publication
<i>Leptohyphes</i> sp A	Traver (1943)	<i>Gen?</i>	

Materials and methods

In the descriptions of the nymphs the term 'gill formula' is used to indicate the number of lamellae present in each abdominal gill. For example 'gill formula: 3/6/6/5/2' means that abdominal gill II is formed by 3 lamellae, gill III by 6, gill IV by 6, gill V by 5 and gill VI by 2. When intraspecific variations occur, the minimum and maximum number of lamellae are given: '3/5–6/5–6/5/2' indicating that in gills III and IV the number of lamellae can be 5 or 6. The tarsal claw denticulation is also represented as a formula (i.e. 5 + 1), indicating first the number of marginal denticles on the basal half of the claw plus the number of apical submarginal denticles. When intraspecific variation occurs the rank is given as explained for the gills.

In the descriptions and discussions the color of the developing wings is used to identify some species; it can be blackish or whitish, depending on the pigments that adult wing membrane will have. It can be seen only in immature nymphs, because it is always blackish in the nymphs ready to molt to subimago. Parts of nymphal legs are named after Hubbard (1995).

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. The deposition of the material is abbreviated as follows: IFML (Instituto-Fundación Miguel Lillo, Tucumán, Argentina), MCBR (Museo de Ciencias Bernardino Rivadavia, Ciudad de Buenos Aires, Argentina), MZSP (Museu de Zoologia de São Paulo, SP, Brazil), FAMU (Florida A&M University, FL, USA); ANSP (Academy of Natural Sciences of Philadelphia, PA, USA) and NMNH (Natural Museum of Natural History, Washington DC, USA).

Results

Key to the nymphs of the South American species of *Leptohiphes*

1. Conspicuous and pointed tubercles present on occiput, pronotum, mesonotum and coxae I–II (Figs. 32–35) [S Brazil, NE Argentina] *L. cornutus* Allen
– Tubercles generally absent, if present, they are small and blunt, not as above 2
2. Hind femora with a distal tubercle as in Figs. 71 and 124 3
– Hind femora without distal tubercles 4
3. Tarsal claw without subapical submarginal denticles (Fig. 72) [Ecuador, Cotopaxi] *L. ecuador* Mayo
– Tarsal claw with a palisade of three subapical submarginal denticles (Fig. 123) [Peru, Tingo María] *L. tuberculatus* Allen
4. Compound eyes of male nymphs divided (Fig. 104) [Brazil, Amazonas] *L. populus* Allen
– Compound eyes of both sexes normal, undivided 5
5. Tarsal claws with a palisade of three or more subapical submarginal denticles (Figs. 67, 114) 6

- Tarsal claws with one or no subapical submarginal denticle (e.g. Figs. 17, 80) 7
- 6. Tubercles present on abdominal terga; denticles on tarsal claws: 3 + 4 (Fig. 67) [Peru, Tingo María] *L. carinus* Allen
– Without tubercles; denticles on tarsal claws: 4 + 5 (Fig. 114) [Peru, Tingo María] *L. setosus* Allen
- 7. Small and blunt tubercles present on mesonotum (Fig. 79); tarsal claw denticulation: 2 + 1 (Fig. 80) [Peru, Tingo María] *L. invictus* Allen
– Without tubercles on mesonotum (e.g. Fig. 81); at least with three marginal denticles on tarsal claw (e.g. Fig. 84) 8
- 8. Spines on dorsal margin of femora II and III inserted in elevated sockets (Figs. 57, 83, 97) 9
– Spines on dorsal margin of femora II and III not inserted in conspicuous elevations as above (Figs. 16, 77, 78, 93, 118) 12
- 9. Two or three rows of branched setae present on dorsum of labrum [Ecuador, Carchi] *L. liniti* Wang et al.
– Without branched setae on labrum 10
- 10. Anterior face of femora II and III with seven or less spines (Fig. 97); tarsal claw denticulation: 3–4 + 0 (Fig. 99) [Peru, Tingo María] *L. petersi* Allen
– Anterior face of femora II and III with 10 or more spines (Figs. 57, 83); tarsal claw denticulation: 3–4 + 1 (Figs. 58, 84) 11
- 11. Anterior face of femora II and III with relatively big spines located in a mediolongitudinal row (Fig. 83) [Peru, Tingo María] *L. jodiannae* Allen
– Anterior face of femora II and III with shorter spines more scattered over the dorsal surface (Fig. 57) [S Brazil, NE Argentina] *L. plaumanni* Allen
- 12. Hind wingpads present in females [Ecuador, Cotopaxi] *L. tacajalo* Mayo
– Hind wingpads absent in females 13
- 13. Femora II and III with short spines on dorsal margin and without spines on ventral margin (Figs. 77, 78) [Peru] *L. illiesi* Allen
– Femora II and III with medium size spines on dorsal margin and short spines on ventral margin (Figs. 16, 93) 14
- 14. Blackish median maculae generally present on abdominal terga II–IX; tarsal claw denticulation: 4 + 0–1 (Figs. 94–95) [Peru, Tingo María] *L. maculatus* Allen
– Abdominal color pattern generally not as above; tarsal claw denticulation: 5–7 + 1 (Fig. 17) [Central and NW Argentina, S Bolivia] *L. eximius* Eaton

Genus *Leptohiphes* Eaton

Leptohiphes Eaton, 1882: 208; Eaton, 1884: 140; Needham & Murphy, 1924: 32; Ulmer, 1933: 206; Traver, 1944: 15; Traver, 1958a: 497; Edmunds et al., 1963: 17; Allen, 1967: 350; Allen, 1978: 541; Kluge, 1992: 6; Hofmann et al., 1999: 65. Type species: *Leptohiphes eximius* Eaton, original designation.

Bruchella Navás, 1920: 56; Demoulin, 1952: 281. Type species: *Bruchella nigra* Navás, original designation.

Cotopaxi Mayo, 1968: 301; McCafferty & Wang, 2000: 58; Wiersema & McCafferty, 2000: 340; Domínguez et al., 2001: 18. Type species: *C. macuchae* Mayo, original designation.
NEW SYNONYM

Description

Imago

Head. Eyes relatively small and separated on meson of head by a distance 3–4 times the width of an eye. Lateral ocelli much larger than median ocellus. Occiput with a pair of small circular sclerites at each side of the median axis, and with a pair of latero-ventral small tubercles on hind margin.

Thorax. Pronotum somewhat translucent, with some irregular sclerotizations on sublateral areas. Mesonotum with parallel posterolateral scutal projections; internal and external parapsidal sutures run independently to each other until reaching the transverse interscutal suture. Superior and inferior dorsoventral suture (mesopleurae) not aligned (Kluge, 1992). Membrane of the base of forewings extended to the tip of mesoscutellum where it develops into a pair of long and slender membranous filaments, that project above the metanotum, reaching the first or second abdominal segment.

Wings. Posterior margin of both pairs of wings fringed with short setae. Forewings: marginal intercalaries present or absent; base of vein ICu1 attached directly with base of CuP (Figs. 1a, 2, 24, 28), free (Fig. 1b) or attached to CuA or CuP by cross veins (Figs. 52, 54); base of CuP present and parallel to base of CuA (Figs. 24, 27) or absent and CuP seems united directly to vein A (Figs. 1a, b, 2, 52, 54); vein MP2 detached at base and united basally to MP1 or CuA by cross veins. Hind wings present on males, with two or three longitudinal veins, and some times with few slightly marked cross veins (Figs. 4, 29); costal projection of male hind wings less than 1/2 of total length of that wing; hind wings of female may be present (Fig. 26), rudimentary or absent.

Legs. Tarsi of all legs four-segmented; pair of tarsal claws of all legs dissimilar, one blunt, paddle like, and the other apically hooked, except in forelegs of male imagines, both blunt.

Abdomen. Cuticle more or less translucent, generally shaded with grayish or blackish, some times with reddish.

Genitalia. Forceps three-segmented, first segment short and stout, second segment long with the wider part located at the base, third segment globular and small. Penes (Figs. 8, 30, 51, 55) with the basal half fused, distal parts divergent in variable angles; lateral margins of penes sclerotized from base, extended at apex as a short spine; medially to each spine a membranous lobe is present; gonopore apparently located between the spine and the lobe (Figs. 9a–d). These membranous lobes are covered by small blisters (probably adhesive glands). In females the genital openings are also

paired and around them the sternal membrane is somewhat sclerotized. Caudal filaments of male (relatively) longer than those of female. Terminal filament 10% longer than cerci, 2–3 times length of forewings in males, and as long as forewings in females.

Subimago

Similar to imago except male genitalia (Fig. 6): distal parts of penes not totally divergent, forceps apparently two-segmented.

Nymph

Head. Hypognathous. Eyes relatively small and well separated on meson of head. Mouthparts: labrum with a shallow anteromedian emargination; mandibles as in Figs. 39 and 41; maxillae: galea-lacinia not fused, palpi three-segmented (Figs. 14, 42, 43); hypopharynx as in Fig. 13 and labium as in Figs. 12 and 38. Genal projections present (Figs. 10, 11, 33, 59), sometimes with dorsal tubercles on occiput (Fig. 33).

Thorax. Pronotum with or without lateral extensions, sometimes with concave posterolateral margins. Mesonotum with (Figs. 33, 59) or without (Fig. 10) projections at antero-lateral corners.

Wings. Hind wingpads present in both sexes, frequently reduced or absent in females.

Legs. Coxae sometimes with dorsal projections (Figs. 34, 35) or not. Anterior face of femora of all legs with a transversal row of spines, generally situated above a ridge; in prothoracic legs this row is situated at middle or 2/3 from base, in meso- and metathoracic legs the row is basal. Spines of fore femora short to medium size (Figs. 15, 34, 56), generally flattened at apex. Ventral margin of all femora with or without spines, dorsal margin with spines (on forelegs only on distal part). Tibiae of all legs with a double longitudinal row of spines on ventral margin, on meta- and mesothoracic tibiae an additional row is generally present on dorsal margin. Middle and hind tibiae and femora with a longitudinal ridge. Tarsi of all legs with a single longitudinal row of spines on ventral margin. Tarsal claws with a variable number of marginal denticles and generally with a single submarginal denticle near apex, rarely the distal denticle is absent or replaced by a palisade of 3–5 denticles.

Abdomen. Segments decreasing in width posteriorly, lateral margins of segments III–VI expanded (as lateral flanges) and hyaline; posterolateral projections sometimes present on segments VII–IX. Gills present on segments II–VI, decreasing in size posteriorly. Gill II opercular (covering remaining gills), formed by a big dorsal sclerotized and oval lamella, with two ventral extensions; these ventral extensions are membranous and one of them (the inferior) has a basal spine directed ventrally (Figs. 19, 45, 46, 60, 61). Gills III–VI formed by a variable number of membranous lamellae ranging from 6/6/5/1 to 10/8/8/5 (numbered from gill III

to VI). Terga with spines of variable length. Terminal filament slightly longer than cerci. Males with 1–3 dark segments at the middle of each caudal filament, in females these dark segments are located near the base of the filaments.

Egg (Figs. 126–129)

Length, 170 µm; width, 80 µm. One polar cap present. Chorion covered by polygonal plates somewhat elevated above egg surface, some of these plates are U-shaped. Generally with one (occasionally two) micropyle per egg, rounded and located near the uncapped pole. Some KCT scarcely distributed on the surface, more numerous toward the capped pole.

