

ORIGINAL ARTICLE

***Leptohyphodes inanis* (Pictet) and *Tricorythodes ocellus* Allen & Roback (Ephemeroptera: Leptoxyphidae): New stages and descriptions**

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Abstract

Leptoxyphodes Ulmer is a poorly known monotypic genus from NE Brazil (Serra do Mar). It is the only known genus in the family Leptoxyphidae that shows divided eyes in the male. In the present paper the genus and species are redescribed, based on new material from all the life stages. The eggs and female adults are described for the first time. Also male imagines of *Tricorythodes ocellus* Allen & Roback are described for the first time, showing markedly plesiomorphic genitalia. *Leptoxyphodes* shows close affinities with the genera *Tricorythodes* and *Haploxyphes*.

Resumen

Leptoxyphodes Ulmer es un género monotípico poco conocido del NE de Brasil (Serra do Mar). Es el único género conocido en la familia Leptoxyphidae que presenta ojos divididos en el macho. En el presente trabajo se describe el género y la especie sobre la base de material nuevo de todos los estadios del ciclo de vida. Los huevos y hembras adultas son descritos por primera vez. También se describe por primera vez a los imagos machos de *Tricorythodes ocellus* Allen & Roback, que muestran genitales masculinos notoriamente plesiomórficos. *Leptoxyphodes* muestra relaciones de parentesco con los géneros *Tricorythodes* y *Haploxyphes*.

Keywords: Taxonomy, redescription, eggs, illustrations

Introduction

The family Leptoxyphidae is distributed from Argentina to Canada but with the greatest diversity found in the Neotropics. Its sister group (family Tricorythidae) is distributed in Africa and Madagascar and the other related groups are also from Gondwanian landmasses.

Since its first description, *Leptoxyphodes* represented an enigmatic taxon with obscure relationships. This genus was established by Ulmer (1920a) for eight male imagines from Brazil described by Pictet (1843) as “*Potamanthus ? inanis*” (but Pictet described this species from 2 male imagines only) and for *Tricorythus australis* Banks (1913) known from male and female imagines. Traver (1944) described the probable nymphs of the genus and later moved (Traver, 1958) Bank’s species to the genus *Tricorythodes*. Thus, the genus *Leptoxyphodes* is currently composed by the type

species, *L. inanis* (Pictet), known from male imagines and *Leptoxyphodes* sp. Traver (1944) known from nymphs. In the present paper, both species are treated as different stages of the same, *L. inanis* (Pictet), for reasons discussed later.

The most unique character of this genus is the large eyes of the male, divided in upper and lower portions. This feature is uncommon for a leptoxyphid, characterized by small undivided eyes in the males. The only exception to this is *Leptoxyphes populus* Allen (1973) known from a male nymph from Amazonas St. (Brazil).

A key to separate all the South American genera of Leptoxyphidae, including *Leptoxyphodes*, can be found in Domínguez et al. (1992, 2001).

The original descriptions and figures of the nymphs and adults do not even suggest the probable relationships of *Leptoxyphodes*. For these reasons the objectives of the present work are to redescribe and illustrate these stages (at generic and specific levels),

describing for the first time the female adults and eggs, and to assess the probable relationships of this enigmatic taxon.

Among the material deposited at Florida A & M University (Tallahassee) were found some male imagines attributable to *Tricorythodes ocellus* Allen & Roback (1969), previously known from nymphs. Here they are described due to the plesiomorphic characteristics of male genitalia, which facilitates the homology of genital structures between the genera of Leptohiphidae.

Materials and methods

The material used in this study was preserved in 80% ethanol. The male genitalia and nymphal parts were dissected and placed in Canada Balsam, wings were mounted dried on microscopic slides. Figures were drawn with the aid of a camera lucida mounted on a stereomicroscope. Eggs were removed from a female imago, dehydrated in a graded ethanol series, and dried by critical point-method using CO₂ in a Bomar apparatus. Eggs were then 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.

Abbreviation of thoracic structures (from Kluge, 1992. external parapsidal suture (EPS), internal parapsidal suture (IPS), inferior dorsoventral suture of lateropostnotum (IS), superior dorsoventral suture of lateropostnotum (SS), posterior scutal protuberances (PSP), transverse interscutal suture (TIS).

