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SYSTEMATICS OF MIROCULIS AND RELATED GENERA  
FROM NORTHERN SOUTH AMERICA  
(EPHEMEROPTERA: LEPTOPHLEBIIDAE)

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published data), it is obvious that *Hermanella thelma* Needham and Murphy and *Hermanellopsis incertans* (Spieth) are neither congeneric nor closely related (Edmunds, Jensen and Berner 1976).

Within collections available to the authors are numerous representatives of *Miroculis*, *Hermanellopsis* and other closely related taxa. A systematic revision of these taxa is provided herein.

#### METHODS AND TYPE DEPOSITION

External cuticular structures to be studied with SEM were found to be maintained if soaked in 100 per cent amyl acetate for roughly 30 minutes, and then air dried prior to coating.

Measurement values represent the total range of variation observed for all specimens available unless the number of specimens (n) measured is provided in parentheses immediately following the range values. The number of specimens measured may also be provided in parentheses when it is necessary to call attention to the limited sample size available for particular measurements that appear to be of diagnostic value.

Values used to represent groups of specimens in Figs. 169-174 are midpoints of the observed range of variation for each character. Males and females of *Miroculis* were treated as separate groups because members of the 3 derived subgenera of *Miroculis*, *M. (Atroari)*, *M. (Yaruma)*, and *M. (Miroculis)*, display sexual differences in wing shape (Figs. 169-171). Values for males of *Miroculis (Ommaethus) mourei* were excluded from calculations and graphs that include body length as available specimens were damaged and body length measurements were unreliable. The reduced major axis regression equation (Teissier 1948; Kermack and Haldane 1950; Ricker 1973), the correlation coefficient  $r$ , probability level  $P$ , and sample size  $n$ , are provided in figure legends for each line plotted.

Correlation and regression analyses were employed to evaluate the effect of size, and relationships between states of continuous characters. Least squares and reduced major axis regression lines were calculated for the original and log transformed data. The two methods produced similar results for both the original and log transformed data. Reduced major axis is preferred because both variables have biological variability, thus, the terms dependent and independent variable of least squares regression have no real meaning (Kermack and Haldane 1950). While statistically it is preferable to use log transformed data (Kermack and Haldane 1950; Hills 1978), we have used the original data in graphs as it is easier for the reader to interpret, and because the log transformed and original data produce very similar results in these cases.

The use of ratios has been subject to much criticism (Pearson 1897; Kendall and Stuart 1969; Sokal and Rohlf 1969; Blackith and Reyment 1971; Atchley and Anderson 1978; Atchley 1978; Albrecht 1978), but this criticism has generally been ignored

tional system and abbreviations proposed by Edmunds and Traver (1954) are used: costa (C), subcosta (Sc), radius (R), radial sector (Rs), medius anterior (MA), intercalary medius anterior (IMA), medius posterior (MP), intercalary medius posterior (IMP), cubitus anterior (CuA), intercalary cubitus (ICu), cubitus posterior (CuP), and anal (A).

In the past, use of venational characters has been limited to veins of the fore wings and the C and Sc of the hind wings. All veins of the fore and hind wings of schematic *Miroculis* wings are labeled in Figs. 4-6. Homologues are based upon the corrugation pattern of convex and concave veins (Edmunds and Traver 1954; Kukulova-Peck 1978) and on comparative study of hind wings in the families Heptageniidae, Ephemeridae, Siphonuridae and primitive Leptophlebiidae such as *Leptophlebia* and *Paraleptophlebia*. The most important feature of hind wing venation in derived genera of Leptophlebiidae is the more medial fusion of vein MA to R<sub>1</sub>, instead of the basal fusion observed in primitive genera and other families. All species of *Miroculis* have veins CuA and CuP of the hind wings fused 1/6 to 1/3 distance from base to margin of vein CuA, while veins CuA and CuP fuse basally to slightly greater than 1/6 distance from base to margin in *Miroculitus* and *Hermanellopsis incertans*. *Hermanellopsis arsia* retains unfused cubitals, while all species of *Microphlebia* lack vein CuP (Savage, in press) in the hind wings.

**WING SHAPE.** The ratio of maximum width to maximum length of fore wings, ratio of maximum width to maximum length of hind wings, ratio of maximum length of hind wings to maximum length of fore wings, and development of the cubital area in fore wings combined with the standard wing shape characters provides a detailed description of the wings for each taxon. Certain wing shape characters are size correlated and while usually reliable as subgeneric and generic criteria, they must be used with caution in phylogenetic reconstruction (Savage, in press).

**MALE PROTHORACIC LEG RATIOS.** The length of each prothoracic leg segment from the femur apically is expressed as a ratio of tibia length. Tibia length in millimeters is given in parentheses.

**STYLIGER PLATE (Figs. 55-80).** Both maximum length along the median line and length along the lateral margin are expressed as ratios over maximum width. The increased number of measurements are necessary to represent the highly evolved states found within *Miroculis* and related genera.

#### *Mature Nymphs*

**CLYPEUS (Figs. 137-138, 142, 148).** Shape of the lateral and anterior margins are generally used as generic characters. However, shape of the lateral margins can separate groups of related genera such as the *Penaphlebia* and *Miroculis* lineages (Fig. 1, Table 2).

**LABRUM (Figs. 137-142, 148).** Ratio of maximum width of labrum to width of distal portion of clypeus, shape of lateral and anterolateral margins, and setation patterns are furnished.

Shape of the nymphal labrum has long been used as a generic character, however,

labral shape and setation patterns may also be used to separate lineages. The ancestral leptophlebiid labrum as observed in the Leptophlebiinae (lineage 1a, Fig. 1), the *Hapsiphlebia* lineage (2a, Fig. 1) and most Ephemeroptera other than members of the Heptageniidae and Oligoneuriidae is characterized by the following: 1) lateral margins are nearly parallel (rectangular shape); 2) maximum width is less than distal width of clypeus (small size); and 3) apical setae are well developed while short, stiff, basal setae are absent. Other lineages of Leptophlebiidae, such as members of the *Miroculis* and *Atalonella* lineages (lineage 3b, Fig. 1), have variable labra, but never as above. Usually the derived condition is a labrum (Figs. 137-138, 142, 148) in which: 1) lateral margins are distally expanded; 2) maximum width is at least equal and usually greater than distal width of clypeus; and 3) basal 2/3 of lateral margins have short, stiff setae with thin, hair-like setae apically. Members of the *Penaphlebia* lineage (3a, Fig. 1) lack stiff basal setae, but the labrum broadens apically in *Penaphlebia*.

SUBAPICAL ROW OF SETAE ON MAXILLAE (Figs. 146, 152, 160-161). Ratio of length of subapical row to length of apical row of setae on the galea-lacinia and number of pectinate spine-like setae in the subapical row are provided.

Survey of specimens available in collections of Florida A&M University indicate the ancestral state, as observed in the Siphonuridae and in members of the Leptophlebiinae (lineage 1a, Fig. 1) is a subapical row of 4-8 setae. Most other genera of Leptophlebiidae have 9-28 setae with the vast majority having 12-25 setae and a subapical/apical row length ratio of roughly 0.5. *Thraulius hsui*, some members of the *Atalophlebioides* lineage and an undescribed genus from New Zealand (D.R. Towns, pers. comm.) have as many as 35 subapical setae, while *Miroculis* has 31-55 setae. The subapical row is most developed in *Petersophlebia inequalis* from Madagascar which has 75-90 subapical setae and a subapical/apical row ratio of roughly 0.7.

### Genus **MIROCOLIS** Edmunds, 1963

Figs. 7-24, 44-70, 81-84, 87-88, 90-92, 96-109, 112-119, 121-132, 137-147, 156-165, 168

*Miroculis* Edmunds, 1963:34

IMAGO. Length of male: body, 3.8-7.8 mm; fore wings, 4.1-6.2 mm; prothoracic legs, 4.0-5.7 mm. Length of female: body, 3.7-5.6 mm; fore wings, 4.1-5.8 mm. Eyes (Figs. 44-54): eyes of male variable, separated on meson of head by a length 1/10 to 1-1/2 width of an upper portion; dorsally upper portion of male eyes circular (Figs. 46, 48), or shaped as in Figs. 50, 52, 54, with large to medium-sized facets, 5-40 facets in longest row, upper portion set on dorsum of head by a long narrow stalk (Figs. 44-46) to short, wide stalk (Figs. 47-48), to stalk absent (Figs. 49-54); width of lower portion of male eyes a little less than to a little greater than height of stalk in stalked-eyed species, or lower portion touching (Figs. 49, 51) to separated by small distance from upper portion (Fig. 53) in species with stalk absent; eyes of female separated on meson of head by a length 3 to 3-1/3 times maximum width of an eye, posterolateral margins

TABLE 1. Diagnostic specific characters for known nymphs of *Miroculis*.

Species	Antero-lateral margins of labrum	Maxilla: setae in subapical row	Gills size & shape	membrane color	Abdomen: dorsum tergum 6 with brownish-black	color pattern segments 2-8	Posterolateral spines developed beyond posterior margin of terga	Caudal filaments
<i>M. (Miroculis) maraliae</i>	slightly flattened	31-39	small, narrow Figs. 121-123	grayish, translucent	submedian marks Figs. 99-101	2-3 dark, 4-5 light, 6-8 dark	3-9	brownish-yellow, articulations darker
<i>M. (Miroculis) fitikau</i>	flattened	44-49	small Figs. 124-125 large	grayish, translucent	median V-shaped mark Fig. 97	2-3 dark, 4-5 light, 6 dark, 7-8 lighter	3-9	light brown, basal 5-9 segments with black bands
<i>M. (Miroculis) brasiliaensis</i>	flattened	35-40	Fig. 126 small	grayish, translucent	median V-shaped mark Fig. 112	2-3 dark, 4-5 light, 6 dark, 7-8 lighter	3-9	articulations brownish-yellow, darker
<i>M. (Atroari) duckensis</i>	flattened	30-33	Fig. 127 large	grayish, translucent	submedian marks Figs. 114-115	2 dark, 3 slightly lighter, 4-8 dark	3-4 to 9	articulations brownish-yellow, darker
<i>M. (Atroari) amazonicus</i>	flattened	40-50	Figs. 128-129	grayish, translucent	submedian marks Fig. 116	2 dark, 3-4 slightly lighter, 5-8 dark	3-5 to 9	articulations of basal segments black
<i>M. (Atroari) colombiensis</i>	flattened	32-37	large Fig. 130	brownish-yellow, translucent	circular submedian marks Fig. 117	2-3 dark 4-8 lighter, progressively darker posteriorly	3-6 to 9	brownish-yellow, articulations darker
<i>M. (Ommaethus) mourei</i>	gently rounded to slightly flattened	44-55	small Fig. 131	grayish, translucent, inner half washed with black	submedian longitudinal bars Fig. 119	2-8 equally dark	5-6 to 9	brownish-yellow, basal 1/5 to 1/3 of segments with black bands

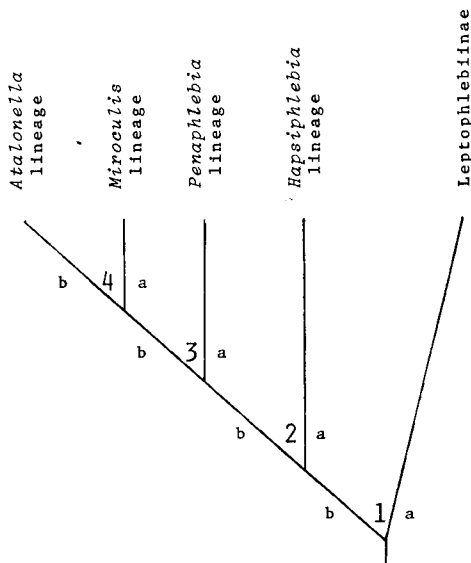


FIGURE 1. Probable phylogenetic relationships among the Leptophlebiinae, and the *Hapsiphlebia*, *Penaphlebia*, *Miroculis* and *Atalonella* lineages of the Atalophlebiinae. Character state distribution is provided in Table 2.

TABLE 2. Character states for lineages of Figure 1. D, derived or apomorphic; A, ancestral or plesiomorphic.

#### FURCATION 1

- | lineage a   | lineage b  |
|---|--|
| 1. (A) posterior margin of styliger plate with very deep, median, ventral cleft           | (D) posterior margin of styliger plate without deep median cleft (Figs. 55, 57, 63, 71, 75, 77), but may have small U or V-shaped indentation (Figs. 58, 65) |
| 2. (A) anteromedian emargination of labrum smooth, without denticles or deep median cleft | (D) anteromedian emargination of labrum with prominent denticles (Figs. 137-143, 148-149) or with deep median cleft  |

- |   |  |
|---|--|
| 3. (A) anterior margin of labrum with thickened submedian setae   | (D) anterior margin of labrum without setae or with hair-like setae (Figs. 137-143, 148-149)   |
| 4. (A) dorsal anteromedian setae of labrum scattered or in one row  | (D) dorsal anteromedian setae of labrum in 2 rows (Figs. 137-142, 148)   |
| 5. (A) outer margin of mandibles relatively straight  | (D) outer margin of mandibles curved to angular (Figs. 147, 153)   |
| 6. (A) lingua of hypopharynx without lateral processes  | (D) lingua of hypopharynx with well developed lateral processes (Figs. 144, 150)   |
| 7. (D) ventral surface of lingua of hypopharynx with submedian and subapical patches of hair-like setae (except <i>Paraleptophlebia</i> ) | (A) ventral surface of lingua of hypopharynx without submedian and subapical patches of hair (hair patterns, if present, occur on apical margin or dorsum) |

## FURCATION 2

**lineage a**

1. (A) lateral margins of labrum are straight and parallel
2. (A) labrum narrower than clypeus
3. (D) outer incisor of right mandible with denticles
4. (A) base of prosthecal tuft blunt or broadly rounded
5. (A) segment 2 of maxillary palpi apically broadened
6. (A) segment 3 of labial palpi triangular and with large spine-like setae on inner margin
7. (D) abdominal terga with prominent setae on lateral margins

**lineage b**

- (D) lateral margins of labrum diverge apically, rounded to angular (Figs. 137-142, 148)
- (D) width of labrum equal to or greater than width of clypeus (Figs. 137-138, 142, 148)
- (A) outer incisor of right mandible smooth or spinose (Figs. 147, 153)
- (D) base of prosthecal tuft elongate
- (D) segment 2 of maxillary palpi slender (Figs. 146, 152)
- (D) segment 3 of labial palpi elongate with stout denticle-like, blade-like or hair-like setae on inner margin (Figs. 145, 151)
- (A) abdominal terga without prominent setae on lateral margins, either bare or with minute setae (Figs. 119-120)

## FURCATION 3

**lineage a**

1. (A) setae on anal and apical margins of subimaginal wings are short
2. (A) fore wings with more than 25 costal cross veins
3. (A) vein Sc of hind wings ends approximately 9/10 distance base to wing apex
4. (A) lateral margins of clypeus straight
5. (A) basal 2/3 of outer margin of labrum without short, stiff setae; setae well developed apically
6. (A) outer margin of mandibles with hairs on basal 1/2-2/3
7. (D) maxillary palpal segment 2 with pectinate setae on inner margin
8. (A) inner margin of segment 3 of labial palpi with a row of denticle-like setae
9. (A) denticles of nymphal claws are variable, they may be progressively larger but apical denticle is not unusually large

**lineage b**

- (D) setae on anal and apical margins of subimaginal wings are long (Figs. 28-31)
- (D) fore wings with less than 25 costal cross veins (Figs. 7, 10, 16, 19, 22, 25, 28, 32, 35)
- (D) vein Sc of hind wings ends 3/4 or less distance base to wing apex (Figs. 9, 11, 15, 18, 21, 24, 27, 30, 34, 37)
- (D) lateral margins of clypeus not straight, curved at least basally (Figs. 137-138, 142, 148)
- (D) basal 2/3 of outer margin of labrum with short, stiff setae (Figs. 137-138, 142, 148)
- (D) outer margin of mandibles with a few hairs on median area or in a median tuft (Figs. 147, 153)
- (A) maxillary palpal segment 2 with non-pectinate setae on inner margin
- (D) inner margin of segment 3 of labial palpi with a row of blade-like setae or with a row of widely spaced hair-like setae (Figs. 145, 151)
- (D) denticles of nymphal claws are progressively larger apically except for apical denticle which is larger (Figs. 154-159)

## FURCATION 4

**lineage a**

1. (D) eyes of male stalked or if unstalked, modified in some fashion, never of the normal or primitive Leptophlebiidae type (Figs. 40-54)
2. (D) prothoracic claws of male imago dissimilar, one apically hooked or with spike-like projection, other pad-like (Figs. 90-95)

**lineage b**

- (A) eyes of male unstalked, of normal or primitive Leptophlebiidae type
- (A) prothoracic claws of male imago similar, both apically hooked



- |   |   |
|---|---|
| 3. (D) fore wings with vein MA branched asymmetrically; MA, straight and MA <sub>2</sub> curved basally (Figs. 7, 10, 13, 16, 19, 22, 25, 28, 32, 35)               | (A) fore wings with vein MA branched more or less symmetrically                       |
| 4. (D) apex of costal projection of hind wings well developed, located from slightly greater than 1/4 to 3/5 distance from base to margin (Figs. 9, 15, 21, 27, 34) | (A) costal projection of hind wings not developed                                     |
| 5. (D) vein Sc of hind wings terminates from slightly less than 1/2 to 3/5 distance from base to wing apex (Figs. 11, 18, 24, 30, 37)                               | (A) vein Sc of hind wings terminates approximately 3/4 distance base to wing apex     |
| 6. (D) apical and anal margins of subimaginal fore and hind wings with branched setae (Figs. 28-31)   | (A) apical and anal margins of subimaginal fore and hind wings with unbranched setae  |
| 7. (D) forceps segment 1 with large spines on inner basal margin (Figs. 55, 58, 63, 68, 73, 77)   | (A) forceps segment 1 with small spines on inner basal margin                         |
| 8. (D) forceps segments 2 and 3 elongate; segment length 3 times or greater than 3 times width (Figs. 57, 61, 65, 71, 75, 78)                                       | (A) forceps segments 2 and 3 short; segment length 2 times or less than 2 times width |
| 9. (D) penes tubular, divided, without appendages (Figs. 55-80)   | (A) penes fused basally, with appendages or spines                                    |
| 10. (D) segment 3 of maxillary palpi less than 3/5 length of segment 2 (Figs. 146, 152)   | (A) segment 3 of maxillary palpi from 3/4 to 1-1/10 length of segment 2               |
| 11. (D) segment 3 of labial palpi less than 3/5 length of segment 2 (Figs. 145, 151)  | (A) segment 3 of labial palpi from 3/4 to 1-1/10 length of segment 2                  |
| 12. (D) inner margin of labial palpal segment 3 with a row of widely spaced hair-like setae (Fig. 164)  | (A) inner margin of labial palpal segment 3 with a row of blade-like setae            |
| 13. (A) glossae of labium prominently curved over ventrally (Figs. 145, 151)  | (D) glossae of labium straight or slightly curved ventrally                           |

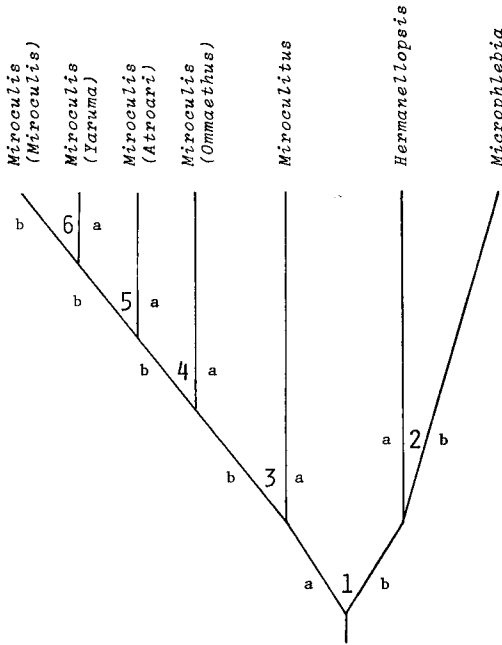


FIGURE 2. Probable phylogenetic relationships among *Microphlebia*, *Hermanellopsis*, *Miroculitus* and the subgenera of *Miroculis*. Character state distribution is provided in Table 3.

TABLE 3. Character states for lineages of Figure 2. D, derived or apomorphic; A, ancestral or plesiomorphic.

FURCATION 1

lineage a

1. (A) vein MP of fore wings forked to vein MP<sub>2</sub> attached at base to MP<sub>1</sub> by a cross vein slightly less than 0.25 to 0.33 distance from base of vein MP to margin
2. (A) marginal intercalaries along posterior margin of fore wings are numerous as in Figs. 7, 10, 13, 16, 19, 22, 25

lineage b

- (D) vein MP of fore wings forked to vein MP<sub>2</sub> attached at base to MP<sub>1</sub> by a cross vein 0.33 to a little less than 0.40 distance from base of vein MP to margin
- (D) marginal intercalaries along posterior margin of fore wings are greatly reduced in number, Figs. 28, 32, 35

- |  |  |
|--|--|
| 3. (A) ratio: maximum length of hind wings/maximum length of fore wings in male imagos is greater than 0.18  | (D) ratio: maximum length of hind wings/maximum length of fore wings in male imagos is less than 0.18  |
| 4. (A) vein Sc of hind wings ends distad to apex of costal projection; distal margin of costal projection gradually tapers as in Figs. 9, 11, 15, 18, 21, 24, 27 | (D) vein Sc of hind wings ends approximately at location of costal projection; distal margin of costal projection is abrupt as in Figs. 30, 34, 37, 39 |
| 5. (A) veins Sc and R of hind wings do not fuse before reaching base of wings (Figs. 9, 18, 21, 24, 27)  | (D) veins Sc and R of hind wings fuse before reaching base of wings (Figs. 30, 34, 37)   |
| 6. (D) eyes of female imago separated on meson of head by a length 3.0-3.3 maximum width of an eye   | (A) eyes of female imago separated on meson of head by a length 5 times maximum width of an eye  |
| 7. (D) lateral margins of nymphal clypeus with apical 1/2 slightly expanded (Figs. 137-138, 142)   | (A) lateral margins of nymphal clypeus with apical 1/2 slightly tapered (Fig. 148)   |
| 8. (D) anteromedian margin of clypeus concave  | (A) anteromedian margin of clypeus very slightly concave   |
| 9. (D) maximum width of labrum from 1-1/10 to 1-1/4 width of distal portion of clypeus (Figs. 137-138, 142)  | (A) maximum width of labrum approximately equal to width of distal portion of clypeus (Fig. 148)   |
| 10. (D) galea-lacinia of maxillae with 31-55 pectinate setae in subapical row (Figs. 146, 160-161)   | (A) galea-lacinia of maxillae with 18-20 pectinate setae in subapical row (Fig. 152)   |
| 11. (A) each gill portion with 3 apical processes, dorsal and ventral portions of gills subequal in size (Figs. 121-132)   | (D) gills plate-like, without apical processes, dorsal portion of gills greatly reduced (Figs. 133-136)  |
| 12. (A) posterolateral spines on abdominal segments 2-3 to 9, spines well developed, acute on segments 5-6 to 9 (Figs. 112-119)                                  | (D) posterolateral spines on abdominal segments 5-6 to 9, spines well developed, acute on segments 8 and 9 (Fig. 120)                                  |

## FURCATION 2

- | lineage a   | lineage b   |
|---|---|
| 1. (A) vein ICu <sub>1</sub> of fore wings is free basally or attached to vein CuA by a cross vein (Figs. 32, 35) | (D) vein ICu <sub>1</sub> of fore wings is attached at base to vein CuA (Fig. 28) |
| 2. (A) cubital area of fore wings is not reduced  | (D) cubital area of fore wings is greatly reduced                                 |

- |  |   |
|--|---|
| <p>3. (A) ratio: maximum length of hind wings/maximum length of fore wings in male imagos from 0.16 to 0.18</p> <p>4. (A) hind wings with apex of costal projection located from 0.40 to 0.50 distance from base to margin of wings</p> <p>5. (A) veins CuA and CuP of hind wings are unfused or fused at base to 0.16 distance from base of vein CuA to margin (Figs. 33-34, 36-39)</p> <p>6. (D) posterior margin of styliger plate with well developed submedian projections (Figs. 77-80)</p> <p>7. (D) penes long, narrow, acute apically, unsculptured (Figs. 77-80)</p> | <p>(D) ratio: maximum length of hind wings/maximum length of fore wings in male imagos from 0.14 to 0.16</p> <p>(D) hind wings with apex of costal projection located from 0.50 to 0.60 distance from base to margin of wings</p> <p>(D) vein CuP of hind wings absent (Figs. 29-30)</p> <p>(A) posterior margin of styliger plate without submedian projections (Figs. 73-75)</p> <p>(A) penes short, blunt apically, sculptured (Figs. 73-75)</p> |
|--|---|

## FURCATION 3

**lineage a**

1. (D) ratio: maximum width of fore wings/maximum length of fore wings in male imagos from 0.38 to 0.40
2. (A) a cross vein connects veins MP and CuA basal to the fusion of MP<sub>1</sub> and MP<sub>2</sub> in fore wings (Fig. 25)
3. (D) vein MP<sub>2</sub> of fore wings attaches at base to vein MP<sub>1</sub> (Fig. 25)
4. (D) vein ICu<sub>1</sub> of fore wings is attached at base to vein CuA (Fig. 25)
5. (A) veins CuA and CuP of hind wings are fused at base to approximately 0.16 distance from base of vein CuA to margin
6. (A) claws of imaginal male prothoracic legs dissimilar, one with apical hook, other pad-like, blunt (Fig. 93, based on subimago).

