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Systematics of the *Terpides* lineage from the Neotropics: Definition of the *Terpides* lineage, methods, and revision of *Fittkaulus* Savage & Peters

(Insecta, Ephemeroptera, Leptophlebiidae)

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Abstract

The monophyletic *Terpides* lineage is established, defined, and distinguished from all other genera of Leptophlebiidae by characters in the imaginal and nymphal stages. This lineage presently includes *Terpides* Demoulin, *Fittkaulus* Savage & Peters, and an undescribed genus. The *Terpides* lineage stems from the base of the Atalophlebiinae very near the basal furcation within the Leptophlebiidae between the subfamilies Atalophlebiinae and Leptophlebiinae. Members of the *Terpides* lineage were isolated on the ancient Guiana and Brazilian Shields of South America during the late Cretaceous and early Tertiary and dispersed northward when the isolation of South America ended with the development of the lower Central American isthmus in Pliocene-Pleistocene times. The genus *Fittkaulus* is revised and two new species are described. *Fittkaulus* is currently known from the eastern Amazon Basin, from river basins draining north from the Eastern Guiana Highlands, and from the northern portion of the Rio Paraguay Basin in Brazil.

Introduction and definition of *Terpides* lineage

Terpides Demoulin, *Fittkaulus* Savage & Peters, and a new genus comprise a distinct monophyletic lineage, herein designated as the *Terpides* lineage. The *Terpides* lineage stems from the base of the Atalophlebiinae very near the basal furcation within the Leptophlebiidae between the subfamilies Atalophlebiinae and Leptophlebiinae. Members of the *Terpides* lineage appear to have been isolated on the ancient Guiana and Brazilian Shields of South America during the late Cretaceous and early Tertiary and dispersed northward when the isolation of South America ended with the development of the lower Central American isthmus in Pliocene-Pleistocene times. Currently, the *Terpides* lineage is widely distributed in the Neotropics from Bolivia north to southern Mexico including the Caribbean island of St. Vincent.

Members of the *Terpides* lineage are placed in the subfamily Atalophlebiinae because they share the following derived states with other Atalophlebiinae: 1) upper portions of ♂ imaginal eyes have square facets; 2) anteromedian emargination of labrum has denticles; 3) anterior margin of labrum lacks thickened, submedian, spine-like setae; and 4) dorsal anteromedian setae of labrum are in 2 rows.

The *Terpides* lineage is a very distinct lineage characterized by a number of very unusual, derived character states in the nymphal stage including: 1) inner apical margin of maxillae has 1 large, non-pectinate, apically curved seta; 2) glossae are curved over ventrolaterally; 3) submentum lacks large setae; 4) anterolateral margins of submentum are developed anteriorly; 5) nymphal claws have basal and sub-apical groups of denticles which are generally separated by a large median denticle (large median denticle absent in *Fittkaulus*); and 6) basal $\frac{2}{5}$ to $\frac{3}{5}$ of nymphal caudal filaments have clusters of long dense setae forming rows, terminal filament with a row of setae on each lateral margin, cerci with a row of se-

tae on inner lateral margin. Nymphs of the *Terpides* lineage also share the ancestral, but very distinctive and taxonomically useful, states of an hypognathous head and a lingua without lateral processes. Combination of the ancestral hypognathous head and the derived setal rows on the caudal filaments is unique among the Leptophlebiidae, and results in a nymph that resembles members of the Baetidae and Siphonuridae. Recent ecological observations by the author in eastern Peru, confirm that the nymphs of most, but not all taxa, within this lineage occupy a Baetidae-like habitat. Nymphs were observed to cling to solid substrates, especially trailing tree roots and vegetation in areas of slow to moderate current, and to employ the slightly flattened abdomen and setal rows on the caudal filaments for swimming in the fashion typical of Baetidae.

Imagines of the *Terpides* lineage share distinctive penes and a number of uncommon character states that serve to distinguish adults, including: 1) vein $1Cu_1$ of the fore wings is attached at base to vein CuA basal to forks of veins MP and Rs ; 2) styli-plate is short, maximum length along median line less than $\frac{2}{5}$ maximum width, and the posterolateral margins are developed; 3) segments 2 and 3 of genital forceps are short, segment 2 less than $\frac{1}{5}$ length of segment 1; and 4) basal $\frac{1}{5}$ or less of forceps segment 1 is expanded. Phenetically, imagines of the *Terpides* lineage often resemble other tropical genera with reduced body size due to shared states of size-associated (SAVAGE 1983) and reduction characters, and modified ♂ imaginal eyes.

Members of the *Terpides* lineage may be easily distinguished from all other genera of Leptophlebiidae by the following combination of characters. In imagines: 1) fore wing vein $1Cu_1$ is attached at base to vein CuA , with attachment basal to forks of veins Rs and MP (Figs. 1, 5, 8, 14); 2) claws of a pair are similar, with apical hook and opposing lobe (Fig. 23); 3) styli-plate is short, with posterolateral margins developed (Fig. 24); 4) segments 2 and 3 of genital forceps are short, with segment 2 less than $\frac{1}{5}$ length of segment 1; 5) basal $\frac{1}{5}$ or less of forceps segment 1 is expanded; 6) penes are short, fused basally, divided apically, and lack apical appendages, spines, setae or flaps (Fig. 24); and 7) sternum 9 of ♀ has a large posteromedian indentation (Figs. 22, 25–26). In nymphs: 1) head is hypognathous; 2) anteromedian emargination of labrum has 5–6 denticles (Figs. 37–38); 3) lingua lacks lateral processes (Fig. 39); 4) maxillae have an inner subapical row of 5–6 pectinate setae, and 1 large pectinate seta and 1 large non-pectinate, apically curved seta on inner apical margin as in Fig. 40; 5) glossae are curved over ventrolaterally (Fig. 41); 6) lateral margins of submentum lack setae; 7) segment 3 of labial palpi have setae as in Fig. 41; and 8) basal $\frac{2}{5}$ to $\frac{3}{5}$ of caudal filaments have clusters of long, dense setae forming rows, terminal filament with a row of setae on each lateral margin, cerci with a row on inner lateral margin (Fig. 49).

This is the first of a series on the systematics of the *Terpides* lineage. The series will include revisions of the genera *Terpides* and *Fittkaulus*, establishment of 1 new genus and 1 new subgenus, description of new species, the transfer of 3 species previously described in the genus *Choroterpes* Eaton to their respective Neotropical genera, keys to genera and species, and delineation of phylogenetic relationships within the lineage and between the *Terpides* lineage and other genera of Leptophlebiidae.

Methods: Specimen deposition and character terminology

Abbreviations for collections in which specimens are deposited are as follows: ANSP, Academy of Natural Sciences of Philadelphia; CAS, California Academy of Sciences; CU, Cornell University; FAMU, Florida A & M University; INPA, Instituto Nacional de Pesquisas da Amazônia; IRSB, Institut Royal des Sciences Naturelles de Belgique; UCVN, Universidad Central de Venezuela, Maracay; USNM, National Museum of Natural History, Washington; USP, Universidade de São Paulo; UU, University of Utah; and ZSBS, Zoologische Staatssammlung München.

Methods, characters, and terminology used in this study follow SAVAGE & PETERS (1982). Wing venational terminology and abbreviations follow SAVAGE (1983) and EDMUNDS & TRAVER (1954). Additional discussion of characters employed herein may be found in: PESCADOR & PETERS (1980); TOWNS & PETERS (1980); and TSUI & PETERS (1975). Therefore, I will discuss only new, seldom used, or problematic characters.

The upper portions of imaginal ♂ eyes in *Terpides* and related genera can be on short, wide stalks or on long, narrow stalks. From the dorsal view, the upper portions are circular in forms with long, narrow stalks, but shape varies from broadly ellipsoidal to circular in forms with short, wide stalks. Ellipsoidal upper portions may have the major axis of the ellipsoids nearly parallel, slightly divergent anteriorly or strongly divergent anteriorly.

The terminology for thoracic sutures including the posterolateral scutal suture follows TSUI & PETERS (1975), except that the term prescutoscutal suture is employed as defined by MATSUDA (1970: 117).

The maximum length of each fore leg segment in ♂ imagines from the femur apically is expressed as a ratio of maximum tibia length, and tibia length in millimeters is given in parentheses. Measurements were made on slide mounted material at 40× and 100×. This method of reporting ratios results in slightly greater values for fore leg tarsus 4 (and also for tarsi 1–3 of the mid and hind legs) than those obtained by measuring a free specimen on a dissecting microscope as the apical extension on tarsus 4 is usually overlooked at lower magnifications.

The size and shape of the small spines on the inner apical margin of the ♂ genital forceps are reported herein for the first time. Information on the function of these spines is not available, and data on character state distribution is limited. *Terpides* has short, wide, flat, round spines that can be easily observed at 200–400×, while *Fittkaulus* and a new genus have very small, rectangular, apically blunt to rounded spines that are definable only when using oil emersion (1 000×).