Material deposition: Instituto-Fundación Miguel Lillo, Tucumán, Argentina (IFML), Florida A & M University, Tallahassee, FL, U.S.A. (FAMU), Museu de Zoologia de São Paulo, SP, Brazil (MZSP).

Results

Generic redescription of Leptohiphodes Ulmer

Leptohiphodes Ulmer, 1920a, 1920b, 1933; Traver, 1944, 1958; Domínguez et al., 1992, 2001. Type species: *Potamanthus inanis* Pictet (original designation).

Imago

Head. Eyes of male big, divided, dorsal portion partially covering head from above (Figure 6b), ventral portion smaller (Figure 6a), hexagonal facets present in both subdivisions, bigger on the dorsal portion. Eyes separated on meson of head by distance approximately equal to 1/2 diameter of an eye (Figure 6b). Eyes of female small, not divided

and inserted laterally (Figure 7a–b); separated on meson of head by a distance 3–4 times diameter of an eye (Figure 7b). Ocelli slightly elevated (Figures 6–7). Antennae as in Figures 6–7.

Thorax. Mesonotum: internal and external parapsidal sutures (IPS and EPS) do not fuse until TIS (Figure 5); sulcus present (concavity between PSP); lateropostnotum with IS and SS not forming a straight line. Membranous filaments on mesoscutellum long, reaching hind margin of abdominal tergum II, with wide base, thinner toward apex (Figure 5). Hind wings absent in both sexes. Fore wing without marked sexual dimorphism, widest part located near MA region (Figures 1a–2). Hind margin of wing fringed with setae (Figure 1b), vein CuP strongly curved, ICu1 free at base but directed toward CuP base (almost forming a triad), MP2 not united directly to MP1. Legs. Femora I and II subequal in length, femora III 20% longer than them; fore tibiae and tarsi of male three times length of middle ones and two times length of hind ones; tarsi five-segmented (Figure 3). Pair of tarsal claws of all legs dissimilar, one acutely pointed and the other paddle-like (Figure 3), except on fore legs of male, both paddle-like (Figure 4).

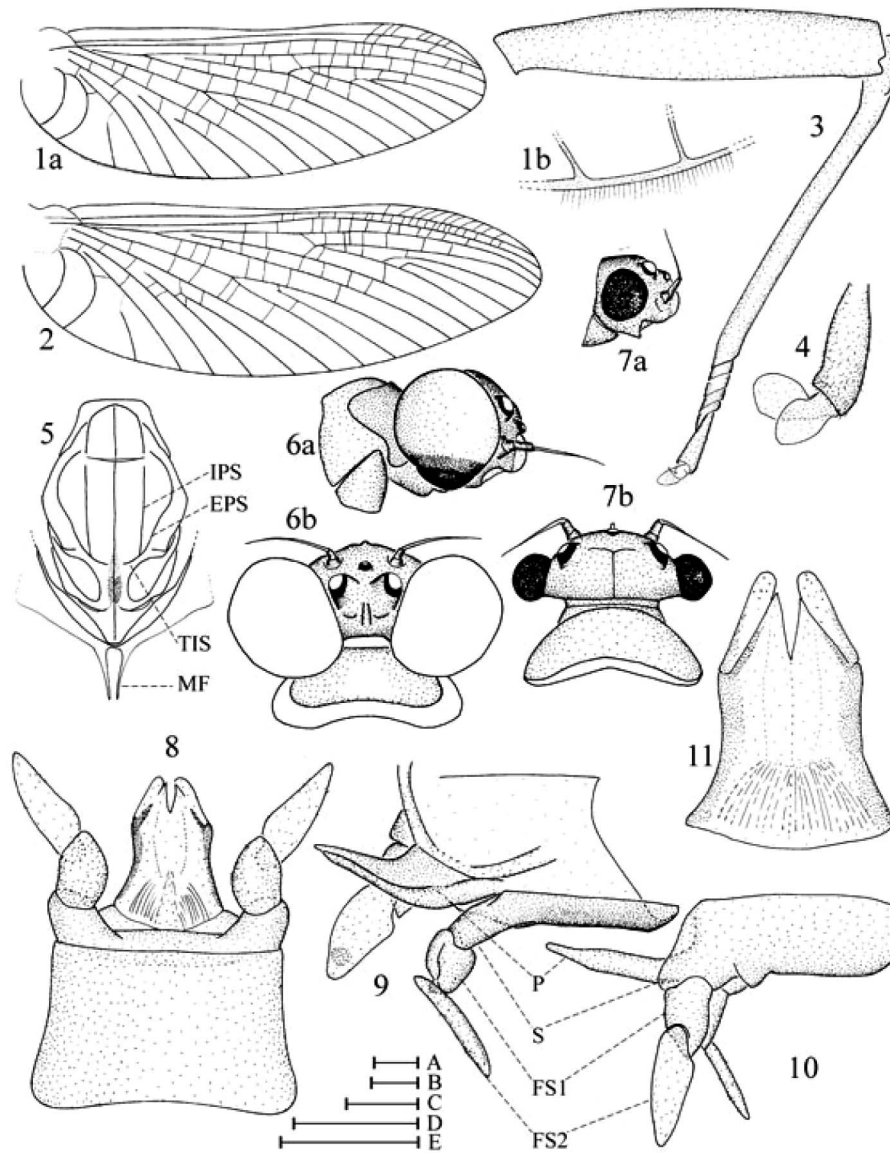
Abdomen. Cylindrical and relatively long. Genitalia (Figures 8–11. forceps (8–10) two-segmented, short and stout; basal segment short and globular (length approximately equal to width), distal segment slightly longer (approximately 1.5 times longer than wide) and leaf-like (Figure 9). Styli plate projected at posterolateral corners (i.e. base of forceps), perpendicularly to main body axis (Figure 10). Penes (Figures 8–11) wide, plate-like, almost completely fused except apical excavation. Ninth female sternite apically blunt, slightly concave. Caudal filaments similar in length to fore wings.