**lineage b**

- (A) ratio: maximum width of fore wings/maximum length of fore wings in male imagos 0.41 or greater
- (D) no cross veins are present between veins MP and CuA basal to the fusion of MP<sub>1</sub> and MP<sub>2</sub> in fore wings (Figs. 7, 10, 13, 16, 19, 22)
- (A) vein MP<sub>2</sub> of fore wings attached by cross veins to MP<sub>1</sub> and CuA (Figs. 13, 16, 19, 22)
- (A) vein ICu<sub>1</sub> of fore wings is free basally or attached at base to vein CuA by a cross vein (Figs. 13, 16, 19, 22)
- (D) veins CuA and CuP of hind wings fuse 0.16 to 0.33 distance from base of vein CuA to margin
- (D) claws of imaginal male prothoracic legs dissimilar, one with a single lateral, long, narrow spike-like projection, other pad-like, blunt (Figs. 90-92)

## FURCATION 4

**lineage a**

1. (D) upper portion of male imaginal eyes unstalked, eyes separated on meson of head by a distance approximately equal to width of an eye, 27-34 facets in longest row (Figs. 51-54)
2. (A) ratio: maximum width of fore wings/maximum length of fore wings in male imagos from 0.41 to 0.43
3. (A) ratio: maximum length of hind wings/maximum length of fore wings in male imagos from 0.20 to 0.23
4. (A) hind wings with apex of costal projection located from 0.34 to 0.44 distance from base to margin of wings
5. (D) posteromedian margin of styliger plate with a large U-shaped indentation as in Figs. 65, 68
6. (A) eyes of female imagos separated on meson of head by a length 3.2-3.3 times maximum width of an eye
7. (A) anterolateral margins of nymphal labrum gently rounded to slightly flattened (Figs. 138-140)

**lineage b**

- (A) upper portion of male imaginal eyes stalked (Figs. 44-48), or if unstalked, eyes separated on meson of head by a distance less than 0.7 width of an eye, 30-40 facets in longest row (Figs. 49-50)
- (D) ratio: maximum width of fore wings/maximum length of fore wings in male imagos from 0.43 to 0.51
- (D) ratio: maximum length of hind wings/maximum length of fore wings in male imagos from 0.24 to 0.32
- (D) hind wings with apex of costal projection located from 0.27 to 0.36 distance from base to margin of wings
- (A) posteromedian margin of styliger plate flat, rounded, or rounded with small median notch (Figs. 55-64)
- (D) eyes of female imagos separated on meson of head by a length approximately 3.0 times maximum width of an eye
- (D) anterolateral margins of nymphal labrum slightly flattened to flattened (Figs. 137, 142)

## FURCATION 5

**lineage a**

1. (A) upper portion of male imaginal eyes unstalked, facets directed laterally (Figs. 49-50)
2. (A) membrane of fore wings with very light brown to dark brown submedian irregular broken transverse bands and numerous blotches near apex (Fig. 19)

**lineage b**

- (D) upper portion of male imaginal eyes set on dorsum of head by a stalk, facets directed dorsally (Figs. 44-48)
- (D) membrane of fore wings without irregular transverse bands on fore wings (Figs. 7, 10, 13, 16)

3. (D) femora/tibiae ratio of male imaginal prothoracic legs approximately 0.42 (A) femora/tibiae ratio of male prothoracic legs from 0.56-0.64

FURCATION 6

lineage a

lineage b

- |  |  |
|--|--|
| <p>1. (A) upper portion of male imaginal eyes with 32-37 medium-sized facets in longest row, set on dorsum of head by a short wide stalk (Figs. 47-48)</p> <p>2. (A) antennae pale yellow</p> <p>3. (A) forceps segments light brown to brown, without brownish-black wash</p> | <p>(D) upper portion of male imaginal eyes with 5-9 large facets in longest row, set on dorsum of head by a long narrow stalk (Figs. 44-46)</p> <p>(D) antennae with scape and pedicel brownish-yellow to brown, usually with brownish-black wash</p> <p>(D) forceps segments brown with brownish-black wash on segments 2 and 3 and apical 1/3 of segment 1</p> |
|--|--|

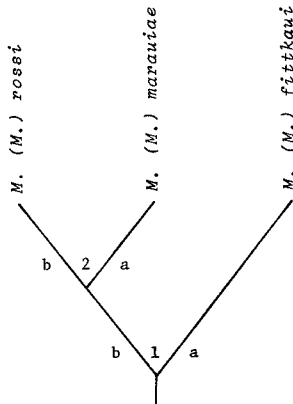


FIGURE 3. Probable phylogenetic relationships among species of *Miroculis* (*Miroculis*). Character state distribution is provided in Table 4.

TABLE 4. Character states for lineages of Figure 3. D, derived or apomorphic; A, ancestral or plesiomorphic.

## FURCATION 1

<b>lineage a</b>	<b>lineage b</b>
1. (A) membrane of wings hyaline to light brown, fore wings darker brown around cross veins and near base (Figs. 10-11)	(D) membrane of wings hyaline (Figs. 7-9, 13-15)
2. (D) basal 1/3-1/2 of forceps segment 1 abruptly narrows apically, distal 1/4 of inner margin developed as in Fig. 58	(A) basal 1/2 of forceps segment 1 gradually narrows apically, distal inner margin not developed (Figs. 55, 57)
3. (D) forceps segment 2 from 0.47-0.58 length of segment 1	(A) forceps segment 2 from 0.33-0.46 length of segment 1
4. (A) posteromedian margin of styliger plate gently rounded with a shallow median indentation as in Fig. 58	(D) posteromedian margin of styliger plate gently rounded as in Figs. 55, 57

## FURCATION 2

<b>lineage a</b>	<b>lineage b</b>
1. (A) upper portion of male imaginal eyes with 8-9 facets in longest row	(D) upper portion of male imaginal eyes with 6 facets in longest row
2. (D) basal 1/2 of caudal filaments with posterior margins of segments black	(A) caudal filaments without black pigment
3. (A) penes without spines (Fig. 57)	(D) penes with a diagonal row of approximately 15 stout spines on a ventral basal ridge as in Figs. 55-56
4. (A) penes from 0.8-1.1 length of forceps segment 1, tubular, apex with notch or excavation (Fig. 57)	(D) penes approximately 2.1 length of forceps segment 1, narrow apically, without notch or excavation (Figs. 55-56)

**SUBIMAGO.** Characters similar to imagos except upper portion of eyes, prothoracic legs and genital forceps of males not fully extended. Head with posteromedian projection between turbinate portion of eyes in species with short, wide, stalked eyes. Wings: membrane translucent, whitish, with long hair on apical and anal margins, hair with small branches, hair not thickened basally.

**MATURE NYMPH.** Head prognathous. Antennae 2 to 2-1/2 length of head. Mouthparts (Figs. 137-147, 160-165): lateral margins of clypeus with basal 1/2

tapered, apical 1/2 slightly expanded; anteromedian margin of clypeus shallowly concave as in Figs. 137-138, 142. Maximum width of labrum 1-1/10 to 1-1/4 width of distal portion of clypeus; anterolateral margins of labrum gently rounded to flattened (Figs. 137-142); dorsal hair on labrum as in Figs. 137-138, 142, short setae on basal 2/3 of lateral margins, submedian areas of hair ventrally; anteromedian emargination with 4 to 5 small, rounded, subequal-sized denticles (Fig. 143). Outer margin of mandibles curved as in Fig. 147, with scattered hair on median area of outer margin; inner basal margin of mandibles with angular bend as in Fig. 147; incisors of left mandible each with 3 apical projections and prostheca as in Fig. 147. Lingua of hypopharynx with well developed lateral processes, anterior margin with a median cleft, submedian lobes and hair as in Fig. 144; superlingua of hypopharynx as in Fig. 144, with hair along anterior margin. Galea-lacinia of maxillae with a subapical row of 31-55 pectinate setae (Figs. 146, 160-161), apical setae as in Figs. 146, 162-163, dense; cardo of maxillae with large setae on outer margin; segment 2 of maxillary palpi 1 to 1-1/4 length of segment 1; segment 3 of maxillary palpi 2/5 to a little less than 3/5 length of segment 2; setae on maxillae as in Fig. 146. Segment 2 of labial palpi 1 to 1-1/4 length of segment 1, outer margin with 3-6 long, thick setae basally and long, thin hairs on apical 2/3, width at base and apex of segment 2 approximately equal (Fig. 145); segment 3 of labial palpi 2/5 to 3/5 length of segment 2, inner margin with widely spaced hair-like setae (Fig. 164) and apex with dense peg-like setae (Fig. 165), meson of segment 3 with a diagonal row of 4-6 large setae as in Fig. 145; glossae curved over ventrally, ventral portion of glossae long, straight; paraglossae wide as in Fig. 145; lateral margins of submentum with setae as in Fig. 145; posteromedian margin of submentum concave, gently rounded. Legs (Figs. 119, 156-159): maximum width of tibiae approximately 2 times maximum width of tarsi, tibiae in cross section circular, tibiae with a row of dense thick spines on inner lateral margin (Fig. 156), outer margin of femora indented near apex so tibiae can draw partially into femora (Fig. 156); apex of claws hooked and narrow, denticles progressively larger apically, except apical denticle much larger (Figs. 156-159). Gills (Figs. 121-132): gills on segments 1-7 similar; dorsal and ventral portions of gills on segments 1-7 dissimilar; gills 1-6 longer than gill 7; dorsal and ventral portions subequal in length with 1 long median apical and 2 short posterolateral projections; dorsal portion asymmetrical with inner posterolateral projection more developed than outer, outer basal margin developed (Figs. 129-130) or not developed anteriorly (Figs. 121-128, 131-132); ventral portion symmetrical with posterolateral projections equally developed (Figs. 121-123, 127, 131-132) to slightly asymmetrical with inner posterolateral projection more developed than outer (Figs. 124-126, 128-130); tracheae unbranched (Figs. 121-125, 127-129, 131-132) to branched (Figs. 126, 130). Posterolateral spines on abdominal segments 2-3 to 9, spines developed beyond posterior margin of terga on segments 3-6 to 9, spines well developed, acute, on segments 5-6 to 9 (Figs. 112-119). Caudal filaments 1-1/2 to 2 times length of body.

ETYMOLOGY: *miror*, L., meaning wonder at; *oculus*, L., meaning eye. Edmunds (1963) did not indicate the gender of *Miroculis* and the -is ending could be either masculine or feminine. The only named species is a patronym. As the generic name refers to the eyes of the male imago, we designate *Miroculis* as masculine.



TYPE SPECIES: *M. (Miroculis) rossi* Edmunds, 1963 by original designation.

SPECIES INCLUDED: *M. (M.) rossi* Edmunds; *M. (M.) marauiae* NEW SPECIES; *M. (M.) fittkau* NEW SPECIES; *M. (M.) brasiliaensis* NEW SPECIES; *M. (Yaruma) wandae* NEW SPECIES; *M. (Atroari) duckensis* NEW SPECIES; *M. (A.) amazonicus* NEW SPECIES; *M. (A.) colombiensis* NEW SPECIES; *M. (Ommaethus) mourei* NEW SPECIES; *M. (O.) froehlich* NEW SPECIES.

DISTRIBUTION: northern South America, including Brazil, Surinam, Colombia and Peru (Fig. 168; localities a-g, i, k, l).

DISCUSSION. *Miroculis* can be distinguished from all other genera of Lep-tophlebiidae by the following combination of characters. In imagos: (1) vein MA of fore wings is forked from slightly greater than 2/5 to slightly greater than 1/2 distance from base of vein to margin, fork asymmetrical as in Figs. 7, 10, 13, 16, 19, 22; (2) vein MP<sub>1</sub> of fore wings is attached at base to veins MP<sub>1</sub> and CuA by cross veins less than 1/4 to 1/3 distance from base of vein MP to margin (Figs. 7, 10, 12, 16, 19, 22) to base of vein MP<sub>1</sub>; greatly shortened and attached to IMP by a cross vein (Fig. 13); (3) marginal intercalaries are numerous along posterior margin of fore wings as in Figs. 7, 13, 16, 19, 22; (4) hind wings are shaped as in Figs. 9, 11, 15, 18, 21, 24; costal projection is developed, apex acute, pointed, apex located from slightly greater than 1/4 to 1/2 distance from base to apex of wings; (5) vein Sc of hind wings ends distad to apex of costal projection as in Figs. 9, 11, 15, 18, 21, 24; (6) veins CuA and CuP of hind wings are fused 1/6 to 1/3 distance from base to margin; (7) claws of male prothoracic legs are dissimilar, one with a single, lateral, spike-like projection, other pad-like, blunt (Figs. 90-92); (8) anterolateral margins of male styliger plate are developed anteriorly to form arms which articulate with the posterior margin of sternum 9 (Figs. 55-70); (9) penes are tubular, divided, without appendages (Figs. 55-70); (10) male genital forceps shaped as in Figs. 55-70; and (11) sternum 9 of female has a deep posteromedian cleft as in Figs. 87-88. In nymphs: (1) gills on segments 1-7 are similar; dorsal and ventral portions of gills are subequal in length, with 1 long, median, apical projection and 2 short posterolateral projections; dorsal portion is asymmetrical with inner posterolateral projection more developed than outer; ventral gill portion is symmetrical to slightly asymmetrical (Figs. 121-132); (2) basal 1/2 of lateral margins of clypeus is tapered; apical 1/2 is slightly expanded (Figs. 137-138, 142); (3) maximum width of labrum is 1-1/10 to 1-1/4 width of distal portion of clypeus, with short setae on basal 2/3 of lateral margins of labrum (Figs. 137-142); (4) outer margin of mandibles is curved with scattered hair on median area (Fig. 147); (5) lingua of hypopharynx has well developed lateral processes; anterior margin has a median cleft and lobes as in Fig. 144; (6) galealacinia of maxillae has a subapical row of 31-55 pectinate setae (Figs. 146, 160-161); (7) glossae of labium are curved over ventrally; ventral portion of glossae is long and straight (Fig. 145); (8) apex of claws are hooked and narrow; denticles are progressively larger apically, except apical denticle is much larger (Figs. 156-159); and (9) posterolateral spines occur on abdominal segments 2-3 to 9; spines are well developed, acute, on segments 5-6 to 9 (Figs. 112-119).

Vein MP<sub>1</sub> of the fore wings is variable within *Miroculis*. Typically, vein MP<sub>1</sub> is attached at base to veins MP<sub>1</sub> and CuA by cross veins (Figs. 7, 10, 16, 19, 22). Vein

MP<sub>2</sub> may be weak and appear broken basally in some small females of *M. (Miroculis) fittkaui* (Fig. 12) and in some male and female specimens of *M. (Atroari) duckensis*. In the small and weak veined species, *M. (Miroculis) marauiae*, vein MP<sub>1</sub> is free basally or attached at base to vein IMP by a cross vein (Fig. 13).

Color of the upper portion of male eyes in mature nymphs is provided in species descriptions. However, eye color of male nymphs is subject to changes associated with development and preservation techniques and is not a reliable character for identification.

Female imagos of *M. (Atroari)* and female imagos and nymphs of *M. (Yaruma)* are unknown. It is not possible to identify female imagos to subgenera, however, some color pattern characters may prove useful. The female genital extension and eyes may provide subgeneric characters but evaluation awaits collection of female imagos of *M. (Yaruma)* and *M. (Atroari)*. As reliable subgeneric characters for nymphs are unknown, distinguishing characters to nymphs of known species are provided in Table 1 and in respective discussion sections.

Keys to male imagos are designed to key to subgenera first and then to known species. Keys to female imagos and nymphs are to known species only, and will not reliably key subgenera.

KEY TO KNOWN MALE IMAGOS OF MIROCULIS

1. Upper portion of eyes on long, narrow stalk (Figs. 44-46), 5-9 large facets in longest row, eyes separated on meson of head by a distance 0.7-1.5 width of an upper portion . . . . . *M. (Miroculis)* . . . . . 4  
 Upper portion of eyes on short, wide stalk (Figs. 47-48), or stalk absent (Figs. 49-54), 27-40 medium-sized facets in longest row, if eyes stalked upper portion separated on meson of head by a distance 0.1-0.2 maximum width of an upper portion . . . . . 2
2. Upper portion of eyes on short, wide stalk (Figs. 47-48), separated by a distance 0.1-0.2 maximum width of an eye; membrane of fore and hind wings hyaline or with very light brown tinge, without darker pigment . . . . . *M. (Yaruma)* . . . . . 6  
 Upper portion of eyes without stalk (Figs. 49-54), separated by a distance 0.5-1.0 width of an upper portion; membrane of fore and hind wings light brown, with brown pigment as in Figs. 19-24. . . . . 3
3. Posteromedian margin of styliger plate rounded (Figs. 63-64); upper portion of eyes separated on meson of head by a distance 0.5-0.6 maximum width of an upper portion (Figs. 49-50); width of fore wings 0.47-0.51 length of fore wings . . . . . *M. (Atroari)* . . . . . 7  
 Posteromedian margin of styliger plate with a large U-shaped indentation (Figs. 65, 68); upper portion of eyes separated on meson of head by a distance approximately equal to maximum width of an upper portion (Figs. 52, 54); width of fore wings 0.41-0.43 length of fore wings . . . . . *M. (Ommaethus)* . . . . . 8

4. Membrane of fore and hind wings hyaline to light brown with darker brown clouds around cross veins (Figs. 10-11); basal 1/3-1/2 of inner margin of forceps segment 1 abruptly narrows apically, distal 1/4 of inner margin developed as in Fig. 58; posteromedian margin of styliger plate gently rounded with shallow indentation (Fig. 58); apical inner margin of each penis lobe excavated as in Fig. 58; abdominal tergum 6 with a large brownish-black V-shaped median mark, with open end of V directed posteriorly (Figs. 97-98) . . . . .  
*M. (Miroculis) fittkaui* NEW SPECIES
- Membrane of fore and hind wings hyaline; basal 1/2 of inner margin of forceps segment 1 gradually narrows apically, distal inner margin not developed (Figs. 55, 57); posteromedian margin of styliger plate gently rounded, without median indentation (Figs. 55, 57); apical margin of each penis lobe excavated as in Fig. 57, or not excavated (Fig. 55); median area of abdominal tergum 6 with submedian brownish-black marks (Figs. 99-100) or washed with brown . . . . . 5
5. Length of penes 2.0-2.2 length of forceps segment 1; penes narrow apically, with a diagonal row of approximately 15 stout spines on ventral, basal ridge as in Figs. 55-56; vein  $MP_2$  of fore wings attached at base to vein  $MP_1$  and CuA by a cross vein (Fig. 7); upper portion of eyes with 6 facets in longest row . . . . .*M. (Miroculis) rossi* Edmunds
- Length of penes 0.8-1.1 length of forceps segment 1; penes tubular, apex of penes excavated as in Fig. 57, without spines; vein  $MP_2$  of fore wings free basally or attached at base to vein IMP by a cross vein (Fig. 13); upper portion of eyes with 8-9 facets in longest row . . . . .  
*M. (Miroculis) marauiae* NEW SPECIES
6. Abdominal terga 5-6 with submedian and sublateral brownish-black marks as in Figs. 103-104 (subimago) . . . . .*M. (Yaruma) wandae* NEW SPECIES
- Abdominal terga 5-6 with faint submedian and sublateral brownish-black marks as in Figs. 105-106. . . . .*M. (Yaruma)* sp.
7. Length of penes 1.7-1.9 length of forceps segment 1; penes shaped as in Fig. 63; forceps segment 2 rectangular (Fig. 63); membrane of fore wings with brown bands and blotches apparent as in Fig. 19; upper portion of eyes separated on meson of head by a distance 0.5 maximum width of an upper portion . . . . .  
*M. (Atroari) amazonicus* NEW SPECIES
- Length of penes 1.1-1.4 length of forceps segment 1; penes shaped as in Fig. 64; forceps segment 2 widens apically (Fig. 64); membrane of fore wings with very light brown bands and blotches; upper portion of eyes separated on meson of head by a distance 0.6 maximum width of an upper portion . . . . .*M. (Atroari) duckensis* NEW SPECIES
8. Body length 3.8-6.0 mm; penes and forceps as in Figs. 65-67; abdominal terga 5-6 brownish-yellow with brownish-black submedian, sublateral and lateral bars (Figs. 107-108); distal 1/3 of forceps segment 1 and all of segments 2 and 3 washed with black; caudal filaments brownish-

- yellow, basal 1/3-1/2 of segments with brownish-black bands . . . . .  
 . . . . . *M. (Ommaethus) mourei* NEW SPECIES  
 Body length 6.0-8.0 mm; penes and forceps as in Figs. 68-70; abdominal  
 terga 5-6 semihyaline, whitish, tergum 6 with faint submedian bars;  
 forceps light yellow; caudal filaments pale yellow . . . . .  
 . . . . . *M. (Ommaethus) froehlichii* NEW SPECIES

KEY TO KNOWN FEMALE IMAGOS OF MIROCULIS

1. Abdominal tergum 6 brownish-yellow with brownish-black submedian, sublateral and lateral bars as in Fig. 109; membrane of fore and hind wings light brown with darker pigment as in Figs. 22-24; sternum 7 with genital extension as in Figs. 83-84; eyes separated on meson of head by a distance 3.2-3.3 times maximum width of an eye . . . . .  
 . . . . . *M. (Ommaethus) mourei* NEW SPECIES
- Abdominal tergum 6 semihyaline, washed lightly with brown, with brownish-black submedian and sublateral marks (Fig. 101) or with a median V-shaped mark, with open end of V directed posteriorly and sublateral marks (Fig. 97); membrane of fore and hind wings hyaline or hyaline to light brown with darker brown clouds around cross veins (Figs. 10-11); sternum 7 with genital extension as in Figs. 81-82; eyes separated on meson of head by a distance approximately 3.0 times maximum width of an eye . . . . . 2
2. Membrane of fore and hind wings hyaline; abdominal terga 6-7 with brownish-black submedian and sublateral marks (Fig. 101); vein MP<sub>2</sub> of fore wings free basally or attached at base to vein IMP by a cross vein (Fig. 13); segments of basal 1/2 of caudal filaments with articulations black . . . . . *M. (Miroculis) marauiae* NEW SPECIES
- Membrane of fore and hind wings hyaline to light brown, fore wings with darker brown clouds around cross veins, hind wings darker brown apically (Figs. 10-12); abdominal terga 6-7 with brownish-black sublateral marks, tergum 6 with median V-shaped mark, open end of V directed posteriorly, tergum 7 with submedian marks (Fig. 97); vein MP<sub>2</sub> of fore wings attached at base to vein MP<sub>1</sub> and CuA by a cross vein (Figs. 10, 12); caudal filaments uniformly light brown . . . . .  
 . . . . . *M. (Miroculis) fittkai* NEW SPECIES

KEY TO KNOWN NYMPHS OF MIROCULIS

1. Abdominal terga 2-6 equally dark with repeating color pattern of longitudinal submedian, sublateral and lateral brownish-black bars as in Fig. 119; anterolateral margins of labrum gently rounded to slightly flattened (Figs. 138-140); abdominal gills small, shaped as in Fig. 131 . . . . .  
 . . . . . *M. (Ommaethus) mourei* NEW SPECIES

- Abdominal terga 2-3 dark, terga 4-5 lighter and tergum 6 dark (Figs. 97, 99, 101, 112-113), or tergum 3 or 4 or terga 3 and 4 slightly lighter, terga 2-6 without a repeating color pattern (Figs. 114-117); anterolateral margins of labrum slightly flattened to flattened (Figs. 137, 141-142); abdominal gills small to large (Figs. 121-130) . . . . . 2
2. Abdominal terga 2-3 dark, terga 4-5 lighter and tergum 6 dark; tergum 6 with a median V-shaped mark (Figs. 97, 112) or terga 6-8 with marks as in Figs. 99-101 . . . . . 3
- Abdominal color pattern on terga 2-6 not as above, tergum 3 or 4 or terga 3 and 4 slightly lighter; terga 4-8 or 5-8 with repeating pattern as in Figs. 116-117, or terga 4-8 variable as in Figs. 114-115, tergum 6 never with a V-shaped mark . . . . . 5
3. Abdominal terga 6-8 with repeating color pattern as in Figs. 99-101; abdominal gills small and narrow, posterolateral projections not greatly developed to reduced (Figs. 121-123) . . . . .
- . . . . . *M. (Miroculis) marauiae* NEW SPECIES
- Abdominal tergum 6 with median V-shaped mark, with open end of V directed posteriorly, terga 7-8 with lighter pattern as in Figs. 97, 112; abdominal gills small to large, posterolateral projections not greatly developed to greatly developed (Figs. 124-126) . . . . . 4
4. Abdominal gills large, posterolateral projections as in Fig. 126; caudal filaments brownish-yellow, basal 5-9 segments with black bands; maxillae with subapical row of 35-40 pectinate setae . . . . .
- . . . . . *M. (Miroculis) brasiliaensis* NEW SPECIES
- Abdominal gills small, posterolateral projections as in Figs. 124-125; caudal filaments uniformly light brown; maxillae with subapical row of 44-49 pectinate setae . . . . . *M. (Miroculis) fittkai* NEW SPECIES
5. Abdominal gills small, posterolateral projections not greatly developed to reduced, dorsal portion of gill with outer basal margin not developed anteriorly (Fig. 127); abdominal color pattern as in Figs. 114-115 . . . . .
- . . . . . *M. (Atroari) duckensis* NEW SPECIES
- Abdominal gills large, posterolateral projections greatly developed, dorsal portion of gills 2-6 with outer basal margin developed anteriorly (Figs. 129-130); abdominal color patterns as in Figs. 116-117 . . . . . 6
6. Abdominal terga 4-8 progressively darker posteriorly with circular submedian marks (Fig. 117); claw of prothoracic leg as in Fig. 159; gill membrane brownish-yellow . . . *M. (Atroari) colombiensis* NEW SPECIES
- Abdominal terga 4-8 equally dark or with tergum 4 slightly lighter, terga 4-8 with submedian marks as in Fig. 116; claw of prothoracic leg as in Fig. 158; gill membrane grayish . . . . .
- . . . . . *M. (Atroari) amazonicus* NEW SPECIES

Subgenus **MIROCULIS** s.s. Edmunds, 1963

Figs. 7-15, 44-46, 55-60, 81-82, 87, 90-91, 96-101, 112-113, 121-126,  
137, 142-147, 157, 168

*Miroculis* Edmunds, 1963:34

IMAGO. Length of male: body, 4.6-6.2 mm; fore wings, 4.1-5.2 mm; prothoracic legs, 4.0-5.5 mm. Length of female: body, 3.7-5.6 mm; fore wings, 4.1-5.8 mm. Eyes (Figs. 44-46): eyes of male separated on meson of head by a length 0.7-1.5 width of an upper portion; dorsally upper portion of male eyes circular with large facets, 5-9 facets in longest row, set on dorsum of head by a long, narrow stalk as in Figs. 44-46; diameter of lower portion of male eyes a little less than to a little greater than height of stalk; eyes of female separated on meson of head by a length approximately 3.0 maximum width of an eye. Ocelli as in Figs. 44-46. Antennae with scape and pedicel brownish-yellow to brown, without wash to washed heavily with brownish-black. Wings (Figs. 7-15): ratio of maximum width to maximum length of fore wings, in males 0.43-0.51, in females 0.39-0.46; ratio of maximum length of hind wings to maximum length of fore wings, in males 0.25-0.32, in females 0.17-0.23; ratio of length to apex of costal projection to length of hind wings, in males 0.27-0.36, in females 0.37-0.49; membrane completely hyaline, or hyaline to light brown with darker brown clouds around cross veins in fore wings and hind wings darker brown near apex as in Figs. 10-11. Legs: ratios of segments in male prothoracic legs, 0.56-0.64: 1.00 (1.61-2.20 mm): 0.02-0.03: 0.36-0.41: 0.25-0.31: 0.17-0.19: 0.06-0.11. Male genitalia (Figs. 55-60): forceps segment 2 rectangular; styliger plate with anterolateral arms well developed, anteromedian area greatly weakened to absent, posterior 1/3 heavily sclerotized, posteromedian margin gently rounded, with (Fig. 58) to without (Figs. 55, 57) shallow median indentation; penes 0.8-2.2 length of forceps segment 1. Sternum 7 of female with small genital extension as in Figs. 81-82.