The arrangement of setae on the inner apical area of the maxillae in members of the *Terpides* lineage is unique and characterized by the following (Fig. 40): an inner subapical row of 5–6 pectinate setae; 1 large pectinate seta and 1 large non-pectinate, apically curved seta on the inner apical margin; and a recessed row of 7–9 setae near the inner, apical margin, with the apical seta larger and thick. This setation pattern is a combination of ancestral, e. g., the inner subapical row of 5–6 pectinate setae, and derived character states, e. g., the large non-pectinate, apically curved seta, and most genera of Leptophlebiidae differ in several respects. Except for members of the *Terpides* lineage, the presence of a large non-pectinate, apically curved seta is observed only in *Habroleptoides* Schoenemund and *Habrophlebia* Eaton of the Leptophlebiinae. These genera also have an inner subapical row of 5–6 pectinate setae and a large pectinate seta on the inner margin, and the setation pattern is similar to that of the *Terpides* lineage. However, these genera differ from the *Terpides* lineage in that the non-pectinate seta is directed anterolaterally and is less conspicuous, and the recessed row of setae is absent or differs in composition.

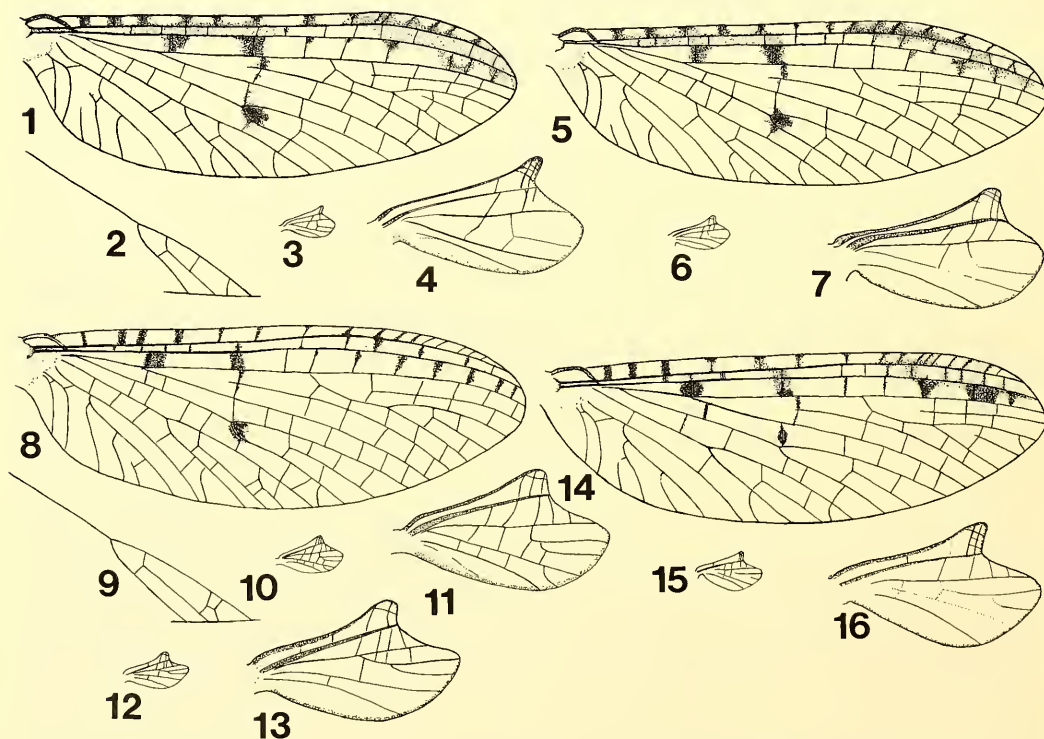
Fittkaulus Savage & Peters

Fittkaulus Savage & Peters, 1978, 8: 293.

Imago. Length of ♂: body, 4.8–6.0 mm; fore wings, 4.8–5.3 mm; fore legs, 4.9–5.4 mm. Length of ♀: body, 5.3–6.8 mm; fore wings, 5.3–6.8 mm. ♂ eyes (Figs. 17–20): upper portions on a long narrow stalk as in Figs. 18, 20; upper portions contiguous to separated by minute distance on meson of head; dorsally upper portions circular (Figs. 17, 19) with square, large-sized facets, 10–13 facets in longest row; from lateral view maximum length of lower portions 1.1–1.2 times maximum length of upper portions; lower portions large, bulbous, facets small, hexagonal, black. ♀ eyes (Fig. 21): separated on meson of head by a distance 1.7–3.4 times maximum width of an eye; margins of head and eyes posterolaterally extended as in Fig. 21; facets small, hexagonal, black. Ocelli with basal portion dark, apical portion light; lateral ocelli enlarged. Wing size (Figs. 1–16): maximum width of fore wings $\frac{1}{3}$ to a little less than $\frac{2}{5}$ length of fore wings; maximum length of hind wings $\frac{1}{10}$ to $\frac{1}{7}$ maximum length of fore wings; maximum width of hind wings a little less than to a little greater than $\frac{2}{5}$ maximum length of hind wings. Fore wings: vein Rs forked $\frac{1}{6}$ to $\frac{1}{5}$ distance from base of vein to margin; vein MA forked a little less than to a little greater than $\frac{1}{2}$ distance from base of vein to margin, fork nearly symmetrical to asymmetrical (Figs. 1, 5, 8, 14); vein MP forked asymmetrically (Fig. 1) to symmetrically (Figs. 8, 14) to vein MP₂ attached to MP₁ and CuA by crossveins (Fig. 5) $\frac{2}{5}$ to slightly greater than $\frac{1}{2}$ distance from base of vein to margin; ICu₁ attached at base to CuA; crossveins moderately numerous (Fig. 8) to reduced in number (Figs. 1, 5), stigmatic crossveins not anastomosed, marginal intercalaries reduced in number; with dark pigment as in Figs. 1, 5, 8, 14. Hind wings: costal projection developed to well developed as in Figs. 4, 7, 10–13, 16, apex located slightly less than $\frac{2}{3}$ to $\frac{4}{5}$ distance from base to apex of wings, apex shaped as in Figs. 4, 7, 10–13, 16, base of projection wide (Figs. 7, 11) to narrow (Fig. 4);

length of vein $Sc^{2/3}$ to a little greater than $4/5$ length of wings; apex of wings obtuse (Figs. 4, 7) to acute (Fig. 13), rounded to broadly rounded; crossveins as in Figs. 4, 7, 11–13, 16. Legs (Fig. 23): all long, length $2/3$ or greater than $2/3$ length of fore wings; ratios of segments in ♂ fore legs, 0.65: 1.00 (2.17–2.21 mm): 0.03–0.05: 0.29–0.31: 0.24: 0.11–0.13: 0.07; claws of a pair similar, with apical hook and opposing lobe (Fig. 23). Abdominal terga 8–9 with large acute posterolateral spines. Styli-ger plate (Fig. 24): maximum length approximately $1/3$ maximum width; maximum length along median line $1/4$ to $3/10$ maximum width; posteromedian margin gently rounded, posterolateral margins developed. Forceps (Fig. 24): forceps 2 segmented; segment 2 from $1/8$ to slightly greater than $1/7$ length of segment 1; segment 1 with bulbous base, apical $1/3$ slightly wider than medial $1/3$, inner margin with long, narrow, pointed spines basally and very small, rectangular, blunt to rounded spines apically; segment 2 shaped as in Fig. 24, with very small rectangular spines on inner margin. Penes (Fig. 24): short, $2/5$ to $1/2$ length of forceps segment 1; tubular, progressively narrower apically, basal $2/3$ fused, apical $1/3$ unfused but penis lobes contiguous, apex as in Fig. 24; without appendages. Sternum 7 of ♀ with very small, broad, flattened to gently rounded genital extension (Figs. 25–26). Sternum 9 of ♀ with large, deep posteromedian indentation and pointed submedian projections (Figs. 22, 25–26). Caudal filaments $1^{3/4}$ to 2 times length of body; cerci and terminal filament subequal in length.