Nymph

Body elongated, covered by thin setae (Figure 12).

Head hypognathous with strong setae on genae, clypeus and labrum. Antennae 3/2–3 times length of head. Eyes of male divided. Mouthparts (Figures 17–22). Labium (Figure 17a–b) with a subcircular submentum, prementum elongated, labial palpi three-segmented, distal segment reduced (Figure 17b); maxillae as in Figure 22, galea and lacinia divided, palp 1-segmented, setiform (arrow in Figure 22b). Mandibles as in Figures 19–20. Hypopharynx as in Figure 18. Labrum deeply cleft medially (Figure 21).

Thorax (Figure 12). Pro- and mesonotal margins fringed with setae, anterolateral corners of pronotum anteriorly projected. Hind wingpads absent in both



Figures 1–11. *Leptohyphodes inanis*. Imago: (1a) male fore wing; (1b) detail of hind margin; (2) female fore wing; (3) male middle leg; (4) male fore tarsus and claws; (5) male mesonotum; (6a) male head, l.v.; (6b) male head, d.v.; (7a) female head, l.v.; (7b) female head, d.v.; (8) male genitalia, v.v.; (9) same (dorsolateral view); (10) male genitalia, l.v.; (11) detail of penes, v.v. EPS = external parapsidal suture, IPS = internal parapsidal suture, MF = membranous filaments, TIS = transverse interscutal suture. Scale bars: A = 0.01 mm (Figures 8–10); B, D, E = 1 mm (Figures 1–2, 5–7); C = 0.1 mm (Figure 3).

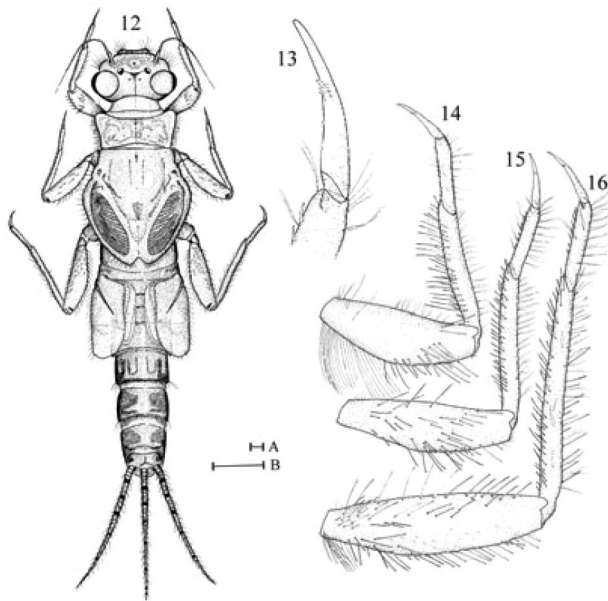
sexes. Legs (Figures 14–16) slender, covered by long setae. Tarsal claws relatively long with 5–6 slightly marked and blunt marginal denticles on basal half and with a double row of 2–3 submarginal denticles on apical 1/3 (Figure 13).