Diagnosis

The genus *Leptohyphes* can be distinguished from the other genera of the family by the following combination of characters, in the imagines: (1) penes fused at basal 1/2, with divergent distal part (Figs. 7, 30, 51); (2) apex of penes formed by a membranous lobe and a more or less sclerotized spine as in Figs. 9a–d; (3) lateral margins of penes sclerotized and some times pigmented as in Figs. 7 and 51; (4) forceps three-segmented; (5) hind wings present on males, with two or three longitudinal veins, and some times with few slightly marked cross veins (Figs. 4, 29); (6) costal projection of male hind wings less than 1/2 of total length of that wing; (7) hind wings of female may be present (Fig. 26), rudimentary or absent; (8) membranous filaments on mesoscutellum long and slender; (9) tails 2–3 times length of forewing in males, and as long as forewing in females. In the nymph: (1) gill on abdominal segment II formed by a dorsal and oval opercular lamella more or less sclerotized, and by a pair of smaller and weaker ventral lamellae parallel to the dorsal one (e.g. Figs. 18, 19); (2) basal spine of gill II present (ventral projection of inferior ventral lamella; Figs. 19, 46, 61); (3) gills III–V formed by numerous lamellae distributed in pairs (e.g. Figs. 20–22); (4) maxillary palpi three-segmented (Figs. 14, 42); (5) galea and lacinia not completely fused; (6) spines on dorsum of fore femora short to medium size (Figs. 15, 34, 56), generally flattened at apex; (7) middle and hind femora with a dorsal row of spines at base (Figs. 16, 35, 57); (8) tarsal claws with a variable number of marginal denticles and generally with a single submarginal denticle near apex (rarely the distal denticle is absent or replaced by a palisade of 3–5 denticles); (9) tails with 1–3 annuli much darker than the rest, very sclerotized and located at base of tails on the female and at 1/2 from base on the male; (10) middle and hind tibiae and femora with a longitudinal ridge.

Discussion

The definition of the genus *Leptohyphes* was improved mainly with the works of Kluge (1992), Hofmann et al. (1999), Baumgardner and McCafferty (2000) and Wiersema

and McCafferty (2000). Some of the characters used here to distinguish *Leptohyphes* were also used by these authors.

In *Leptohyphes*, there are two groups of species clearly different: one with penes 'T' shaped and hind wings present in females and those with 'Y' shaped penes and hind wings absent in females. As some intermediates exist in the angle of separation of penes lobes, to be sure to what group these males belong, it is indispensable to know the female or nymph. The nymphs of both groups are quite similar but they can be separated from each other (besides the presence/absence of hind wingpads in females) by the presence of a small but conspicuous ventral projection on the most dorsal lamellae of abdominal gill V. These groups are not defined formally because all the stages are necessary to be sure in what group fits a particular species, and this knowledge is only available for few species. Moreover, *L. cornutus* Allen (treated below) shows some intermediate characters between these groups, and does not fit in any of them, probably constituting a third group in the genus. Only one of the described South American species, *L. tacajalo* Mayo, is probably from the group of species with 'T' shaped penes, but is known only as nymph. The male genitalia of this species, when known, are expected to be of the 'T' type. Four other undescribed species of this group from Colombia and Ecuador were studied by the author but they will be published separately. The majority of the described species fits in the group with 'Y' shaped genitalia.

Cotopaxi, the monotypic genus described by Mayo (1968) for a single specimen from Ecuador is here proposed to be a junior synonym of *Leptohyphes*. The holotype is apparently a gynandromorph with teratological genitalia. The genitalia are a complex asymmetric structure, where only the penes are recognizable, although somewhat deformed. The structures described by Mayo as forceps and 'median lobes' are not easily assignable to any normal structure. The body and wings correspond well with a female of *Leptohyphes* but the presence of penes and other teratological structures on the IXth sternum indicate that it would be a gynandromorphic individual. The characters that serve to assign this species to *Leptohyphes* are the following: (1) longitudinal vein ICu1 not united basally to CuA or CuP, ending free in the membrane (Figs. 1–3 of Mayo, 1968); (2) vein ICu2 attached at base to vein ICu1 (Figs. 1–3 of Mayo, 1968); (3) membranous filaments on the mesoscutellum long and slender (Fig. 3 of Mayo, 1968); (4) general aspect of thorax and abdomen (Fig. 3 of Mayo, 1968). This kind of cubital venation is only shared by *Haplohyphes*, but adults of this genus do not have membranous filaments on the mesoscutellum, as does the holotype of *Cotopaxi macuchae*. For all these reasons I propose to treat *Cotopaxi macuchae* Mayo (1968) as a *Nomen Dubium*.

Material

Cotopaxi macuchae holotype slides from Ecuador, Cotopaxi Province, Macuchi, Braden Quebrada, 6/VI/1945, V. K. Mayo Col. Deposited in FAMU.

Biology

The adults of *Leptohyphes* generally perform the nuptial flight at early morning, emerging as subimagines the previous day (generally at dusk). They molt to subimago during the night or early morning and immediately take flight. The swarms are not very numerous, ranging from 5–10 males to no more than about 50. The swarms are more or less ovoid in form, located above the water or near the shore above some landmark. The observed landmarks were mainly rapids or big blocks emerging from the river or at the banks. The females fly in a straight pattern directly above the swarm, until detected and grabbed by a male. Some females were observed to enter the same swarm 2–4 times, each time abandoning it for a moment with a different male. Males were observed to return to the swarm after each mating. Only one species from Colombia was observed to fly at dusk.

Nymphs are relatively bad swimmers inhabiting rivers and streams of variable conditions. In some silty rivers they were found as the most numerous component of the mayfly fauna. The darker segments on the caudal filaments function as weak points where the filaments can break when forced. The opercular gills of each side move independently. If disturbed they are maintained against the abdomen protecting the functional gills, and after a few seconds they are lifted slightly to permit the respiratory movements of the remaining gills.

Analysis of gut content showed only organic and inorganic detritus, supporting the general idea that they are collectors of particulate matter.

Leptohyphes eximius Eaton (Figs. 1–23, 126, 127)

L. eximius Eaton, 1882: 208; Eaton, 1884: 140; Ulmer 1920: 122; Needham & Murphy, 1924: 32; Navás; 1930: 130; Lestage, 1931: 60; Traver, 1958a: 497; Traver, 1958b: 81; Kimmins, 1960: 305; Edmunds et al., 1976: 254; Hubbard, 1982: 273; Domínguez, 1984: 103; Kluge & Naranjo, 1990; Kluge, 1992: 6–9; Domínguez et al., 1994; Hofmann et al., 1999: 66; Molineri: 2001a: 129.

Leptohyphes bruchi Navás, 1931: 322; Hubbard, 1982: 273; Domínguez, 1984: 103. NEW SYNONYM

Bruchella nigra Navás, 1920: 56; Demoulin, 1952: 281; Traver, 1958a: 494. NEW SYNONYM

Leptohyphes nigra; Edmunds, Allen & Peters, 1963: 17.

Leptohyphes niger; Hubbard, 1982: 274; Domínguez, 1984: 103.

Description

Male imago (in alcohol)

Length: body, 5.5–5.6 mm; forewings, 6.7–7.0 mm; hind wings, 1.3–1.5 mm. General coloration orange-brown.

Head. Yellowish white heavily tinged with black between ocelli. Antennae yellowish white very slightly shaded with gray at apex of pedicel.

Thorax. Pronotum yellowish shaded with black. Mesonotum orange-brown shaded with black on carinae and anterolateral corners of anteroscutum and shaded with gray on a median and two sublateral longitudinal bands; mesoscutellum yellowish translucent completely washed with black, membranous filaments whitish translucent. Metanotum orange-yellow. Propleurae and prosternum whitish translucent washed with black on prosternum. Pleurae and sterna of meso- and metathorax orange-yellow tinged with gray on carinae, coxae and mesosternum.

Legs. Forelegs: coxae and trochanters yellowish, remaining segments whitish slightly tinged with gray on dorsum of femora, tibiae and tarsi, and with yellow on dorsum of femora and base of tibiae. Middle and hind legs whitish with yellowish coxae, trochanters, margins of femora and base of tibiae; shaded with gray on coxae and on dorsum of femora.

Wings (Figs. 2–4). Membrane of forewings hyaline very slightly tinged with yellow, longitudinal veins yellowish washed slightly with gray, cross veins yellowish.

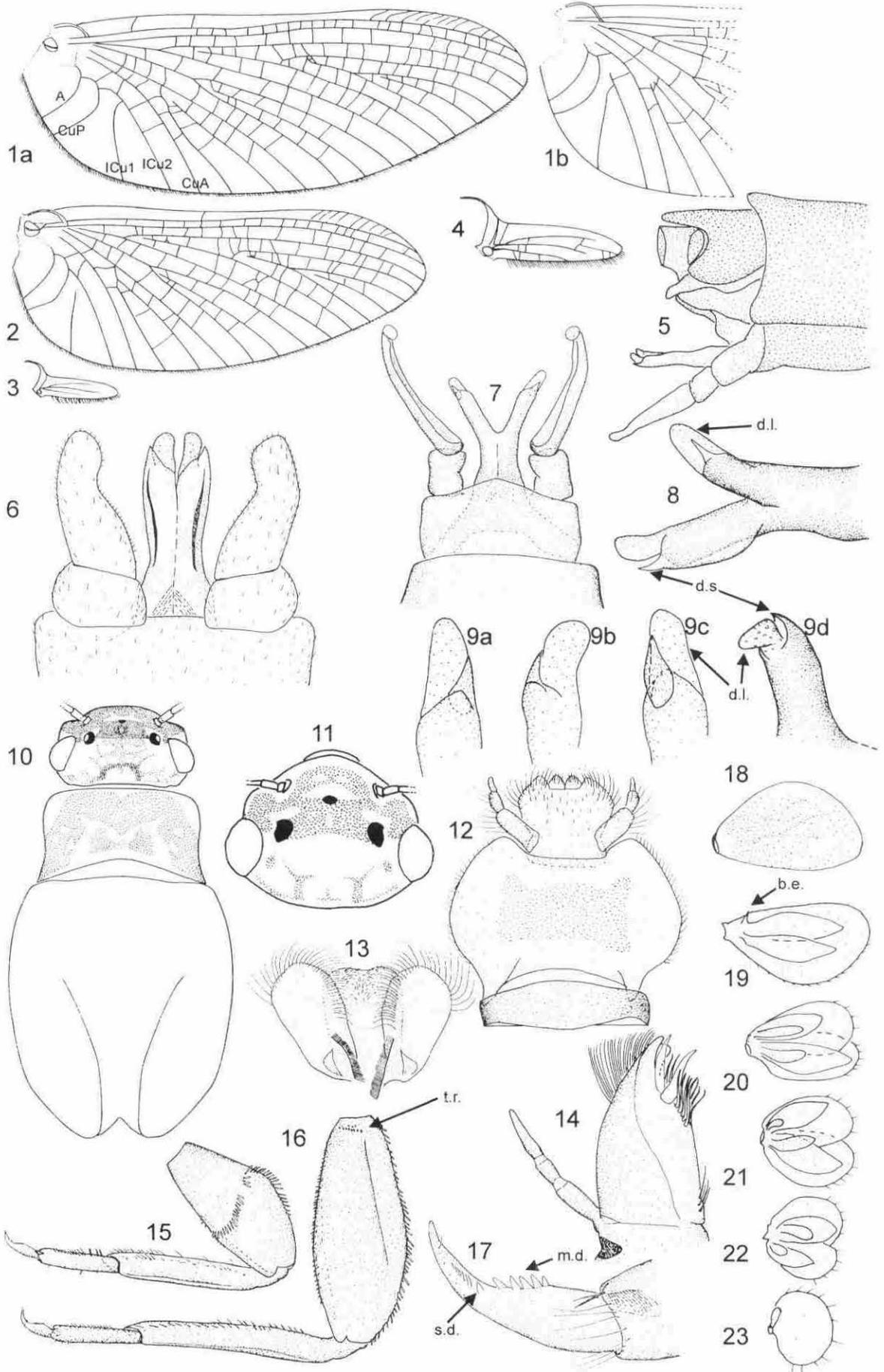
Abdomen. Yellowish translucent, terga completely shaded with black except on intersegmental membranes, shaded more markedly on a pair of submedian lines on terga I–VI and a single median line on tergum X. Abdominal sterna slightly washed with gray darker on a median ovoid mark.