Mature nymph. Head hypognathous. Antennae $2^{1/2}$ to $3^{1/2}$ times maximum length of head. Clypeus (Fig. 37): lateral margins straight, tapered apically as in Fig. 37; anteromedian margin relatively straight to slightly convex. Labrum (Figs. 37–38): maximum width of labrum subequal to width of distal portion of clypeus (Fig. 37); maximum length from $1/2$ to slightly greater than $3/5$ width; anterome-



Figs. 1–16. Fore wings, hind wings, and hind wings enlarged: 1–7, *Fittkaulus maculatus*, (1–4, ♂), with variation in vein MP (2), (5–7, ♀); 8–13, *Fittkaulus cuiabae*, ♀, with variation in vein MP (9) and hind wings (10–13); 14–16, *Fittkaulus curruensis*, ♀.

dian emargination developed to well developed (Fig. 37) with 6 very small, apically flattened denticles (Fig. 38); dorsum with apical setae as in Fig. 37, ventrum with setae submedially and laterally. Mandibles (Figs. 42–43): outer margin of left mandible relatively straight as in Fig. 42, outer margin of right mandible broadly curved; outer incisors with 4 teeth, inner incisor of left mandible with 3 teeth, inner incisor of right mandible with 2 teeth; outer incisor of right mandible broad with 3 apical teeth and 1 tooth on inner lateral margin, and median setae as in Fig. 43. Hypopharynx (Fig. 39): lingua lacks lateral processes, lingua widens distally as in Fig. 39 with broad, median indentation; superlinguae and lingua with apical setae as in Fig. 39. Maxillae (Fig. 40): galea-lacinia with an inner subapical row of 5–8 pectinate setae, inner apical margin with 1 large pectinate seta and 1 large non-pectinate apically curved seta as in Fig. 40, inner lateral margin with a row of long setae and a recessed row of 7–9 setae near apical margin, apical seta of recessed row larger, thick; segment 2 of palpi $\frac{7}{10}$ to $\frac{9}{10}$ length of segment 1; segment 3 of palpi from $\frac{7}{10}$ to a little less than length of segment 2; setae as in Fig. 40. Labium (Fig. 41): segment 2 of palpi a little greater than $\frac{1}{2}$ to $\frac{3}{4}$ length of segment 1; segment 3 of palpi from $\frac{3}{4}$ to a little greater than length of segment 2; segment 3 conical with spine-like setae on inner margin, dorsum with a diagonal row of large setae medially, ventrum with narrow hair-like setae on outer margin and subapically; segment 2 widens slightly to strongly apically with hair-like setae on outer margin and on inner apical margin; segment 1 shaped as in Fig. 41, with setae on inner and outer margins, setae on outer margin thicker; paraglossae and glossae with dense setae as in Fig. 41; glossae curved over ventrolaterally, large; paraglossae broadly rounded laterally (Fig. 41) to slightly tapered laterally; anterolateral corners of submentum developed anteriorly, median area of basal margin variable, gently rounded, concave to relatively straight, lateral margins of submentum without setae. Legs (Figs. 44–47): hind legs longer than fore and mid legs, fore femora shorter and slightly fatter (greater width/length ratio) than mid and hind femora, femora indented on apical $\frac{1}{5}$ – $\frac{2}{5}$ of inner margin so tibiae can draw partially into femora, maximum width of tibiae 1.4–1.8 times maximum width of tarsi, fore tibial and tarsal cross sections as in Figs. 46–47, inner and outer margins of femora and inner margins of tibiae and tarsi with thick setae, inner basal margin of fore femora with a row of setae as in Fig. 44, mid and hind tibiae without numerous thick setae on outer margin and medial area, outer margins with scattered long hair-like setae as in Fig. 44; claws weakly hooked and narrow apically, with a basal group of 5–6 short, fat denticles along inner margin, denticles slanted, directed anterolaterally, and a slightly recessed row of 4–5 narrow, pointed denticles subapically as in Fig. 45. Gills (Figs. 50–54): gills on segments 1–7, ventral portion of gills $\frac{3}{5}$ to $\frac{4}{5}$ length of dorsal portion, tracheae of gills 1 and 7 branched or unbranched, tracheae of gills 2–6 branched; gills on segments 2–6 similar, dorsal and ventral portions of gills 2–6 dissimilar; dorsal portion of gills 2–6 large, tapering basally, outer basal margin not developed anteriorly, apical margin with large inner lobe, very small outer lobe and a narrow median projection as in Fig. 51; ventral portion of gills 2–6 short, subelliptic with narrow apical projection as in Figs. 51–52; dorsal and ventral portions of gill 1 lanceolate, slender, gradually tapered apically except dorsal portion with narrow projection as in Fig. 50; dorsal and ventral portions of gill 7 similar, lanceolate, except dorsal portion wider and longer, ventral portion roughly $\frac{3}{4}$ length of dorsal portion, dorsal portion with outer median margin developed and abruptly tapering to median apex as in Fig. 53. From lateral view, posterolateral margins of terga and sterna 3–6 and 8–9 form spines, spines large and acute on 8–9, segment 7 without spines, segments 1–2 without to with small spines (Fig. 48). Basal $\frac{2}{5}$ to $\frac{3}{5}$ of caudal filaments with clusters of long dense setae forming rows, terminal filament with a row of setae on each lateral margin, cerci with a row of setae on inner lateral margin (Fig. 49).

Type- Species: *Fittkaulus maculatus* Savage & Peters, 1978.

Species included: *F. maculatus* Savage & Peters; *F. cuiabae* spec. nov. and *F. cururuensis* spec. nov.

Distribution (Fig. 55): Surinam; and the Brazilian states of Pará and Mato Grosso.

Discussion: *Fittkaulus* can be distinguished from all other genera of Leptophlebiidae by the following combination of characters. In imagines: 1) upper portions of ♂ eyes are on long, narrow stalks (Figs. 17–20), and each upper portion has 10–13 large, square facets in longest row; 2) vein ICu₁ of fore

wings is attached at base to vein CuA basal to forks of veins MA and MP, and the fore wings have dark pigment as in Figs. 1, 5, 8, 14; 3) hind wings are small, length less than $\frac{1}{7}$ length of fore wings, and the costal projection is developed to well developed as in Figs. 4, 7, 11–13, 16; 4) all legs are long, length $\frac{2}{3}$ or greater than $\frac{2}{3}$ length of fore wings; claws of a pair are similar, with apical hook and opposing lobe (Fig. 23); 5) styliar plate is short, maximum length approximately $\frac{1}{3}$ width; posterolateral margins are developed (Fig. 24); 6) forceps are 2 segmented, segment 2 is short and the base of segment 1 is bulbous but not broad (Fig. 24); 7) penes are short and tubular, basal $\frac{2}{3}$ fused, apical $\frac{1}{3}$ unfused but penis lobes contiguous, without projections or appendages (Fig. 24); and 8) sterna 7–9 of ♀ are as in Figs. 22, 25–26; sternum 9 has a large, deep, posteromedian indentation and pointed submedian projections. In nymphs: 1) head is hypognathous; 2) clypeus and labrum are shaped as in Figs. 37–38; anteromedian emargination of labrum is developed with 6 small flattened denticles; 3) lingua lacks lateral processes and widens distally with a broad median indentation on apical margin as in Fig. 39; 4) galea-lacinia of maxillae has an inner subapical row of 5–8 pectinate setae, and 1 large pectinate seta, and 1 large non-pectinate, apically curved, seta on inner apical margin as in Fig. 40; 5) labium is as in Fig. 41; palpal segment 3 is conical; glossae are curved over ventrolaterally; anterolateral corners of submentum are developed anteriorly; lateral margins of submentum lack setae; 6) fore legs are shaped as in Figs. 44–47, fore femora have a row of setae on inner basal margin; mid and hind tibiae lack numerous thick setae on outer margin and medial area; 7) claws are weakly hooked and narrow apically, with a basal group of 5–6 short, fat denticles along inner margin, denticles slanted, directed anterolaterally, and a slightly recessed row of 4–5 narrow, pointed denticles subapically as in Figs. 44–45; 8) ventral portion of gills is $\frac{3}{5}$ to $\frac{4}{5}$ length of dorsal portion; dorsal and ventral portions of gills 1 and 7 are similar in general shape, lanceolate; gills on segments 2–6 are similar, but dorsal and ventral portions are dissimilar; apical margin of dorsal portion of gills 2–6 has a large inner lobe, small outer lobe and a narrow median projection (Fig. 51), dorsal portion narrows basally; ventral portion of gills 2–6 is subelliptic and has a apicomedian projection (Figs. 51–52); 9) posterolateral margins of abdominal terga and sterna 3–6 and 8–9 form spines, spines are large and acute on 8–9, segment 7 distinctly lacks spines (Fig. 48); and 10) basal $\frac{2}{5}$ to $\frac{3}{5}$ of caudal filaments have clusters of long, dense setae forming rows, terminal filament with a row of setae on each lateral margin, cerci with a row of setae on inner lateral margin (Fig. 49).