Abdomen (Figures 12, 23–24) cylindrical, elongated, gills present on segments II–V (Figure 24). Posterior margins of terga I–VI glabrous or with fine setae, posterior margins of terga VII–X with small spines and fine setae. Gills II (Figures 25–27) operculate, subtriangular to subrectangular with a transverse weak medial line (not always well marked), completely covering remaining gills; ventral lamellae dorsally festooned with smaller lobes,

and with a small remnant of a second ventral lamella (arrow in Figure 27). Operculate gills may touch each other on meson of abdomen, if totally retracted. Gills III–IV (Figures 28–29) formed by three lamellae, the ventralmost, festooned; gill V (Figure 30) formed by two lamellae. Lateral flanges and posterolateral spines absent. Three caudal filaments present, less than 1/2 length of body (Figure 12).

Egg

Length, 130–170 μm ; maximum width, 60–75 μm . One polar cap present, conical and elongated (Figure 31). One micropylar area per egg,



Figures 12–16. *Leptohyphodes inanis*. Nymph: (12) nymphal habitus, d.v.; (13) detail of fore tarsal claw; (14) fore leg; (15) middle leg; (16) hind leg. Scale bars: A = 0.1 mm (Figures 14–16); B = 1 mm (Figure 12).

subcircular, surrounded by five chorionic plates (Figure 32). Chorionic plates subcircular, contiguous on uncapped pole but separating from each other toward capped pole (Figures 31–32). Adhesive filaments relatively long, slowly widening toward the apex as in Figures 33–34.

Diagnosis

Leptohyphodes can be distinguished from all other genera of Leptohiphidae by the following combination of characters. Imago: (1) male fore wings without extended cubitoanal lobe (Figure 1a); (2) hind wings absent in both sexes; (3) female caudal filaments relatively long; (4) membranous filaments of mesoscutellum long and slender (Figure 5); (5) male forceps two-segmented, distal segment leaf-like (Figures 8–10); (6) penes plate-like, fused except on apical excavation (Figure 11); (7) eyes of male big and divided (Figures 6a–b). Nymph: (1) hind wingpads absent in both sexes; (2) operculate gills subtriangular, dorsally with two ridges and a median weaker band (Figure 26); (3) number of lamellae per gill (II–V. 2-3-3-2, lamellae subtriangular (Figures 27–30); (4) femora I with a subdistal transverse row of long setae (Figure 14); (5) femora II and III with a subdistal transverse row of setae (Figures 15–16); (6) maxillary palp small, setiform (Figure 22a–b); (7) labrum with a deep median cleft (Figure 21); (8) tarsal claw with 5–6 slightly marked and blunt marginal denticles on basal half and with a double row of 2–3 submarginal denticles on apical

1/3 (Figure 13); (9) frontal and genal projections present; (10) body elongated, not heavily sclerosed and covered by numerous long setae; (11) 3–4 small imbricated lobes on ventral lamellae of gills II–IV (Figures 27–29).

Discussion

Traver (1958) stated that gills are present on segments II–VI. Here it is confirmed that gills are present only on segments II–V as Traver originally described (Traver, 1944).

Leptohyphodes appear more nearly related to *Tricorythodes* and *Haplohyphes* than to any other Leptohiphid genus. These three taxa share a similar body shape (long and slender, abdomen cylindrical), mouthparts (mainly form of labrum and labium), legs (form and setation), and gills (form and number of lamellae).