Genitalia (Figs. 5–9). Styliiger plate yellowish white washed with gray, with yellow lateral margins; forceps and penes whitish translucent washed with gray at base of first segment of forceps and with yellow on lateral margins of penes. Tails whitish translucent completely washed with gray, darker on basal joinings.

Female imago (in alcohol)

Length: body, 6.6–6.8 mm; forewings (Fig. 1a, b), 7.5–8.0 mm. General coloration orange-brown. Head as male except occiput paler. Thorax as male except shaded with black more

Figs. 1–23. *Leptohyphes eximius*. Adult: 1a. ♀ forewing; 1b. same, variation in cubital venation; 2. ♂ forewing; 3. ♂ hind wing; 4. detail of ♂ hind wing; 5. ♂ abdominal segments IX–X, l.v.; 6. genitalia of ♂ subimago, v.v.; 7. genitalia of male imago, v.v.; 8. penes, ventrolateral view; 9a–d. details of apex of penes lobes (different positions). Nymph: 10. dorsal aspect of head and thorax (mesothoracic coloration omitted); 11. head (color pattern variation), d.v.; 12. labium, v.v.; 13. hypopharynx, d.v.; 14. apex of maxillae, d.v.; 15. foreleg, d.v.; 16. hind leg, d.v.; 17. detail of claw; 18. gill II, d.v.; 19–23. gills II–VI, v.v.; b.e. = basal spine; d.l. = distal lobe; d.s. = distal spine; m.d. = marginal denticles; s.d. = submarginal denticles; t.r. = transversal row of spines.



marked. Legs and wings as in male, except hind wings absent or extremely reduced to a small membranous flap. Abdomen as in male, IX sternum yellowish washed with black with slightly concave hind margin. Tails as in male but relatively shorter.

Mature nymph (in alcohol)

Length of male: body, 4.8–5.6 mm; mesonotum + wingpads, 2.0–2.2 mm; hind femora, 1.3–1.5 mm; terminal filament, 3.6–4.0 mm; cerci, 3.2–3.5 mm. Length of female: body, 5.5–6.7 mm; mesonotum + wingpads, 2.3–2.5 mm; hind femora, 1.4–1.6 mm; terminal filament, 4.5–5.2 mm; cerci, 4.0–4.2 mm. General coloration: cuticle yellowish translucent without marks, hypodermis varies from yellowish white to whitish yellow with gray or black markings. Head yellowish white tinged with black as in Figs. 10, 11. Antennae yellowish white. Mouthparts yellowish white shaded with gray on center of submentum and dorsal portion of mandibles. Thorax. Pronotum yellowish white with gray markings as in Fig. 10. Mesonotum whitish yellow with longitudinal gray bands. Metanotum yellowish white shaded with gray at margins. Legs (Figs. 15–16). Whitish yellow, except tarsi yellowish, with diffuse longitudinal gray bands on femora. Tarsal claws with 4–5 marginal denticles and one unpaired submarginal denticle near apex (Fig. 17). Abdomen yellowish white almost completely washed with blackish on terga I–IX, washed more markedly on median band; tergum X with blackish median band and lateral regions. Segments III–VI laterally expanded and yellowish translucent, posterolateral spines present on segments VII–IX. Abdominal sterna whitish except posterolateral spines and distal half of IX sternum yellowish. Gills (Figs. 18–23) whitish translucent tinged with blackish on basal half of opercular lamellae and very slightly at base of remaining gills; gill formula 3/6/6/6/2. Tails yellowish.

Egg

Polar cap generally triangular (Fig. 126), some with a distal constriction (see Fig. 3e in Kluge, 1992). Chorionic plates polygonal and contiguous on uncapped pole, becoming U-shaped and more separated toward capped pole (Fig. 126). Small ovoid fibrous scales (probably KCT, but greatly transformed) sparsely distributed between the plates, and lying above a small groove (Fig. 127). Micropyle circular or polygonal, surrounded by 5–6 chorionic plates, generally located near the uncapped pole (Fig. 127).

Variations

Some individuals have femora very slightly shaded with gray and others only conserve the distal part of the blackish band on femora in the form of a subapical mark. The vein ICu1 of male and female forewings may be attached (Fig. 1a, (2) or not (Fig. 1b) to CuP or CuA. Female hind wings are gener-

ally absent but in some females a little membranous remnant of the wings can be found.

Life cycle association

Association between adults and nymphs were made by rearing of nymphs of both sexes. Male and female imagines where captured in the same swarms.

Material

Leptohyphes eximius Eaton: 2 male imagines (pinned, deposited at MACN) from Argentina, Córdoba, Alta Gracia, La Granja, 29/II/1925, C. Bruch Col.; 80 male imagines, 4 female imagines, 4 male subimagines, 6 female subimagines and 45 nymphs (IFML) from ARGENTINA, Córdoba, Los Espinillos, Río Los Espinillos, 13–16/IX/1997, C. Molineri & C. Nieto Cols. *Leptohyphes bruchi* Navás: 1 male subimago ("typus", pinned, MACN) from Argentina, Córdoba, Alta Gracia, La Granja, 7/II/1927, C. Bruch Col. *Bruchella nigra* Navás: 1 male imago ("typus", pinned, MACN) from Argentina, Córdoba, Alta Gracia, La Granja, 1–8/IV/1920, C. Bruch Col. Numerous adults and nymphs (many of them reared) from different localities in Argentina (Jujuy, Salta, Catamarca, Tucumán, La Rioja, San Luis, San Juan, Córdoba, Mendoza and Neuquén Provinces) are housed in IFML.

Diagnosis

This species can be differentiated from the others of the genus by the following combination of characters, in the imagines: (1) membrane of wings almost hyaline; (2) wing veins yellowish; (3) occiput whitish yellow with black markings as Figs. 10, 11; (4) abdominal segments IX–X and base of tails without bright orangish brown *in vivo*. Nymph: (1) occiput whitish or with an arc-shaped blackish mark as in Figs. 10, 11; (2) tarsal claws with 4–5 marginal denticles and one unpaired submarginal denticle near apex (Fig. 17); (3) pronotum with black markings as in Fig. 10; (4) basal half of opercular lamellae shaded with black; (5) gill formula 3/6/6/6/2; (6) basal 1/3 of tails with whorls of long setae at each intersegmental joining.

Discussion

The type material of *L. eximius* is represented by a single female imago thoroughly studied by Kluge (1992). Although this material was not available for the present study, the descriptions from Eaton and Kluge permit the assignation of the material to this species with certainty. The type material of *Leptohyphes bruchi* Navás and *Bruchella nigra* Navás are pinned, dried specimens from the same locality as *L. eximius* Eaton. These names are synonymized here because all of them proved to be of the same species, described first by Eaton as *L. eximius*. The presence of two pinned male imag-

ines (see Material) correctly identified as *L. eximius* by Navás shows that this author knew the male of this species, but never described it.

Biology

Populations of nymphs of this species studied during a period of two years in a foothill stream in NW Argentina showed a multivoltine type of life cycle. Nymph of different stages and adults were collected all the year around, each generation lasting 2 to 4 months.

Leptohyphes cornutus Allen (Figs. 24–50, 128, 129)

L. cornutus Allen, 1967: 357; Hubbard, 1982: 273.

Description

Male imago (in alcohol)

Length: body, 6.3–6.5 mm; forewings, 7.7–8.2 mm; hind wings, 1.3–1.4 mm. General coloration grayish brown.

Head. Blackish except base of antennae and ocelli whitish. Eyes brownish black. With a pair of small and blunt tubercles between lateral ocelli. Antennae: scape whitish washed with brown ventrally, pedicel yellowish translucent, flagellum whitish translucent.

Thorax. Pronotum heavily shaded with black, posterior margin extended rearward forming a pair of projections. Meso- and metanotum brown slightly shaded with black, with black margins and carinae. Propleurae and prosternum whitish completely shaded with black; mesopleura yellowish brown tinged with black on base of coxae, mesosternum brown tinged with black at middle; mesoscutellum translucent yellowish brown with a pair of grayish membranous filaments; metapleurae and metasternum whitish completely shaded with black.

Legs. Coxae of all legs black, trochanters yellowish brown partially washed with black; femora whitish with brown margins, shaded with black on distal half of forefemora and almost completely on middle and hind femora; tibiae and tarsi of all legs yellowish white washed with light gray except on middle and hind tarsi.

Wings (Figs. 27–29). Membrane of both wings hyaline tinged with yellowish brown, C and Sc sectors of forewings darker than rest of wing; longitudinal veins yellowish brown shaded with black; cross veins light brown, some of them connecting longitudinal veins with hind margin; base of vein CuP present and parallel to base of vein CuA. Hind wings relatively large, with two longitudinal veins, and curved costal projection.

Abdomen. Whitish translucent completely tinged with grayish brown except on lateral zones of segments II–V slightly shaded with gray; segments VII–X darker than the rest, tergum X with a brown longitudinal band at middle; with black pleural folds.

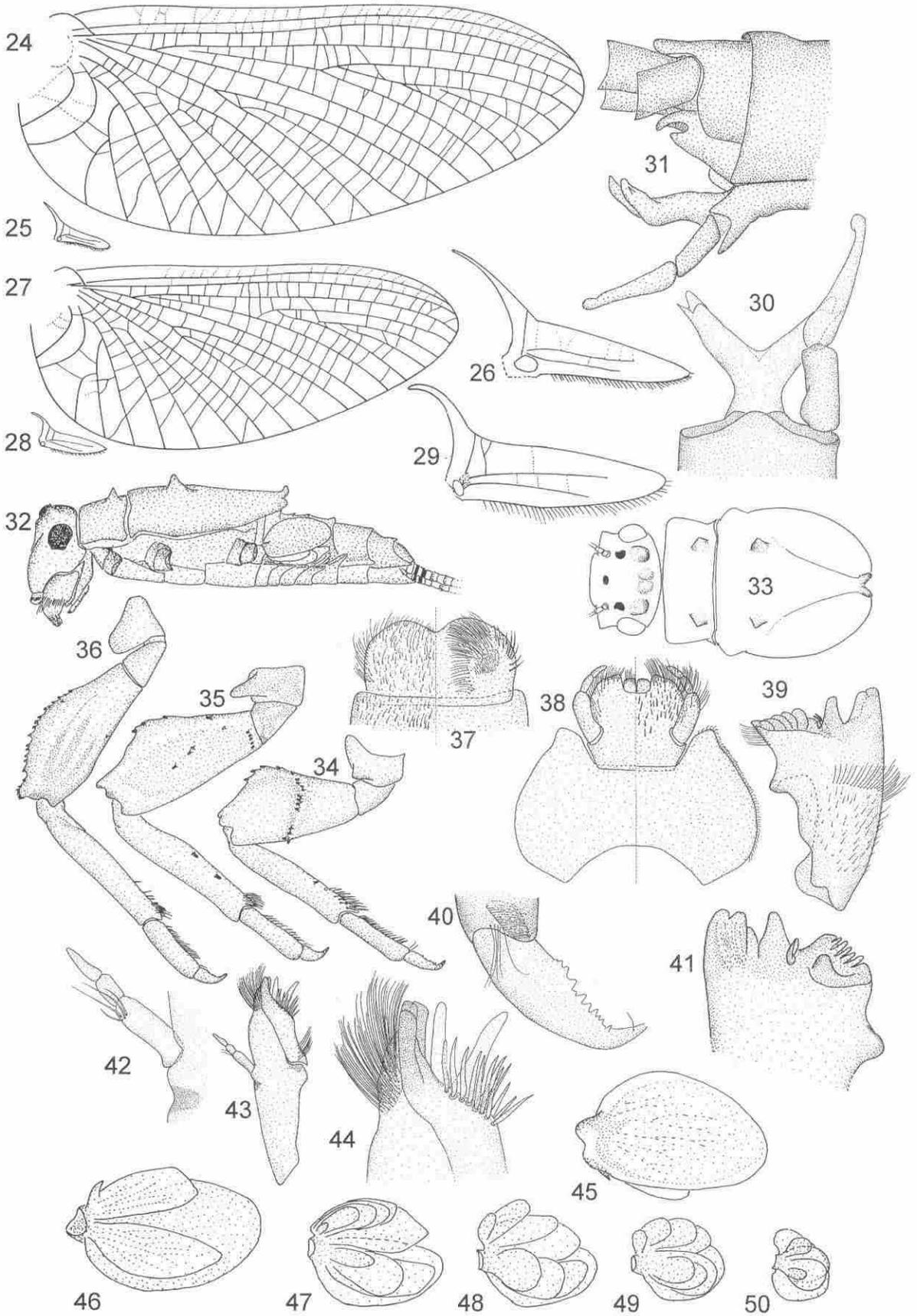
Genitalia (Figs. 30, 31). Styliiger plate yellowish brown shaded with gray; forceps and penes translucent yellowish white, slightly shaded with yellowish brown on segment I of forceps and with light gray on penes. Tails yellowish white slightly shaded with gray. On living individuals the base of tails and abdominal segments IX–X are bright reddish brown, but this coloration immediately fades when immersed in alcohol.