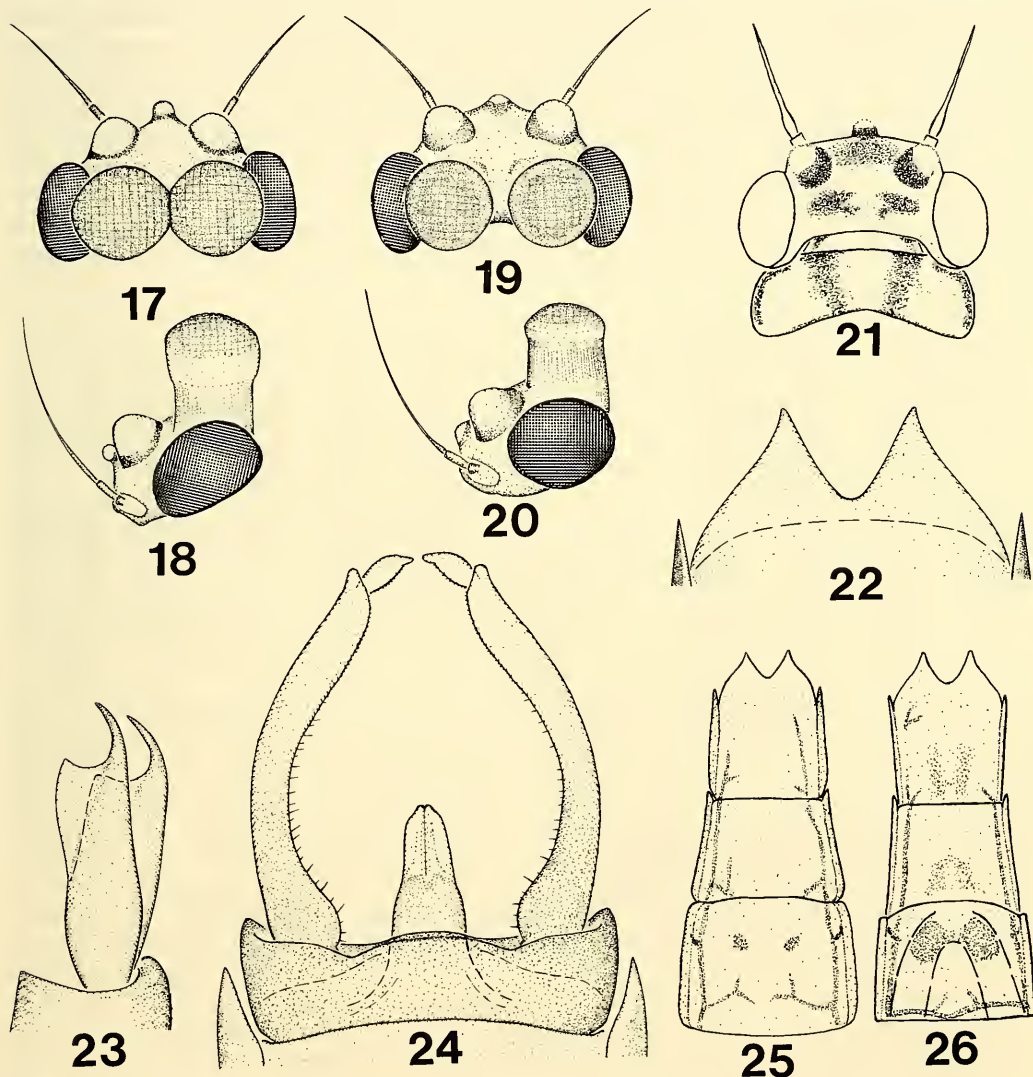
In addition to the three nominal species the following nymphs identified as *Fittkaulus* sp. (Fig. 55) were also examined: 1 immature nymph, Brazil: Pará State, Mapiyí Creek, nr. Rio Tapajóz, nr. Santarém, 8-XI-1940, H. Sioli; 1 nymph, Brazil: Pará State, Rio Cupari at mouth, a tributary of Rio Tapajóz, 29-VII-1946, H. Sioli; 3 nymphs, Brazil: Pará State, Varginha Creek, Mulato, 21-IX-1954, H. Sioli; 1 nymph, Surinam: Brokopondo Dist., Creek on N. edge of Brokopondo, 100 m, 27-XII-1968, W. L. & J. G. Peters.

Gill shape for mature nymphs of *Fittkaulus* is as described and figured (Figs. 50–54) except that the inner apical lobe on the dorsal portion of gills 2–6 may be more pointed than in Fig. 51, and the apical margin of the ventral portion may be slightly wider and flatter. In a specimen from Pará, Brazil, identified as *Fittkaulus* sp., the ventral portion of gills 2–6 have very small, lateral lobes apically as in Fig. 52. Immature nymphs may differ from the description for mature nymphs by the following: 1) the apical lobes on the dorsal portion of gills 2–6 may be small, especially on gill 6; 2) the ventral portion of gill 6 may be narrow such that the ventral portion appears lanceolate without a distinct apical projection; and 3) the dorsal portion of gill 1 may be lanceolate without a distinct apical projection.

Key to the known imagines of *Fittkaulus* Savage & Peters

- 1. Fore wings with a dark macula at fork of vein MA (Figs. 1, 5, 8); pleura of ♀ with brownish black median stripe extending entire length of thorax; abdominal sterna 1–2 lack small posteromedian brownish black marks 2

- Fore wings without a dark macula at fork of vein MA, dark marks as in Fig. 14; pleura of ♀ without a dark stripe entire length of thorax, propleuron and mesopleuron washed with brownish black near lateral margins of pronotum, episternites of mesopleuron and metapleuron brownish black; abdominal sterna 1–2 with small posteromedian brownish black marks *F. cururuensis* spec. nov.
- 2. Hind wings shaped as in Figs. 4, 7, apex of wings obtuse, broadly rounded, costal projection well developed with apex located $\frac{7}{10}$ or greater distance from base to apex of wings; vein MP of fore wings forked asymmetrically (Figs. 1, 5); ♂ genitalia as in Fig. 24 *F. maculatus* Savage & Peters
- Hind wings shaped as in Figs. 10–13, apex of wings acute, rounded, costal projection developed with apex located less than $\frac{7}{10}$ distance from base to apex of wings; vein MP of fore wings forked symmetrically (Figs. 8–9) *F. cuiabae* spec. nov.



Figs. 17–25. *Fittkaulus maculatus*, imagines except where noted (19–20): 17–18, ♂ head (17, dorsal; 18, lateral); 19–20, ♂ head, subimago, (19, dorsal; 20, lateral); 21, ♀ head and pronotum; 22, ♀, posterior portion of abdominal segment 9, ventral; 23, ♂ fore claw; 24, ♂ genitalia, ventral; 25, ♀ abdominal segments 7–9, ventral. Fig. 26. *Fittkaulus cuiabae*, ♀ imago, abdominal segments 7–9, ventral.

Fittkaulus maculatus Savage & Peters

Figs. 1–7, 17–25, 27–33, 37–51, 53–55

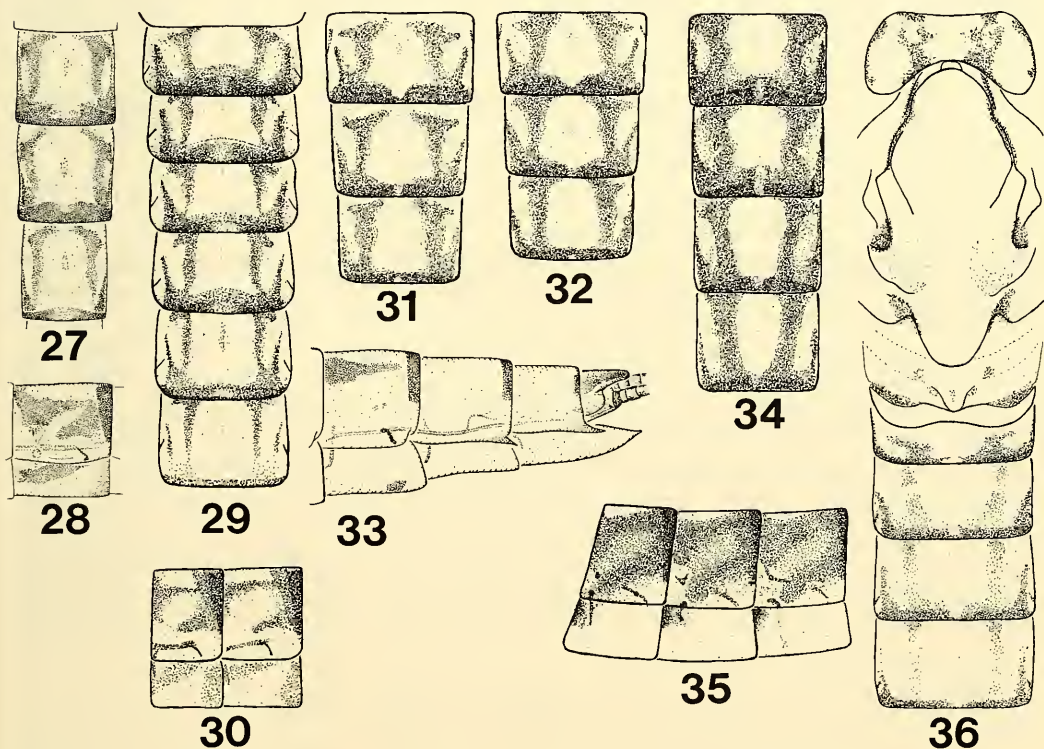
Fittkaulus maculatus Savage & Peters, 1978, 8: 294.