A closer relationship between *Leptohyphodes* and *Tricorythodes* is favored here, because gills of basal species of *Tricorythodes* (Molineri 2002) show striking similarities with those of *Leptohyphodes*. Both are easily derived from a common ancestor that excludes *Haplohyphes* for the higher number of lamellae present in the gills of that genus. Also, the absence of hind wings in both sexes of *Tricorythodes* and *Leptohyphodes* gives additional support to a sister group relationship between these taxa. Provided that the plesiomorphic state (hind wings present in both sexes) is shown by *Haplohyphes*.

Specific redescription of *Leptohyphodes inanis* (Pictet) (Figures 1–34)

Potamanthus? inanis Pictet, 1843; Walker, 1853; Eaton, 1871, 1887.

Leptohyphodes inanis Ulmer, 1920a, 1920b.

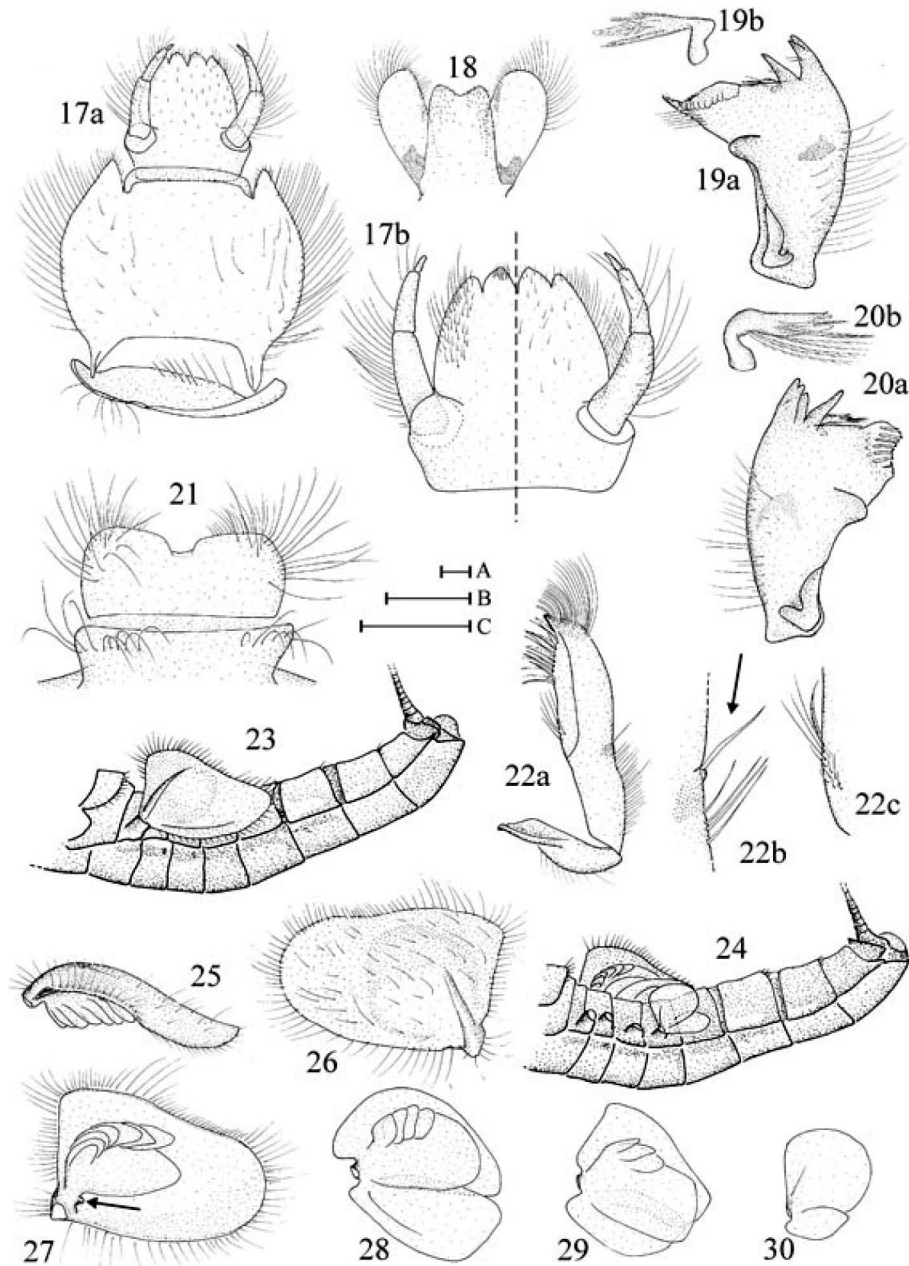
Leptohyphodes sp. Traver, 1944.