MATURE NYMPH. Labrum (Figs. 137, 142-143): anteromedian emargination with 5 small, subequal-sized denticles; anterolateral margins slightly flattened to flattened (Figs. 137, 142). Posterolateral spines developed beyond posterior margin of terga on abdominal segments 3-9.

TYPE SPECIES: *M. (Miroculis) rossi* Edmunds, 1963.

SPECIES INCLUDED: *M. (M.) rossi* Edmunds, 1963; *M. (M.) marauiae* NEW SPECIES; *M. (M.) fittkau* NEW SPECIES; *M. (M.) brasiliaensis* NEW SPECIES.

DISTRIBUTION: Loreto Province, PERU; Amazonas State, Pará State, and Goiás State, BRAZIL (Fig. 168, localities c, f, g, i, l).

DISCUSSION. *M. (Miroculis)* can be distinguished from all other subgenera of *Miroculis* by the following combination of characters. In imagos: (1) upper portion of male eyes are on a long, narrow, stalk, with 5-9 large facets in longest row (Figs. 44-46); (2) eyes of female are separated on meson of head by a length approximately 3.0 maximum width of an eye; (3) ratio of maximum width to maximum length of fore wings in male imagos is 0.43-0.51; (4) ratio of maximum length of hind wings to maximum length of fore wings in male imagos is 0.25-0.32; (5) posteromedian margin of styliger plate is gently rounded, with (Fig. 58) or without (Figs. 55, 57)

shallow median indentation; and (6) sternum 7 of female has a small genital extension as in Figs. 81-82.

### **Miroculis (*Miroculis*) rossi** Edmunds

Figs. 7-9, 44, 55-56, 90, 168

*Miroculis rossi* Edmunds, 1963:34

MALE IMAGO (in alcohol). Length: body, 4.7 mm; fore wings, 5.0 mm; prothoracic legs, 4.3 mm. Eyes (Fig. 44): apex of upper portion separated on meson of head by a distance approximately equal to diameter of an upper portion; stalked turbinate portion long, light brown at base, paler apically; facets of turbinate portion large, 6 complete facets in longest row, brownish-yellow, separated by brown grooves; facets of lower portion black, small. Head dark brown. Scape and pedicel brown, flagellum brownish-yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum brown, submedian carinae and lateral edges brownish-black; remainder of thorax brown, mesonotum darker, carinae brownish-black. Wings (Figs. 7-9): longitudinal and cross veins brown; membrane hyaline, apical 1/3 of cells of C and Sc of fore wings translucent, whitish. Legs (Fig. 90): ratios of segments in prothoracic legs, 0.64: 1.00(1.61 mm): 0.03: 0.39: 0.31: 0.19: 0.11; coxae and trochanters of all legs yellowish-brown, carinae darker; prothoracic legs light yellowish-brown, femora with medial area brownish-black, femora and tibiae with distal black band, [mesothoracic and metathoracic legs broken off and missing]; prothoracic claws as in Fig. 90. Abdomen: terga 2-7 semihyaline, washed with brown, terga 1 and 8-10 opaque, brown; terga 2-4 with posteromedian 1/2 washed with dark brown, terga 5-8 with posterior 1/2-2/3 washed with dark brown, terga 9-10 dark brown; spiracles black, tracheae smoky; sterna 1-7 semihyaline, yellowish-brown, sterna 8-9 yellowish-brown. Forceps (Fig. 55): segment 3 approximately 0.9 (n = 1) length of segment 2; segment 2 approximately 0.46 (n = 1) length of segment 1; basal 1/2 of inner margin of segment 1 gradually narrows apically, distal inner margin not developed (Fig. 55); apical 1/2 of segment 1 and all of segments 2 and 3 washed with black. Styliiger plate (Fig. 55): maximum length along lateral margin approximately 0.83 (n = 1) maximum width; maximum length along median line approximately 0.48 (n = 1) maximum width; posteromedian margin gently rounded (Fig. 55); brown. Penes (Figs. 55-56): length approximately 2.1 (n = 1) length of forceps segment 1, penes gradually narrow apically with diagonal row of approximately 15 stout spines on a ventral basal ridge as in Figs. 55-56; brown. Caudal filaments uniformly light brown.

FEMALE IMAGO: Unknown.

MATURE NYMPH: Unknown.

TYPE LOCALITY: PERU: Yurac, 67 road miles E. of Tingo Maria (Fig. 168; locality 1).

DEPOSITION OF TYPE: 1 male imaginal holotype and 2 male imaginal paratypes are deposited in collections of CAS.

SPECIMENS EXAMINED: 2 male imaginal paratypes, PERU: Yurac, 67 road miles E. of Tingo Maria, 28-IV-1954, E.S. Ross and E.I. Schlinger.

LIFE CYCLE ASSOCIATION: None.

DISCUSSION. Male imagos of *M. rossi* can be distinguished from male imagos of all other species within *M. (Miroculis)* by the following combination of characters: (1) membrane of wings is hyaline (Figs. 7-9); (2) ratio of femora to tibiae of male prothoracic legs is approximately 0.64; length of prothoracic tibiae is approximately 1.6 mm; (3) posteromedian 1/2-2/3 of tergum 6 is washed with dark brown; (4) basal 1/2 of inner margin of forceps segment 1 gradually narrows apically, distal margin is not developed (Fig. 55); (5) styliger plate is as in Fig. 55, with posteromedian margin gently rounded; and (6) penes are approximately 2.0-2.2 length of forceps segment 1; penes gradually narrow apically, with a diagonal row of approximately 15 stout spines on a ventral, basal ridge (Fig. 56).

Paratypes are in poor condition and it was necessary to rely upon the description of abdominal color pattern given by Edmunds (1963).

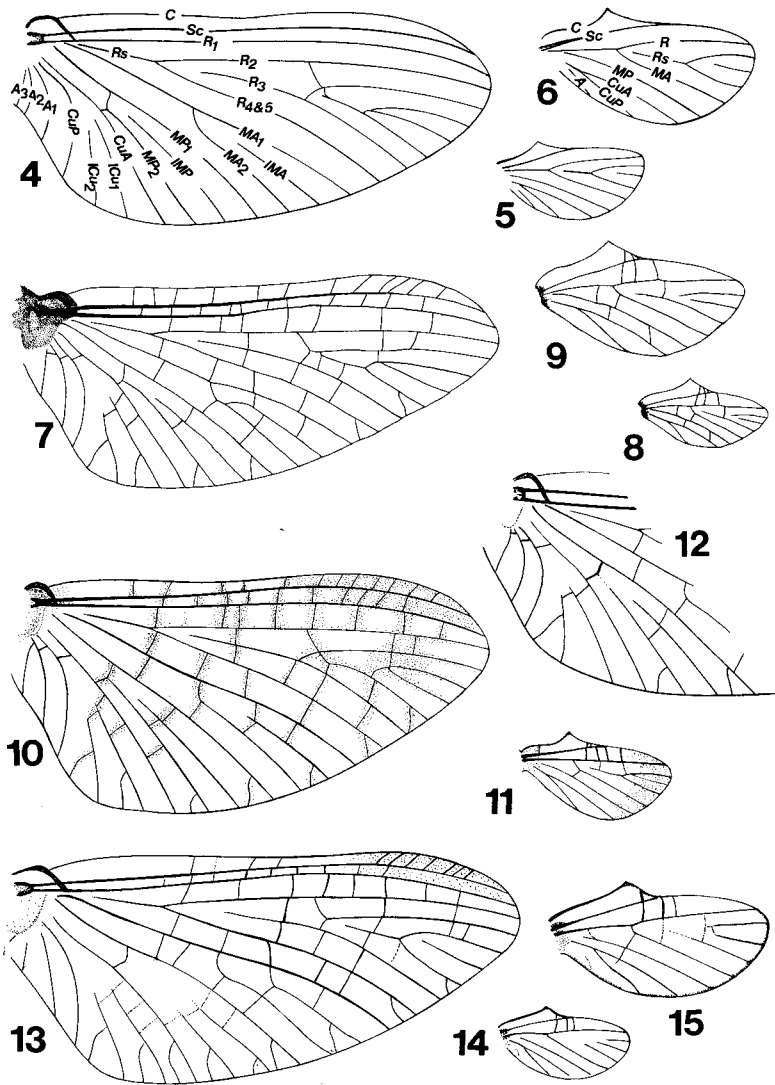
BIOLOGY. Edmunds (1963) reported that specimens were collected in a tropical rain-forest zone at approximately 300 meters elevation. Collection records indicate that imagos of *M. rossi* emerge in late April.

### ***Miroculis (Miroculis) marauiae* NEW SPECIES**

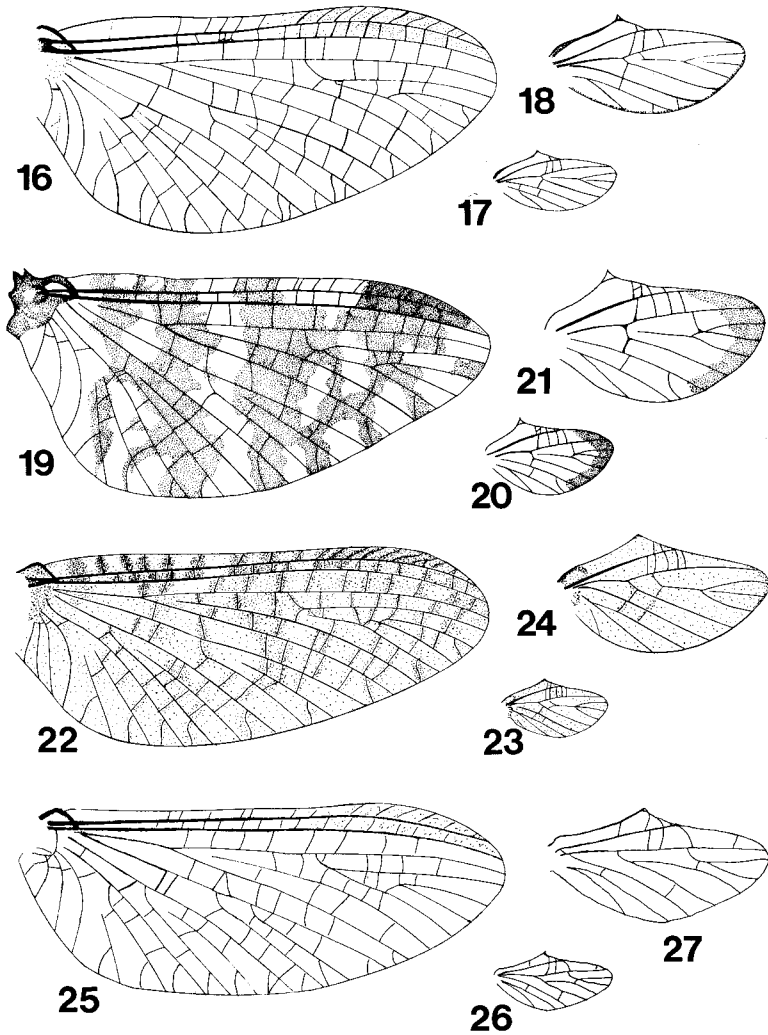
Figs. 13-15, 57, 99-101, 121-123, 142-147, 157, 168

MALE IMAGO (in alcohol). Length: body, 4.6-6.0 mm; fore wings, 4.1-4.7 mm; prothoracic legs, 4.0-4.3 mm. Eyes: apex of upper portion separated on meson of head by a length 0.7-1.3 diameter of an upper portion; stalked turbinate portion long, light brown at base, paler apically; facets of turbinate portion large, 8-9 complete facets in longest row, light yellow, separated by dark brown grooves; facets of lower portion black, small. Head light brown, ventral surface darker, carinae brownish-black. Scape and pedicel light brown, washed with brownish-black, flagellum pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum brown, submedian carinae and outer margins brownish-black, remainder of nota dark brown, carinae dark brown to brownish-black; sterna brown, carinae and lateral margins of sclerites dark brown; pleura light brown, washed with brownish-black, margins of sclerites and carinae with wash heavy. Wings (Figs. 13-15): longitudinal veins very light brown with C, Sc and R of fore wings darker, cross veins very weakly developed and hyaline except light brown anterior to R in fore wings; membrane hyaline, apical 1/3 of cells of C and Sc of fore wings translucent, whitish. Legs: ratios of segments in prothoracic legs, 0.59: 1.00(1.61-1.62 mm): 0.02-0.03: 0.36-0.41: 0.26-0.31: 0.17-0.18: 0.09; coxae brown, remainder of legs light brown except a large median brownish-black macula on both sides of femora, femora and tibiae with a black band near apex. Abdomen (Figs. 99-100): terga 1-7 semihyaline, washed with brown, posterior 1/2 of tergum 7 and entire terga 8-10 light brown; posterior margin of terga 1-10 washed lightly with brownish-black, terga 1-9 with brownish-black sublateral marks, terga 1-2 with large median brownish-black marks, tergum 3 with submedian brownish-black marks, terga 4-5 with to without small submedian brownish-black macula near margin, terga 6-8 with





FIGURES 4-15. Imaginal fore and hind wings. Schematic wings, with abbreviations of venational terminology: 4, fore wing; 5, hind wing; 6, hind wing enlarged. *Miroculis (M.) rossi*, male: 7, fore wing; 8, hind wing; 9, hind wing enlarged. *M. (M.) fittkai*: 10, male fore wing; 11, male hind wing; 12, female, basal 1/3 of fore wing. *M. (M.) marauiaie*, male: 13, fore wing; 14, hind wing; 15, hind wing enlarged.



FIGURES 16-27. Male imaginal fore and hind wings. *Miroculis (Yaruma)* sp.: 16, fore wing; 17, hind wing; 18, hind wing enlarged. *Miroculis (Atroari) amazonicus*: 19, fore wing; 20, hind wing; 21, hind wing enlarged. *Miroculis (Ommaethus) mourei*: 22, fore wing; 23, hind wing; 24, hind wing enlarged. *Miroculitus emersoni*: 25, fore wing; 26, hind wing; 27, hind wing enlarged.

brownish-black submedian marks which expand apically as in Figs. 99-100, tergum 10 with posteromedian 1/2 washed with brownish-black; spiracles brownish-black, tracheae light brown; sterna 1-7 semihyaline, washed with brown, sterna 8-9 light brown. Forceps (Fig. 57): segment 3 from 0.80-0.88 (n = 5) length of segment 2; segment 2 from 0.33-0.43 (n = 5) length of segment 1; basal 1/2 of inner margin of segment 1 gradually narrows apically, distal inner margin not developed (Fig. 57); distal 1/3 of segment 1 and all of segments 2 and 3 washed with black. Styli-plate (Fig. 57): maximum length along lateral margin 0.50-0.53 (n = 5) maximum width; maximum length along median line 0.34-0.38 (n = 5) maximum width; posteromedian margin gently rounded as in Fig. 57; brown. Penes (Fig. 57): length 0.86-1.02 (n = 5) length of forceps segment 1, tubular, apex excavated as in Fig. 57; brown. Caudal filaments light brown, subequal in length, basal 1/2 of caudal filaments with articulations of segments black.

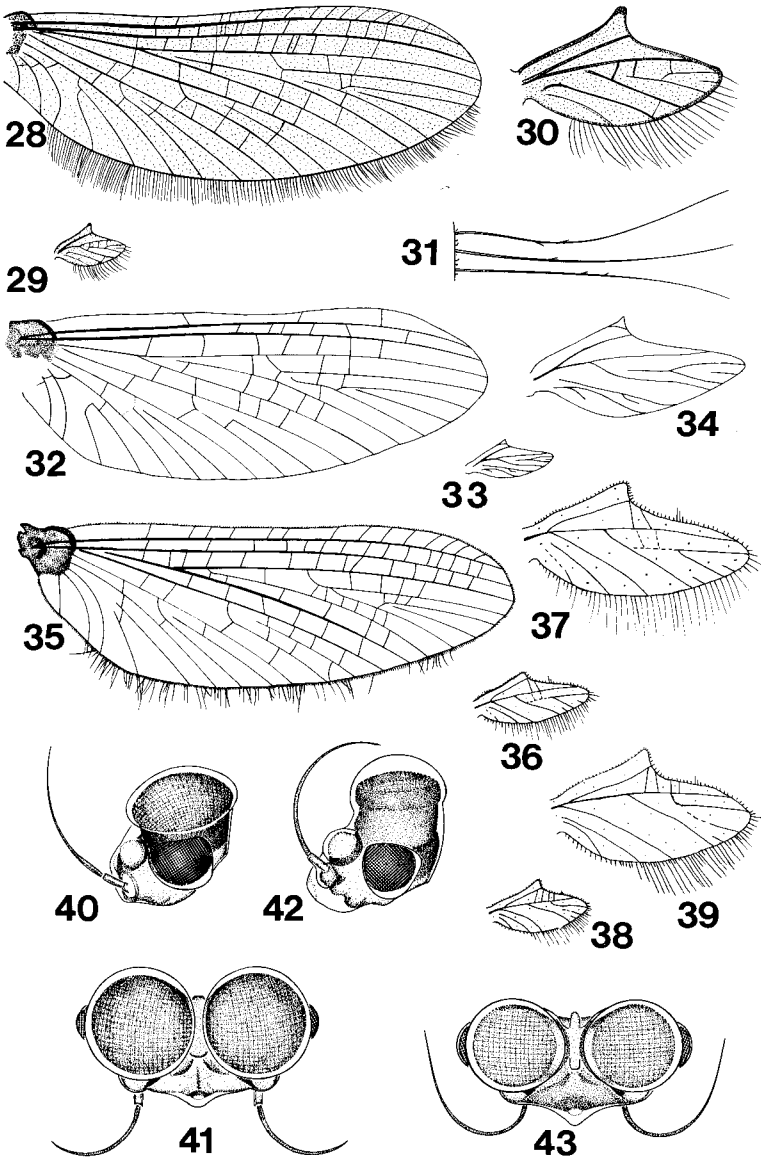
**FEMALE IMAGO** (in alcohol). Length: body, 4.5 mm; fore wings, 4.5 mm. Eyes black. Head light brown, ventral surface and carinae of dorsal surface brownish-black. Scape and pedicel dark brown, flagellum pale yellow. Ocelli as in male imago. Thorax: color and marks as in male imago. Wings: veins and color as in male imago. Legs: [broken from specimen at coxae and missing]. Abdomen (Fig. 101): color and marks on terga as in male imago except brownish-black wash heavy such that color pattern obscured producing submedian marks on terga 2-8 as in Fig. 101, submedian marks on terga 4 and 8 lighter; spiracles and tracheae as in male imago; sterna 1-6 semihyaline, washed very lightly with brown, sterna 7-9 light brown, washed with brownish-black. Caudal filaments: [broken off specimen and missing].

**MATURE NYMPH** (in alcohol). Body length, 4.0-5.5 mm. Eyes: eyes of female black; upper portion of eyes of male yellow, lower portion black. Head brownish-yellow, lateral edges of genae brownish-black. Basal 2/3 of ocelli black, apical 1/3 white. Scape and pedicel light brown, washed heavily with brownish-black, flagellum pale yellow. Mouthparts (Figs. 142-147): anterolateral margins of labrum slightly flattened (Fig. 142); length of subapical row of setae on maxillae 0.47-0.60 (n = 4) length of apical row, subapical row with 31-39 (n = 4) pectinate setae, segment 2 of maxillary palpi 1.07-1.20 (n = 4) length of segment 1, segment 3 of maxillary palpi 0.50-0.57 (n = 4) length of segment 2; segment 2 of labial palpi 1.11-1.25

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FIGURES 28-39. Fore and hind wings. *Microphlebia surinamensis*, male subimago: 28, fore wing; 29, hind wing; 30, hind wing enlarged; 31, wing setae enlarged. *Hermanellopsis incertans*, male imago: 32, fore wing; 33, hind wing; 34, hind wing enlarged. *Hermanellopsis arsia*, male subimago with hind wing variation: 35, fore wing; 36, hind wing; 37, hind wing enlarged; 38, hind wing; 39, hind wing enlarged.

FIGURES 40-43. Subimaginal male eyes of *Microphlebia*. *M. pallida*: 40, lateral view; 41, dorsal view. *M. surinamensis*: 42, lateral view; 43, dorsal view.



(n = 4) length of segment 1, segment 3 of labial palpi 0.45-0.48 (n = 4) length of segment 2, labium light yellow, base of submentum brownish-black. Thorax: nota and sterna brownish-yellow, brownish-black marks on pronotum as in male imago, mesonotum with margins washed with brownish-black; pleura brownish-yellow, washed with brownish-black. Legs (Fig. 157): brownish-yellow, brownish-black marks as in male imago, except median macula prominent only on metathoracic legs; prothoracic claw as in Fig. 157. Abdomen: brownish-yellow, tergum 3 with 2 submedian marks to 1 large median brownish-black mark, remainder of terga as in male or female imago; sterna 1-9 with posterolateral corners brownish-black. Posterolateral spines on abdominal segments 2-3 to 9, developed beyond posterior margin of terga on segments 3-9, spines well developed on segments 5-6 to 9. Gills (Figs. 121-123): small, posterolateral projections not greatly developed (Fig. 121) to greatly reduced (Fig. 123), outer basal margin of dorsal portion not developed anteriorly; membrane grayish, translucent; tracheae black, unbranched. Caudal filaments brownish-yellow, basal 5 segments with articulations dark brown to brownish-black.

**SPECIMENS EXAMINED** (Fig. 168; locality f): Holotype male imago, BRAZIL: *Amazonas State*, Rio Marauia, 3 days trip above S. Antonio Mission, N.W. of Taparuquara, 28-I-1963, E.J. Fittkau. Allotype female imago, same data as holotype. Paratypes: 43 male imagos, same data as holotype; 3 male imagos, same data as holotype except date of collection is 25-I-1963; 1 male subimago and 12 nymphs, same data as holotype except date of collection is 24-I-1963; 2 nymphs, BRAZIL: *Amazonas State*, mountain stream II, near Rio Marauia, 3 days trip above S. Antonio Mission, N.W. of Taparuquara, 26-27-I-1963, E.J. Fittkau; 1 nymph, BRAZIL: *Amazonas State*, below waterfall, S. Antonio Creek, near S. Antonio Mission, Rio Marauia, N.W. of Taparuquara, 9-I-1963, E.J. Fittkau.

Holotype, allotype, 8 male imaginal and 3 nymphal paratypes are deposited in INPA collections. Eighteen male imaginal, 1 male subimaginal and 6 nymphal paratypes are deposited in collections of FAMU. Fourteen male imaginal and 3 nymphal paratypes are deposited in collections of UU. Six male imaginal and 3 nymphal paratypes are deposited in ZSBS.

**LIFE CYCLE ASSOCIATIONS:** Male and female imagos are associated by the unique condition of vein MP<sub>2</sub> of the fore wings (Fig. 13), and by shared color patterns. Nymphs are associated with imagos by shared abdominal color patterns. All specimens were collected in the same area over a 4 day period.

**ETYMOLOGY:** Species is named for Rio Marauia, type locality. Noun in the genitive case.

**DISCUSSION.** Imagos of *M. marauiae* can be distinguished from imagos of all other species within *M. (Mirocolis)* by the following combination of characters: (1) upper portion of male eye has 8-9 facets in longest row; (2) vein MP<sub>2</sub> of fore wings is free basally to attached at base to vein IMP by a cross vein (Fig. 13); (3) membrane of wings is hyaline; (4) ratio of femora to tibiae of male prothoracic legs is approx-

imately 0.59; length of prothoracic tibiae is approximately 1.6 mm; (5) median area of abdominal terga 6-8 has brownish-black submedian marks as in Figs. 99-101; (6) basal 1/2 of inner margin of forceps segment 1 gradually narrows apically, distal margin is not developed (Fig. 57); (7) male styliiger plate is as in Fig. 57, with posteromedian margin gently rounded; (8) penes are 0.8-1.1 length of forceps segment 1; penes are tubular, apex excavated as in Fig. 57; and (9) basal 1/2 of caudal filaments with articulations of segments black.

Nymphs of *M. marauiae* can be distinguished from all known nymphs of *Miroculis* by the following combination of characters: (1) anterolateral margins of labrum are slightly flattened as in Fig. 142; (2) abdominal terga have alternating pattern, terga 2-3 dark, terga 4-5 light, terga 6-8 dark (Fig. 99); (3) abdominal terga 6-8 are brownish-yellow with median and sublateral brownish-black marks (Figs. 99-101); (4) gills are small and narrow, posterolateral projections are not greatly developed to reduced (Figs. 121-123); and (5) caudal filaments are brownish-yellow, articulations of segments darker.