Female imago (in alcohol)

Length: body, 7.0–8.7 mm; forewings, 10.0–11.2 mm; hind wings, 1.0–1.1 mm. General coloration grayish brown. Head and thorax as in male, except meso- and metapleurae yellowish brown washed with black on metapleurae. Legs as in male except fore femora completely shaded with black, tibiae of all legs yellowish translucent and tarsi of all legs whitish translucent. Wings. Forewings (Fig. 24) as in male except with more cross veins connected with hind margin; hind wings (Figs. 25, 26) relatively smaller and with longer costal projection. Abdomen as in male, except sterna I–VII strongly convex; tergum IX with black posterolateral spines. Sternum IX extended posteriorly with shallow apical notch. Tails as male but relatively shorter.

Mature female nymph (in alcohol)

Length: body, 7.3 mm; mesonotum, 2.7 mm; terminal filament, 5.0 mm; cerci, 4.0 mm. General coloration blackish brown. Maxillary palp with setae on apex of segment I (Fig. 42). Head and thorax with cuticle marks not visible, with hypodermic marks as in female imago. With a pair of small and blunt tubercles dorsally on meson of head and another pair of larger and pointed tubercles behind eyes (Fig. 33). Pronotum with a pair of tubercles near hind margin (Figs. 32, 33); mesonotum with a pair of similar tubercles at middle and with an additional pair of tubercles formed by the extended posterior margin of wingpads (Figs. 32, 33). Legs (Figs. 34–36). Fore and middle coxae with a dorsal projection, blunt and small on coxae I, but pointed and large on coxae II; short and blunt spines present in all femora; tibiae I and II with a pair of blunt spines on inner margin, all tibiae with a group of acute spines at apex; tarsi of all legs with a row of spines on inner margin; tarsal claws (Fig. 40) with a row of 9–11 irregular marginal denticles and with a single submarginal denticle near apex. Abdomen brown turning blackish brown on segments VIII–X, with a pair of dorsolateral blunt spines on segments IV–VIII; segments III–VII laterally expanded; segments VII–IX with posterolateral spines, those on VII dorsally directed. Gills (Figs. 45–50): gill II black, gills III–V with numerous additional lamellae, gill VI with a dorsal bigger lamella and two pairs of smaller ventral leaves (gill formula 3/10/8/8/5). Tails yellowish brown with blackish brown basal rings and with whorls of brownish setae on some intersegmental joinings.



Egg

Polar cap generally triangular (Fig. 128). Chorionic plates polygonal and contiguous on uncapped pole, turning U-shaped (not as marked as in *L. eximius*) and more separated toward capped pole (Fig. 128). Fibrous scales (KCT?) longer and thinner than in *L. eximius*, sparsely distributed between the plates (Fig. 129). Micropyle circular or polygonal, rounded by 5–6 chorionic plates, generally located near the uncapped pole (Fig. 129).

Life cycle association

Male and female adults are associated because they were captured at nuptial flight, and share forewing venation and color pattern. Nymphs and adults are associated by rearing.

Biology

Nuptial flight was observed before sunrise at 5:30 h AM, and disappeared at 6:30 h AM. Groups of 7–10 males flew about 1 m above water level, in riffle zones. Each male went up and down continuously about 40–60 cm. Females displayed a straight flight above the swarm. Only three nymphs could be collected, two mature nymphs (one of them reared to subimago) and the other very immature; they were found on a substrate composed mainly by a rock floor covered with submersed vegetation.

Material

Holotype slides (head and mouthparts, legs) from Brazil, Rio Irany, IV-1963, F. Plaumann [probably for Rio Irani from Brazil, Santa Catarina St., Near Nova Teutonia]. Other material studied: 2 nymphs (one very immature), 1 female subimago, 3 female imagines, 37 male imagines and 1 reared male subimago with its nymphal exuviae from Argentina, Misiones, Parque Provincial Urugua-í, Arroyo Uruzú, 23–24/XI/1998, E. Domínguez, C. Molineri, C. Nieto & F. Romero Cols.; 2 immature nymphs, 1 female and 6 male imagines same locality except date and collector: 7–11/XII/1999, C. Molineri Col.; 34 male imagines from Argentina, Misiones, Dpto. San Pedro, confluencia ríos Alegría y Pirai Guazú, 22–23/XI/1998, E. Domínguez, C. Molineri, C. Nieto & F. Romero Cols.; 1 immature nymph from Brazil, Rio de Janeiro, Nova Friburgo, Mun. water supply, 20/IV/1977, C. M. & O. S. Flint Jr.; 2 mature nymphs from Brazil, Santa Catarina, Xanxerê, Rio Toldo, no data of collectors; and 2 mature nymphs from Brazil, GO, Rio

Itiquira, 19/II/1970, C. G. Froehlich Col. The holotype slides and 4 male and 1 female imagines are deposited in FAMU, the nymph from Rio de Janeiro is deposited in NMNH, 2 nymphs are housed in MZSP and the remaining material in IFML.

Diagnosis

L. cornutus can be differentiated from the other species of the genus by the following combination of characters, in the imagines: (1) membrane of wings tinged with yellowish brown; (2) wing veins yellowish brown shaded with black; (3) head widely shaded with black; (4) abdominal segments IX–X and base of tails bright orange-brown *in vivo*; (5) genitalia as in Figs. 30, 31; (6) base of CuP present and parallel to base of CuA (Figs. 24, 27); (7) attached marginal intercalaries present (Figs. 24, 27). Nymph: (1) occiput widely washed with black; (2) tarsal claws with 9–11 irregular marginal denticles and one unpaired submarginal denticle near apex (Fig. 40); (3) head, pronotum and mesonotum with pairs of tubercles as in Figs. 32, 33; (4) opercular lamellae widely shaded with black; (5) coxae I and II with a dorsal projection (Figs. 34, 35), bigger in coxa II; (6) maxillary palp with setae on apex of segment I (Fig. 42); (7) gill formula 3/10/8/8/5 (Figs. 46–50).

Leptohyphes plaumanni Allen (Figs. 51–65)

Leptohyphes sp. Edmunds, Allen & Peters, 1963, pl. 14, Fig. 72.
Leptohyphes plaumanni Allen, 1967: 355; Hubbard, 1982: 274;
Da Silva, 1993: 314.

Leptohyphes pereirae Da Silva, 1993: 313. NEW SYNONYM

Description

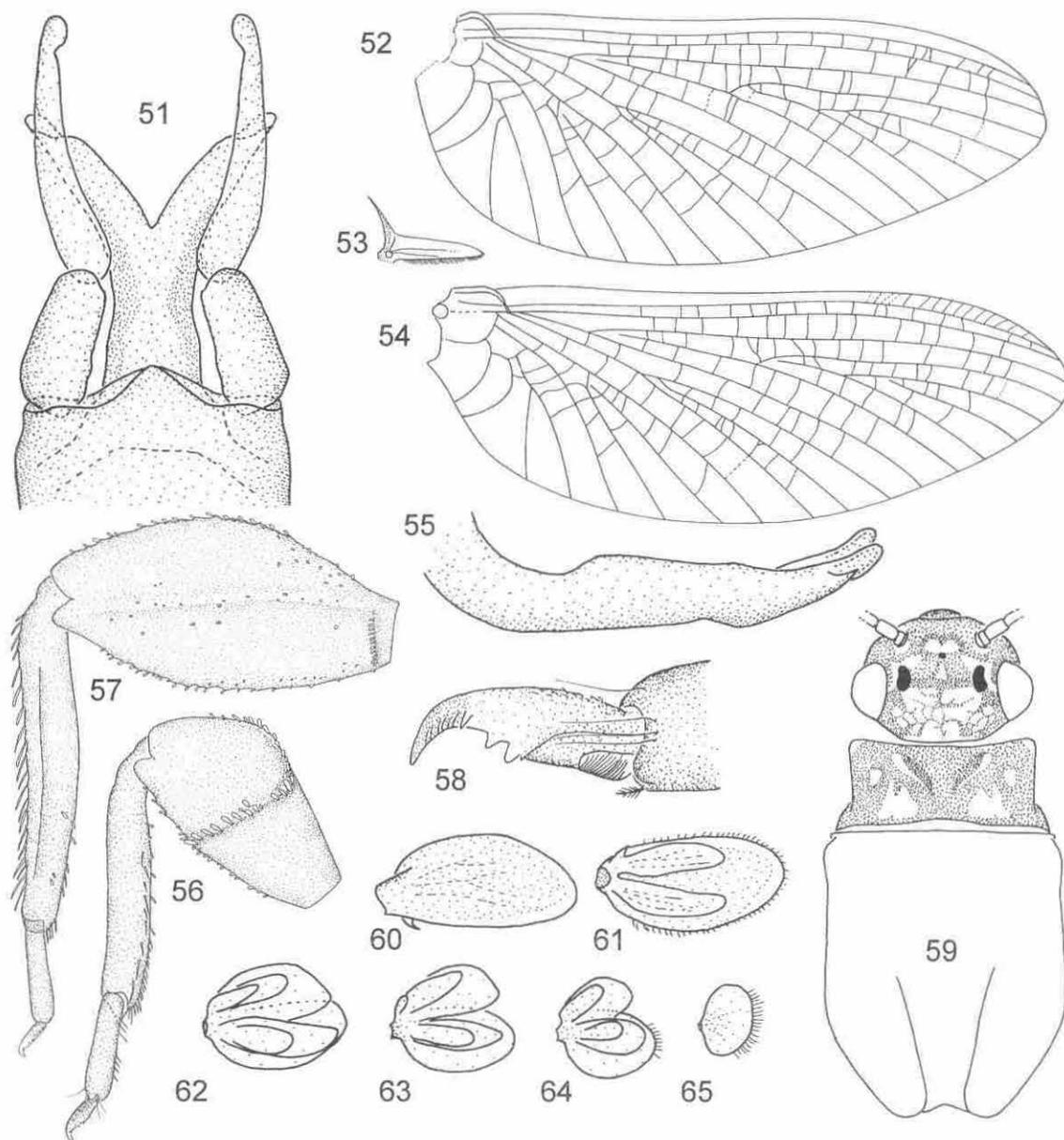
Male imago (in alcohol)

Length: body, 4.9–5.3 mm; forewings, 5.3–5.5 mm; hind wings, 0.8–0.9 mm. General coloration yellowish brown.

Head. Yellowish white washed with black dorsally. Eyes blackish, ocelli whitish rounded with black. Antennae yellowish white washed with light brown on scape.