♂ Imago (in alcohol). Length: body, 4.8–6.0 mm; fore wings, 4.8–5.3 mm; fore legs, 4.9–5.4 mm. Eyes (Figs. 17–20): 12–13 facets in longest row, (subimagines with 10–13 facets in longest row), facets and grooves light yellow. Head whitish yellow ventrally to light brownish yellow dorsally, stalk of upper portions of eyes light brownish yellow streaked with brownish black. Scape and pedicel white to pale yellow, flagellum light brownish yellow. Cervix whitish yellow, washed heavily with brownish black dorsally. Thorax: pronotum brownish yellow, with anterosubmedian marks, marks narrow to absent posteriorly, margins washed with brownish black, wash light to absent on posterolateral margins; mesonotum light brownish yellow to light brown, lighter posteromedially, carinae brown, with heavy brownish black wash forming small marks on anterolateral margins, lateral subposterior margins just anterior to lateral subposterior humps lightly to heavily washed with brownish black, posteromedian portion and margins washed with brownish black; metanotum light brown, posterolateral scutal suture and median carinae of scutum washed with brownish black, median area of scutum with a long narrow black mark that widens anteriorly; prosternum brownish yellow to yellowish brown, carinae darker, meso- and metasternum whitish yellow to yellowish brown, carinae darker; pleural membrane whitish yellow, sclerites yellowish brown, median longitudinal area of pleura washed irregularly with brownish black. Wings (Figs. 1–4): vein MP in fore wings forked asymmetrically to vein MP₂ attached to MP₁ by a crossvein; hind wings with well developed costal projection as in Figs. 3–4, apex located $\frac{7}{10}$ or greater distance from base to apex of wings; apex of hind wings obtuse, broadly rounded (Figs. 3–4); costal brace brownish black; longitudinal veins of fore wings light brown to hyaline, veins C, Sc and R₁ darker, posterior veins lighter, crossveins of fore wings light brownish yellow to hyaline except when covered by darker pigment as in Fig. 1; longitudinal veins and crossveins of hind wings hyaline except vein Sc light brownish yellow; membrane of fore wings with blackish brown to brownish black clouds around crossveins as in Fig. 1, including a dark macula at fork of vein MA, light brown pigment surrounds veins Sc and R and covers the medial and apical portions of cell Sc and apical portion of cell R₁ as in Fig. 1, apical $\frac{1}{3}$ of cells C and Sc translucent, whitish, washed with brown; membrane of hind wings hyaline. Legs (Fig. 23): ratios of segments in fore legs, 0.65: 1.00 (2.17–2.21 mm): 0.03–0.05: 0.29–0.31: 0.24: 0.11–0.13: 0.07; fore femora brownish yellow, remainder of legs pale yellow, except tibia-tarsus articulations darker, mid coxae with small brownish black macula and hind coxae with 2 small brownish black maculae; claws as in Fig. 23. Abdomen (Figs. 27–30): terga pale yellow, semihyaline to light brownish yellow washed lightly with brownish black; terga 1–8 with posterior brownish black band, band with lighter posteromedian area and darker submedian areas, band widens medially on terga 2–6; terga 1–8 with posterosublateral brownish black marks, marks widen posteriorly fusing to posterior band on terga 1–6, marks faint posteriorly on tergum 7, marks light to absent on tergum 8; terga 2–7 with longitudinal submedian brownish black marks that widen anteriorly, posterior portion of marks faint on tergum 7 (Fig. 29); terga 2–7 with a small, narrow, median, light brownish black mark (Figs. 27, 29), mark faint to absent on tergum 2; tergum 10 with posteromedian brownish black mark and wash submedially and posterolaterally; spiracles black, tracheae smoky; sterna brownish yellow washed with brownish black; sterna 1–6 with wash forming posterior light brownish black band, sternum 7 with to without posterior band; sterna 2–6 with heavy wash forming lateral marks, marks widen anteriorly (Figs. 28, 30), marks progressively smaller on posterior segments, sterna 2–3 without to with anterolateral wash continuing along anterior margin of sterna, sterna 7–8 with to without lateral marks. Genitalia (Fig. 24): shaped as in Fig. 24; styliger plate yellowish brown; basal $\frac{1}{4}$ of forceps segment 1 brownish yellow, apical $\frac{3}{4}$ of segment 1 and segment 2 pale yellow; penes brownish yellow basally, pale yellow apically. Caudal filaments pale yellow.

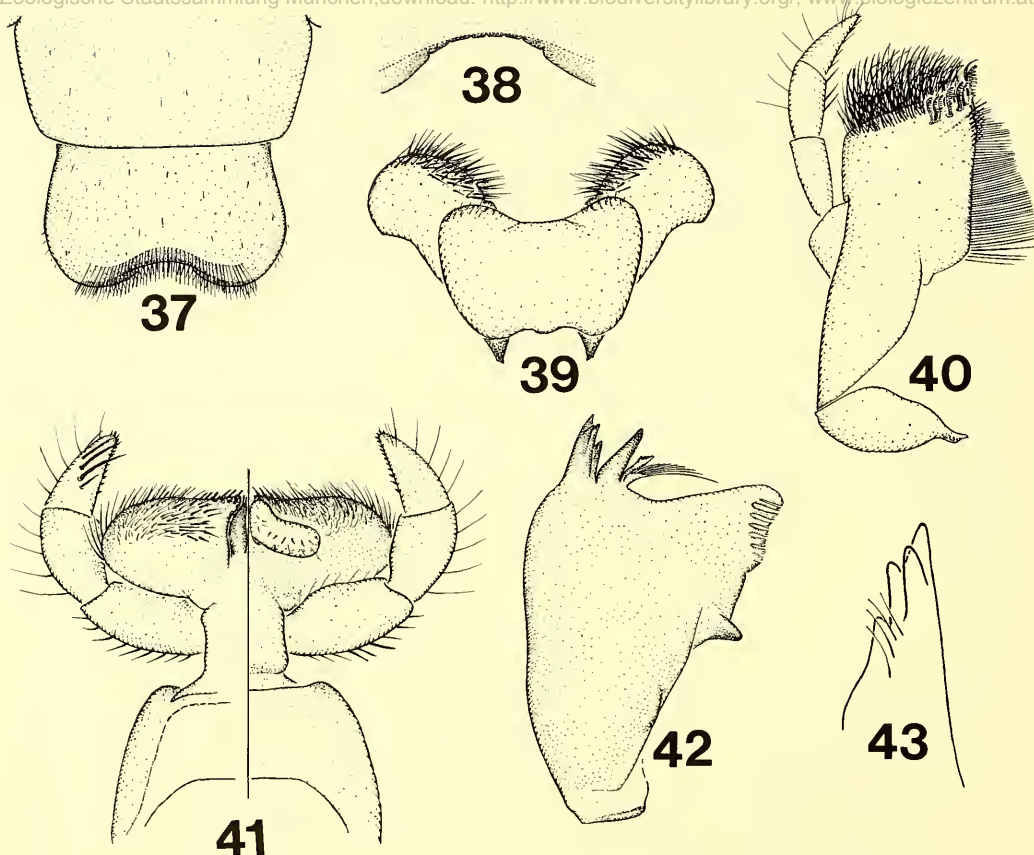
♀ Imago (in alcohol). Length: body, 5.5–6.8 mm; fore wings, 5.3–6.0 mm. Eyes (Fig. 21): separated on meson of head by a distance 1.7–2.8 times maximum width of an eye. Head: color as in ♂

except dorsum with submedian brownish black marks between compound eyes and heavy brownish black wash anteriorly between ocelli as in Fig. 21. Antennae as in ♂. Cervix whitish yellow, with brownish black wash laterally. Thorax (Fig. 21): color and marks similar to ♂, except pronotum with brownish black wash heavier and with distinct submedian longitudinal brownish black marks (Fig. 21), and pleura with median longitudinal brownish black wash forming a distinct stripe entire length of thorax. Wings (Figs. 5–7): veins and color similar to ♂ except vein MP_2 attached to MP_1 nearer to base and fork shaped as in Fig. 5. Legs: femora brownish yellow, tibia-tarsus articulations darker, remainder of legs pale yellow. Abdomen (Figs. 22, 25, 31–33): color and marks similar to ♂ except terga 6–7 with to without median marks; tergum 10 with submedian brownish black marks, and sterna 1–6 with to without brownish black wash forming posterior band; posterior portion of lateral oviducts washed with brownish black forming submedian circular marks on sternum 7 as in Fig. 25; genital extension as in Fig. 25; sternum 9 as in Figs. 22, 25. Caudal filaments as in ♂.