Male imago

Length: body, 5.6–7.6 mm; fore wings, 8.0 mm. General coloration: thorax chestnut, abdomen whitish.

Head. Pale chestnut shaded with gray, upper portion of compound eyes cream, lower portion blackish. Antennae whitish yellow.

Thorax. Pronotum chestnut shaded with gray, surrounded by a membranous whitish band. Mesonotum chestnut slightly shaded with gray, stronger between PSP. Metanotum pale chestnut. Membranous filaments of mesoscutellum yellowish translucent. Thoracic pleurae and sterna brownish yellow, except membranes whitish yellow. Legs. Coxae and trochanters brownish yellow, remaining segments of all legs whitish yellow, except fore tibiae and tarsi whitish. Wings. Membrane hyaline shaded



Figures 17–30. *Leptohyphodes inanis*. Nymph: (17a) labium, v.v.; (17b) detail of prementum, right ventral, left dorsal; (18) hypopharynx, v.v.; (19a) right mandible, d.v.; (19b) detail of prostheca; (20a) left mandible, d.v.; (20b) detail of prostheca; (21) labrum, d.v.; (22a) maxilla, v.v.; (22b) detail of maxillary palp (arrow); (22c) detail of basal setae on lacinia; (23) abdomen, l.v.; 24, idem but gills II–IV omitted; (25) gill II, lateroventral view; (26) gill II, d.v.; (27) gill II, v.v.; (28–30), gills III–V, v.v. Scale bars: A = 0.1 mm (Figures 17–22); B, C = 1 mm (Figures 23–30).

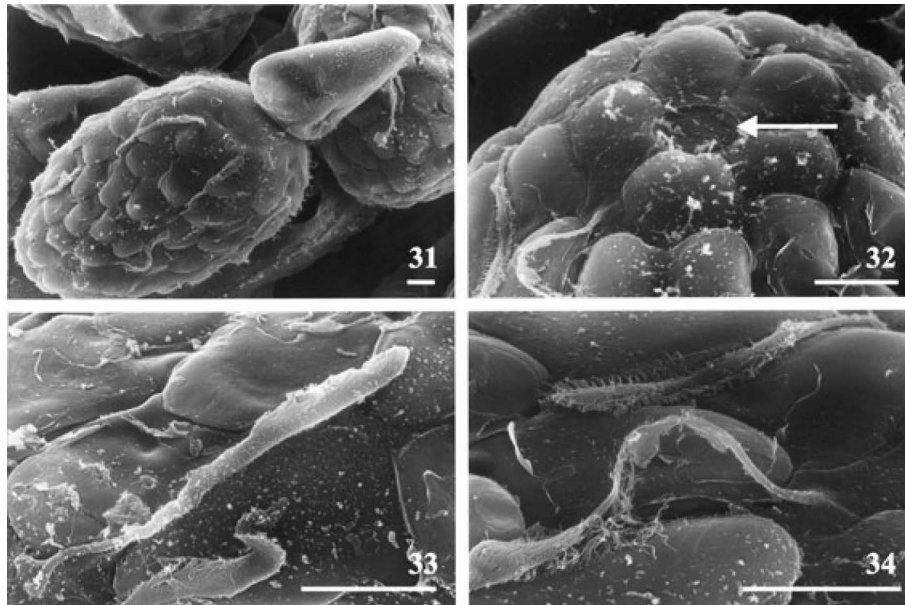
with gray on C and Sc areas, longitudinal veins brownish gray, cross veins whitish yellow.

Abdomen. Whitish translucent, intersegmental membranes hyaline; shaded with brownish gray on lateral zones of segments I–V and more extensively and strongly on segments VI–X. Sterna whitish slightly shaded with gray, lateral margins darker. Genitalia: styliiger plate yellowish white shaded with gray, hind margin brownish gray; forceps whitish, distal segment surrounded by a brownish line; penes

whitish with lateral margins brownish yellow. Caudal filaments whitish shaded with gray, and with some blackish joinings.