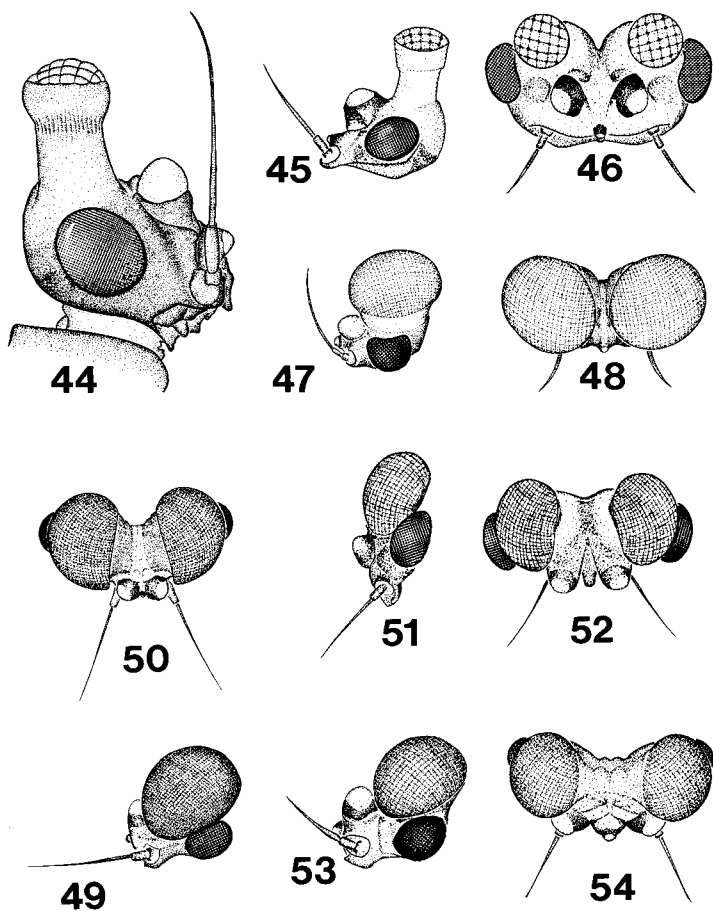
Longitudinal and cross veins of wings in *M. marauiae* are very weak and cross veins may often appear broken. Vein  $MP_2$  is not attached at base to vein  $MP_1$  by a cross vein in any of the 48 imaginal specimens available. In the majority of specimens vein  $MP_2$  is free basally (Fig. 13). However, vein  $MP_2$  may be attached at base to vein  $IMP_2$  by a cross vein.

Within the single locality, 3 days trip above S. Antonio Mission, abdominal color patterns of nymphs and imagos vary. Typically, the observed color pattern of terga 3-8 is as in Figs. 99-101. However, in some nymphal specimens, the submedian marks of tergum 3 may fuse to form a single median mark. Terga 4-5 usually lack submedian marks, although some imaginal specimens do have small brownish-black submedian maculae near the posterior margin. The submedian marks on terga 6-8, especially tergum 6, often coalesce basally to produce a V-shaped mark with the open end of the V directed posteriorly. Also, in highly pigmented specimens tergum 1 may be completely brownish-black.

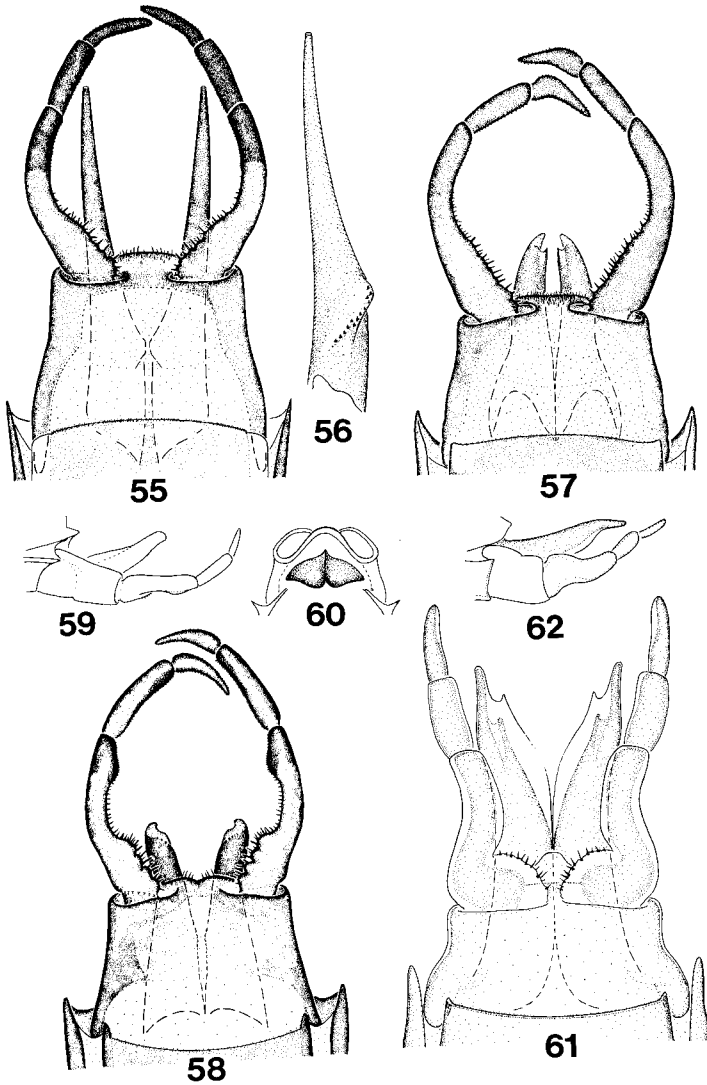
The posterolateral projections of nymphal gills are usually present, but not greatly developed as in Fig. 121. However, in small specimens the posterolateral projections of the dorsal gill portion may be greatly reduced to absent (Fig. 122). The main tracheal trunk of nymphal gills may bend back upon itself. The bend is usually located near the apex of the gill body and may appear as a black spot (Fig. 123). This phenomenon has also been observed in *M. (Ommaethus) mourei*, *M. (Miroculis) fittkai* and in *Leptophlebia intermedia* from Rocky Comfort Creek in Northwest Florida.

**BIOLOGY.** Collection records indicate that imagos of *M. marauiae* emerge in January and February.

Most nymphs were collected from leaves in fast current. However, 2 specimens were collected on leaves and sticks in an area of little or no current. (Translated from Dr. E.J. Fittkau's field notes).

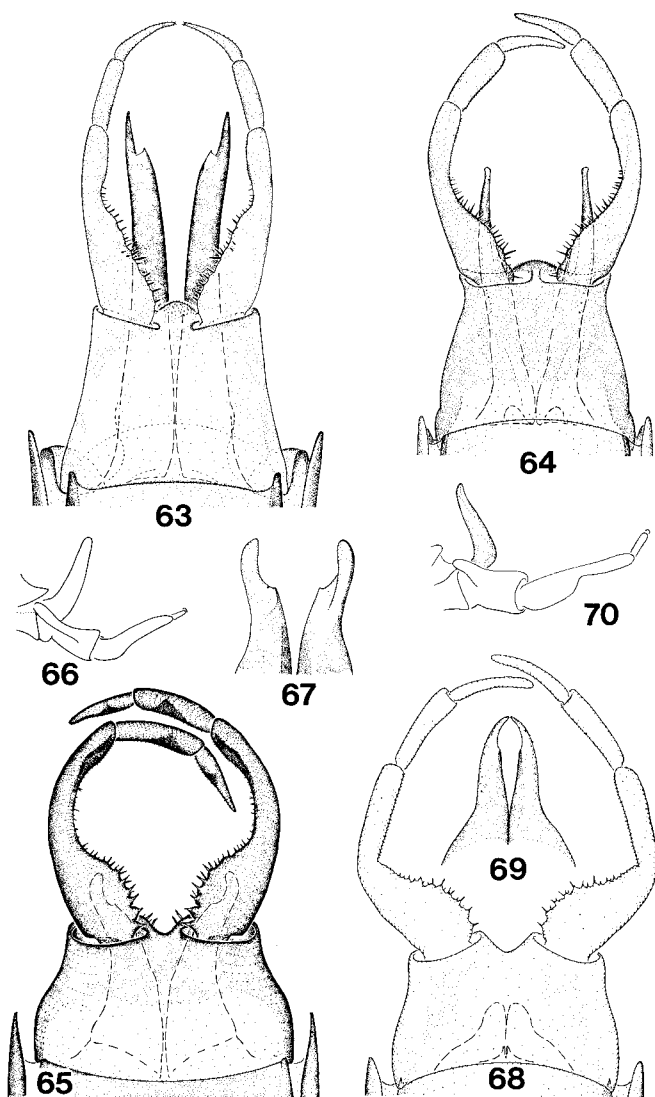


FIGURES 44-54. Male imaginal eyes of *Miroculis*. *M. (M.) rossi*: 44, lateral view (from Edmunds 1963). *M. (M.) fittkai*: 45, lateral view; 46, dorsal view. *M. (Yaruma)* sp.: 47, lateral view; 48, dorsal view. *M. (Atroari) duckensis*: 49, lateral view; 50, dorsal view. *M. (Ommaethus) mourei*: 51, lateral view; 52, dorsal view. *M. (O.) froehlichii*: 53, lateral view; 54, dorsal view.

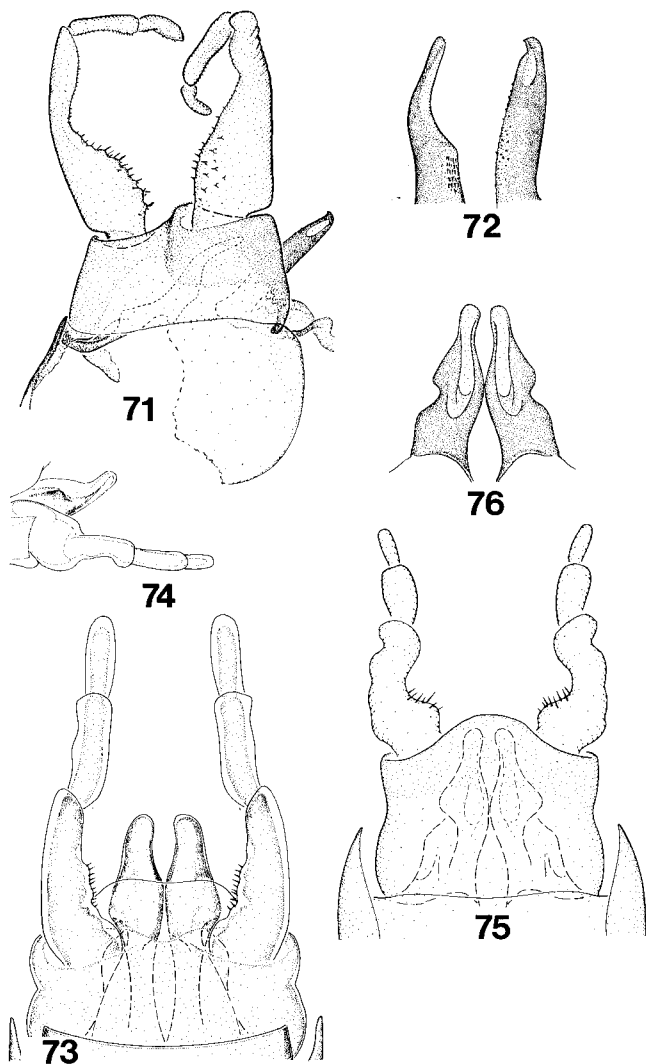


FIGURES 55-62. Male genitalia of *Miroculis*. *M. (Miroculis) rossi*, imago: 55, ventral view; 56, ventral view of penis lobe. *M. (M.) marauiae*, imago: 57, ventral view. *M. (M.) fittkaui*, imago: 58, ventral view; 59, lateral view; 60, posterodorsal view. *M. (Yaruma) wandae*, subimago: 61, ventral view; 62, lateral view.

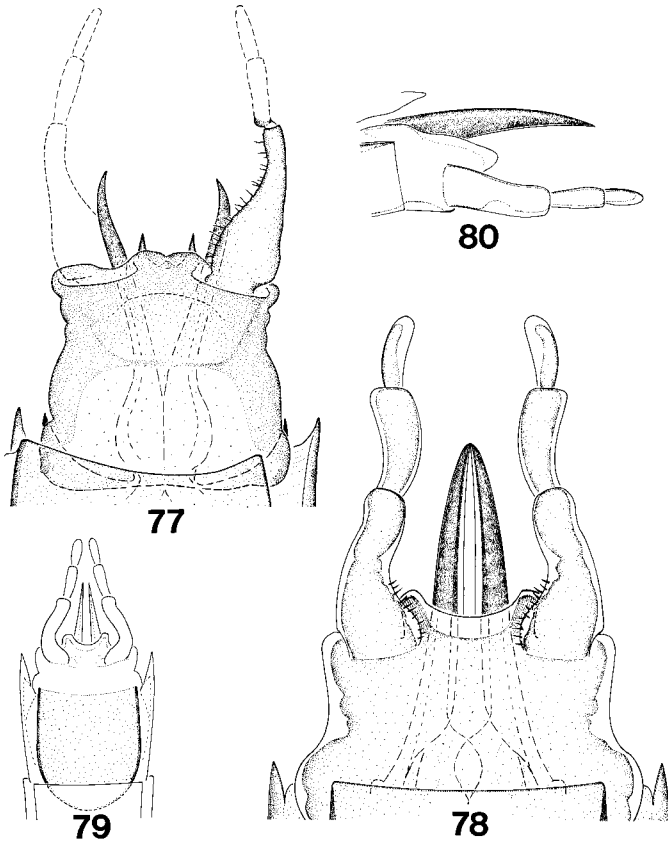




FIGURES 63-70. Male imaginal genitalia of *Miroculis*. *M. (Atroari) amazonicus*: 63, ventral view. *M. (A.) duckensis*: 64, ventral view. *M. (Ommaethus) mourei*: 65, ventral view; 66, lateral view; 67, dorsal (left) and ventral (right) views of apex of penis lobe. *M. (O.) froehlichii*: 68, ventral view; 69, ventral view of penes; 70, lateral view.



FIGURES 71-76. Genitalia of male. *Miroculitus emersoni*, imago: 71, ventral view; 72, apical portion of penes enlarged. *Mirophlebia surinamensis*, subimago: 73, ventral view; 74, lateral view. *Mirophlebia pallida*, subimago: 75, ventral view; 76, ventral view of penes.



FIGURES 77-80. Male genitalia of *Hermanellopsis*. *H. incertans*, imago: 77, ventral view. *H. arsia*, subimago: 78, ventral view; 79, ventral view of sternum 9 and genitalia; 80, lateral view.

**Miroculis (Miroculis) fittkaui** NEW SPECIES

Figs. 10-12, 45-46, 58-60, 81-82, 87, 91, 96, 97-98, 124-125, 137, 168

MALE IMAGO (in alcohol). Length: body 4.9-6.2 mm; fore wings, 4.5-5.2 mm; prothoracic legs, 4.9-5.5 mm. Eyes (Figs. 45-46): apex of upper portion separated on meson of head by a length 0.8-1.5 diameter of an upper portion; stalked turbinate portion long, light brown at base, paler apically; facets of turbinate portion large, 5-6 complete facets in longest row, light yellow, separated by dark brown grooves; facets of lower portion black, small. Head light brown, washed with brownish-black. Scape and pedicel brownish-yellow with light brownish-black wash, flagellum pale yellow. Basal 1/2 of ocelli brownish-black, apical 1/2 white. Thorax: pronotum brownish-yellow, remainder of thorax brown, carinae and margins of sclerites dark brown to brownish-black; sterna brown, carinae and margins of sclerites dark brown; pleura brown, washed with brownish-black, margins of sclerites darker, median areas lighter. Wings (Figs. 10-11): longitudinal and cross veins brown; membrane hyaline to very light brown, fore wings darker brown near base, and with darker brown clouds around cross veins, apical 1/3 of cells of C and Sc of fore wings translucent and whitish, hind wings of uniform color to darker brown near apex. Legs (Fig. 91): ratios of segments in male prothoracic legs, 0.56-0.61: 1.00(1.90-2.20 mm): 0.02-0.03: 0.36-0.39: 0.26-0.31: 0.17-0.19: 0.06-0.09; light brown, a small brownish-black macula on both sides of femora near middle, paler on prothoracic legs, apical 1/5 of femora brownish-black, paler on prothoracic legs, a brownish-black band near apex of tibiae, paler on prothoracic legs; prothoracic claws as in Fig. 91. Abdomen (Figs. 97-98): terga 1-7 semihyaline, washed lightly with brown to light brown, terga 8-10 brownish-yellow to light brown; terga 1-10 with posterior margins brownish-black, terga 1-9 with sublateral brownish-black marks, terga 1-3 with brownish-black submedian marks, terga 4-5 with or without brownish-black submedian marks, tergum 6 with a median brownish-black V-shaped mark, with open end of V directed posteriorly (Figs. 97-98), terga 7-9 with brownish-black submedian marks, submedian marks faded on tergum 9; spiracles brownish-black, tracheae very light brown washed with brownish-black; sterna 1-7 semihyaline, washed lightly with brown to light brown, sternum 8 brownish-yellow to light brown, sternum 9 brown. Forceps (Figs. 58-60): segment 3 from 0.57-0.80 (n=9) length of segment 2; segment 2 from 0.47-0.58 (n=9) length of segment 1; basal 1/3-1/2 of inner margin of segment 1 abruptly narrows apically, distal 1/4 of inner margin developed (Fig. 58); distal 1/3 of segment 1 and all of segments 2 and 3 washed lightly to heavily with black. Styliger plate (Figs. 58-60): maximum length along lateral margin 0.50-0.70 (n=9) maximum width; maximum length along median line 0.40-0.48 (n=9) maximum width; posteromedian margin gently rounded with a shallow median indentation as in Fig. 58; brown. Penes (Figs. 58-60): length 0.92-1.29 (n=9) length of forceps segment 1, tubular, apex excavated as in Fig. 58; brown. Caudal filaments uniformly light brown, subequal in length.

FEMALE IMAGO (in alcohol). Length: body, 3.7-5.6 mm; fore wings, 4.1-5.8 mm. Eyes black. Head yellowish-black, carinae brownish-black. Scape and pedicel brownish-yellow, flagellum pale yellow. Ocelli as in male imago. Thorax: color and

marks as in male imago. Wings (Fig. 12): longitudinal and cross veins as in male imago, except  $MP_2$  may appear broken basally (Fig. 12); membrane as in male imago, except darker brown clouds around cross veins well developed to absent. Legs (Fig. 96): light brown, color marks as in male imago; prothoracic claws as in Fig. 96. Abdomen (Figs. 81-82, 87): brown, color pattern as in male imago except darker; genital extension as in Figs. 81-82; sternum 9 as in Fig. 87. Caudal filaments light brown to brown.

MATURE NYMPH (in alcohol). Body length, 4.3-6.2 mm. Eyes: eyes of female black; upper portion of eyes of male yellow, lower portion black. Dorsum of head brownish-yellow, anterolateral margins of genae washed with brownish-black; venter pale yellow. Basal 2/3 of ocelli black, apical 1/3 white. Scape and pedicel brownish-yellow, washed lightly with brownish-black, flagellum pale yellow. Mouthparts (Fig. 137): anterolateral margins of labrum flattened (Fig. 137); length of subapical row of setae on maxillae 0.52-0.59 ( $n=4$ ) length of apical row, subapical row with 44-49 ( $n=4$ ) pectinate setae, segment 2 of maxillary palpi 1.02-1.09 ( $n=4$ ) length of segment 1, segment 3 of maxillary palpi 0.41-0.51 ( $n=4$ ) length of segment 2; segment 2 of labial palpi 1.00-1.22 ( $n=4$ ) length of segment 1, segment 3 of labial palpi 0.50-0.60 ( $n=4$ ) length of segment 2, labium light yellow. Thorax: mesonotum and metanotum light brown, remainder of thorax brownish-yellow, marks as in male imago. Legs: brownish-yellow, brownish-black marks as in male imago. Abdomen: brownish-yellow, brownish-black marks as in male imago. Posterolateral spines on abdominal segments 2-9, developed beyond posterior margin of terga on segments 3-9, spines well developed on segments 6-9. Gills (Figs. 124-125): small, posterolateral projections not greatly developed, outer basal margin of dorsal portion not developed anteriorly; membrane grayish, translucent; tracheae black, unbranched. Caudal filaments uniformly light brown.

SPECIMENS EXAMINED (Fig. 168; localities g, i): Holotype male imago, BRAZIL: *Pará State*, Akahe Creek, near Tiriyo Mission, near Brazil-Surinam border, 15-III-1962, E.J. Fittkau. Allotype, female imago, same data as holotype. Paratypes: 29 male imagos, 20 female imagos, 13 nymphs, same data as holotype; 25 female imagos, BRAZIL: *Pará State*, Moeneni Creek, near Tiriyo Mission, near Brazil-Surinam border, 30-III-1962, E.J. Fittkau; 3 male imagos, 7 female imagos, SURINAM: *Brokopondo Dist.*, Kreek on N. edge of Brokopondo, 300', 23-XII-1968, W.L. and J.G. Peters; 1 nymph, same as previous paratypes except date of collection is 26-XII-1968; 4 nymphs, SURINAM: *Para Dist.*, Carolina Kreek, 6 km. N. of Zauderij, 200', 20-XII-1968, W.L. and J.G. Peters; 16 female imagos, SURINAM: *Brokopondo Dist.*, Brokopondo, road to Brownsweag, Km 13 stream-let, 22-I-1969, N. Nieser; 39 female imagos, SURINAM: *Para Dist.*, Zanderij savanne, Carolina Kreek, 25-VIII-1969, Ephemeroptera lying dead on sand flat, N. Nieser; 19 female imagos, SURINAM: *Saramacca Dist.*, Coesewijne Project, source region of the Coesewijne River, stream-let 17 km. W. of Saramacca-Brug, 23-IV-1970, small bare sand-flat, N. Nieser.

Holotype, allotype, 5 male imaginal, 8 female imaginal and 3 nymphal paratypes are deposited in the collections of INPA. Twelve male imaginal, 35 female imaginal and 7 nymphal paratypes are deposited in FAMU collections. Nine male imaginal,

35 female imaginal and 5 nymphal paratypes are deposited in collections of UU. Four male imaginal, 12 female imaginal and 3 nymphal paratypes are deposited in ZSBS collections. Two male imaginal and 20 female imaginal paratypes are deposited in collections of RNH.

LIFE CYCLE ASSOCIATIONS: Rearing by Dr. E.J. Fittkau.

ETYMOLOGY: Species is named for Dr. E.J. Fittkau, Zoologische Sammlung des Bayerischen Staates.

DISCUSSION. Imagos of *M. fittkai* can be distinguished from imagos of all other species within *M. (Miroculis)* by the following combination of characters: (1) membrane of wings is hyaline to very light brown, fore wings with darker brown clouds around cross veins (Figs. 10-11); (2) ratio of femora to tibiae of male prothoracic legs is 0.56-0.61; length of male prothoracic tibiae is 1.9-2.2 mm; (3) median area of abdominal tergum 6 has a median brownish-black V-shaped mark, with open end of V directed posteriorly (Figs. 97-98); (4) basal 1/3-1/2 of inner margin of forceps segment 1 abruptly narrows apically, distal 1/4 of inner margin is developed (Fig. 58); (5) male styliiger plate is shaped as in Figs. 58-60, posteromedian margin is gently rounded with a shallow median indentation; and (6) penes are 0.9-1.3 length of forceps segment 1; penes are tubular, excavated apically as in Fig. 58.

Nymphs of *M. fittkai* can be distinguished from known nymphs of all species within *Miroculis* by the following combination of characters: (1) anterolateral margins of labrum are flattened (Fig. 137); (2) subapical row of maxillae has 44-49 pectinate setae; (3) abdominal terga have alternating color pattern, terga 2-3 dark, terga 4-5 light, tergum 6 dark, terga 7-8 lighter (Fig. 97); (4) abdominal tergum 6 has a brownish-black median V-shaped mark with open end of V directed posteriorly (Figs. 97-98); (5) gills are small, posterolateral projections are not greatly developed (Figs. 124-125); and (6) caudal filaments are uniformly light brown.

Nymphs of *M. fittkai* and *M. (Miroculis) brasiliaensis* have similar abdominal color patterns which may confuse identification. However, nymphs of *M. fittkai* can be distinguished from *M. brasiliaensis* by characters 2, 5 and 6 listed above, and by the color pattern of abdominal tergum 3 (Fig. 97) which does not have submedian pale spots as in *M. brasiliaensis* (Fig. 112).

*Miroculis fittkai* is known from Brazil, near the Brazil-Surinam border (Fig. 168, g), and north-central Surinam (Fig. 168, i). Specimens from these two countries differ in several respects. The abdomen of imagos and subimagos from Surinam, especially females, is darker, while the abdomen of Brazilian specimens is lighter. In specimens from Surinam, the hind wings are of uniform color, while they are darker brown near the apex in specimens from Brazil (Fig. 11). Only 3 male imagos are known from Surinam, but the limited data suggest that prothoracic femora/tibiae ratios are larger in specimens from Surinam [0.59-0.61/1.00(1.90-2.07 mm)], than in specimens from Brazil [0.56-0.59/1.00(2.00-2.20 mm)]. Imagos from Brokopondo and Para Districts of Surinam are smaller than the Brazilian specimens. However, female imagos from Saramacca District, Surinam, are by far the largest known specimens of *M. fittkai*. Nymphs from the two countries appear very similar, however, the inner posterolateral projection of the dorsal gill portion is longer in the specimens from Surinam (Fig. 125) than in those from Brazil (Fig. 124).

Fore and hind wings of females are more variable than those of males. Wings of all males and most females from Akahe Creek, Brazil, have color patterns as in Figs. 10-11. However, small females generally have reduced pigment and a few specimens retain dark brown pigment only on the cross veins. Females from Moeneni Creek, Brazil, are smaller than those from Akahe Creek and most have reduced pigmentation. Vein  $MP_2$  of fore wings may appear broken (Fig. 12), and cross veins may be reduced in number in small specimens.

The inner basal margin of forceps segment 1 is usually corrugated in males of *Miroculis* (Fig. 58). However, 1 of the 30 male specimens from Akahe Creek, Brazil, has a smooth inner margin. Within these 30 specimens, the posteromedian indentation of the styliiger plate varies from well developed (Fig. 58) to very weakly developed.

In a limited number of specimens from all localities the V-shaped mark on abdominal tergum 6 (Figs. 97-98) appears as 2 diagonal lines which are not fused anteriorly.

The main tracheal trunk of nymphal gills may bend back upon itself. The bend is usually located near the apex of the gill body and may appear as a black spot. This phenomenon has also been observed in *M. (Miroculis) marauiae* (Fig. 123), *M. (Ommaethus) mourei* and in *Leptophlebia intermedia* from Rocky Comfort Creek in Northwest Florida.

**BIOLOGY.** Collection records indicate that imagos of *M. fittkai* emerge in March and April in northern Brazil, and in April, August, December and January in Surinam.

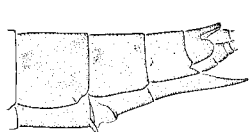
In Brazil, nymphs were collected in streams 3-5 m wide, 20-50 cm deep, with sandy bottoms and partly exposed bedrock. Most nymphs were found on leaves and

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FIGURES 81-86. Genital extension of female imago. *Miroculis (M.) fittkai*: 81, lateral view of segments 7-10; 82, ventral view of posterior margin of sternum 7. *M. (Ommaethus) mourei*: 83, lateral view of segment 7; 84, ventral view of posterior margin of sternum 7. *Hermanellopsis incertans*: 85, lateral view of segment 7; 86, ventral view of posterior margin of sternum 7.