Thorax. Pronotum whitish translucent medially, turning yellowish toward margins, completely washed with gray. Mesonotum yellowish brown diffusely washed with gray, membranous filaments on mesoscutellum grayish white. Metanotum light yellowish brown. Propleura and prosternum whitish washed with gray and with brown carinae, pleura and sterna of meso- and metathorax light yellowish brown shaded with gray on carinae.

Figs. 24–50. *Leptohyphes cornutus*. Adult: 24. ♀ forewing; 25. ♀ hind wing; 26. same, enlarged; 27. ♂ forewing; 28. ♂ hind wing; 29. same, enlarged; 30. ♂ genitalia (one forceps omitted), v.v.; 31. ♂ abdominal segments IX–X, l.v. Nymph: 32. lateral aspect; 33. dorsal outline of head and thorax; 34–36. fore, median and hind legs, d.v.; 37. labrum, left d.v., right v.v.; 38. labium, idem; 39. right mandible, d.v.; 40. tarsal claw; 41. detail of apex of left mandible, v.v.; 42. maxillary palp; 43. maxilla, v.v.; 44. apex of maxilla, detail; 45. gill II, d.v.; 46–50. gills II–VI, v.v.



Figs. 51–65. *Leptohyphes plaumanni*. Adult: 51. ♂ genitalia, v.v.; 52. ♂ forewing; 53. ♂ hind wing; 54. ♀ forewing; 55. penes, l.v. Nymph: 56. foreleg; 57. hind leg; 58. tarsal claw; 59. dorsal outline of nymphal head and thorax; 60. gill II, d.v.; 61–65. gills II–VI, v.v.

Legs. Coxae and trochanters of all legs light yellowish brown shaded with gray, rest of legs yellowish white with yellowish brown margins and shaded completely with gray, shaded more markedly on middle and hind legs.

Wings (Figs. 52, 53). Membrane of forewings hyaline tinged with yellowish light brown, darker on basal half of C and Sc areas, longitudinal veins grayish brown, cross veins brownish.

Abdomen. Whitish translucent completely washed with grayish brown, except on intersegmental membranes; segments VIII–X darker than rest of abdomen; shaded with gray on pleural fold of segment II, and on a double submedian

row on terga II–VI; tergum X with a brownish mediolongitudinal band.

Genitalia (Figs. 51, 55). Styliiger plate yellowish brown with lateral margins brownish; forceps and penes whitish translucent tinged with yellowish on forceps segment I and lateral margins of penes. Tails grayish with hyaline intersegmental joints.

Female imago (in alcohol)

Length: body, 4.5–5.7 mm; forewings, 7.3 mm. General coloration orange-brown. Head as in male. Thorax, legs and

wings (Fig. 54) as in male except for common sexual dimorphism. Hind wings absent. Abdomen as in male except washed with grayish brown more markedly. Egg mass yellowish translucent. Tails whitish translucent slightly washed with gray.

Mature nymph (in alcohol)

Length of male: body, 3.6–4.4 mm; mesonotum + wingpads, 1.5–1.6 mm; hind femur, 1.2 mm; terminal filament, 4.2–4.3 mm; cerci, 3.9–4.1 mm. Length of female: body, 6.2–6.6 mm; mesonotum + wingpads, 2.2 mm; hind femur, 2.7 mm; terminal filament, 5.5–6.0 mm; cerci, 5.0–5.5 mm. General coloration yellowish brown with gray markings, ventrally paler. Head dorsally washed with black as in Fig. 59. Antennae yellowish translucent. Thorax. Pronotum widely tinged with black except on sublateral irregular and yellowish marks, hind margin blackish. Mesonotum widely tinged with blackish, darker at base of wings. Anterolateral corners of pro- and mesonotum somewhat extended forming a right angle. Thoracic sterna whitish yellow very slightly shaded with gray. Legs yellowish light brown with short brown spines as in Figs. 56, 57, widely washed with gray, basal 2/3 of tarsi orange-brown; coxae II with a dorsal blackish mark at the base of a small dorsal projection; tarsal claws with 3–4 marginal denticles and one unpaired submarginal denticle near apex (Fig. 58). Abdomen yellowish brown widely tinged with blackish with short brown spines on terga I–IX, these spines are small and scattered over terga, but two of them are bigger and located medially on hind margins of terga; tergum X without spines and washed with black on mediolongitudinal band. Gills (Figs. 60–65): opercular gill grayish with whitish margins, remaining gills whitish translucent slightly washed with gray at base; gill formula 3/5–6/5–6/5/1. Tails yellowish translucent with blackish joints at base on females and at 1/2 from base to apex on males, with whorls of brown and small spines on each intersegmental joining.

Life cycle association

Association between adults and nymphs were made by reared nymphs of both sexes. Male and female imagines were captured at the same hour.

Material

L. plaumanni: 13 nymphs paratypes and 7 nymphal slides paratypes from Brazil, Nova Teutonia, Rio Ariranha, XI/1961, Fritz Plaumann Col (FAMU, No. E2007). Other material studied from the following localities in Argentina, Misiones Province: 1 reared male subimago from Ruta Prov. 203, 15 km E San José, Arroyo Loquiño, 17/IX/1998, Domínguez, Molineri and Nieto (= "D, M & N" below); 3 nymphs, 1 male imago and 1 reared male subimago from Dpto. San Pedro, confluencia ríos Alegría y Piray Guazú,

22–23/XI/1998, D, M & N; 10 nymphs, 1 reared female imago, 1 male imago, 1 female and 1 male subimagines from Dpto Candelaria, 2 km E Bonpland, río del camping, 18/XI/1998, D, M & N; 2 nymphs and 14 male imagines from Aristóbulo del Valle, Ruta Prov. 7, Río Cuñá-Pirú, 19–20/XI/1998, D, M & N; 15 nymph and 2 female imagines from Parque Prov. Urugua-í, Arroyo Uruzú, 23–24/XI/1998, D, M & N; 2 nymphs same locality except date and collector: 7–11/XII/1999, C. Molineri; 7 nymphs from INTA Cuartel Victoria, 10 km NE San Vicente, 20/XI/1998, D, M & N; 22 nymphs from Puerto Mado, 3 km W María Magdalena, Arroyo Yacutinga, 19–20/XI/1998, D, M & N; 12 nymphs, 1 reared female subimago and 1 reared male subimago from Arroyo 25 km S El Soberbio, 21/XI/1998, D, M & N. The paratypes are housed in FAMU, the remaining material in IFML.

Diagnosis

Leptohyphes plaumanni can be differentiated from the other species of the genus by the following combination of characters, in the imagines: (1) membrane of wings tinged with yellowish light brown; (2) wing veins grayish brown; (3) occiput widely shaded with black; (4) abdominal segments IX–X and base of tails bright orange-brown *in vivo*. Nymph: (1) occiput widely washed with black as in Fig. 59; (2) tarsal claws with 3–4 marginal denticles and one unpaired submarginal denticle near apex (Fig. 58); (3) pronotum with black markings as in Fig. 59; (4) opercular lamellae widely shaded with gray; (5) basal 1/3 of tails with whorls of short spines at each intersegmental joining; (6) gill formula 3/5–6/5–6/5/1 (Figs. 60–65).

Discussion

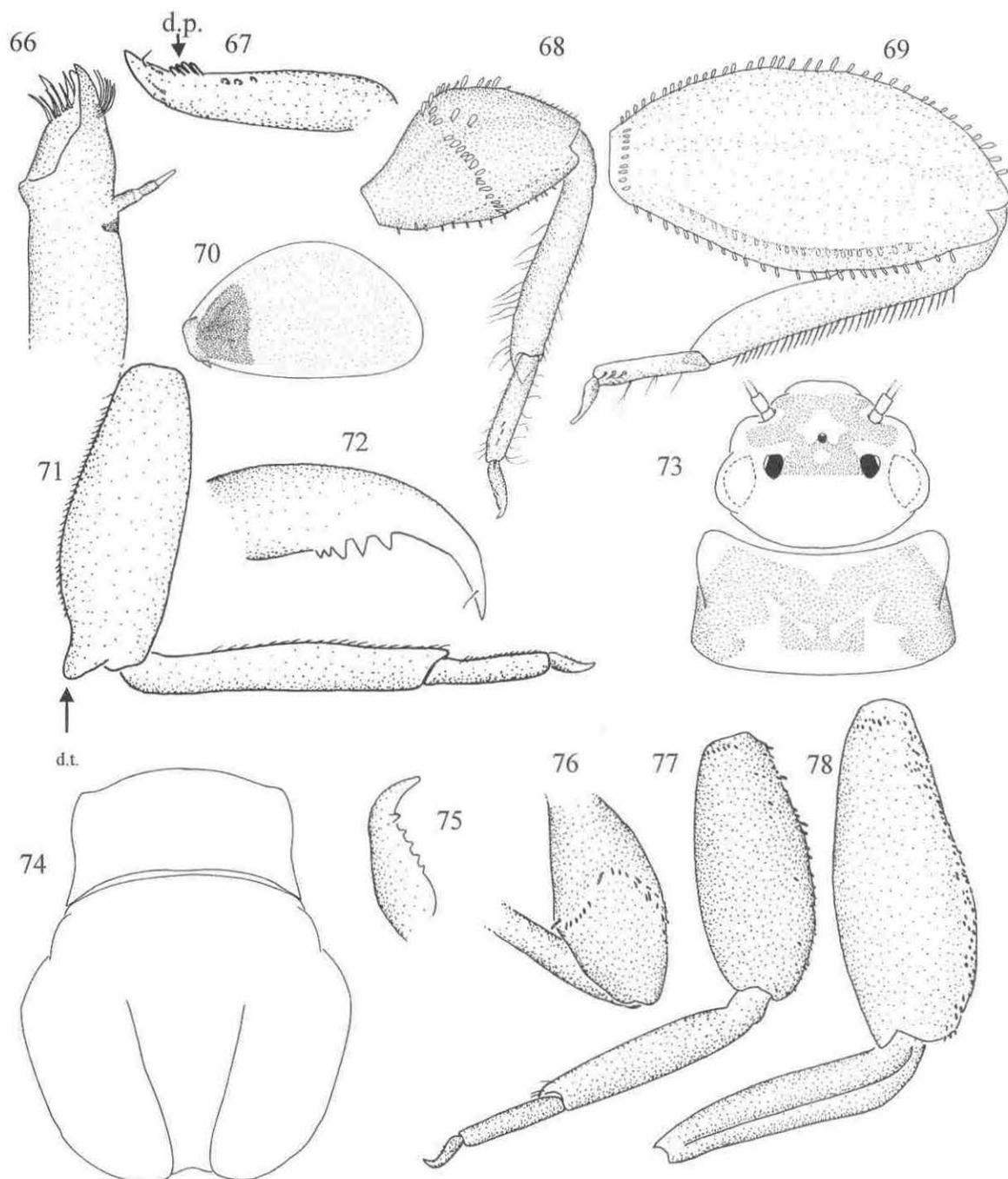
Leptohyphes pereirae Da Silva is synonymized with *L. plaumanni* Allen because the characters postulated to distinguish them (number of denticles on tarsal claws and spines on dorsum of femora II and III) are no longer valid. In the same population of *L. plaumanni* were observed nymphs with 3 or 4 marginal denticles, showing that this variation is intraspecific, so the presence of a small fourth denticle on *L. pereirae* is not sufficient to maintain it as a valid species. Also the spiculation of dorsum of femora, the general aspect of the nymphs and color pattern are similar in both species.

Leptohyphes carinus Allen (Figs. 66–70)

Leptohyphes carinus Allen, 1973: 365; Hubbard, 1982: 273.

Material

Four holotype slides from PERU: Huallaga, 25-IX-1963, M. Pandura. Deposited in FAMU.