Female imago

Length: body, 5.5–6.2 mm; fore wing, 8.0–8.7 mm. Coloration as in male except head, pronotum and abdomen shaded with blackish gray; fore tibiae and tarsi whitish yellow.



Figures 31–34. *Leptohyphodes inanis*. Eggs, SEM photographs: (31) general view of egg; (32) micropylar area; (33–34) details of chorion and adhesive filaments. Scale bars = 10 μm .

Nymph

Length: body, 8.3–8.5 mm; mesonotum, 2.4 mm; hind femora, 1.5 mm; caudal filaments, 3.0–3.5 mm. General coloration brownish gray to grayish chestnut.

Head. Shaded with grayish between ocelli. Mouthparts yellowish shaded with gray. Antennae translucent yellowish.

Thorax. Pro- and mesonotum shaded with gray, thoracic sterna paler than dorsum. Developing wings with blackish veins and costal margin, turning paler toward apex. Legs whitish yellow without marks.

Abdomen. Yellowish gray except intersegmental membranes whitish, shaded widely with gray, stronger on longitudinal band. Gills translucent whitish shaded with gray at base. Sterna paler than dorsum. Caudal filaments yellowish.

Material

All the material is from Brazil, São Paulo, Campos do Jordão, Parque Estadual: 7 male and 1 female imagines from Ríó Sapucaí and Córrego Galharada, 7-8/I/1986, light, C.G.Froehlich (C.G.F.) and L.G.Oliveira (L.G.O.); 1 male imago, no river data, 14-16/XII/1987, C.G.F. & L.G.O.; 10 nymphs from Córrego Galharada, 21-22/X/1987, C.G.F. et al.; 11 nymphs, idem, 10/XI/1985, C.G.F. & L.G.O.; 1 nymph, idem, 1/XI/1986, C.G.F.; 3 female and 6 male imagines from Riberão Casquilho, 26/XI/1986, C.G.F.; 4 female and 2 male imagines, no river data, 22/XII/1986, C.G.F. All the material is housed in MZSP, except 3 male and 2 female imagines and 5 nymphs in IFML.

Discussion

The nymphs described by Traver as *Leptohyphodes* sp. are associated with the adults described by Pictet on the basis of shared color pattern and unique morphological features. The descriptions here presented were made upon material of both stages not associated by rearing but that undoubtedly pertain to the same species because they were collected at the same localities and dates and show the same color pattern and size. Furthermore, pharate subimagines of both sexes show adult coloration and structures inside nymphal cuticle. The new material was identified as *L. inanis* following Ulmer (1920a) and Traver (1944) descriptions and figures.

Specific description of *Tricorythodes ocellus* Allen & Roback (Figures 34–38)

Tricorythodes sp. Roback, 1966: 150.

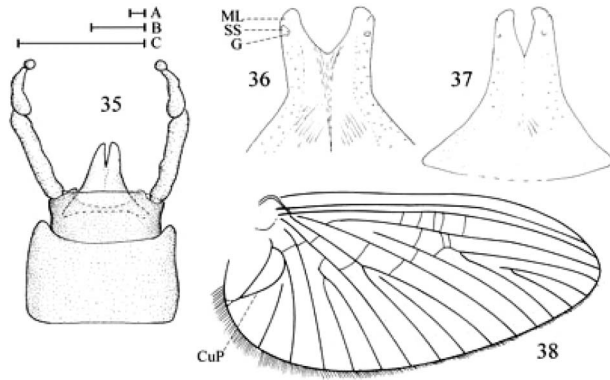
Tricorythodes (*Tricorythodes*) *ocellus* Allen & Roback, 1969: 378.

Tricorythyphes ocellus Wiersema & McCafferty, 2000: 353.

Male imago. Length: body, 2.9–3.1 mm; fore wings, 3.0–3.2 mm. General coloration chestnut, abdomen blackish.

Head. Blackish chestnut except around antennae and ventrally, paler. Antennae: scape and pedicel chestnut, flagellum hyaline.