FIGURES 87-89. Ventral view of sternum 9 of female imago. *Miroculis (M.) fittkai*: 87. *M. (Ommaethus) mourei*: 88. *Hermanellopsis incertans*: 89.

FIGURES 90-96. Prothoracic claws of adult. *Miroculis (M.) rossi*: 90, male imago. *M. (M.) fittkai*: 91, male imago. *M. (Ommaethus) mourei*: 92, male imago. *Miroculitus emersoni*: 93, male subimago. *Hermanellopsis arsia*: 94, male subimago. *Microphlebia surinamensis*: 95, male subimago. *Miroculis (M.) fittkai*: 96, female imago.



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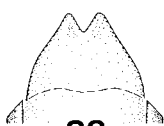
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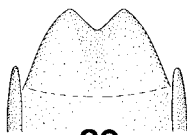
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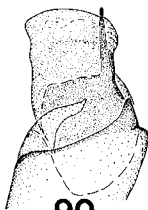
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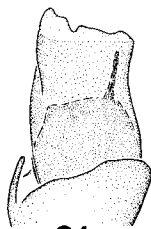
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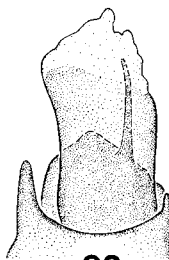
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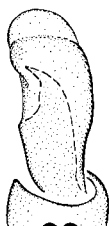
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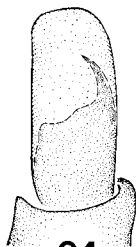
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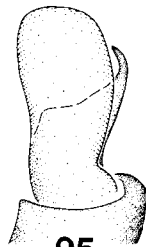
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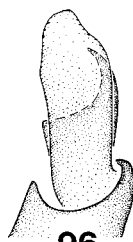
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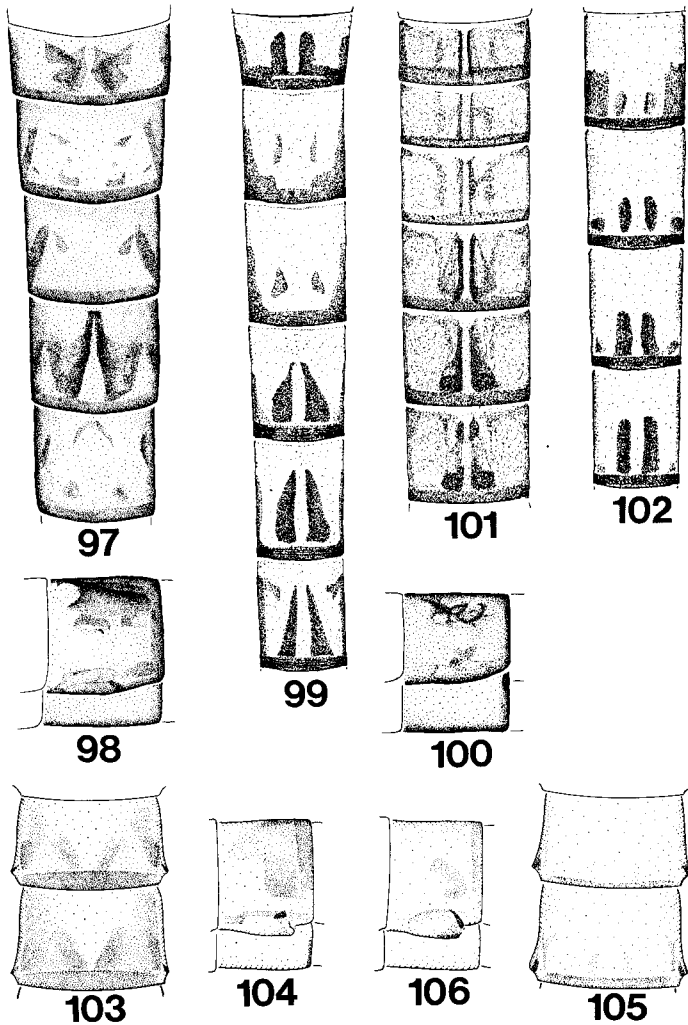


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FIGURES 97-106. Abdominal color patterns of adult. *Miroculis* (*M.*) *fittkai*, male: 97, dorsal view of segments 3-7; 98, lateral view of segment 6. *M. (M.) marauia*: 99, male, dorsal view of segments 3-8; 100, male, lateral view of segment 6; 101, female, dorsal view of segments 3-8. *M. (Atroari) amazonicus*, male: 102, dorsal view of segments 4-7. *M. (Yaruma) wandae*, male: 103, dorsal view of segments 5-6; 104, lateral view of segment 6. *M. (Yaruma) sp.*, male: 105, dorsal view of segments 5-6; 106, lateral view of segment 6.

other large detrital fragments in areas of slow current. A few specimens were collected from fine detritus and sand in calm areas. (Translated from Dr. E.J. Fittkau's field notes).

### **Miroculis (Miroculis) brasiliaensis** NEW SPECIES

Figs. 112-113, 126, 168

MALE IMAGO: Unknown.

FEMALE IMAGO: Unknown.

MATURE NYMPH (in alcohol). Body length, 4.6-4.8 mm. Eyes: eyes of female black; upper portion of eyes of male blackish-gray, lower portion black. Head light brown, genae brownish-black. Basal 2/3 of ocelli black, apical 1/3 white. Scape and pedicel brownish-black, flagellum pale yellow. Mouthparts: anterolateral margins of labrum flattened; length of subapical row of setae on maxillae 0.48-0.51 (n=2) length of apical row, subapical row with 35-40 (n=2) pectinate setae, segment 2 of maxillary palpi 1.15-1.22 (n=2) length of segment 1, segment 3 of maxillary palpi 0.50-0.52 (n=2) length of segment 2; segment 2 of labial palpi 1.01-1.04 (n=2) length of segment 1, segment 3 of labial palpi 0.46-0.57 (n=2) length of segment 2, labium light yellow. Thorax: nota light brown, pronotum with submedian carinae and margins brownish-black, mesonotum and metanotum with carinae dark brown to brownish-black, mesonotum with anterolateral corners brownish-black; sterna brownish-yellow, posterior margin of prosternum and metasternum, anterior margin of mesosternum, lateral margins of mesosternum and metasternum brownish-black; pleura brownish-yellow, outer edges of sclerites brownish-black. Legs: brownish-yellow with prominent apical black bands on femora and tibiae, femora with faint median brownish-black macula, tibiae with faint brownish-black streak near base, prothoracic femora with brownish-black streak on dorsal basal edge. Abdomen (Figs. 112-113): terga brownish-yellow; terga 1-7 and tergum 10 with posterior margin brownish-black; terga 1-9 with sublateral brownish-black marks, lighter on terga 7-9; terga 1-2 with brownish-black median and sublateral marks; terga 3-9 with brownish-black submedian and sublateral marks, lighter on terga 8-9; terga 1-5 with all marks fused along posterior margin of each tergum; terga 1-2 with median and sublateral marks fused along anterior margin to enclose pale spots; tergum 3 with submedian and sublateral marks fused along anterior margin to enclose pale spots (Fig. 112); tergum 6 with submedian marks fused anteriorly to produce V-shaped mark, open end of V directed posteriorly (Figs. 112-113); spiracles brownish-black, tracheae light brown; sterna brownish-yellow. Posterolateral spines on abdominal segments 2-9, developed beyond posterior margin of terga on segments 3-9, spines well developed on segments 5-6 to 9. Gills (Fig. 126): large, posterolateral projections greatly developed, outer basal margin of dorsal portion not developed anteriorly; membrane grayish, translucent; tracheae black, branched apically (Fig. 126). Caudal filaments light brown, basal 5-9 segments with a black band on each segment.

SPECIMENS EXAMINED (Fig. 168; locality c): Holotype mature nymph, BRAZIL: Goiás State, Brasília, Creek on Belém Street, 16-XI-1960, W. Sattler. Paratypes: 6 nymphs, same data as holotype.

Holotype and 1 nymphal paratype are deposited in the USP collections. Five nymphal paratypes are deposited in FAMU collections.

LIFE CYCLE ASSOCIATIONS: None.

ETYMOLOGY: Species is named for the city of Brasília, type locality.

DISCUSSION. *Miroculis brasiliaensis* is known only from the nymphal stage. *M. brasiliaensis* can be distinguished from all known nymphs within *Miroculis* by the following combination of characters: (1) anterolateral margins of labrum are flattened; (2) subapical row of maxillae has 35-40 pectinate setae; (3) abdominal terga have alternating color pattern, terga 2-3 dark, terga 4-5 light, tergum 6 dark, terga 7-8 light (Fig. 112); (4) abdominal tergum 6 has a brownish-black median V-shaped mark, with open end of V directed posteriorly (Figs. 112-113); (5) abdominal tergum 3 has pale submedian spots enclosed by brownish-black marks (Fig. 112); (6) gills are large, posterolateral projections are greatly developed (Fig. 126); and (7) caudal filaments are light brown, basal 5-9 segments with black band on each segment.

Nymphs of *M. brasiliaensis* and *M. fittkai* both have a V-shaped mark on tergum 6 which could confuse identification. However, *M. brasiliaensis* nymphs can be distinguished from *M. fittkai* by characters 2, 5, 6 and 7 listed above.

Two male nymphal specimens are in the last nymphal instar and some submarginal structures are visible. The upper portion of the male eye appears to have 7-8 large facets on a stalk, and *M. brasiliaensis* is assigned to *M. (Miroculis)* on the basis of this character state.

Abdominal color patterns may be obscured by a light brown wash on some specimens.

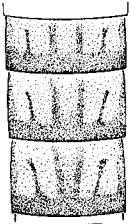
BIOLOGY: Collection of late instar nymphs indicates that *M. brasiliaensis* probably emerges at least from mid-November through December.

Nymphs were collected from a small creek in the city of Brasília.

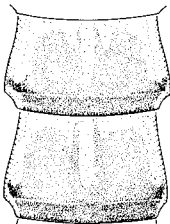
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FIGURES 107-111. Abdominal color patterns of adult. *Miroculis (Ommaethus) mourei*: 107, male, dorsal view of segments 4-6; 108, male, lateral view of segment 6; 109, female, dorsal view of segment 6. *Microphlebia surinamensis*, male: 110, dorsal view of segments 5-6; 111, lateral view of segment 6.

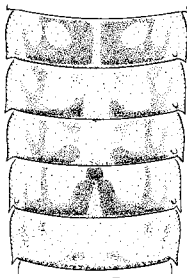
FIGURES 112-118. Abdominal color patterns of nymph. *Miroculis (M.) brasiliaensis*, mature nymph: 112, dorsal view of segments 3-7; 113, lateral view of segments 4-5. *M. (Atroari) duckensis*: 114, mature nymph, dorsal view of segments 2-10; 115, immature nymph, dorsal view of segments 2-10. *M. (A.) amazonicus*, mature nymph: 116, dorsal view of segments 2-10. *M. (A.) colombiensis*, mature nymph: 117, dorsal view of segments 4-10. Probable nymph of *M. (Ommaethus) froehlichii*, immature nymph: 118, dorsal view of segments 2-10.



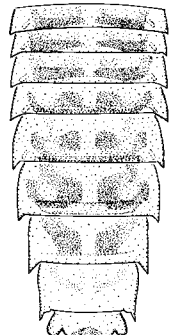
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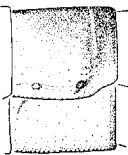
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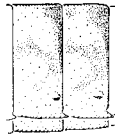
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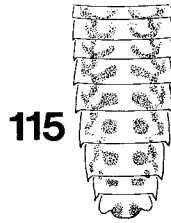
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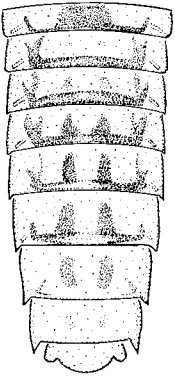
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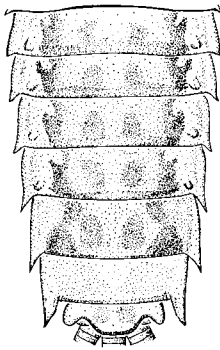
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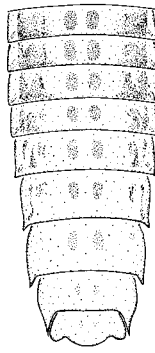
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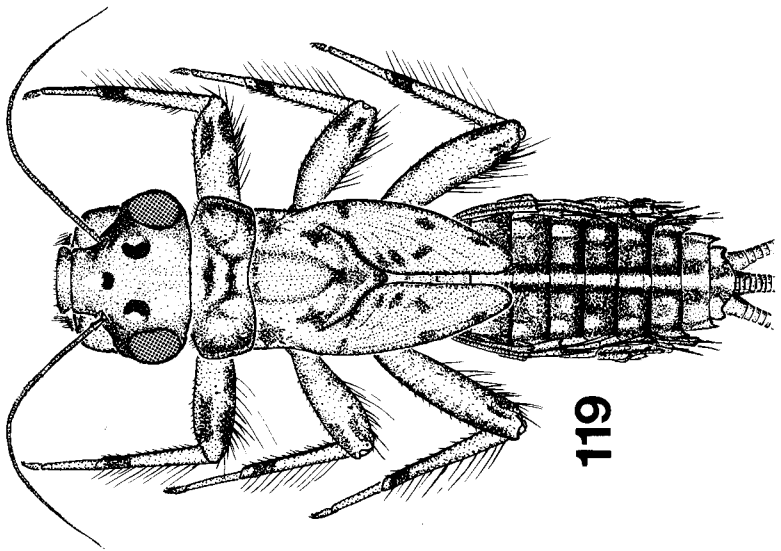
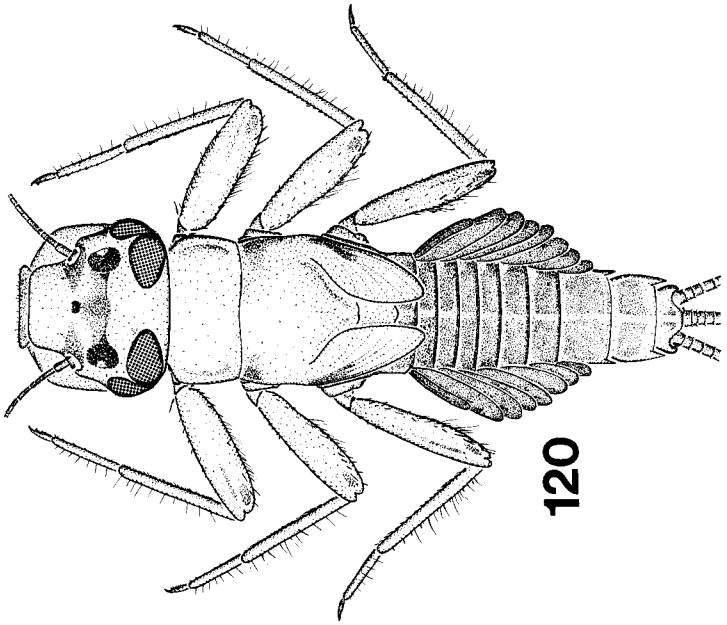
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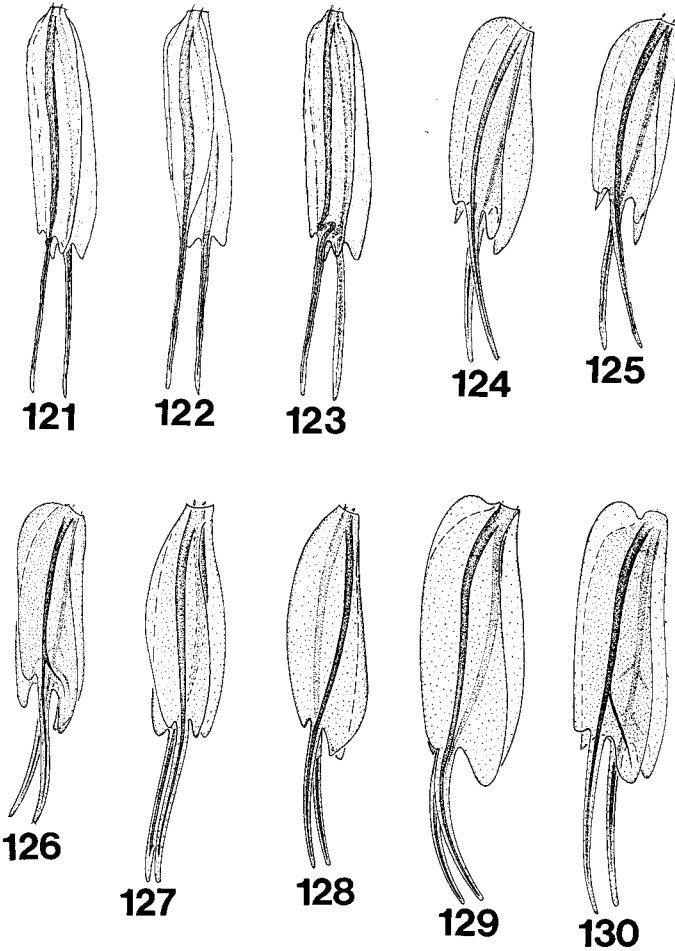
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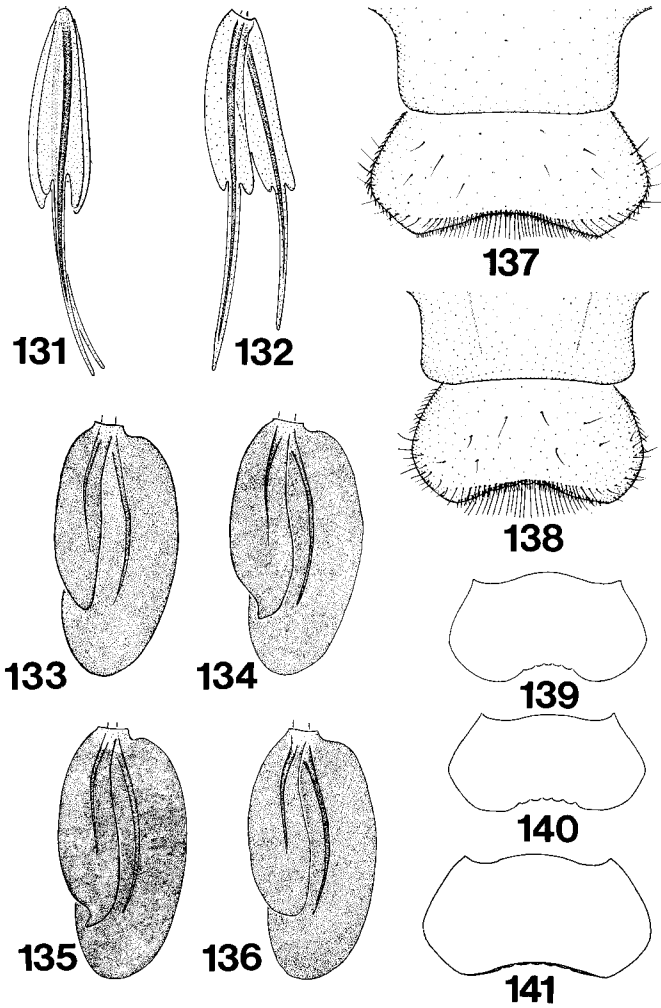
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FIGURES 119-120. Dorsal view of mature nymph. *Miroculis (Ommaethus) mourei*: 119, female. *Microphlebia surinamensis*: 120, male.

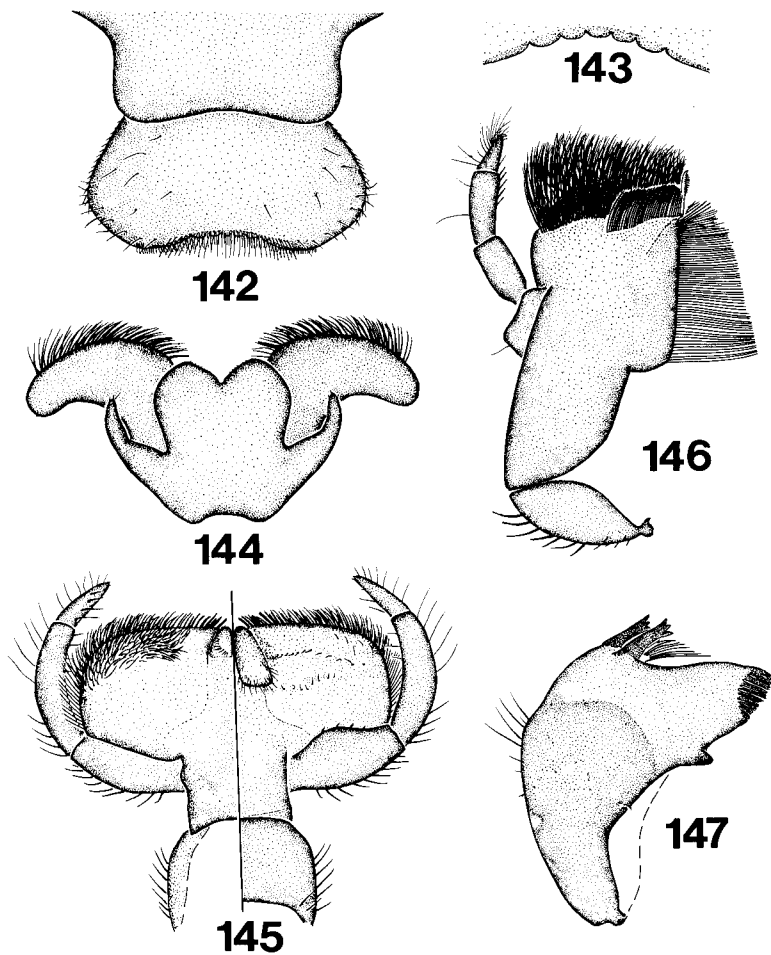


FIGURES 121-130. Left abdominal nymphal gill of *Miroculis*. *M. (M.) marauiae*: 121, typical gill 4; 122, gill 4 with posterolateral projections reduced; 123, gill 4 with aberrant trachea. *M. (M.) fittkai*: 124, gill 4 from Brazilian population; 125, gill 4 from population in Surinam. *M. (M.) brasiliaensis*: 126, gill 4. *M. (A.) duckensis*: 127, gill 4. *M. (A.) amazonicus*: 128, gill 1; 129, gill 4. *M. (A.) colombiensis*: 130, gill 4.



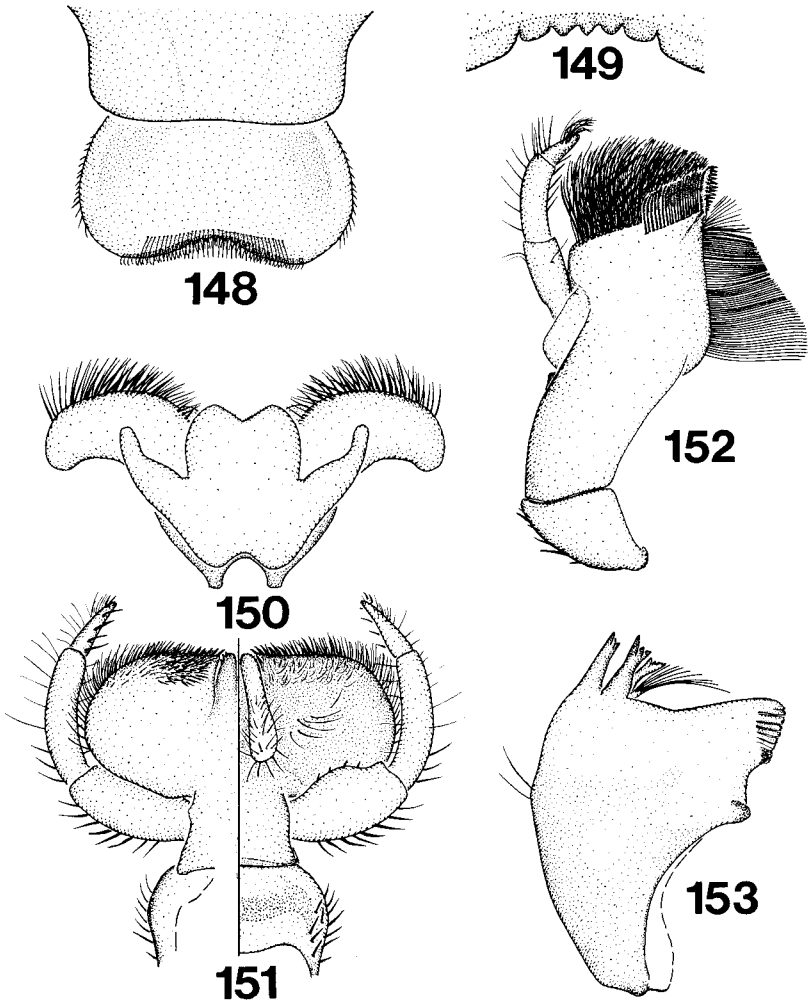
FIGURES 131-136. Left abdominal gill of nymph. *Miroculis (Ommaethus) mourei*: 131, gill 4. Probable immature nymph of *M. (O.) froehlichii*: 132, gill 4. *Microphlebia surinamensis*: 133, gill 1; 134-135, gill 4; 136, gill 7.

FIGURES 137-141. Nymphal clypeus and labrum of *Miroculis*. *M. (M.) fittkaui*: 137, labrum and clypeus. *M. (Ommaethus) mourei*: 138, labrum and clypeus; 139-140, variability in shape of labrum. Probable nymph of *M. (O.) froehlichii*: 141, shape of labrum.