Mature nymph (in alcohol). Body length, 4.5–6.8 mm. Head brownish yellow to yellowish brown, lateral edges of genae darker. Antennae pale yellow. Mouthparts (Figs. 37–43): maximum length of labrum approximately $\frac{3}{5}$ maximum width, anteromedian emargination well developed (Fig. 37) with 6 very small, apically flattened denticles (Fig. 38); segment 2 of labial palpi a little greater than $\frac{1}{2}$ to $\frac{3}{4}$ length of segment 1, segment 3 of labial palpi a little greater than $\frac{3}{4}$ to a little greater than length of segment 2. Thorax: color and marks as in ♂ imago except median mark on metanotum often appears as distinct triangle. Legs (Figs. 44–47): brownish yellow, fore legs slightly darker; fore claws as



Figs. 27–36. Color patterns of *Fittkauulus*. 27–33, *F. maculatus*, abdomens, imagines except where noted (29–30): 27, ♂, terga 4–6; 28, ♂, segment 5, lateral; 29, ♂ subimago, terga 2–7; 30, ♂ subimago, segments 3–4, lateral; 31–32, ♀, terga 4–6, variation; 33, ♀, segments 7–10, lateral. 34–35, *F. cuiabae*, ♀ imaginal abdomen: 34, terga 4–7; 35, segments 3–5, lateral. 36, *F. cururuensis*, ♀ imago, thorax and terga 1–4.



Figs. 37–43. Mouthparts of mature nymphs. *Fittkaulus maculatus*: 37, clypeus and labrum; 38, enlargement of denticles on labrum; 39, hypopharynx; 40, right maxilla; 41, labium, dorsum (left) and venter (right); 42, left mandible; 43, enlargement of outer incisor of right mandible.

in Fig. 45. Abdomen (Figs. 48–49): terga and sterna brownish yellow washed lightly with brownish black; terga 1–6 with brownish black posterior bands as in ♂ imago except narrower, terga 7–8 with to without narrow posterior bands; terga 1–6 with small posterosublateral brownish black marks, light brownish black wash may connect posterosublateral marks and posterior band on terga 1–5; terga 2–6 with anteromedian, brownish black marks as in Fig. 49, marks lighter on tergum 6; terga 2–6 with light brownish black median mark as in Fig. 49; tergum 7 with heavier wash anteromedially and posteromedially; terga 8–9 with heavier wash sublaterally; tergum 10 with heavier wash posteriorly. Gills (Figs. 50–51, 53–54): membrane translucent, tracheae washed lightly to heavily with brownish black. Caudal filaments brownish yellow.

Type locality: Brazil, Pará State, Akahe Creek, near Tiriyo Mission, near Brazil-Surinam border.

Deposition of Type: holotype deposited in collections of INPA.

Specimens examined: holotype ♂ imago, Brazil: Pará State, Akahe Creek, near Tiriyo Mission, near Brazil-Surinam border, 15-III-1962, E. J. Fittkau; ♀ allotype, wing slide only, same data as holotype; 7 ♂ and 5 ♀ subimaginal paratypes, same data as holotype; 5 nymphal paratypes, same data as holotype.

In addition to the type material, the following specimens of *F. maculatus*, which are in poor condition, were examined: 1 ♀ subimago (reared) and exuviae, Brazil: Pará State, Rio Paru, nr. Tiriyo Mission, nr. Brazil-Surinam

border, 22-III-1962, E. J. Fittkau; 1 ♀ subimago, 1 ♀ imago, 1 ♂ subimago, Brazil: Pará State, Akahe Creek, nr. Tiriyo Mission, nr. Brazil-Surinam border, 15-III-1962, E. J. Fittkau; 2 immature nymphs, Brazil: Pará State, Iveraca I Creek, nr. Brazil-Surinam border, 17-18-IV-1962, E. J. Fittkau. The above additional specimens are deposited in ZSBS collections.

Discussion. Imagines of *F. maculatus* may be distinguished from all remaining species of *Fittkaulus* by the following combination of characters: 1) fore wings have dark pigment as in Figs. 1, 5, including a dark macula at fork of vein MA; 2) vein MP of fore wings is forked asymmetrically to vein MP₂ attached to MP₁ by a crossvein (Figs. 1, 5); 3) apex of hind wings is obtuse, broadly rounded; costal projection of hind wings is as in Figs. 4, 7; 4) pleura of ♀ has heavy brownish black wash forming distinct, median, longitudinal stripe entire length of thorax; 5) mesonotum has heavy brownish black wash forming marks on anterolateral margins, anterolateral sutures are dark brown but not heavily washed with brownish black; lateral subposterior margins just anterior to lateral subposterior humps are washed lightly to heavily with brownish black; 6) legs lack brownish black markings; 7) color pattern of abdominal terga is as in Figs. 27–33, terga 3–5 have small median dark marks; 8) abdominal sterna 1–2 lack small posteromedian brownish black marks; 9) ♂ genitalia is as in Fig. 24; and 10) sterna 7–9 of ♀ are as in Fig. 25.

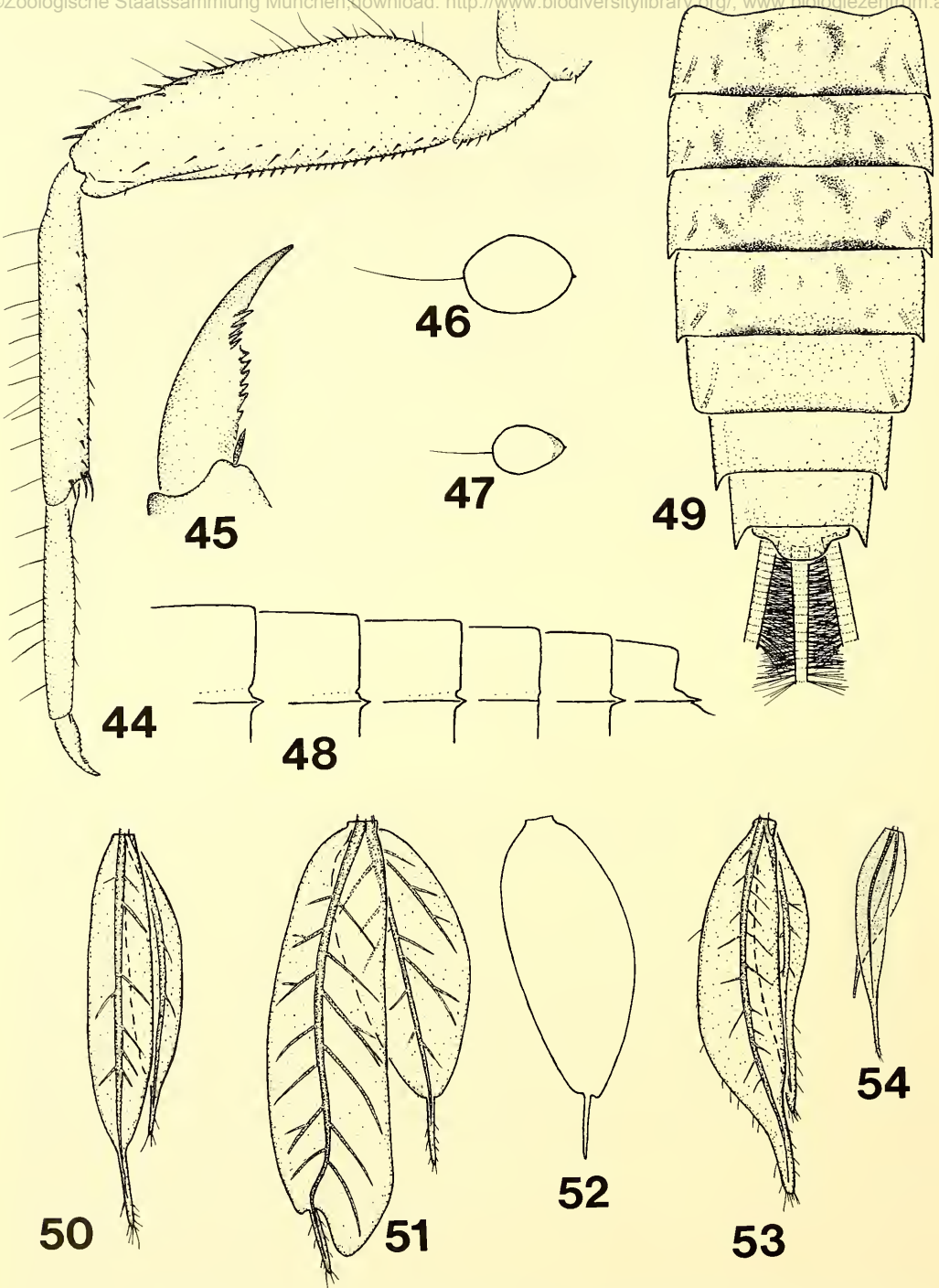
Mature nymphs of *F. maculatus* may be distinguished by the following characters: 1) anteromedian emargination of labrum is well developed (Fig. 37) with 6 very small, apically flattened denticles (Fig. 38); 2) fore claws are as in Fig. 45; 3) abdominal terga have brownish black markings as in Fig. 49; 4) gills are as in Figs. 50–51, 53; 5) metanotum has a median longitudinal mark that widens anteriorly, mark often appears as a distinct triangle; 6) legs lack brownish black markings (Fig. 44); and 7) labium is as in Fig. 41.