Figs 66–70. *Leptohyphes carinus*, nymph. 66. Maxillae, d.v.; 67. fore tarsal claw, v.v.; 68. foreleg; 69. hind leg; 70. gill II, d.v.

Figs. 71, 72. *Leptohyphes ecuador*, nymph. 71. Hind leg; 72. detail of tarsal claw.

Figs. 73–78. *Leptohyphes illiesi* nymph. 73. Head and pronotum; 74. general outline of pro- and mesonotum; 75. tarsal claw; 76–78. fore, middle and hind legs; d.p. = distal palisade of denticles; d.t. = dorsal tubercle.

Diagnosis

Only the nymphal stage is known, and can be separated from the others of the genus by the following combination of characters: (1) abdomen with dorsal tubercles; (2) tarsal claw with 3 marginal denticles and 4 submarginal denticles near apex (Fig. 67); (3) spines on anterior face of femora II and III absent (Fig. 69); (4) elevated sockets absent.

Discussion

This species is very similar to *L. setosus*, described from the same locality, but can be separated from it by “abdomen with dorsal tubercles on some terga” (Allen). The presence of hind wingpads in the females could not be scored, because only males were studied; this would help with the future association with adults.

Leptohyphes ecuador Mayo (Figs. 71, 72)

Leptohyphes ecuador Mayo, 1968: 305; Hubbard, 1982: 273.

Material

Three female paratypes nymphs (alcohol, FAMU: E2034.T) from ECUADOR: Macuchi, Braden Quebrada, June 6, 1945, V. K. Mayo.

Diagnosis

Only nymphs are known. This species can be separated from the other of the genus by the following combination of characters: (1) occiput with a pair of blunt tubercles, pro- and mesonotum each with a pair of smaller tubercles, all of them with spicules on the apex; (2) inner margin of forewingpads with a row of a few spicules; (3) hind wingpads absent in female; (4) tarsal claws with 5 marginal denticles but no submarginal denticles near apex (Fig. 72); (5) hind femora with a distal tubercle (Fig. 71); (6) spines on anterior face of femora absent; (7) elevated sockets absent.

Leptohyphes illiesi Allen (Figs. 73–78)

Leptohyphes illiesi Allen, 1967: 368; Hubbard, 1982: 273.

Material

Holotype nymph (in alcohol, parts on slide, FAMU: (E2018.1T) from PERU: Rio Chillon, Station IV (343-D), 1100 m, 3-V-1958, J. Illies.

Diagnosis

Only the nymph is known and it can be separated from the other of the genus by the following combination of characters: (1) tarsal claws with 4–5 marginal denticles and one submarginal denticle near apex (Fig. 75); (2) hind wingpads absent in female; (3) developing wings whitish; (4) spines on anterior face of femora present near the dorsal margin (Figs. 77, 78); (5) elevated sockets absent; (6) anterolateral corners of pro- and mesonotum projected as in Figs. 73, 74; (7) occiput apparently without color markings (Fig. 73).

Leptohyphes invictus Allen (Figs. 79, 80)

Leptohyphes invictus Allen, 1973: 368; Hubbard, 1982: 274.

Material

Holotype male nymph (alcohol, FAMU: E2042.1T) from PERU, San Martin Prov., Tulumayo, 20 km. E Tingo Maria, 23-VI-1963, W. L. Peters.

Diagnosis

Only the nymphal stage is known and only males were studied. This species can be differentiated from the others of the genus by the following combination of characters: (1) denticles on tarsal claws: 2 + 1 (Fig. 80); (2) small tubercles on mesonotum (Fig. 79); (3) anterolateral corners of pro- and mesonotum projected as in Fig. 79; (4) occiput apparently without color markings (Fig. 79).

Leptohyphes jodiannae Allen (Figs. 81–85)

Leptohyphes jodiannae Allen, 1967: 358; Hubbard, 1982: 274.

Material

Paratypes: 3 nymphs (FAMU: E2011.T) from PERU, San Martin Prov., Rio Septa Grande [Supte Grande in Allen, 1967], 10 km. E. Tingo Maria, 26/VI/1963, W. L. Peters.

Diagnosis

The nymphs of this species can be separated from the other of the genus by the following combination of characters: (1) denticles on tarsal claws: 3 + 1 (Fig. 84); (2) mesonotum with spicules; (3) with a small and acute projection on anterolateral corners (Fig. 81); (4) hind wingpads absent in female; (5) developing wings whitish; (6) femoral spines relatively long and located on elevated sockets (Figs. 82, 83); (7) spines on anterior face of femora II and III present (as a median longitudinal row of 12–13 spines, Fig. 83); (8) ventral margin of tibiae I appear to be expanded (Fig. 82).

Discussion

This species is very similar to *L. petersi* but can be distinguished from it by tarsal claw denticulation and number of spines on dorsum of femora.

Leptohyphes liniti Wang et al.

Leptohyphes liniti Wang, Sites & McCafferty, 1998: 69.

Diagnosis

This species was not studied but from the original description and figures the following combination of characters to distinguish it was extracted: (1) head, body and legs without tubercles; (2) tarsal claw: 4–5 + 0; (3) developing wings blackish; (4) elevated sockets present; (5) anterolateral corners of pronotum projected anteriorly; (6) occiput with a reticulated color pattern; (7) branched setae present on dorsum of labrum.

Discussion

The following characters could not be scored but would be important for a better definition of this species: (1) presence



Figs. 79, 80. *Leptohyphes invictus*, nymph. 79. General outline of head and thorax, d.v.; 80. tarsal claw.

Figs. 81–85. *Leptohyphes jodiannae*, nymph. 81. General outline of head and thorax, d.v.; 82. foreleg; 83. hind leg; 84. tarsal claw; 85. detail of femoral spines.

Figs. 86–95. *Leptohyphes maculatus*, nymph. 86. General outline of head and thorax (left and right sides of head showing intraspecific variation); 87. head, d.v.; 88. general outline of head and thorax (other variation); 89. opercular gill, d.v.; 90. maxillae, d.v.; 91a–b. variation in femoral spines; 92. foreleg; 93. hind leg; 94–95. variation in tarsal claws; m.r. = mediolongitudinal row of dorsal spines.

or absence of hind wingpads in females; (2) form, number and distribution of spines on femora; (3) form and number of lamellae of the abdominal gills.

Leptohyphes maculatus Allen (Figs. 86–95)

Leptohyphes sp. 3 Roback [partim] 1966: 151.

Leptohyphes maculatus Allen, 1967: 360; Allen & Roback, 1969: 376; Hubbard, 1982: 274.

Leptohyphes sp. Illies, 1965: Fig. 3e.

Leptohyphes comatus Allen, 1967: 368; Hubbard, 1982: 273.
NEW SYNONYM

Leptohyphes sp. 4 Roback, 1966: 151.

Leptohyphes hirsutus Allen & Roback, 1969: 374; Hubbard, 1982: 273. NEW SYNONYM

Leptohyphes sp. 2 Roback, 1966: 151.

Leptohyphes myllonotus Allen & Roback, 1969: 375; Hubbard, 1982: 274. NEW SYNONYM

Material

Leptohyphes maculatus. Paratypes: 2 nymphs from PERU: Huanuco, Río Huallaga, Tingo Maria, 10–12/VII/1963, W. L. Peters (= WLP below); 8 slides from different localities near Tingo Maria: Río Huallaga, 14–16/VIII/1963, WLP (2 slides); Río Pendescia, 24 km E de Tingo Maria, 22/VII/1963, WLP; Río Tulumayo, 20 km E Tingo Maria, 19/VII/1963, WLP (3 slides); Río Bella junction Río Monzon, 25/VII/1963, WLP; all of them deposited in FAMU. *Leptohyphes comatus*. Holotype nymph (in alcohol, FAMU E2014.T) from PERU: Huallaga, Station Va, no date, 373-D, 1800m, J. Illies. Paratype slide (Illies collection) from: PERU, Huanuco, Huallaga, 1900m, 321-D, no date, J. Illies. *Leptohyphes hirsutus*. Holotype nymph (alcohol, ANSP), 2 paratype nymphs (alcohol) and 4 paratype slides from: PERU, near Tingo Maria, Puente Perez River, 1–2/X/1955, S.S. Roback. *Leptohyphes myllonotus*. Holotype slides (ANSP) de Peru, Porto Nuevo, 24-IX-1955, S. S. Roback. 3 paratype slides and 2 nymphs in alcohol from Peru Tulumayo R., 24-IX-1955, S. S. Roback. 3 paratypes nymphs from Peru, R. Monzon, near Tingo Maria, 27-IX-1955, S. S. Roback.

Diagnosis

L. maculatus is known from subimagines and nymphs, and can be distinguished from the other species of the genus by the following combination of characters. In the adults: (1) female hind wings absent; (2) penes ‘Y’ shaped; (3) membrane of wings not strongly tinged with brown or black. In the nymphs: (1) body and legs completely covered with thin whitish setae (not drawn in Figs. 92, 93); (2) occiput with variable marks (Figs. 86–88); (3) tarsal claw denticulation: 3–5 + 0/1 (Figs. 94, 95); (4) developing wings whitish.

Discussion

Leptohyphes myllonotus, *L. maculatus*, *L. hirsutus* and *L. comatus* are treated here as subjective synonyms because the types of these species are undistinguishable from each other, and represent small intraspecific variations of only one species. Moreover, all of these nymphs were collected in the same area. The name *Leptohyphes maculatus* Allen (1967) has date and page priority above the others.

Leptohyphes mollipes Needham & Murphy

Leptohyphes mollipes Needham & Murphy, 1924: 32; Lestage, 1931: 60; Traver, 1958a; Hubbard, 1982: 274.

Discussion

Material of this species was not studied. It is known from adults of both sexes from Brazil, Cordisboro. From the original drawings the male genitalia seems typical of the genus. Forewings show an unusual cubital venation with ICu2 longer than normal; whether this is an error on the drawing or a real pattern cannot be established without the material. The hind wings are veinless from description and illustration.

Leptohyphes nigripunctum Traver

Leptohyphes nigripunctum Traver, 1943: 82; Hubbard, 1982: 274.

Discussion

This species is only known from a male subimago from Venezuela (Antimano). Traver stated that the genitalia was of the ‘peterseni type’ (similar to the type species of *Leptohyphes*) but reported that it was lost while being prepared for mounting. For these reasons the assignment to *L. nigripunctum* should be done after a carefully comparison with the holotype.

Leptohyphes peterseni Ulmer

“Genus Nov” Esben-Petersen, 1909: 553.

Leptohyphes peterseni Ulmer, 1919: 46; Ulmer, 1920: 122; Lestage, 1924: 45; Needham & Murphy, 1924: 32; Lestage, 1931: 60; Hubbard, 1982: 274; Dominguez, 1984: 103.

Discussion

This species is known from male and female subimagines from Brazil (Santa Catarina), Bolivia and Argentina. It constitutes the first description of a male of *Leptohyphes*, and Ulmer assigned it to this genus because the wing venation was similar to that of the female of *L. eximius* Eaton (type species of the genus). The material is represented by numerous male and female subimagines, but between them probably more than one genus are represented. I suspect this

because Ulmer described some males with penes not divergent at the tip, a situation known to occur in males of some recently described groups of the region. Moreover, the divergent penes of *Leptohyphes* species are always well separated in subimagines and imagines. This situation cannot be confirmed until the type material can be studied. The genitalia drawn by Ulmer is quite similar to that described here for the males of *L. plumannii* (Fig. 51), and as they are the only *Leptohyphes* species with this type of genitalia in this region (besides *L. cornutus* Allen, also described here), probably they will show to be synonyms after detailed study.

Leptohyphes petersi Allen (Figs. 96–103)

Leptohyphes nymph no. 2 Needham & Murphy, 1924: 34.
Leptohyphes petersi Allen, 1967: 364; Hubbard, 1982: 274.