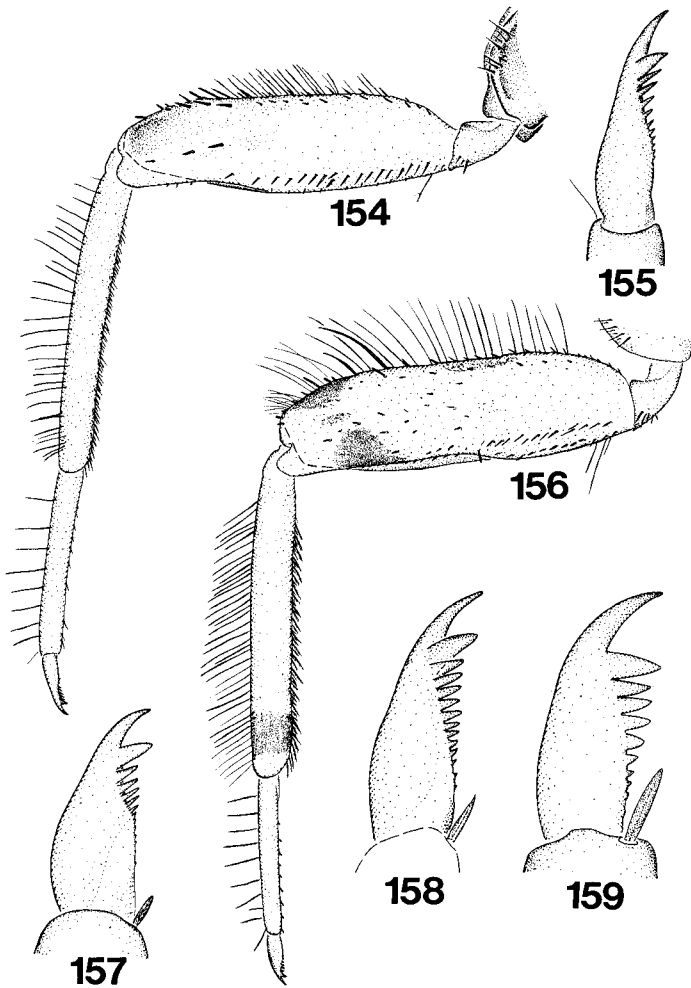


FIGURES 142-147. Mature nymphal mouthparts of *Miroculis* (*M.*) *marauiae*: 142, labrum and clypeus; 143, enlargement of denticles on labrum; 144, hypopharynx; 145, labium, dorsal (left) and ventral (right); 146, right maxilla; 147, left mandible.

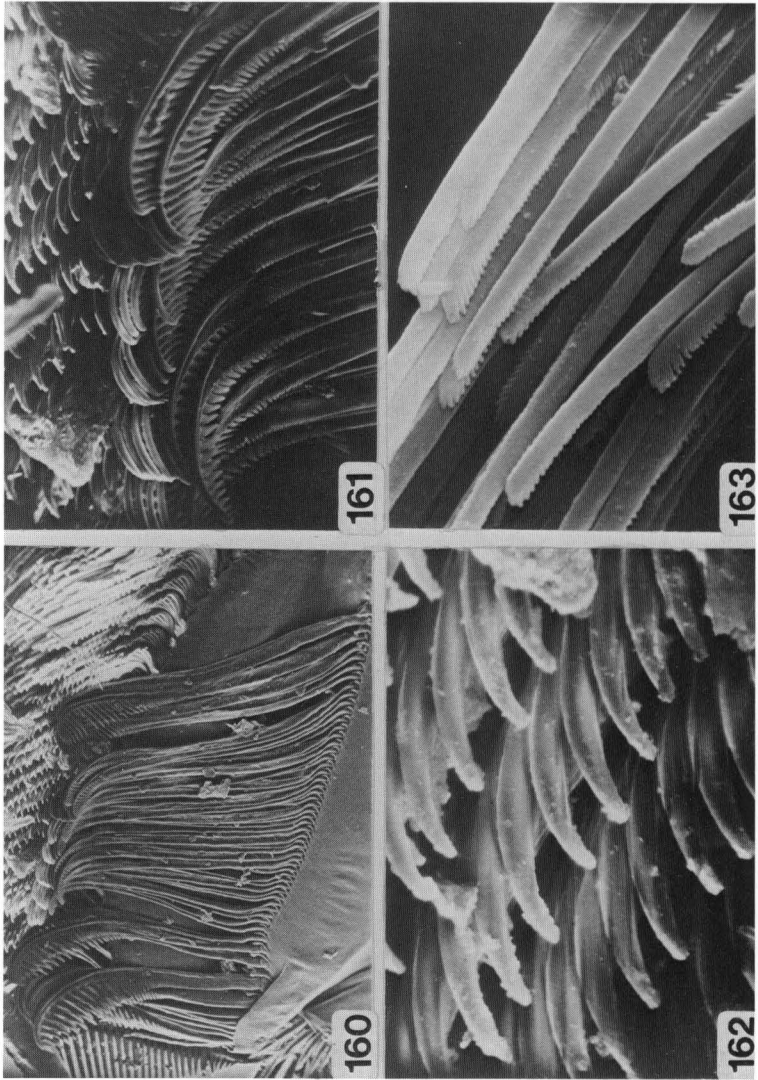




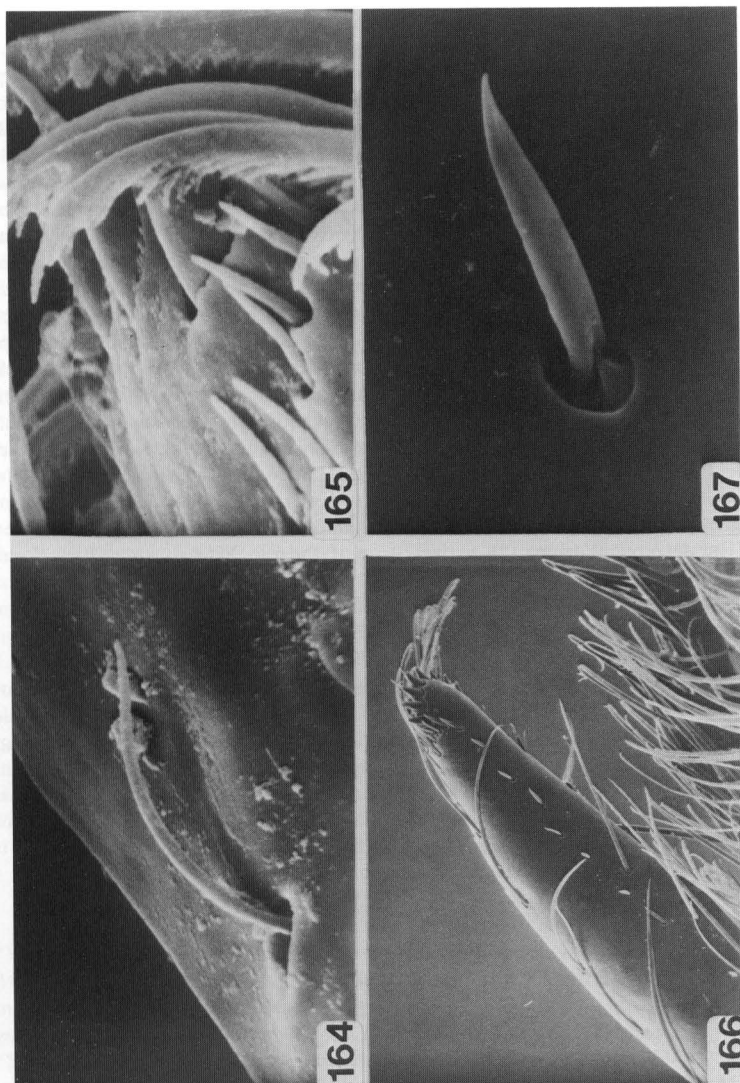
FIGURES 148-153. Mature nymphal mouthparts of *Microphlebia surinamensis*: 148, labrum and clypeus; 149, enlargement of denticles on labrum; 150, hypopharynx; 151, labium, dorsal (left) and ventral (right); 152, right maxilla; 153, left mandible.



FIGURES 154-159. Nymphal prothoracic legs and claws. *Microphlebia surinamensis*: 154, leg; 155, claw enlarged. *Miroculis (Ommaethus) mourei*: 156, leg. *M. (Miroculis) marauiae*: 157, claw enlarged. *M. (Atroari) amazonicus*: 158, claw enlarged. *M. (A.) colombiensis*: 159, claw enlarged.



FIGURES 160-163. SEM micrographs of nymphal maxilla. *Miroculis* (*Ommaethus*) *mourei*: 160(356X)-161(1106X), setae of subapical row (foreground) and dorsal portion of apical row (background) of galea-lacinia; 162(3469X), setae of dorsal portion of apical row; 163(3263X), setae of ventral portion of apical row.



FIGURES 164-167. SEM micrographs of nymphal labium. *Miroculis (Ommaethus) mourei*: 164(4967X), hair-like seta of lateral margin of segment 3 of labial palpi; 165(5005X), apex of segment 3 of labial palpi. *Atalonella ophis*: 166(366X), segment 3 of labial palpi; 167(4928X), seta of lateral margin of segment 3 of labial palpi.

**Miroculis (Yaruma) NEW SUBGENUS**

Figs. 16-18, 47-48, 61-62, 103-106, 168

MALE IMAGO: Length of male: body, 4.9-5.1 mm; fore wings, 4.5 mm; prothoracic legs [broken off specimens and missing]. Eyes (Figs. 47-48): eyes of male separated on meson of head by a length 0.1-0.2 width of an upper portion, dorsally upper portion of eyes circular with medium-sized facets, 32-37 facets in longest row, set on dorsum of head by a short, wide stalk as in Fig. 47; width of lower portion of eyes subequal to a little greater than height of stalk. Ocelli as in Fig. 47. Antennae pale yellow. Wings (Figs. 16-18): ratio of maximum width to maximum length of fore wings, in males 0.43-0.46; ratio of maximum length of hind wings to maximum length of fore wings, in males 0.24-0.26; ratio of length to apex of costal projection to length of hind wings, in males 0.35-0.36; membrane hyaline to with very light brown tinge. Legs: [male prothoracic legs broken off specimens and missing]. Male genitalia (Figs. 61-62): forceps segment 2 rectangular; styliger plate with anterolateral arms well developed, anteromedian area greatly weakened to absent, posterior 1/3 heavily sclerotized, posteromedian margin rounded (Fig. 61); penes roughly 2.0 length of forceps segment 1.

FEMALE IMAGO: Unknown.

MATURE NYMPH: Unknown.

ETYMOLOGY: Yaruma, an extinct tribe of the Rio Xingu region, Pará State, Brazil (Cowell 1973); masculine.

TYPE SPECIES: *M. (Yaruma) wandae* NEW SPECIES

SPECIES INCLUDED: *M. (Y.) wandae* NEW SPECIES

DISTRIBUTION: Amazonas State, BRAZIL (Fig. 168; localities e, f).

DISCUSSION. *M. (Yaruma)* can be distinguished from all other subgenera of *Miroculis* by the following combination of characters. In imagos: (1) eyes of male are separated on meson of head by a length 0.1-0.2 width of an upper portion (Fig. 48); (2) upper portion of male eyes are on a short, wide, stalk, with 32-37 medium-sized facets in longest row (Fig. 47); (3) antennae pale yellow; (4) ratio of maximum width to maximum length of fore wings in male imagos is 0.43-0.46; (5) ratio of maximum length of hind wings to maximum length of fore wings in male imagos is 0.24-0.26; and (6) posteromedian margin of styliger plate is rounded (Fig. 61).

**Miroculis (Yaruma) wandae NEW SPECIES**

Figs. 61-62, 103-104, 168

MALE IMAGO: Unknown.

MALE SUBIMAGO (in alcohol). Length: body, 5.0 mm; fore wings, 4.5 mm; prothoracic legs [broken off specimen and missing]. Eyes: apex of upper portion

separated on meson of head by a length approximately 0.1 diameter of an upper portion; stalked turbinate portion short, wide, brownish-black at base, light yellow apically; facets of turbinate portion medium-sized, 32-37 facets in longest row, facets and grooves yellow; facets of lower portion black, small. Head with postero-medial projection between turbinate portion of eyes, brownish-yellow, washed with brownish-black, ventral surface washed heavily with brownish-black. Antennae pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum brownish-yellow, lateral margins and carinae brownish-black, remainder of notum light brown, carinae dark brown; sterna brownish-yellow, edges of sclerites dark brown; pleura brownish-yellow, washed with brownish-black, anterodorsal margin of mesopleura brownish-black. Wings: longitudinal and cross veins very light brown, with C, Sc and R of fore wings darker; membrane whitish with brown tinge, translucent. Legs: [broken off specimen and missing]. Abdomen (Figs. 103-104): terga whitish-yellow; terga 1-10 with posterior margin brownish-black, terga 1-8 with sublateral brownish-black marks, tergum 1 with median brownish-black mark, terga 2-10 with submedian brownish-black marks as in Fig. 103, marks lighter on tergum 9; spiracles brownish-black, tracheae washed lightly with brownish-black; sterna whitish-yellow. Forceps (Figs. 61-62): segment 3 approximately 1.00 ( $n = 1$ ) length of segment 2; segment 2 approximately 0.44 ( $n = 1$ ) length of segment 1; basal 1/2 of inner margin of forceps segment 1 gradually narrows apically, distal inner margin not developed; yellowish-white. Styli plate (Figs. 61-62): maximum length along lateral margins approximately 0.66 ( $n = 1$ ) maximum width; maximum length along median line approximately 0.45 ( $n = 1$ ) maximum width; posteromedial margin rounded as in Fig. 61; yellowish-white. Penes (Figs. 61-62): length approximately 2.20-2.30 ( $n = 1$ ) length of forceps segment 1, apex excavated as in Fig. 61; whitish-yellow. Caudal filaments [broken off specimen and missing].

FEMALE IMAGO: Unknown.

MATURE NYMPH: Unknown.

SPECIMENS EXAMINED (Fig. 168; locality f): Holotype male subimago, BRAZIL: Amazonas State, Rio Marauia, 1 day's trip above S. Antonio Mission, N.W. of Taparauquara, at light, 3-II-1963, E.J. Fittkau.

Holotype deposited in collections of INPA.

LIFE CYCLE ASSOCIATIONS: None.

ETYMOLOGY: Species is named for Wanda Diane Colbert.

DISCUSSION. The subgenus *M. (Yaruma)* includes *M. (Y.) wandae* and *M. (Yaruma)* sp. *Miroculis (Y.) wandae* is represented by a single male subimago, while *M. (Yaruma)* sp. is known from a single male imago with damaged genitalia. The male imago is described as *M. (Yaruma)* sp. as it is impossible to compare the genitalia of the 2 specimens. *M. (Y.) wandae* can be distinguished from *M. (Yaruma)* sp. by abdominal color patterns on segments 5-6 (Figs. 103-104).

BIOLOGY: Collection records indicate that imagos of *M. wandae* emerge in January and February.

**Miroculis (Yaruma) sp.**

Figs. 16-18, 47-48, 105-106, 168

MALE IMAGO (in alcohol). Length: body, 4.9-5.1 mm; fore wings, 4.5 mm; prothoracic legs [broken off specimen and missing]. Eyes (Figs. 47-48): apex of upper portion separated on meson of head by a length 0.1-0.2 diameter of an upper portion; stalked turbinate portion short, wide, brown at base, brownish-yellow apically; facets of turbinate portion medium-sized, approximately 35 facets in longest row, facets and grooves light brownish-yellow; facets of lower portion black, small. Head yellowish-brown, washed heavily with brownish-black. Antennae pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum brownish-yellow, lateral margins and carinae brownish-black, remainder of notum light brown, carinae dark brown to brownish-black; sterna brownish-yellow; pleura brownish-yellow, washed with brownish-black, anterodorsal margins of mesopleura brownish-black. Wings (Figs. 16-18): longitudinal and cross veins brown, membrane hyaline to with very light brown tinge, apical 1/3 of cells of C and Sc of fore wings translucent, whitish. Legs: [prothoracic legs broken off specimen and missing]; remaining legs brownish-yellow, femora and tibiae with subapical black bands, femora with median black macula, base of tibiae washed with light black. Abdomen (Figs. 105-106): terga 1-6 semihyaline, brownish-yellow, terga 7-10 brownish-yellow; terga 1-8 with posterior margins brownish-black and with sublateral and very light submedian brownish-black marks as in Fig. 105; spiracles black, tracheae smoky; sterna 1-6 semihyaline, whitish-yellow, sterna 7-9 light brownish-yellow. Forceps: segment 3 approximately 0.9 (n = 1) length of segment 2; segment 2 approximately 0.22-0.27 (n = 1) length of segment 1; basal 1/2 of inner margin of forceps segment 1 gradually narrows apically, distal inner margin not developed; brown. Styli: plate: [damaged], maximum length along lateral margin roughly 1/2 maximum width; maximum length along median line roughly 1/4 maximum width; posterior margin [damaged]; light brown. Penes: [damaged], roughly 2 times length of forceps segment 1, similar to Fig. 61; dark brown. Caudal filaments [broken off specimen and missing].

FEMALE IMAGO: Unknown.

MATURE NYMPH: Unknown.

SPECIMENS EXAMINED (Fig. 168; locality e): Male imago, BRAZIL: Amazonas State, Aduja Creek, near Rio Itu, 10-II-1962, E.J. Fittkau. Specimen is in collections of FAMU.

LIFE CYCLE ASSOCIATIONS: None.

DISCUSSION. The taxonomic status of *M. (Yaruma) sp.* is uncertain. *Miroculis (Yaruma) sp.* is known from a single male imago with damaged genitalia and comparisons with *M. (Y.) wandae* which is known from a male subimago are not possible. Thus, the male imago is described as *M. (Yaruma) sp.* *Miroculis (Yaruma) sp.* can be distinguished from *M. (Y.) wandae* by the faint abdominal color pattern on segments 5-6 (Figs. 105-106).

BIOLOGY: Collection records indicate *M. (Yaruma) sp.* emerges in February.

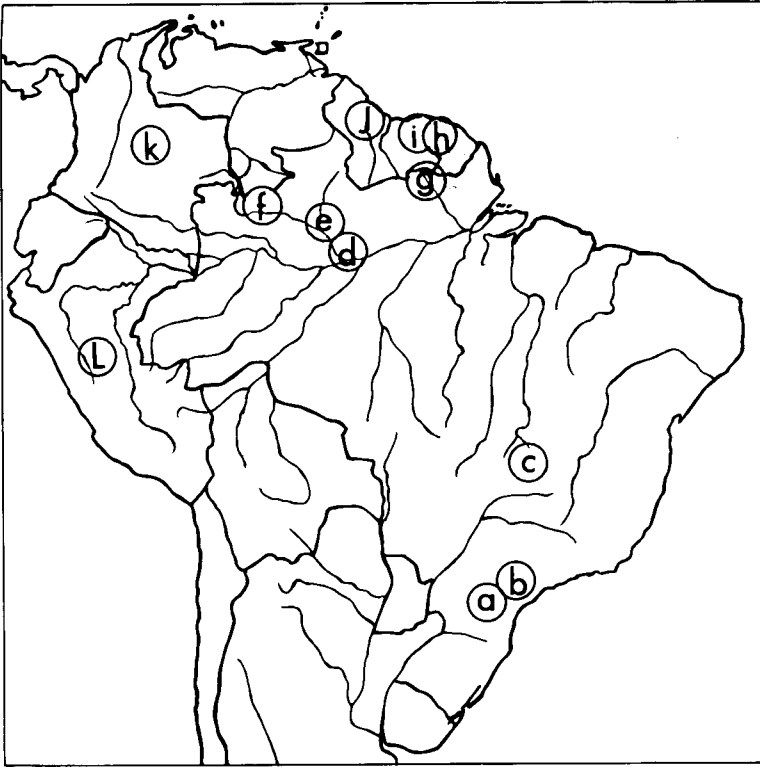


FIGURE 168. Known distribution for species of *Miroculis*, *Miroculitus*, *Microphlebia* and *Hermanellopsis*: *Miroculis* (*M.*) *rossi*, l; *M. (M.) marauiaie*, f; *M. (M.) fittkaui*, g, i; *M. (M.) brasiliaensis*, c; *M. (Yaruma) wandae*, f; *M. (Yaruma)* sp., e; *M. (Atroari) duckensis*, d; *M. (A.) amazonicus*, f; *M. (A.) colombiensis*, k; *M. (Ommaethus) mourei*, a; *M. (O.) froehlichii*, b; *Miroculitus emersoni*, j; *Microphlebia surinamensis*, i; *M. pallida*, d; *Hermanellopsis incertans*, h; *H. arisia*, d.

### ***Miroculis (Atroari)* NEW SUBGENUS**

Figs. 19-21, 49-50, 63-64, 102, 114-117, 127-130, 158-159, 168

MALE IMAGO: Length of male: body, 4.8-6.0 mm; fore wings, 4.4-4.6 mm; prothoracic legs, 5.6-5.7 mm. Eyes (Figs. 49-50): eyes of male separated on meson of



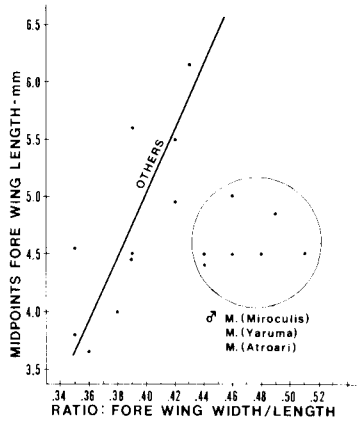


FIGURE 169. Relationship between midpoints of fore wing length (mm) and fore wing width/length ratio for 17 groups within *Miroculis* and related genera. Values for male imagos of lineage 4b (Fig. 2) are enclosed by a circle. Regression line: others,  $Y = 28.48x - 6.34$ ,  $r = 0.79$ ,  $P = 0.006$ ,  $n = 10$ .

head by a length 0.5-0.6 width of an upper portion; upper portion large, round, with medium-sized facets, 30-40 facets in longest row, stalk absent (Figs. 49-50); lower portion of eyes touching upper portion as in Fig. 49. Ocelli close together as in Fig. 50. Antennae pale yellow. Wings (Figs. 19-21): ratio of maximum width to maximum length of fore wings, in males 0.47-0.51; ratio of maximum length of hind wings to maximum length of fore wings, in males 0.24-0.28; ratio of length to apex of costal projection to length of hind wings, in males 0.27-0.29; membrane very light brown to light brown, fore wings with very light brown to dark brown submedian irregular broken transverse bands and numerous blotches near apex, hind wings darker near apex (Figs. 19-21). Legs: ratio of segments in male prothoracic legs, 0.42: 1.00(2.45 mm): 0.01-0.02: 0.37: 0.25: 0.20: 0.06. Male genitalia (Figs. 63-64): styliger plate with anterolateral arms well developed, anteromedian area greatly weakened to absent, posterior 1/3 heavily sclerotized, posteromedian margin rounded (Figs. 63-64); penes 1.1-1.9 length of forceps segment 1.

FEMALE IMAGO: Unknown.

MATURE NYMPH: Labrum: anteromedian emargination with 5 small, subequal-sized denticles; anterolateral margins flattened. Posterolateral spines developed beyond posterior margin of terga on abdominal segments 3-6 to 9.

ETYMOLOGY: Atroari, an Indian tribe that resides north of Manaus in the region of the Rio Alalau (Cowell 1973); masculine.

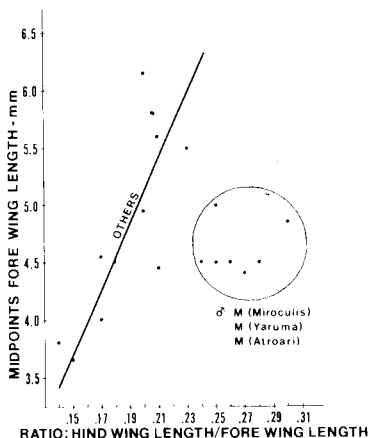


FIGURE 170. Relationship between midpoints of fore wing length (mm) and hind wing length/fore wing length ratio for 17 groups within *Miroculis* and related genera. Values for male imagos of lineage 4b (Fig. 2) are enclosed by a circle. Regression line: others,  $Y = 28.68x - 0.62$ ,  $r = 0.79$ ,  $P = 0.007$ ,  $n = 10$ .

TYPE SPECIES: *M. (Atroari) duckensis* NEW SPECIES.

SPECIES INCLUDED: *M. (A.) duckensis* NEW SPECIES; *M. (A.) amazonicus* NEW SPECIES; *M. (A.) colombiensis* NEW SPECIES.

DISTRIBUTION: Amazonas State, BRAZIL; and Department Meta, COLOMBIA (Fig. 168; localities d, f, k).

DISCUSSION: *M. (Atroari)* can be distinguished from all other subgenera of *Miroculis* by the following combination of characters. In imagos: (1) eyes of male are unstalked, large and round with 30-40 facets in longest row (Figs. 49-50); (2) eyes of male are separated on meson of head by a length 0.5-0.6 width of an upper portion; (3) antennae are pale yellow; (4) ratio of maximum width to maximum length of fore wings in male imagos is 0.47-0.51; (5) ratio of maximum length of hind wings to maximum length of fore wings in male imagos is 0.24-0.28; (6) membrane of wings is very light brown to light brown, fore wings with very light brown to dark brown submedian irregular broken transverse bands and numerous blotches near apex, membrane of hind wings darker near apex (Figs. 19-21); and (7) posteromedian margin of styliger plate is rounded (Figs. 63-64).

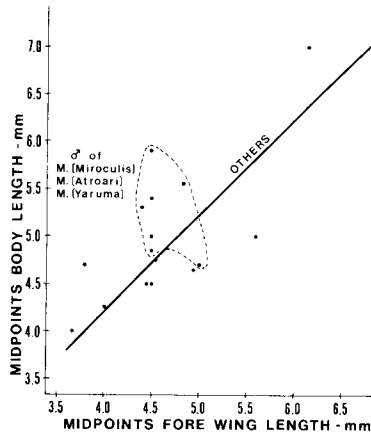


FIGURE 171. Relationship between midpoints of body length (mm) and fore wing length (mm) for 16 groups within *Miroculis* and related genera. Values for male imagoes of lineage 4b (Fig. 2) are enclosed by dashes. Regression line: others,  $Y = 1.02x + 0.12$ ,  $r = 0.84$ ,  $P = 0.005$ ,  $n = 9$ .

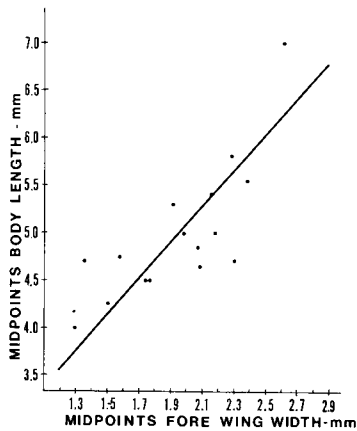


FIGURE 172. Relationship between midpoints of body length (mm) and fore wing width (mm) for 16 groups within *Miroculis* and related genera. Regression line: all,  $Y = 1.89x + 1.32$ ,  $r = 0.78$ ,  $P < 0.001$ ,  $n = 16$ .