***Fittkaulus cuiabae* spec. nov.**

Figs. 8–13, 26, 34–35, 55

♂ Imago and mature nymph: Unknown.

♀ Imago (in alcohol). Length: body, 5.3–6.5 mm; fore wings, 5.6–6.8 mm. Eyes: separated on meson of head by a distance 2.4–3.4 times maximum width of an eye. Head whitish yellow ventrally to light brownish yellow dorsally, with submedian brownish black marks between compound eyes and with to without light brown to blackish brown wash anteriorly between ocelli. Scape and pedicel white to pale yellow, flagellum light brownish yellow. Cervix whitish yellow with brownish black wash laterally. Thorax: pronotum brownish yellow, margins heavily washed with brownish black except wash absent on posterolateral margins, heavy brownish black wash forming irregular submedian longitudinal marks; mesonotum light brownish yellow to brown, lighter posteromedially, with small brownish black marks on anterolateral margins, lateral subposterior margins just anterior and posterior to lateral subposterior humps washed with brownish black, posteromedian portion with very heavy brownish black wash, carinae dark brown; metanotum light brown, posterolateral scutal suture and median carinae and posteromedian margin of scutum with heavy brownish black wash; membrane of prosternum white, heavily washed with brownish black, sclerites of prosternum brownish yellow to yellowish brown, carinae darker, meso- and metasternum whitish yellow to yellowish brown, mesobasis sternum and median portion of mesofurcasternum lighter, posterolateral corners of metasternum with to without heavy brownish black wash forming narrow marks; pleural membrane whitish yellow, sclerites yellowish brown, pleura with heavy brownish black wash forming a distinct median longitudinal stripe entire length of thorax. Wings (Figs. 8–13): vein MP in fore wings forked symmetrically (Figs. 8–9); hind wings with costal projection as in Figs. 10–13, apex located less than to $\frac{7}{10}$ distance from base to apex of wings; apex of hind wings acute, rounded; costal brace light brownish yellow, portions heavily washed with brownish black; longitudinal veins of fore wings light brownish yellow to hyaline, veins C, Sc and R₁ darker, posterior veins lighter, crossveins of fore wings hyaline except when covered by



Figs. 44–54. Mature nymph of *Fittkaulus maculatus* except where noted (52, 54): 44, fore leg; 45, fore claw; 46, cross section of tibia; 47, cross section of tarsus; 48, abdominal segments 4–9, lateral; 49, terga 3–10; 50, gill 1; 51, gill 4; 52, ventral portion of gill 4, *Fittkaulus* sp. from Pará, Brazil; 53, gill 7; 54, gill 7 of immature nymph.

darker pigment as in Fig. 8; vein Sc and basal portion of C of hind wings light brownish yellow, remainder of longitudinal veins and crossveins of hind wings hyaline; membrane of fore wings hyaline with blackish brown to brownish black clouds around crossveins as in Fig. 8, including a dark macula at fork of vein MA, apical $\frac{1}{3}$ of cells of C and Sc translucent, whitish; membrane of hind wings hyaline except basal portion of cell C light yellow. Legs: [fore and mid legs broken off and missing]; coxae and hind legs light brownish yellow, mid coxae without to with small brownish black macula, hind coxae with 2 brownish black maculae, one large, dark and prominent, other small, light and obscure, hind femora with a brownish black mark on outer margin located approximately $\frac{3}{5}$ length from base to apex and subapical marks on inner and outer margins, and washed very lightly with brownish black at base. Abdomen (Figs. 26, 34–35): terga and sterna semihyaline to light brownish yellow washed with brownish black, wash with to without reddish cast; terga 1–9 with posterior brownish black band, band lighter on terga 8–9, band with posteromedian area lighter on terga 1–7, band slightly wider medially on terga 2–6; terga 1–8 with posterosublateral brownish black marks, marks large on terga 1–4 nearly reaching anterior margin, progressively smaller on posterior segments, marks widen posteriorly fusing to posterior band on terga 1–6 (Figs. 34–35), marks well developed to faint posteriorly on tergum 7, marks light to absent on tergum 8; tergum 1 with submedian brownish black wash, heavier wash forming anterior and posterior submedian marks; terga 2–7 with longitudinal submedian brownish black marks that widen anteriorly (Figs. 34–35); area between sublateral and submedian marks on terga 1–7 washed with brownish black, wash very light to heavy; terga 2–7 without to with a small, narrow, median, light brownish black mark; tergum 9 with heavy submedian brownish black wash; tergum 10 with prominent submedian marks; spiracles black, tracheae smoky; sternum 1 with median area washed with brownish black to with wash forming wide median transverse band; sterna 2–6 with heavy wash forming anterolateral marks (Fig. 35), sterna 2–3 without to with anterolateral wash continuing along anterior margin of sterna; sterna 8–9 with anterosubmedian brownish black wash as in Fig. 26; posterior portion of lateral oviducts washed with brownish black forming submedian marks on sternum 7 as in Fig. 26; genital extension and sternum 9 as in Fig. 26. Caudal filaments [broken off at base and missing].

Specimens examined: holotype ♀ imago, Brazil: Mato Grosso, bridge on Rio Aricá, on Cuiabá to Rondonópolis Rd., near km 391 marker, black light trap run 5: 45–6: 45 pm, 22-IV-1981, D. P. Wojcik; paratypes, 24 ♀ imagines, same data as holotype.

Holotype deposited in USP collections; 20 paratypes deposited in FAMU collections; and 4 paratypes deposited in ZSBS collections.

Etymology: Cuiabá, a city near the type-locality; noun in the genitive case.

Discussion. Imagines of *F. cuiabae* may be distinguished from all remaining species of *Fittkaulus* by the following combination of characters: 1) fore wings have dark pigment as in Fig. 8, including a dark macula at fork of vein MA; 2) vein MP of fore wings is forked symmetrically (Figs. 8–9); 3) apex of hind wings is acute, rounded; costal projection of hind wings is as in Figs. 10–13; 4) pleura of ♀ has heavy brownish black wash forming distinct, median, longitudinal stripe entire length of thorax; 5) mesonotum has heavy brownish black wash forming marks on anterolateral margins, anterolateral sutures are dark brown but not heavily washed with brownish black; lateral subposterior margins just anterior and posterior to lateral subposterior humps are washed with brownish black; 6) hind femora have a brownish black mark on outer margin located approximately $\frac{3}{5}$ length from base to apex, subapical marks on inner and outer margins, and very light brownish black wash at base [fore and mid legs missing]; 7) color pattern of abdominal terga is as in Figs. 34–35, terga without to with small median dark marks; 8) abdominal sterna 1–2 lack small posteromedian brownish black marks, sternum 1 is washed with brownish black medially; and 9) sterna 7–9 of ♀ are as in Fig. 26.

Fittkaulus cuiabae is very closely related to *F. maculatus*, but may be distinguished from *F. maculatus* by characters 2, 3, 5 (in part), 6, 7 (in part), 8 (in part) and 9 listed above. In addition, ♀ imagines of *F. cuiabae* differ from *F. maculatus* in the following coloration characters: 1) cell Sc and stigmatic area of fore wings lack brown pigment other than clouds; 2) hind coxae have 2 brownish black maculae, one

large and prominent and the other small and obscure; 3) the area between the ocelli is washed with light brown, or occasionally with light brownish black, rather than the heavy brownish black wash observed in *F. maculatus*; and 4) brownish black wash is usually apparent between the sublateral and submedian marks on terga 2–7 in *F. cuiabae* and absent in *F. maculatus*.

The abdomen of gravid ♀ is yellow to brownish yellow due to the presence of bright yellow eggs, while the abdomen of ♀ without eggs appears semihyaline to pale yellow.

The dark color pattern on the abdomen is relatively constant; however, differences result from variation in the intensity of the brownish black wash. The anteromedian portions of the submedian marks on terga 2–7 may bend medially resulting in a lightly pigmented anteromedian margin, or on rare occasions, the anteromedian portions may curve posteromedially to produce an anteromedian mark that narrows posteriorly and terminates near the center of the tergum. The terga of most specimens have brownish black wash between the sublateral and submedian marks and the terga appear as in Figs. 34–35; however, in a few dark specimens the distinction between the sublateral and submedian marks is obscured by heavy wash, and in very light specimens the terga may resemble those of *F. maculatus* (Figs. 31–32). The small, median marks of terga 2–7 are not apparent on most specimens (roughly 70%), but are easily seen on dark specimens. The wash on the submedian areas of sterna 8–9, and the lateral oviducts generally appears as in Fig. 26; but the wash on sterna 8–9 is often lighter while the wash on the oviducts is occasionally much darker.