Thorax. Pronotum laterally yellowish chestnut, blackish on median zone; propleurae hyaline, prosternum whitish, shaded with gray. Mesonotum chestnut with blackish margins, mesopleurae and



Figures 35–38. *Tricorythodes ocellus*. Male imago: (35) genitalia, v.v.; (36–37) details of penes, v.v.; (38) fore wing. Abbreviations: FS1=first forceps segment, FS2=second forceps segment, ML=membranous lobes, P=penes, S=styliiger plate, SS=sclerotized spines, G=gonopore. Scale bars: A=0.01 mm (Figures 36–37); B=0.1 mm (Figure 35); C=1 mm (Figure 38).

mesosternum yellowish chestnut; membranous filaments of mesoscutellum short, not extending beyond tip of this sclerite. Metanotum slightly lighter than mesonotum. Wings (Figure 38. membrane hyaline shaded with gray on costal margin; longitudinal veins grayish, cross veins whitish translucent. Legs yellowish, shaded with gray only on fore tibiae and fore tarsi.

Abdomen. Whitish yellow shaded completely with grayish black, except lateral zones of terga III–VII; shaded more markedly on segments VIII–X. Terga II–VII with a pair of submedian longitudinal darker lines, between them extends a lighter thin band. Genitalia (Figure 35. styliiger plate shaded with gray; forceps whitish translucent, first segment extremely elongated, basal swelling on second segment weakly developed; penes (Figures 36–37) yellowish white, with a deep apical cleft (sometimes widely open), each distal penean arm show a membranous medial lobe and a slightly marked sclerotized spine; the gonopore is sometimes visible below the sclerotized spines. Caudal filaments heavily shaded with blackish gray at base, turning whitish towards the apex.

Material

Holotype male mature nymph from Perú, near Tingo María, Río Tulumayo, 25 September 1955, S. S. Roback. Paratype nymph (body in alcohol, parts on slides) same data as holotype (FAMU). Other material: 5 male imagines from Perú, Huanuco Prov., Tingo María, Río Huallaga, December 1963, M. Rojas Col.; 7 male imagines, same locality except: 17–19 August 1963, W.L. Peters Col.; 2 male imagines, idem, except date, 2–5 August 1963; and 4 male imagines, idem, except date, 14–16

August 1963. All the material is deposited in FAMU except 4 male imagines in IFML.

Diagnosis. Male imagines of *T. ocellus* can be distinguished from the other species of *Tricorythodes* by the following combination of characters: (1) abdominal segments uniformly shaded with blackish gray, except on the zone covered by gills in the nymphal stage, abdominal segments VIII–X and base of caudal filaments shaded with black more markedly than the rest of the abdomen; (2) tibiae and tarsi without subapical blackish marks; (3) femora without marks; (4) ratio length of forceps segment 1/length of segment 2 = 1.5–1.7; (5) vein CuP present (Figure 38); (6) wide penes, with a median cleft (Figures 36–37).

Discussion

The male imagines here described as the adults of *T. ocellus* are tentatively associated with the nymphs described by Allen and Roback (1969). This association is based on the similarities shown in color markings, body size and development of lateral ocelli. Moreover adults and nymphs were collected in the same area.

Male genitalia and particularly the penes of this species seem to be plesiomorphic for *Tricorythodes*. The penes still show a distinctive median cleft, with a pair of membranous lobes and sclerotized spines, also present in the penes of *Leptoiphodes*, *Haploiphodes* and *Leptoiphodes*. The nymphal stage has been recently revised and its systematic position among the other species of the genus was postulated (Molineri, 2002). The new information available from male genitalia suggests a more basal position for this species.

Wiersema and McCafferty (2000) divided *Tricorythodes* in several genera: *Asioplax*, *Epiphrades*, *Homoleptoiphodes*, *Tricoryhodes* and *Tricorythodes*. Molineri (2002) proved that some of these taxa are highly supported monophyletic groups (*Asioplax* and *Epiphrades*) but others are not (*Tricoryhodes* and *Tricorythodes*). Molineri (2002) did not include *Homoleptoiphodes* in his analysis, but suggested continuing the use of the traditional definition of *Tricorythodes* until a better knowledge of the group could be achieved. In the present paper, generic placement of *Tricorythodes ocellus* follows the findings of Molineri (2002).

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