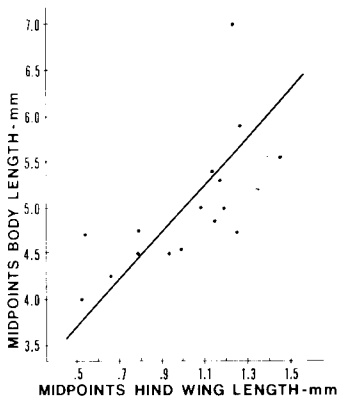


FIGURE 173. Relationship between midpoints of body length (mm) and hind wing length (mm) for 16 groups within *Miroculis* and related genera. Regression line: all,  $Y = 2.63x + 2.35$ ,  $r = 0.67$ ,  $P = 0.004$ ,  $n = 16$ .

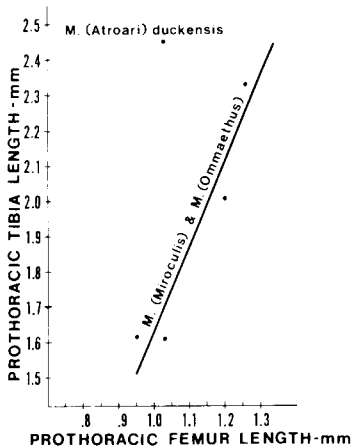


FIGURE 174. Relationship between midpoints of prothoracic tibia length (mm) and femur length (mm) in male imagos of 5 species of *Miroculis*. Regression line: *Miroculis* (*Miroculis*) and *M. (Ommaethus)*,  $Y = 2.44x - 0.81$ ,  $r = 0.96$ ,  $P < 0.05$ ,  $n = 4$ .

**Miroculis (Atroari) duckensis** NEW SPECIES

Figs. 49-50, 64, 114-115, 127, 168

MALE IMAGO (in alcohol). Length: body, 4.8-6.0 mm; fore wings, 4.4-4.6 mm; prothoracic legs, 5.6-5.7 mm. Eyes (Figs. 49-50): upper portion separated on meson of head by a length approximately 0.6 maximum width of an upper portion; facets of upper portion brownish-yellow, separated by light brown grooves; facets of lower portion black, small. Head brownish-yellow, carinae brownish-black, ventral surface washed heavily with brownish-black. Antennae pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum yellowish-brown, carinae, submedian sutures, and margins brownish-black, mesonotum and metanotum light brown, carinae dark brown to brownish-black; sterna yellowish-brown, margins of sclerites dark brown; pleura yellowish-brown washed lightly with brownish-black. Wings: longitudinal and cross veins brown; membrane very light brown, fore wings with very light brown submedian irregular broken transverse bands and numerous blotches near apex, apical 1/3 of cells of C and Sc translucent, brownish, hind wings darker near apex. Legs: ratio of segments in prothoracic legs, 0.42: 1.00(2.45 mm): 0.01-0.02: 0.37: 0.25: 0.20: 0.06; legs light brown, with apical black bands on femora and tibiae, femora with faint median brownish-black macula, median macula on femora faint to absent on prothoracic and mesothoracic legs. Abdomen: terga semihyaline, washed with yellowish-brown; posterior margin of terga 1-8 brownish-black, terga 1-3 washed lightly with brownish-black medially and sublaterally, terga 4-8 washed lightly with brownish-black submedially and sublaterally, very light on terga 4-5; spiracles brownish-black, tracheae semihyaline, lightly washed with brown; sterna 1-6 semihyaline, washed with yellowish-brown, sterna 7-8 yellowish-brown, sternum 9 brown. Forceps (Fig. 64): segment 3 from 0.93-0.96 (n = 2) length of segment 2; segment 2 from 0.37-0.41 (n = 2) length of segment 1; basal 1/2 of inner margin of forceps segment 1 gradually narrows, distal 1/4 of inner margin not developed; segment 2 widens slightly apically; light brown. Styli-ger plate (Fig. 64): maximum length along lateral margin approximately 0.86-0.88 (n = 2) maximum width; maximum length along median line approximately 0.60-0.62 (n = 2) maximum width; posteromedian margin rounded (Fig. 64); brown. Penes (Fig. 64): length approximately 1.12-1.38 (n = 2) length of forceps segment 1, apex as in Fig. 64; dark brown. Caudal filaments yellowish-brown [broken off specimens apically and missing].

FEMALE IMAGO: Unknown.

MATURE NYMPH (in alcohol). Body length, 4.0-5.5 mm. Eyes: eyes of female black; upper portion of eyes of male yellow, lower portion black. Dorsum of head brownish-yellow, anterolateral margins of genae and anterior margin of clypeus washed with brownish-black; venter pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Scape and pedicel brownish-yellow, washed lightly with brownish-black, flagellum pale yellow. Mouthparts: anterolateral margins of labrum flattened; length of subapical row of setae on maxillae 0.45-0.52 (n = 3) length of apical row, subapical row with 30-33 (n = 3) pectinate setae, segment 2 of maxillary palpi 0.95-1.17 (n = 3) length of segment 1, segment 3 of maxillary palpi 0.45-0.59 (n = 3)

length of segment 2; segment 2 of labial palpi 0.85-1.13 ( $n=4$ ) length of segment 1, segment 3 of labial palpi 0.47-0.54 ( $n=4$ ) length of segment 2, labium light yellow. Thorax: pronotum brownish-yellow, with brownish-black marks as in male imago, mesonotum and metanotum brownish-yellow, with carinae brown to brownish-black, anterolateral corners of mesonotum brownish-black; sterna brownish-yellow; pleura brownish-yellow, carinae washed with brownish-black. Legs: brownish-yellow, with brownish-black marks as in male imago. Abdomen (Figs. 114-115): terga brownish-yellow, washed with brownish-black; terga 1-8 with posterior margins brownish-black, tergum 1 washed heavily with brownish-black, terga 2-10 with brownish-black wash darker submedially forming submedian marks as in Figs. 114-115, terga 2-8 with brownish-black wash darker sublaterally and laterally as in Figs. 114-115; spiracles and tracheae brownish-yellow washed with brownish-black; sterna brownish-yellow. Posterolateral spines on abdominal segments 2-9, developed beyond posterior margin of terga on segments 3-4 to 9, spines well developed on segments 6-7 to 9 (Fig. 114). Gills (Fig. 127): small, posterolateral projections not greatly developed to reduced, outer basal margin of dorsal portion not developed anteriorly; membrane grayish, translucent; tracheae black, unbranched to branched in apical 1/3. Caudal filaments brownish-yellow, articulations darker.

**SPECIMENS EXAMINED** (Fig. 168; locality d): Holotype male imago, BRAZIL: *Amazonas State*, Acará Rapids, near Acapamento, Reserva Ducke, N. of Manaus, at light, 26-VI-1961, E.J. Fittkau. Paratypes: 1 male imago, 4 nymphs, BRAZIL: *Amazonas State*, rapids, gigante creek, Reserva Ducke, N. of Manaus, 3-VII-1961, E.J. Fittkau; 2 nymphs, as in previous paratypes except date of collection is 1-VIII-1961; 6 nymphs, BRAZIL: *Amazonas State*, Barro Branco Creek, Reserva Ducke, N. of Manaus, 10-V-1961, E.J. Fittkau; 3 nymphs, BRAZIL: *Amazonas State*, Passarinho Creek, Reserva Ducke, N. of Manaus, 27-VI-1961, E.J. Fittkau; 6 nymphs, BRAZIL: *Amazonas State*, Bica Creek, nr. Ponta Negra, Rio Negro, N. of Manaus, 23-VI-1961, E.J. Fittkau; 1 nymph, BRAZIL: *Amazonas State*, gigante creek, nr. Ponta Negra, Rio Negro, N. of Manaus, 23-VI-1961, E.J. Fittkau.

Holotype and 4 nymphal paratypes are deposited in collections of INPA. One male imaginal and 9 nymphal paratypes are deposited in FAMU collections. Nine nymphal paratypes are deposited in UU collections.

**LIFE CYCLE ASSOCIATIONS:** Mature nymphs are associated with male imagos by shared color patterns on the abdomen and legs, and by the structure of the male eyes.

**ETYMOLOGY:** Species is named for Reserva Ducke, type locality.

**DISCUSSION.** Male imagos of *M. duckensis* can be distinguished from male imagos of all other species within *M. (Atroari)* by the following combination of characters: (1) penes are approximately 1.1-1.4 length of forceps segment 1, with apex as in Fig. 64; (2) styliiger plate is shaped as in Fig. 64; (3) forceps segments are shaped as in Fig. 64; (4) ratio of femora to tibiae of male prothoracic legs is approximately 0.42; length of prothoracic tibiae is approximately 2.45 mm; and (5) membrane of fore wings has very light brown submedian irregular broken transverse bands and numerous blotches near apex.

Nymphs of *M. duckensis* can be distinguished from known nymphs of all species

within *Miroculis* by the following combination of characters: (1) anterolateral margins of labrum are flattened; (2) subapical row of maxillae has 30-33 pectinate setae; (3) median brownish-black maculae on prothoracic and mesothoracic legs are faint to absent; (4) abdominal terga 2-8 with similar pattern becoming darker posteriorly (Figs. 114-115); (5) abdominal tergum 6 has heavy brownish-black wash submedially, sublaterally and laterally as in Figs. 114-115; and (6) gills are small, posterolateral projections are not greatly developed to reduced (Fig. 127).

**BIOLOGY.** Collection records indicate imagos of *M. duckensis* emerge in June and July.

Barro Branco Creek is a small (1 meter wide), shallow, sandy bottomed stream. Acará is 3-4 meters wide with alternating areas of sandy bottom, exposed bedrock and small waterfalls. Nymphs inhabit logs and other detritus in areas of medium current.

### ***Miroculis (Atroari) amazonicus* NEW SPECIES**

Figs. 19-21, 63, 102, 116, 128-129, 158, 168

**MALE IMAGO** (in alcohol). Length: body, 5.9 mm; fore wings, 4.6 mm; prothoracic legs [broken off specimen and missing]. Eyes: upper portions separated on meson of head by a length approximately 0.5 maximum width of an upper portion; facets of upper portion brownish-yellow, separated by dark brown grooves; facets of lower portion black, small. Head brown, carinae dark brown to brownish-black, ventral surface washed heavily with brownish-black. Antennae pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum brownish-yellow, carinae, lateral margins and submedian sutures brownish-black; mesonotum and metanotum brown, carinae dark brown to brownish-black; sterna brownish-yellow, margins of sclerites dark brown; pleura brownish-yellow, washed with brownish-black. Wings (Figs. 19-21): longitudinal and cross veins brown; membrane light brown, fore wings with brown submedian irregular broken transverse bands and numerous blotches near apex as in Fig. 19, apical 1/3 of cells of C and Sc of fore wings translucent, brownish, hind wings darker near apex. Legs: [prothoracic and mesothoracic legs broken off specimen and missing]; metathoracic legs brownish-yellow, femora and tibiae with black band near apex. Abdomen (Fig. 102): terga 1-7 semihyaline with posterior 2/3 of each tergum brownish-yellow, terga 8-10 brownish-yellow; posterior margin of terga 1-10 brownish-black, tergum 1 brownish-black, terga 2 with median and lateral brownish-black marks, terga 3-8 with submedian and lateral brownish-black marks, lateral marks lighter on terga 5-8 (Fig. 102); spiracles brownish-black, tracheae semihyaline, brownish-yellow; sterna semihyaline, brownish-yellow. Forceps (Fig. 63): length of segment 3 from 0.97-1.00 (n=1) length of segment 2; segment 2 from 0.32-0.34 (n=1) length of segment 1; basal 1/2 of inner margin of forceps segment 1 gradually narrows apically, distal 1/4 of inner margin weakly developed; segment 2 rectangular; light brown. Styliiger plate (Fig. 63): maximum length along lateral margin approximately 0.78 (n=1) maximum width; maximum length along median line approximately 0.53 (n=1) maximum

width; posteromedian margin rounded; light brown. Penes (Fig. 63): length from 1.75-1.81 ( $n=1$ ) length of forceps segment 1, apex as in Fig. 63; dark brown. [Caudal filaments broken off specimen and missing].

FEMALE IMAGO: Unknown.

MATURE NYMPH (in alcohol). Body length, 4.0-6.0 mm. Eyes: eyes of female black; upper portion of eyes of male yellow, lower portion black. Head brownish-yellow, lateral edges of genae washed with brownish-black. Basal 2/3 of ocelli black, apical 1/3 white. Scape and pedicel brownish-yellow, flagellum pale yellow. Mouthparts: anterolateral margins of labrum flattened; length of subapical row of setae of maxillae 0.49-0.54 ( $n=2$ ) length of apical row, subapical row with 40-50 ( $n=2$ ) pectinate setae, segment 2 of maxillary palpi 1.02-1.18 ( $n=2$ ) length of segment 1, segment 3 of maxillary palpi 0.48-0.58 ( $n=2$ ) length of segment 2; labial palpi [not measurable], light yellow. Thorax: color and marks as in male imago, except anterolateral corners of mesonotum brownish-black. Legs (Fig. 158): brownish-yellow, femora and tibiae with a brownish-black band near apex, tibiae with light streaks of brownish-black on inner basal margin; prothoracic claw as in Fig. 158. Abdomen (Fig. 116): terga brownish-yellow, posterior margins of terga 1-10 brownish-black, lighter on tergum 9, tergum 1 brownish-black, tergum 2 with median and lateral brownish-black marks, terga 3-8 with submedian and lateral brownish-black marks (Fig. 116), submedian marks lighter on tergum 3, lateral marks lighter on terga 5-8, tergum 9 with or without faint submedian brownish-black maculae, tergum 10 with submedian brownish-black maculae; spiracles and tracheae as in male imago except tracheae washed with brownish-black; sterna brownish-yellow. Posterolateral spines on abdominal segments 2-3 to 9, developed beyond posterior margin of terga on segments 3-5 to 9, spines well developed on segments 6 to 9. Gills (Figs. 128-129): large, posterolateral projections greatly developed, outer basal margin of dorsal portion developed anteriorly on gills 2-6 (Fig. 129), not developed anteriorly on gills 1 (Fig. 128) and 7; membrane grayish, translucent; tracheae black, unbranched (Figs. 128-129). Caudal filaments brownish-yellow, articulations of basal segments black.

SPECIMENS EXAMINED (Fig. 168; locality f): Holotype male imago, BRAZIL: *Amazonas State*, Rio Marauia, near S. Antonio Mission, N.W. of Taparuquara, at light, 10-I-1963, E.J. Fittkau. Paratypes, 1 mature female nymph and 3 mature male nymphs, BRAZIL: *Amazonas State*, below waterfall, S. Antonio Creek, near S. Antonio Mission, N.W. of Taparuquara, 9-I-1963, E.J. Fittkau.

Holotype male imago is deposited in collections of INPA. One female and 1 male nymphal paratype are deposited in FAMU collections. Two male nymphal paratypes are deposited in collections of UU.

LIFE CYCLE ASSOCIATIONS: Mature nymphs are associated with imagos by shared abdominal color patterns and by the structure of the developing eyes and male genitalia. All specimens were collected in the same area over a two day period.

ETYMOLOGY: Species is named for the *Amazonas State*, type locality.

DISCUSSION. Male imagos of *M. amazonicus* can be distinguished from male imagos of all other species within *M. (Atroari)* by the following combination of characters: (1) penes are approximately 1.7-1.9 length of forceps segment 1, with



apex as in Fig. 63; (2) styliger plate is shaped as in Fig. 63; (3) forceps segments are shaped as in Fig. 63; (4) membrane of fore wings has brown submedian irregular transverse bands and numerous blotches near apex (Fig. 19); and (5) abdominal terga 5-6 have submedian and lateral brownish-black marks (Fig. 102).

Nymphs of *M. amazonicus* can be distinguished from all known nymphs of *Miroculis* by the following combination of characters: (1) anterolateral margins of labrum are flattened; (2) subapical row of maxillae has 40-50 pectinate setae; (3) abdominal terga 3-8 have submedian brownish-black marks, marks light on terga 3 and 4, dark on terga 5-8 (Fig. 116); (4) abdominal tergum 6 has brownish-black submedian and lateral marks as in Fig. 116; (5) gills are large, posterolateral projections are greatly developed (Figs. 128-129); (6) outer basal margin of dorsal portion of gills 2-6 is developed anteriorly (Fig. 129); and (7) caudal filaments are brownish-yellow, articulations of basal segments black.

**BIOLOGY:** Collection records indicate that imagos of *M. amazonicus* emerge in January.

### ***Miroculis (Atroari) colombiensis* NEW SPECIES**

Figs. 117, 130, 159, 168

**MALE IMAGO:** Unknown.

**FEMALE IMAGO:** Unknown.

**MATURE NYMPH** (in alcohol). Length: body, 5.0-5.6 mm. Eyes: eyes of female black; upper portion of eyes of male grayish-yellow, lower portion black. Head yellowish-brown, genae and carinae brownish-black. Basal 2/3 of ocelli black, apical 1/3 white. Scape and pedicel brownish-black, flagellum pale yellow. Mouthparts: anterolateral margins of labrum flattened; length of subapical row of setae on maxillae 0.46-0.52 ( $n=3$ ) length of apical row, subapical row with 32-37 ( $n=3$ ) pectinate setae, segment 2 of maxillary palpi 1.00-1.12 ( $n=3$ ) length of segment 1, segment 3 of maxillary palpi 0.50-0.53 ( $n=3$ ) length of segment 2; segment 2 of labial palpi 1.07-1.18 ( $n=3$ ) length of segment 1, segment 3 of labial palpi 0.46-0.50 ( $n=3$ ) length of segment 2, labium light yellow, mentum and submentum washed lightly with brownish-black. Thorax: pronotum yellowish-brown, submedian carinae and outer margins brownish-black; mesonotum and metanotum brown with carinae dark brown to brownish-black, anterolateral corners of mesonotum brownish-black; sterna yellowish-brown, margins of mesosternum dark brown; pleura light brown, washed with brownish-black. Legs (Fig. 159): brownish-yellow, femora and tibiae with brownish-black subapical bands, femora with median brownish-black macula, inner basal margin of tibiae washed with brownish-black; claws with denticles as in Fig. 159. Abdomen (Fig. 117): terga brownish-yellow, terga 1-8 with sublateral brownish-black marks, terga 1-2 with median brownish-black marks, terga 3-8 with circular submedian brownish-black marks (Fig. 117), tergum 10 with posterior margin brownish-black; spiracles brownish-black, tracheae brownish-yellow; sterna brownish-yellow, posterior margin of sterna 2-8 brownish-black, darker laterally. Posterolateral spines on abdominal segments 2-9, developed

beyond posterior margin of terga on segments 3-6 to 9, spines well developed on segments 6-9 (Fig. 117). Gills (Fig. 130): large, posterolateral projections greatly developed, outer basal margin of dorsal portion developed anteriorly on gills 2-6, not developed to developed anteriorly on gills 1 and 7; membrane brownish-yellow, translucent; tracheae black, branched near base and apically (Fig. 130). Caudal filaments brownish-yellow, articulations of segments darker brown.

**SPECIMENS EXAMINED** (Fig. 168; locality k): Holotype, mature male nymph, COLOMBIA: *Department Meta*, Hacienda Mozambique, 16 km. S.W. of Puerto Lopez, Pond 2 in palm forest, E. of Hacienda, 7-III-1971, S.S. Roback. Paratypes, 2 mature male nymphs and 1 mature female nymph, same data as holotype.

Holotype and 1 nymphal paratype are deposited in ANSP collections. Two nymphal paratypes are deposited in collections of FAMU.

**LIFE CYCLE ASSOCIATIONS:** Unknown.

**ETYMOLOGY:** Species is named for the country of Colombia, type locality.

**DISCUSSION.** *M. colombiensis* is known from mature nymphal specimens only. *M. colombiensis* can be distinguished from all known nymphs of *Miroculis* by the following combination of characters: (1) anterolateral margins of labrum are flattened; (2) abdominal terga 2-3 are dark, terga 4-8 with similar pattern becoming darker posteriorly (Fig. 117); (3) abdominal tergum 6 has brownish-black sublateral and circular submedian marks (Fig. 117); (4) gills are large, posterolateral projections are greatly developed (Fig. 130); (5) outer basal margin of dorsal portion of gills 2-6 is developed anteriorly (Fig. 130); (6) membrane of gills is brownish-yellow, translucent; and (7) caudal filaments are brownish-yellow, segment articulations darker brown.

It is difficult to assign nymphs of *Miroculis* to subgenera. In this case, nymphal-specimens are very mature and subimaginal structures are visible. The upper portion of the male eyes is indicative of *M. (Atroari)* and the developing penes are long with the apex similar to those of *M. (A.) duckensis*.

**BIOLOGY.** Collection records of mature nymphs indicate imagoes of *M. colombiensis* emerge in March and April.

Nymphs were collected from a pond in a palm forest.

### ***Miroculis (Ommaethus)* NEW SUBGENUS**

Figs. 22-24, 51-54, 65-70, 83-84, 88, 92, 107-109, 118-119,  
131-132, 138-141, 156, 160-165, 168

**IMAGO.** Length of male: body, 3.8-7.8 mm; fore wings, 5.4-6.2 mm; prothoracic legs, 5.3-5.4\*mm. Length of female: body, 4.9-5.1\*mm; fore wings, 5.5-5.7\*mm. Eyes (Figs. 51-54): eyes of male separated on meson of head by a length approximately equal to width of an upper portion; upper portion of male eyes shaped as in Figs. 51-54, with medium-sized facets, 27-34 facets in longest row, stalk absent; lower portion of male eyes touching upper portion (Fig. 51) to separated by small distance (Fig. 53); eyes of female separated on meson of head by a length 3.2-3.3

maximum width of an eye. Ocelli as in Figs. 51-54. Antennae with scape and pedicel brown, washed with brownish-black. Wings (Figs. 22-24): ratio of maximum width to maximum length of fore wings, in males 0.41-0.43, in females roughly 0.39; ratio of maximum length of hind wings to maximum length of fore wings, in males 0.20-0.23, in females roughly 0.21-0.22; ratio of length to apex of costal projection to length of hind wings, in males 0.33-0.44, in females roughly 0.38; membrane light brown, fore wings with darker brown clouds around cross veins and brownish-black clouds around cross veins of cells of C and Sc (Fig. 22). Legs: ratios of segments in male prothoracic legs, 0.54: 1.00(2.33\*mm): 0.02: 0.30: 0.22: 0.17: 0.07. Male genitalia (Figs. 65-70): styliiger plate with anterolateral arms not well developed, anteromedian area only slightly weakened, posterior 1/3 sclerotized, posteromedian margin with a large U-shaped indentation as in Figs. 65, 68; penes 0.8-1.0 length of forceps segment 1. Sternum 7 of female with small genital extension as in Figs. 83-84.

**MATURE NYMPH.** Labrum (Figs. 138-141): anteromedian emargination with 4-5 small, subequal-sized denticles; anterolateral margins gently rounded to slightly flattened as in Figs. 138-141. Posterolateral spines developed beyond posterior margin of terga on abdominal segments 5-6 to 9 (Fig. 119).

**ETYMOLOGY:** omma, Gr., meaning eye; aethes, Gr., meaning strange, unusual; masculine.

**TYPE SPECIES:** *M. (Ommaethus) mourei* NEW SPECIES.

**SPECIES INCLUDED:** *M. (O.) mourei* NEW SPECIES; *M. (O.) froehlichii* NEW SPECIES.

**DISTRIBUTION:** southern Brazil; Paraná and São Paulo States (Fig. 168; localities a, b).

**DISCUSSION:** *M. (Ommaethus)* can be distinguished from all other subgenera of *Miroculis* by the following combination of characters. In imagos: (1) eyes of male are unstalked, shaped as in Figs. 51-54, with 27-34 facets in longest row; (2) eyes of male are separated on meson of head by a length subequal to width of an upper portion (Figs. 52, 54); (3) eyes of female are separated on meson of head by a length 3.2-3.3 maximum width of an eye; (4) ratio of maximum width to maximum length of fore wings in male imagos is 0.41-0.43; (5) ratio of maximum length of hind wings to maximum length of fore wings in male imagos is 0.20-0.23; (6) membrane of wings is light brown, fore wings have darker brown clouds around cross veins and brownish-black clouds around cross veins of cells of C and Sc (Fig. 22); (7) posteromedian margin of styliiger plate has a large U-shaped indentation as in Figs. 65, 68; (8) penes are 0.8-1.0 length of forceps segment 1; and (9) sternum 7 of female has a small genital extension as in Figs. 83-84.

Male prothoracic legs and tibiae lengths, and female body and fore wing lengths are marked with an asterisk (\*) to indicate values represent only *M. (O.) mourei*. Male prothoracic legs and female imagos of *M. (O.) froehlichii* are unknown. As *M. (O.) froehlichii* is larger than *M. (O.) mourei* the upper values should be larger than represented.

**Miroculis (Ommaethus) mourei** NEW SPECIES

Figs. 22-24, 51-52, 65-67, 83-84, 88, 92, 107-109, 119,

131, 138-140, 156, 160-165, 168

MALE IMAGO (in alcohol). Length: body, 3.8-4.6\*mm; fore wings, 5.4-5.6 mm; prothoracic legs, 5.3-5.4 mm. Eyes (Figs. 51-52): upper portions separated on meson of head by a length approximately equal to maximum width of an upper portion; upper portion shaped as in Figs. 51-52; 27-29 facets in longest row, facets brownish-yellow, separated by dark brown grooves; lower portion touching upper portion as in Fig. 51, facets black, small. Head brown, washed heavily with brownish-black. Scape and pedicel brown, washed with brownish-black, flagellum pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum yellowish-brown to light brown, washed with brownish-black, carinae, margins and submedian sutures black; mesonotum and metanotum brown, carinae brownish-black; sterna brownish-yellow, except prosternum brown, margins of sclerites brownish-black; pleura yellowish-brown, washed heavily with brownish-black. Wings (Figs. 22-24): longitudinal and cross veins brown; membrane light brown, fore wings with darker brown clouds around cross veins and brownish-black clouds around cross veins of cells of C and Sc. Legs (Fig. 92): ratios of segments in prothoracic legs, 0.54: 1.00(2.33mm); 0.02: 0.30: 0.22: 0.17: 0.07; coxae brown, remainder of legs brownish-yellow with a large brownish-black mark on both sides of femora near apex, metathoracic femora with median brownish-black mark, tibiae with a brownish-black band near apex; prothoracic claws as in Fig. 92. Abdomen (Figs. 107-108): terga brownish-yellow, tergum 1 washed heavily with brownish-black, posterior 1/3-1/4 of terga 1-10 brownish-black with longitudinal submedian, sublateral and lateral brownish-black bars, lateral and sublateral bars light on terga 9-10; spiracles and tracheae brownish-black; sterna 1-9 brownish-yellow with posterior 1/3 brownish-black. Forceps (Figs. 65-66): segment 3 from 0.72-0.79 (n = 1) length of segment 2; segment 2 from 0.38-0.42 (n = 1) length of segment 1; basal 1/2 of inner margin of segment 1 narrows apically as in Fig. 65, distal inner margin not developed; segment 2 rectangular; distal 1/3 of segment 1 and all of segments 2 and 3 washed with black. Styliiger plate (Figs. 65-66): maximum length along lateral margin approximately 0.51 (n = 1) maximum width; maximum length along median line approximately 0.28 (n = 1) maximum width; posteromedian margin as in Fig. 65; brown. Penes (Figs. 65-67): length 0.87-0.89 (n = 1) length of forceps segment 1, apex excavated as in Figs. 65, 67; brown. Caudal filaments brownish-yellow, basal 1/3-1/2 of segments with brownish-black bands.