Material

Paratype slides from PERU, Río Bella junction Río Monzon, 25-VII-1963, WLP. Paratype slides from PERU, Río Huallaga, Tingo María, 14–16/VIII/1963, WLP; 5 female and 5 male imagines (in alcohol) from Peru, Río Huallaga, Tingo María, 1/VIII/1963, WLP (No. 2024T). Deposited in FAMU.

Diagnosis

Among the type material studied at FAMU there was one female with hind wings; the other four females differ a little in coloration with the first one and do not have hind wings. Here it is assumed that the female with hind wings was included by error in the type series and that it belongs to a different species. *L. petersi* can be separated from the other species of the genus by the following combinations of characters. In the adults: (1) female hind wings absent; (2) penes as in Figs. 103a–c, distal spines longer than inner membranous lobes; (3) membrane of wings not strongly tinged with black or brown; (4) hind wings as in Fig. 102. In the nymphs: (1) femoral spines medium in length (Fig. 100); (2) elevated sockets present (Fig. 97); (3) tarsal claw denticulation: 3–4 + 0 (Fig. 99); (4) maxillar palpi long and slender (Fig. 101); (5) hind wingpads absent in female; (6) developing wings blackish or whitish; (7) pro- and mesonotum with projected anterolateral corners (Fig. 98).

Discussion

The presence of nymphs with blackish and whitish developing wings (black tint not due to maturity) could reveal the

presence of two rather than one species in the type material. The same applies to the female subimago with hind wings. The nymphs are similar to *L. jodiannae* but can be distinguished from it by the characters discussed in this species.

Leptohyphes populus Allen (Figs. 104–111)

Leptohyphes populus Allen, 1973: 366; Hubbard, 1982: 274.

Material

Holotype slides E2048.T from Brazil, Amazonas St., Rio Marauia, 26–27/I/1963, Fittkau. FAMU.

Diagnosis

This species is only known from the nymphal stage and can be distinguished from the other species of the genus by the following combination of characters: (1) eyes of male divided (Fig. 104); (2) without tubercles on body or legs; (3) tarsal claw denticulation: 3–4 + 0 (Fig. 105); (4) spines on anterior face of femora absent (Fig. 111); (5) elevated sockets present (Fig. 110, 111).

Discussion

This is the only species of *Leptohyphes* known to have divided eyes in the male. This situation permits a rapid identification but creates doubts about its generic position. Except this, all the structures of the material studied show that *L. populus* belongs to *Leptohyphes*. In the family Leptohiphidae, divided eyes in males are only known for *Leptohiphodes inanis* (Pictet), from which I have studied newly collected material and that represents a totally different group.

Leptohyphes setosus Allen (Figs. 112–116)

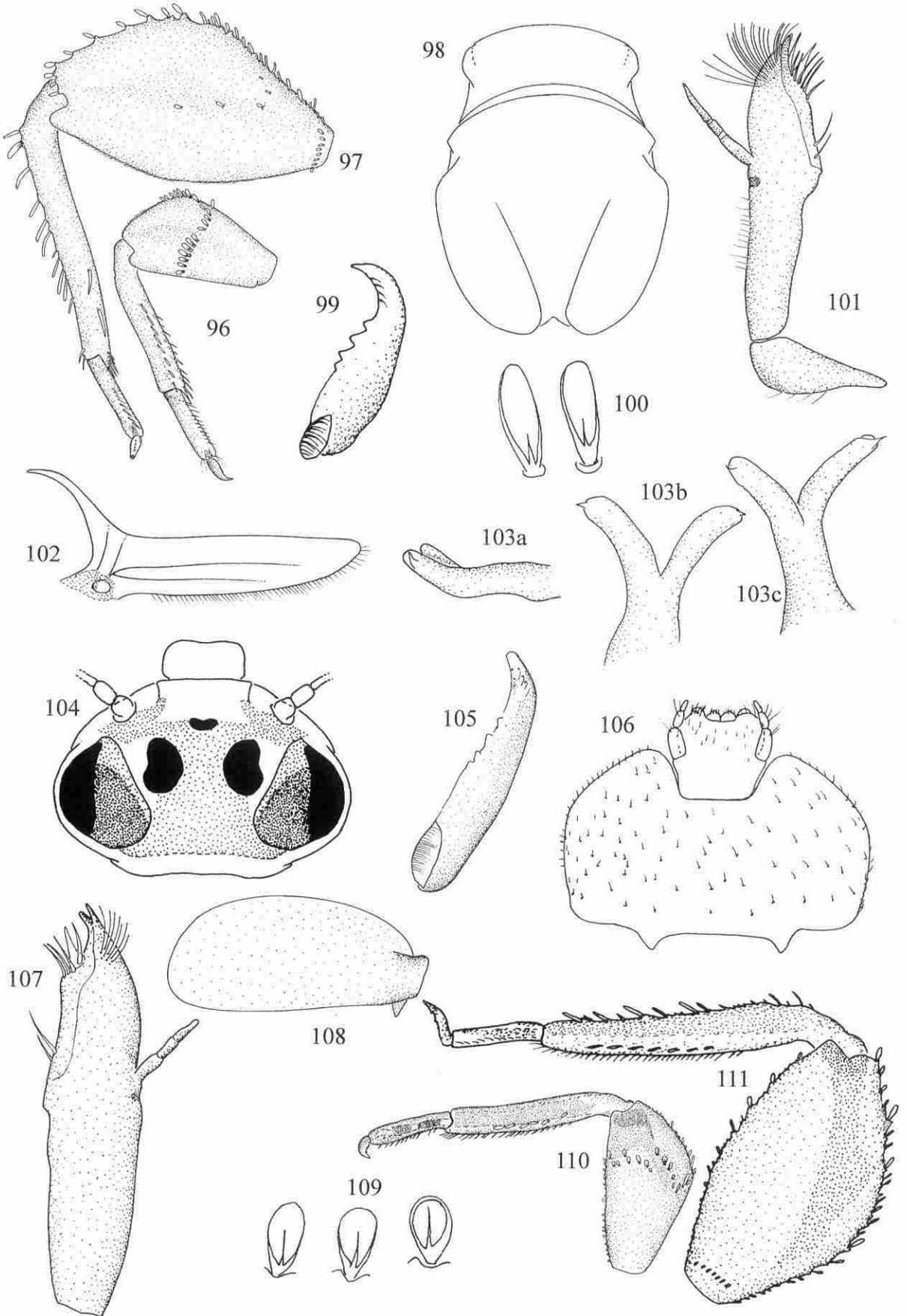
Leptohyphes sp. 3 Roback [partim] 1966: 151.
Leptohyphes setosus Allen, 1967: 362; Allen & Roback, 1969: 378; Hubbard, 1982: 274.
Leptohyphes sp. 5 Roback, 1966: 151.
Leptohyphes echinatus Allen & Roback, 1969: 375; Hubbard, 1982: 273. NEW SYNONYM

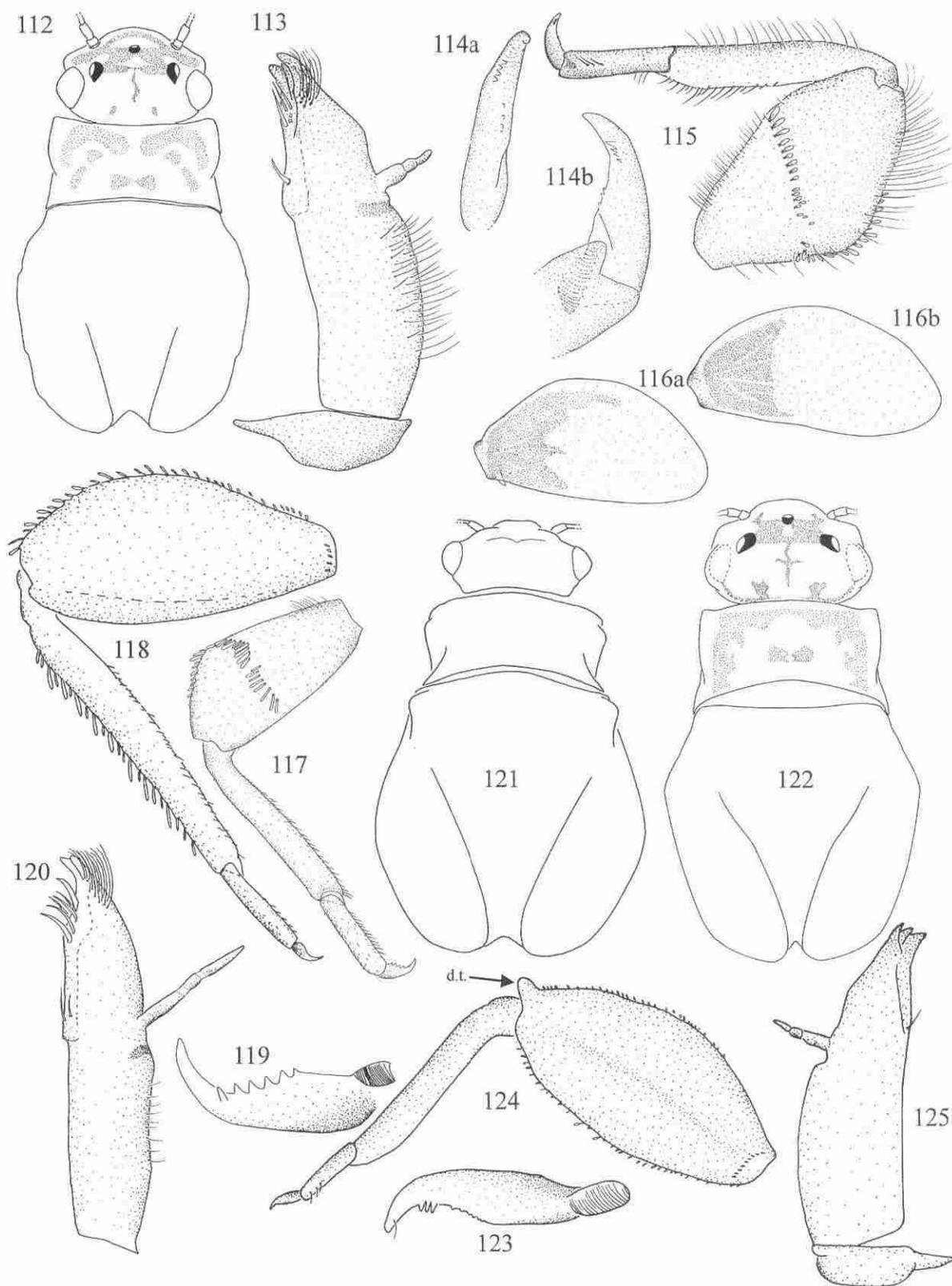
Material

Leptohyphes setosus. Holo- and paratype nymphs in alcohol from Peru, Loreto Prov., Río Aguaytia, Aguaytia,

Figs. 96–103. *Leptohyphes petersi*. Nymph: 96. foreleg; 97. hind leg; 98. general outline of thorax, d.v.; 99. tarsal claw. Adult: 100. detail of femoral spines; 101. maxillae, d.v.; 102. male hind wing; 103a. penes, l.v.; 103b, c. penes, v.v.

Figs. 104–111. *Leptohyphes populus*. Nymph: 104. head, d.v.; 105. tarsal claw; 106. labium, v.v.; 107. maxillae, d.v.; 108. opercular gill, d.v.; 109. detail of femoral spines; 110. foreleg; 111. hind leg.





Figs. 112–116. *Leptohiphes setosus*, nymph. 112. General outline of head and thorax, d.v.; 113. maxillae, d.v.; 114a, b. detail of tarsal claw; 115. foreleg; 116a, b. variation on opercular gill, d.v.

Figs. 117–121. *Leptohiphes tacajalo*, nymph. 117. Foreleg; 118. hind leg; 119. tarsal claw; 120. maxillae, d.v.; 121. general outline of head and thorax, d.v.