Fittkaulus cururuensis spec. nov.

Figs. 14–16, 36, 55

♂ Imago and mature nymph: Unknown.

♀ Imago (in alcohol). Length: body, 5.8–6.1 mm; fore wings, 5.9 mm. Eyes: separated on meson of head by a distance 2.8–3.0 times maximum width of an eye. Head yellowish white ventrally to light

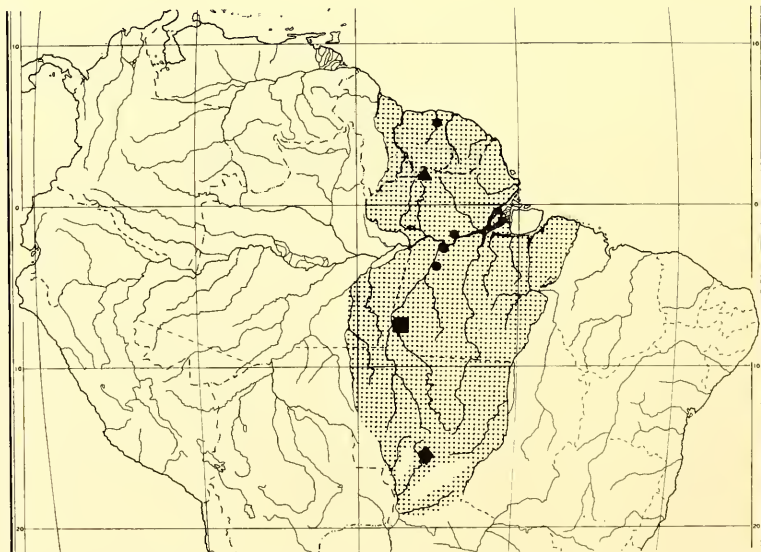


Fig. 55. Distribution of *Fittkaulus*. Conservative estimate of continuous distribution for genus is indicated by stippling. *F. maculatus*, triangle; *F. cuiabae*, diamond; *F. cururuensis*, square; nymphs identified as *Fittkaulus* sp., dots.

brownish yellow dorsally, with submedian brownish black wash between compound eyes. Scape and pedicel whitish; flagellum whitish to light brownish yellow, darker apically. Cervix yellowish white. Thorax (Fig. 36): pronotum whitish yellow, anterosubmedian, posterosubmedian and lateral margins with heavy brownish black wash, heavy brownish black wash forming irregular submedian longitudinal marks; mesonotum whitish yellow to light brown, lighter posteromedially, anterolateral margins and areas surrounding prescutoscutal sutures with heavy brownish black wash producing anterosublateral stripes slightly longer than $\frac{1}{3}$ length of mesonotum, lateral subposterior humps whitish yellow, washed with brownish black, lateral subposterior margins with very heavy brownish black wash forming 2 marks on each side, 1 just anterior and 1 just posterior to lateral subposterior humps, posteromedian margin without to with light brownish black wash; metanotum light brown, posterolateral scutal suture and median carinae of scutum washed with brownish black; sternum whitish yellow to brownish yellow; pleura light yellow to light brownish yellow, propleuron and mesopleuron washed with brownish black near lateral margins of pronotum, episternites of meso- and metapleura with heavy brownish black wash. Wings (Figs. 14–16): vein MP in fore wings forked symmetrically (Fig. 14); hind wings with well developed costal projection as in Figs. 15–16, apex located approximately $\frac{7}{10}$ distance from base to apex of wings; apex of hind wings acute, rounded as in Figs. 15–16; costal brace light yellow, portions with heavy brownish black wash; longitudinal veins of fore wings light brownish yellow to hyaline, veins Sc and R₁ darker, posterior veins lighter, basal and apical portions of veins Sc and R₁ with to without light brown to brownish black wash, vein Rs-R₂ washed with brownish black near fork Rs, crossveins hyaline with light brown to brownish black wash as in Fig. 14, except stigmatic crossveins hyaline to brownish yellow with darker wash; membrane of fore wings hyaline with light brown to brownish black clouds around crossveins as in Fig. 14, clouds surrounding crossveins in cell Sc, in posterior portion of cell C, and along anterior margin of cell R₁ lighter than remaining clouds, apical $\frac{1}{3}$ of cells C and Sc translucent, whitish to brownish white; membrane and all veins of hind wings hyaline. Legs: coxae light yellow, washed with brownish black apically, mid coxae with 1 large brownish black macula, hind coxae with 2 large brownish black maculae; fore femora and apical portion of mid and hind femora yellowish brown, femora with brownish black wash forming subapical marks on inner and outer margins and with light brownish black wash near base, remainder of legs light yellow. Abdomen (Fig. 36): terga and sterna semihyaline to light brownish yellow; terga 1–9 with posterior brownish black band, band with posteromedian area lighter, band narrower on terga 7–9; terga 1–7 with posterosublateral brownish black marks, marks well developed on terga 1–4, small on tergum 5, light and small on 6–7, marks widen posteriorly fusing to posterior band on terga 1–5; tergum 1 with brownish black posterosubmedian marks, terga 2–6 with brownish black wash forming light longitudinal submedian marks (Fig. 36), tergum 7 with to without light brownish black wash submedially; spiracles black, tracheae semihyaline, portions smoky; sterna 1–2 with a small light brownish black posteromedian mark, sterna 2–5 with anterolateral brownish black marks, marks large on sternum 2; posterior portion of lateral oviducts with light brownish black wash forming submedian marks on sternum 7; genital extension and sternum 9 similar to Figs. 25–26. Caudal filaments [broken off at base and missing].

Specimens examined: Holotype ♀ imago, Brazil: Pará State, Rio Cururu at Cururu Mission, at light, 6-II-1961, E. J. Fittkau; paratype, one ♀ imago, same data as holotype.

Holotype is deposited in USP collections; one paratype is deposited in UU collections.

Etymology: Rio Cururu, type-locality; adj.

Discussion. Imagines of *F. cururuensis* may be distinguished from all remaining species of *Fittkauulus* by the following combination of characters: 1) fore wings have dark pigment as in Fig. 14, fork of vein MA lacks a dark macula; 2) vein MP of fore wings is forked symmetrically (Fig. 14); 3) apex of hind wings is acute, rounded; costal projection of hind wings is as in Figs. 15–16; 4) pleura of ♀ lack a submedian brownish black stripe entire length of thorax; propleuron and mesopleuron are washed with brownish black near lateral margins of pronotum, and episternites of mesopleuron and metapleuron are very heavily washed with brownish black; 5) anterolateral margins and areas surrounding pre-

scutoscotal sutures are heavily washed with brownish black producing anterosublateral stripes slightly longer than $\frac{1}{3}$ length of mesonotum; lateral subposterior margins have very heavy brownish black wash forming 2 marks on each side, 1 just anterior and 1 just posterior to lateral subposterior humps (Fig. 36); 6) femora have subapical brownish black marks on inner and outer margins and light brownish black wash near base; 7) color pattern of abdominal terga is as in Fig. 36, terga without small median dark marks; and 8) abdominal sterna 1–2 have small posteromedian brownish black marks.

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Zusammenfassung

Die monophyletische *Terpides*-Gruppe wird aufgestellt, definiert und von allen anderen Gattungen der Leptophlebiidae durch Merkmale an den Imaginal- und Nymphenstadien unterschieden. Die Gruppe umfaßt gegenwärtig *Terpides* Demoulin, *Fittkaulus* Savage & Peters und eine noch unbeschriebene Gattung. Die *Terpides*-Gruppe entspringt von der Basis der Atalophlebiinae ganz nahe der basalen Gabelung innerhalb der Leptophlebiidae zwischen den Unterfamilien Atalophlebiinae und Leptophlebiinae. Angehörige der *Terpides*-Gruppe wurden auf den sehr alten Schilden Guyanas und Brasiliens während des Tertiärs isoliert und breiteten sich nach Norden aus, als die Isolierung von Südamerika mit der Entwicklung der niedrigeren zentralamerikanischen Landenge im Pliozän-Pleistozän endete. – Eine Revision der noch schlecht bekannten Gattung *Fittkaulus* wird vorgelegt. *Fittkaulus* ist gegenwärtig bekannt aus dem östlichen Amazonasbecken, von Flußbecken, die von den östlichen Hochländern Guyanas nach Norden entwässern, und vom nördlichen Teil des Rio Paraguay Beckens in Brasilien.

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