Figs. 122–125. *Leptohiphes tuberculatus*, nymph. 122. General outline of head and thorax, d.v.; 123. tarsal claw; 124. hind leg; 125. maxilla, d.v.; d.t. = dorsal tubercle.

15-VII-1963, WLP, and paratype slide from Peru, Tingo María, Río Huallaga, no date, WLP (FAMU, No. 2010T). *Leptohyphes echinatus*. Holotype (whole nymph on slide) and paratype slides (ANSP, No. 20.55) from Tulumayo R., 25-IX-1955, S.S. Roback. 8 paratype nymphs Tulumayo, Porto Nuevo, near Tingo Maria, 25-IX-1955, S.S. Roback.

Diagnosis

Leptohyphes setosus is known from male subimagines and nymphs and it can be distinguished from the others of the genus by the following combination of characters. In the adults: (1) genitalia of the 'peterseni' type; no more data except for the abdominal color pattern (Allen, 1967, Fig. 32). In the nymphs: (1) body and legs completely covered with thin and whitish setae; (2) without projections on legs or abdomen; (3) maxillae stout with enlarged apical canines, recurved setae of distal brush short and scarce, denticulae small and reduced in number, palpi short and robust (Fig. 113); (4) tibiae wide, ventral margin extended (Fig. 115); (5) tarsal claw denticulation: 3-4 + 4-5 (Fig. 114a, b); (6) femora wide, femoral spines relatively short (Fig. 115); (7) hind wingpads absent in females; (8) abdominal color pattern as in Figs. 31, 32 of Allen (1967).

Discussion

Leptohyphes echinatus Allen and Roback (1969) is here synonymized with *Leptohyphes setosus* Allen (1967) because they are indistinguishable, showing identical color pattern, form of maxilla, tarsal claw denticulation, and leg and body setation.

Leptohyphes tacajalo Mayo (Figs. 117-121)

Leptohyphes tacajalo Mayo, 1968: 307; Hubbard, 1982: 274.
Leptohyphes albus Mayo, 1968: 305; Hubbard, 1982: 273. NEW SYNONYM

Material

Leptohyphes tacajalo. Holotype female nymph (intact, in alcohol) from ECUADOR: Macuchi, Braden Quebrada, June 6, 1945, V. K. Mayo; paratypes: 10 female and 5 male nymphs (alcohol), same data as holotype. ERROR: holotype slide, FAMU: E2023.T from Ecuador R. Amayo, Macuchi, 30 June 1943. *L. albus*. Holotype nymph (alcohol, parts on slide, FAMU: E2022.1T) from ECUADOR: Macuchi, Río Amayo, 7 July 1942, V. K. Mayo; paratypes: 2 nymphs (alcohol), same data as holotype. All deposited in FAMU.

Diagnosis

The nymphs of this species, the only known stage, can be separated from the others of the genus by the following combination of characters: (1) tarsal claw denticulation: 4-5 + 1

(Fig. 119); (2) pronotum with a small lateral and somewhat acute projection as in Fig. 121; (3) hind wingpads present in female; (4) developing wings whitish; (5) spines on anterior face of femora II and III absent (Fig. 118); (6) elevated sockets absent; (7) mesonotum with projected anterolateral corners (Fig. 121).

Discussion

The type material of *L. albus* and *L. tacajalo* was studied and it was impossible to find characters to distinguish them. Mayo described them as two species because the maxillary palp of *L. albus* was two-segmented. Actually, the last segment is lost in the holotype slide but its insertion on the second segment is clear. Moreover, the paratypes have normal, three-segmented maxillary palpi. Also in Mayo's Fig. 8 the labial palpi of *L. albus* appear two-segmented, but this is a teratological labium as shown by the paratype nymphs that have normal, three-segmented labial palpi. Another difference proposed was on tarsal claws, *L. albus* having five marginal denticles and *L. tacajalo* four marginal denticles, but this showed to be spurious for some paratypes of *L. tacajalo* that have five marginal denticles. It seems better to conserve the name *L. tacajalo* because its type material is more numerous and does not show teratological structures.

Leptohyphes tuberculatus Allen (Figs. 122-125)

Leptohyphes sp. 6 Roback, 1966: 152.
Leptohyphes tuberculatus Allen, 1967: 369; Allen & Roback, 1969: 378; Hubbard, 1982: 274.

Material

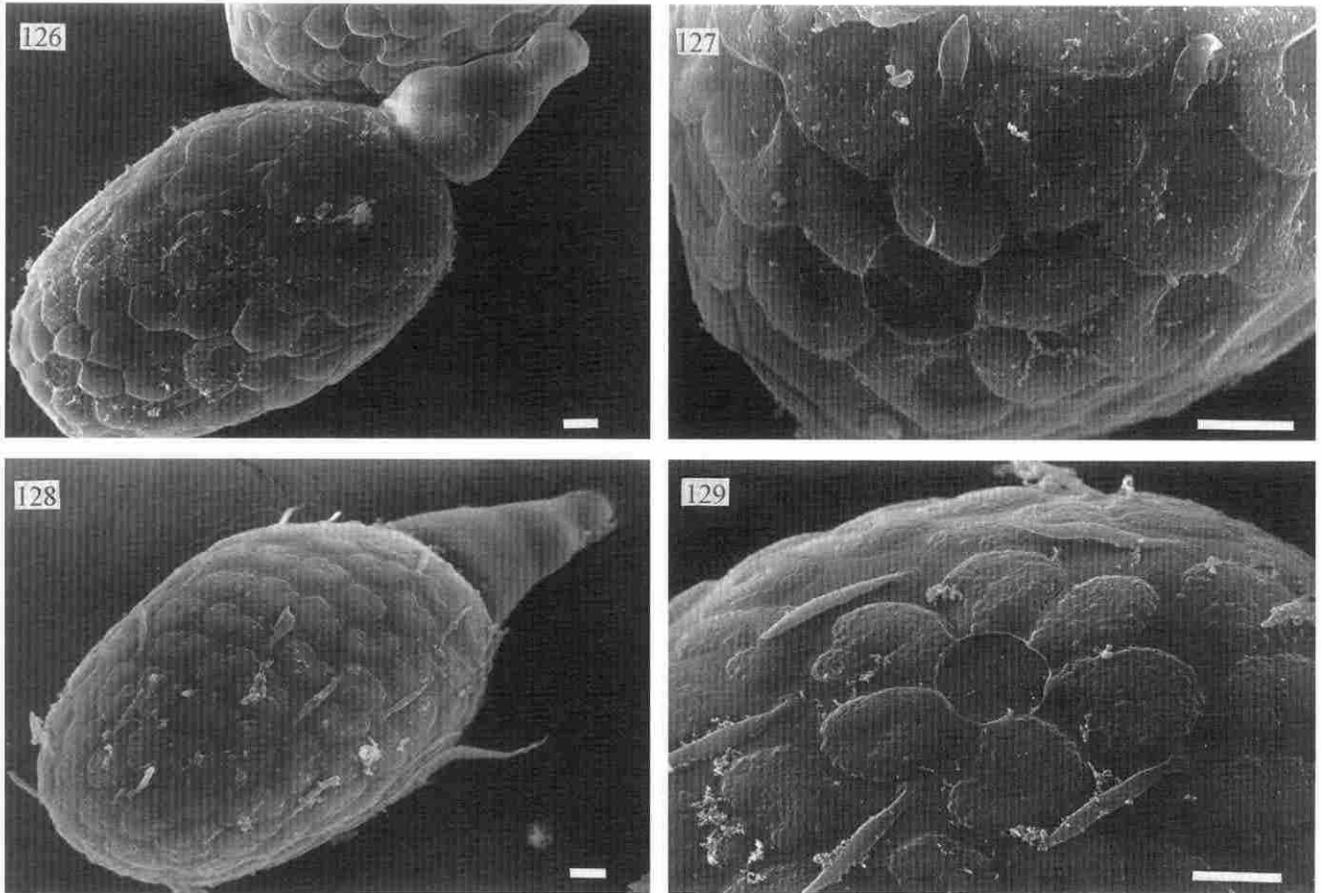
Paratypes: 3 nymphs from Peru, Río Huallaga, Tingo María, 26-VII-1963, WLP. FAMU E2028.

Diagnosis

This species is only known from nymphs that can be separated from the other of the genus by: (1) hind femora with a distal tubercle (Fig. 124); (2) hind wingpads absent in female; (3) tarsal claw denticulation: 6 + 3 (Fig. 123); (4) spines on anterior face of femora II and III absent (Fig. 124); (5) elevated sockets absent; (6) pro- and mesonotum without projected anterolateral corners (Fig. 122); (7) occiput patterned as in Fig. 122; (8) maxillae as in Fig. 125.

Discussion

Only *L. ecuador* shares with *L. tuberculatus* the presence of a tubercle on apex of hind femora, but they can be separated by: tarsal claw denticulation, absence of tubercles on the head of the latter species, and form of femora.



Figs. 126–129. Eggs, SEM photographs. Figs. 126, 127: *Leptohiphes eximius*. 126. General aspect of egg; 127. detail of micropyle and KCT. Figs. 128, 129. *L. cornutus*. 128. General aspect of egg; 129. detail of micropyle and KCT. Scale bar = 10.0 μm .

Discussion

As a result of the present study, in South America, the species of *Leptohiphes* now known from males and nymphs are six: *L. cornutus* Allen, *L. eximius* Eaton, *L. maculatus* Allen, *L. plaumanni* Allen, *L. setosus* Allen and *L. petersi* Allen (1967). Three species are known only from male adults: *L. mollipes* Needham and Murphy (1924), *L. nigripunctum* Traver (1943) and *L. peterseni* Ulmer (1919). And nine, described as nymphs only, remain as valid species congeneric with *L. eximius*: *L. illiesi*, *L. jodiannae*, *L. tuberculatus* (Allen, 1967); *L. carinus*, *L. populus*, *L. invictus* (Allen, 1973); *L. tacajalo*, *L. ecuador* (Mayo, 1968) and *L. liniti* Wang et al. (1998).

The remaining South American species originally described in *Leptohiphes* and listed below are not congeneric with *Leptohiphes eximius*: *L. asperulus* Allen (1967: 366), *L. edmundsi* Allen (1973: 363), *L. gibbus* Allen (1967: 358), *L. indicator* Needham and Murphy (1924: 33), *L. minimus* Allen (1973: 369), *L. nicholsae* Wang et al. (1998: 69), *L. rallus* Allen (1967: 363), *L. spinosus* Allen and Roback (1969: 150), *L. tinctus* Allen (1973: 368), *L. undulatus* Allen (1967: 357) and *L. viriosus* Allen (1973: 369), *Leptohiphes* sp. A Traver (1944: 15). Most of them have been changed to

other genera (*Tricorythopsis*, Molineri 2001b; *Allenhiphes* and *Tricorythodes*, Wiersema and McCafferty 2000, Molineri in press) or were the bases for new generic descriptions (*Allenhiphes*, Hofmann et al. 1999; *Traverhiphes*, Molineri 2001a; *Vacupernius*, Wiersema and McCafferty 2000). The actual or probable status of these species is presented in Table 1.

From the present study the following conclusions can be drawn:

- *Leptohiphes*, as restricted here, is a well defined group of Leptohiphidae supported by numerous characters at nymphal and adult stages.
- Some characters may vary in individuals of the same species, for example in the nymphs some variations occur in: details on color markings of head and body, body size, degree of development of the covering of fine setae on the body, little variations in the number of denticles on tarsal claws; and in the adults: details of cubital venation, body size, degree of development of the remnants of female hind wings.
- New species to be described in the future should be accurately defined (and fully illustrated) to avoid the problems accumulated in the group.

- The numerous species described from nymphs from Río Huallaga (near Tingo María, Peru) need further study and correct associations with the alate stages. Some synonymies are still expected in this group of species.

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