FEMALE IMAGO: Unknown.

FEMALE SUBIMAGO (in alcohol). Length: body, 4.9-5.1 mm; fore wings, 5.5-5.7 mm. Eyes black. Head brownish-yellow, washed with brownish-black, carinae and ventral surface brownish-black. Scape and pedicel brownish-black, flagellum light yellow. Ocelli as in male imago. Thorax: color and marks as in male imago. Wings: color and marks as in male imago. Legs: brownish-yellow, marks as in male imago.

Abdomen (Figs. 83-84, 88, 109): terga brownish-yellow, with marks as in male imago (Fig. 109); sterna brownish-yellow, posterior margins brownish-black, lighter on sterna 7-8; genital extension as in Figs. 83-84; sternum 9 as in Fig. 88. Color and marks on caudal filaments as in male imago.

**MATURE NYMPH** (in alcohol). Body length, 4.0-5.0 mm. Eyes: eyes of female black; upper portion of eyes of male brownish-yellow, lower portion black. Head brownish-yellow, genae brownish-black (Fig. 119). Basal 2/3 of ocelli black, apical 1/3 white. Scape and pedicel brownish-black, flagellum pale yellow. Mouthparts (Figs. 138-140, 160-165): anterolateral margins of labrum gently rounded to slightly flattened (Figs. 138-140); length of subapical row of setae on maxillae 0.57-0.64 (n = 5) length of apical row, subapical row with 44-55 (n = 5) pectinate setae (Figs. 160-161), setae of apical row as in Figs. 162-163, segment 2 of maxillary palpi 1.09-1.24 (n = 5) length of segment 1, segment 3 of maxillary palpi 0.45-0.54 (n = 5) length of segment 2; segment 2 of labial palpi 1.05-1.21 (n = 5) length of segment 1, segment 3 of labial palpi 0.45-0.54 (n = 5) length of segment 2, setae of segment 3 of labial palpi as in Figs. 164-165, labium light yellow, base of mentum and anterolateral margins of submentum brownish-black. Thorax: brownish-yellow, brownish-black marks as in Fig. 119. Legs (Figs. 119, 156): brownish-yellow, femora with apical brownish-black marks as in Figs. 119, 156, tibiae with brownish-black band near apex. Abdomen (Fig. 119): brownish-yellow, terga washed with brownish-black, brownish-black marks as in male imago except submedian bars darker (Fig. 119). Posterolateral spines on abdominal segments 2-9, developed beyond posterior margin of terga on segments 5-6 to 9, spines well developed on segments 6-9 (Fig. 119). Gills (Figs. 119, 131): small, posterolateral projections not greatly developed, outer basal margin of dorsal portion not developed anteriorly; membrane grayish, translucent, inner 1/2 of membrane washed very lightly with black; tracheae black, unbranched. Caudal filaments brownish-yellow, basal 1/5-1/3 of segments with black bands.

**SPECIMENS EXAMINED** (Fig. 168; locality a): Holotype male imago, BRAZIL: *Paraná State*, Rio Ipiranga, Estrada do Itupaua, altitude 2,400', 21-23-II-1969, W.L. and J.G. Peters. Paratypes: 2 male subimagos, 2 female subimagos and 31 nymphs, same data as holotype; 3 nymphs, BRAZIL: *Paraná State*, Rio dos Patos, 3 km E. of Prudentópolis, 2,300', 3-III-1969, W.L. and J.G. Peters.

Holotype and 5 nymphal paratypes are deposited in collections of USP. One male subimaginal, 1 female subimaginal and 19 nymphal paratypes are deposited in FAMU collections. One male subimaginal, 1 female subimaginal and 10 nymphal paratypes are deposited in collections of UU.

**LIFE CYCLE ASSOCIATIONS:** Male and female imagos are associated by shared color patterns of the wings, abdomen and caudal filaments. Nymphs are associated with imagos by shared color patterns of the abdomen and caudal filaments. All specimens except for 3 nymphs were collected from the same locality over a period of 2 days.

**ETYMOLOGY:** Species is named for Padre Mouré, S.J., Universidade do Paraná.

**DISCUSSION.** Imagos of *M. mourei* can be distinguished from imagos of all other species within *M. (Ommaethus)* by the following combination of characters: (1)

body length of male imagos is 3.8-6.0 mm; (2) upper portion of male eyes are shaped as in Figs. 51-52; (3) lower portion of male eyes touches upper portion as in Fig. 51; (4) ratio of femora to tibiae of male prothoracic legs is approximately 0.54; length of prothoracic tibiae is approximately 2.3 mm; (5) abdominal terga 5-6 are brownish-yellow with submedian, sublateral, and lateral brownish-black bars as in Figs. 107-109; (6) basal 1/2 of forceps segment 1 gradually narrows apically; forceps segment 2 is rectangular (Fig. 65); (7) distal 1/3 of forceps segment 1 and all of segments 2 and 3 are washed with black; (8) penes are shaped as in Figs. 65-67; and (9) caudal filaments are brownish-yellow, basal 1/3-1/2 of segments with brownish-black bands.

Nymphs of *M. mourei* can be distinguished from known nymphs of all species within *Miroculis* by the following combination of characters: (1) anterolateral margins of labrum are gently rounded to slightly flattened as in Figs. 138-140; (2) subapical row of maxillae has 44-55 pectinate setae (Figs. 160-161); (3) abdominal terga 2-8 are dark with repeating color pattern as in Fig. 119; (4) abdominal tergum 6 is brownish-yellow, with lateral, sublateral and prominent submedian longitudinal bars as in Figs. 107-109, 119; (5) gills are small, posterolateral projections are not greatly developed (Fig. 131); and (6) caudal filaments are brownish-yellow, basal 1/5-1/3 of segments with black bands.

Male imagos of *M. mourei* have been allowed to dry out, and body lengths of freshly collected specimens would likely be larger than recorded here. I have indicated this with an asterisk(\*) in the description. In keys and listed diagnostic characters body length is shown to range up to 6.0 mm, which should include the upper size limit of *M. mourei*.

Color patterns of mature nymphs are relatively constant, however, the intensity of the brownish-black wash and marks varies greatly within the 31 nymphal specimens collected from the Rio Ipiranga. In some nymphs, the brownish-black wash on the abdominal terga is very light and only the submedian longitudinal bars are prominent, while in other nymphs the wash is so dark that the color pattern is nearly obscured. The posterior margins of the nymphal sterna are usually brownish-black, but in lightly pigmented or young nymphs only the posterolateral corners of each sternum will be brownish-black. Likewise, black bands on nymphal caudal filaments usually appear only on mature specimens. Gills of *M. mourei* usually have a light black wash on the dorsal half, however, the intensity of wash is highly variable and is not a reliable species character.

The main tracheal trunk of nymphal gills may bend back upon itself. The bend is usually located near the apex of the gill body and may appear as a black spot. This phenomenon has also been observed in *M. (Miroculis) marauiae* (Fig. 123), *M. (M.) fittkaui* and in *Leptophlebia intermedia* from Rocky Comfort Creek in Northwest Florida.

Shape of the anterolateral margins of the labrum varies from gently rounded to slightly flattened (Figs. 138-140) within *M. mourei*, and a series of specimens would be necessary to reliably use this character to identify nymphs.

BIOLOGY. Collection records indicate that imagos of *M. mourei* emerge in late February and March.

All specimens except for 3 nymphs were collected from the Rio Ipiranga in the Serra do Mar at an altitude of 800 meters. At the collecting site, the river is 20 to 30 meters wide, deep with huge boulders and very fast current.

Three nymphs were collected from the Rio do Patos at an altitude of 760 m. At this site, the river is roughly 50 m wide, and shallow with medium to slow current. The river bottom consists of exposed bedrock with a covering of rubble (W.L. and J.G. Peters, pers. comm.).

### ***Miroculis (Ommaethus) froehlichii* NEW SPECIES**

Figs. 53-54, 68-70, 118, 132, 141, 168

**MALE IMAGO** (in alcohol). Length: body, 6.2-7.8 mm; fore wings, 5.8-6.5 mm; prothoracic legs [broken off specimens and missing]. Eyes (Figs. 53-54): apex of upper portion separated on meson of head by a length approximately equal to maximum width of an upper portion; upper portion shaped as in Figs. 53-54; 27-34 facets in longest row, facets brownish-yellow, separated by dark brown grooves; lower portion separated dorsally from upper portion by a small distance as in Fig. 53, facets black, small. Head yellowish-brown, washed with brownish-black, carinae and ventral surface brownish-black. Scape and pedicel brown, washed with brownish-black, flagellum pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum yellowish-brown with margins, carinae and submedian sutures brownish-black, remainder of notum brown, carinae dark brown to brownish-black; sterna yellowish-brown, carinae dark brown to brownish-black; pleura yellowish-brown, washed with brownish-black, margins of sclerites and anterodorsal corner of mesopleura brownish-black. Wings: longitudinal and cross veins brown; membrane very light brown, fore wings with darker brown clouds around cross veins and brownish-black clouds around cross veins of C and Sc, hind wings darker brown near apex. Legs: [prothoracic and mesothoracic legs broken off specimens and missing], metathoracic legs brownish-yellow. Abdomen: terga and sterna 1-6 and anterior 1/2 of 7 semihyaline, whitish, terga and sterna 8-10 and posterior 1/2 of 7 pale yellow; terga 1-3 with faint brownish-black sublateral marks, tergum 1 with faint submedian brownish-black bars, tergum 2 and terga 6-8 with faint brownish-black submedian bars; spiracles brownish-black, tracheae semihyaline, whitish. Forceps (Figs. 68, 70): segment 3 from 0.98-1.02 (n = 2) length of segment 2; segment 2 from 0.44-0.49 (n = 2) length of segment 1; inner margin of forceps segment 1 forming an angular bend approximately 1/2 distance from base as in Fig. 68, distal inner margin not developed; segment 2 widens apically; pale yellow. Styliger plate (Figs. 68, 70): maximum length along lateral margin from 0.88-0.92 (n = 2) maximum width; maximum length along median line from 0.42-0.46 (n = 2) maximum width; posteromedian margin as in Fig. 68; pale yellow. Penes (Figs. 68-70): length 0.83-0.86 (n = 2) length of forceps segment 1, apex excavated as in Fig. 69; brown. Caudal filaments pale yellow.

**FEMALE IMAGO:** Unknown.

**MATURE NYMPH:** Unknown.

PROBABLE NYMPH (in alcohol). Body length, 4.0 mm. Eyes: eyes of female black; [eyes of male unknown]. Head brownish-yellow, genae brownish-black. Basal 1/2 of ocelli black, apical 1/2 white. Scape and pedicel brownish-yellow, washed very lightly with brownish-black; flagellum pale yellow. Mouthparts (Fig. 141): anterolateral margins of labrum slightly flattened (Fig. 141); length of subapical row of setae on maxillae 0.53-0.55 (n = 1) length of apical row, subapical row with 39-41 (n = 1) pectinate setae, segment 2 of maxillary palpi 1.20-1.30 (n = 1) length of segment 1, segment 3 of maxillary palpi 0.40-0.50 (n = 1) length of segment 2; segment 2 of labial palpi 1.16-1.26 (n = 1) length of segment 1, segment 3 of labial palpi 0.44-0.48 (n = 1) length of segment 2, labium light yellow. Thorax: nota brownish-yellow, anterior margin of pronotum, anterolateral corners and posteromedian area of mesonotum brownish-black; sterna brownish-yellow; pleura brownish-yellow, washed heavily with brownish-black. Legs: brownish-yellow, femora with apical brownish-black marks similar to Fig. 156, dorsal margin of femora washed with brownish-black, metathoracic femora with faint median brownish-black macula, tibiae with apical brownish-black band. Abdomen (Fig. 118): brownish-yellow, lateral 1/3 of terga 1-7 washed with brownish-black, wash darker laterally and sublaterally as in Fig. 118, terga 1-10 with submedian brownish-black marks as in Fig. 118, submedian marks light on tergum 9; spiracles and tracheae brownish-black; sterna brownish-yellow. Posterolateral spines on abdominal segments 2-9, developed beyond posterior margin of terga on segments 5-6 to 9; spines well developed on segments 6-9. Gills (Fig. 132): long, narrow, posterolateral projections not greatly developed to reduced, outer basal margin of dorsal portion not developed anteriorly; membrane grayish, translucent; tracheae black, unbranched. Caudal filaments brownish-yellow.

SPECIMENS EXAMINED (Fig. 168; locality b): Holotype male imago, BRAZIL: *São Paulo State*, Estação Biologica de Paranapiacaba, near Paranapiacaba, 15-X-1963, C.G. Froehlich. Paratype, 1 male imago, same data as holotype. One immature, female nymph, which is not included in the type series, was also examined; same data as holotype except date of collection is 5-XI-1963.

Holotype is deposited in collections of USP. One male imaginal paratype, and 1 immature female nymph which is not included in the type series are deposited in collections of FAMU.

LIFE CYCLE ASSOCIATIONS: Male imagos and the probable nymph are tentatively associated as both were collected at the same locality. This life cycle association must be considered tentative at this time, as rearing and/or the collection of mature male nymphal specimens is required for positive association.

ETYMOLOGY: Species is named for Dr. C.G. Froehlich, Universidade de São Paulo.

DISCUSSION: Imagos of *M. froehlichii* can be distinguished from imagos of all other species within *M. (Ommaethus)* by the following combination of characters: (1) body length of male imagos is 6.0-8.0 mm; (2) upper portion of male eyes are shaped as in Figs. 53-54; (3) lower portion of male eyes are separated from upper portion by a small distance (Fig. 53); (4) legs are uniformly brownish-yellow; (5) abdominal terga 5-6 are semihyaline, whitish; tergum 6 has faint submedian brownish-



black bars; (6) inner margin of forceps segment 1 is angularly bent approximately  $1/2$  distance from base as in Fig. 68; forceps segment 2 widens apically; (7) forceps are pale yellow; (8) penes are shaped as in Figs. 68-70; and (9) caudal filaments are pale yellow.

The probable nymph of *M. froehlich* can be distinguished from known nymphs of all species within *Miroculis* by the following combination of characters: (1) anterolateral margins of labrum are slightly flattened (Fig. 141); (2) subapical row of maxillae has 39-41 pectinate setae; (3) abdominal terga 1-7 have a repeating color pattern as in Fig. 118; (4) abdominal tergum 6 is brownish-yellow, with prominent brownish-black submedian marks, and dark brownish-black wash sublaterally and laterally as in Fig. 118; (5) gills are long and narrow, posterolateral projections are not greatly developed to reduced (Fig. 132); and (6) caudal filaments are brownish-yellow.

Knowledge of character variation within *M. froehlich* is precluded by the restricted sample size.

BIOLOGY. Collection records indicate that imagos of *M. froehlich* emerge in October.

### MIROCULITUS NEW GENUS

Figs. 25-27, 71-72, 93, 168

MALE IMAGO. Length of male: body, 4.0-5.0 mm; fore wings, 4.3-5.4 mm. Head [broken off specimen and missing, see description of male subimago]. Wings (Figs. 25-27): maximum width of fore wings a little less than  $2/5$  to  $2/5$  maximum length of fore wings; maximum width of hind wings a little greater than  $1/2$  to less than  $3/5$  length of hind wings; maximum length of hind wings slightly less than  $1/5$  to a little less than  $1/4$  maximum length of fore wings; vein Rs of fore wings forked a little greater than  $1/7$  to a little less than  $1/5$  distance from base of vein to margin; vein MA of fore wings forked a little greater than  $2/5$  to a little less than  $1/2$  distance from base of vein MA to margin, fork asymmetrical; vein MP of fore wings forked  $3/10$  to  $1/3$  distance from base of vein MP to margin, fork asymmetrical; a cross vein connects veins MP and CuA basal to the fusion of MP<sub>1</sub> and MP<sub>2</sub>; vein ICu<sub>1</sub> attached at base to vein CuA, cubital area as in Fig. 25; cross veins of fore wings numerous; marginal intercalaries numerous along posterior margin of fore wings as in Fig. 25. Hind wings with costal projection well developed, apex acute, pointed, base of projection wide, apex located from  $2/5$  to a little greater than  $2/5$  distance from base to margin of wings; length of vein Sc from  $1/2$  to a little greater than  $2/3$  length of hind wings; veins CuA and CuP fuse near base to a little greater than  $1/6$  distance from base of vein CuA to margin; apex of wings acute, slightly rounded; cross veins as in Figs. 26-27. Legs: [legs broken from specimen and missing, see description of male subimago]. Genitalia: forceps segment 3 from  $6/10$  to  $7/10$  length of segment 2, forceps segment 2 approximately  $3/10$  length of segment 1, segment 1 with basal  $1/2$  expanded, with spines on inner basal margin, segments 2 and 3 as in Fig. 71; styliiger plate [damaged] with anterolateral margins developed anterior-

ly to form arms which articulate with posterior margin of sternum 9, maximum length of styliger plate along lateral margin roughly  $1/2$  maximum width, maximum length of styliger plate along median line [damaged, not measurable], posterior margin as in Fig. 71; penes tubular, short, divided, without appendages (Figs. 71-72). Caudal filaments [broken off specimen and missing].

**MALE SUBIMAGO.** Eyes: eyes of male contiguous on meson of head; dorsally upper portion of eyes circular with medium-sized facets, 30-40 facets in longest row, upper portion set on dorsum of head by a short, wide stalk; diameter of lower portion of eyes 2-3 times height of stalk. Head with posteromedian projection between turbinate portion of eyes. Legs: claws of a pair dissimilar; one apically hooked, other pad-like, blunt (Fig. 93). Wings: membrane translucent, whitish, with long hair on apical and anal margins, hair with small branches, hair not thickened basally. Remainder of characters as in male imago except genital forceps not fully extended.

**FEMALE IMAGO:** Unknown.

**MATURE NYMPH:** Unknown.

**ETYMOLOGY:** *Miroculis*, a genus of Leptophlebiidae; itus, L., meaning having the nature of, pertaining to; masculine.

**TYPE SPECIES:** *Choroterpes emersoni* Needham and Murphy.

**SPECIES INCLUDED:** *Miroculitus emersoni* (Needham and Murphy), NEW COMBINATION.

**DISTRIBUTION:** Bartica District, British Guiana (Guyana), (Fig. 168; locality j).

**DISCUSSION.** *Miroculitus* can be distinguished from all other genera of Leptophlebiidae by the following combination of characters. In imagos: (1) upper portion of male eyes are on a short, wide stalk; (2) vein MA of fore wings is forked from a little greater than  $2/5$  to a little less than  $1/2$  distance from base of vein to margin, fork asymmetrical (Fig. 25); (3) vein MP of fore wings is forked from  $3/10$  to  $1/3$  distance from base of vein to margin, fork asymmetrical (Fig. 25); (4) vein ICu<sub>1</sub> of fore wings is attached at base to vein CuA; cubital area as in Fig. 25; (5) marginal intercalaries of fore wings are numerous along posterior margin of fore wings as in Fig. 25; (6) hind wings are shaped as in Figs. 26-27; costal projection is developed, apex acute, pointed, apex located from  $2/5$  to a little greater than  $2/5$  distance from base to apex of wings; (7) vein Sc of hind wings ends distad to apex of costal projection as in Figs. 26-27; (8) veins CuA and CuP of hind wings fused near base to a little greater than  $1/6$  distance from base of vein CuA to margin; (9) claws of a pair are dissimilar, one apically hooked, other pad-like (Fig. 93); (10) penes are tubular, divided, without appendages (Figs. 71-72); and (11) male genital forceps shaped as in Fig. 71.

The wings, especially the hind wings, and male genitalia of *Miroculitus* and *Miroculis* are very similar in general appearance. However, imagos of *Miroculitus* can be distinguished from those of *Miroculis* by the following characters: (1) vein MP of fore wings is forked asymmetrically as in Fig. 25; (2) a cross vein connects veins MP and CuA basal to the fusion of MP, and MP; (Fig. 25); (3) vein ICu<sub>1</sub> of fore wings is attached at base to vein CuA (Fig. 25); (4) maximum width of fore wings is a little less than  $2/5$  to  $2/5$  maximum length of fore wings; and (5) veins CuA and CuP of hind wings fuse at base to a little greater than  $1/6$  distance from base of vein CuA to margin (Figs. 26-27).

**Miroculitus emersoni** (Needham and Murphy),  
NEW COMBINATION

Figs. 25-27, 71-72, 93, 168

*Choroterpes emersoni* Needham and Murphy, 1924, 24, Entomol. Ser. 4:47-48; Traver, 1946, 17:427; Traver, 1947, 18:154-155.

MALE IMAGO (in alcohol). [Wings and genitalia are on slides, remainder of body is lost. Description is based on original description (Needham and Murphy 1924) and examination of slide material]. Length: body [lost]; fore wings, 5.2 mm; prothoracic legs [broken from specimens and missing]. Eyes: [unknown, see subimago]. Head reddish-brown to black. Antennae: [unknown]. Ocelli: [unknown]. Thorax: brown. Wings (Figs. 25-27): longitudinal and cross veins of fore and hind wings light brown; membrane of fore and hind wings hyaline, apical 1/3 of cells of C and Sc of fore wings translucent, whitish. Legs: brownish-yellow, prothoracic femora washed with brownish-black, meso- and metathoracic femora with faint submedian and apical brownish-black marks, tibiae with brownish-black apical bands. Abdomen: posterior margin and lateral carinae of terga brownish-black. Forceps (Fig. 71): segment 3 roughly 0.65 (n = 1) length of segment 2, segment 2 roughly 0.3 (n = 1) length of segment 1; light brown. Styliiger plate (Fig. 71): [damaged], maximum length along lateral margin roughly 1/2 maximum width; light brown. Penes (Figs. 71-72): length roughly 0.7 (n = 1) length of forceps segment 1, penes narrow apically with rows of spines basally (Figs. 71-72); dark brown. Caudal filaments light yellow, joints of segments narrowly marked with brown.

MALE SUBIMAGO (in alcohol). Length: body, 4.0-5.0 mm; fore wings, 4.2-4.7 mm; prothoracic legs [broken from specimens and missing]. Eyes: stalked turbinate portion pale yellow apically, brownish-black basally; 30-40 facets in longest row of upper portion, facets yellow; facets of lower portion black, small. Head brownish-yellow, ventral surface washed heavily with brownish-black. Antennae light yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum brownish-yellow, lateral margins and carinae brownish-black, remainder of nota brown; sterna brownish-yellow; pleura brown. Wings: longitudinal and cross veins as in imago; membrane of fore and hind wings white, translucent. Legs: brownish-yellow; prothoracic claws as in Fig. 93. Abdomen: tergal-sternal fold brownish-black; tergum 1 light brown, opaque; terga 2-9 brownish-yellow, semitransparent, with light submedian and lateral brown marks, sterna brownish-yellow, semitransparent. Genitalia: [on slide, in poor condition, see discussion]. Caudal filaments pale brown basally, brownish-yellow apically.

FEMALE IMAGO: Unknown.

MATURE NYMPH: Unknown.

TYPE LOCALITY: BRITISH GUIANA, *Bartica District*, Kalacoon (Fig. 168, locality j).

DEPOSITION OF TYPE: Holotype male imago (wings and genitalia) deposited at CU.

SPECIMENS EXAMINED: 1 male imaginal holotype (wings and genitalia only), BRITISH GUIANA, *Bartica District*, Kalacoon, March 23, 1918, A.E. Emerson; 4 male subimaginal specimens (damaged, BRITISH GUIANA, *Bartica District*, Penal Settlement, March 27, 1919, collector unknown).

The body of the holotype is missing while the additional specimens have been poorly preserved.

Needham and Murphy (1924) described *Choroterpes emersoni* based on 1 female and 3(?) male specimens collected from a spider web that overhung Kalacoon Brook. Traver (1946) noted that the allotype slide of *Choroterpes emersoni* contained a female body of *Hagenulopsis*, an assortment of male legs, a male head, and pieces of caudal filaments. Traver (1946, 1947) identified the female allotype of *Choroterpes emersoni* as *Hagenulopsis minutus* Spieth. She also recognized two males of *Hagenulopsis* in the type series of *Choroterpes emersoni*, but stated that the body of the holotype of *C. emersoni* was missing.

Traver (1947) associated 4 male subimaginal specimens with the holotype slides of *Choroterpes emersoni*. This association appears justified as the penes have rows of spines as in the holotype, however, the genitalia were poorly mounted and all other details are obscured.

The male head on the allotype slide could belong to a number of genera including *Miroculis*, *Miroculitus*, *Microphlebia* or *Hagenulopsis*. The stalked eyes are so similar among these taxa that differentiating characters are not evident in the dried specimen on slide. *Hagenulopsis* might be favored because of the small size of the head.

The imaginal claws on the allotype slide are of a type common to many genera, including *Hagenulopsis*, but not *Miroculis*. The non-pad like claw is hooked, not straight or spike-like as in *Miroculis*. However, the claws are similar to claws of genera related to *Miroculis* and *Miroculitus* such as *Hermanellopsis* and *Microphlebia*. The claws of the subimagos later associated with *Miroculitus emersoni* by Traver (1947) are also hooked (Fig. 93). The ratios for the 2 prothoracic legs with claws on the allotype slide are as follows: 0.46-0.47; 1.00(1.58-1.59 mm); 0.03; 0.30; 0.21; 0.07-0.12; 0.06. The femora are washed heavily with brownish-black and the tibiae have brownish-black apical bands. While it is possible that these legs belong to *Miroculitus emersoni*, it appears most likely that they belong to the two male specimens of *Hagenulopsis* originally included in the type series.

The caudal filaments on the allotype slide show evidence of annulations at articulations of the basal segments. This character state is observed in *Hagenulopsis* and some species of *Miroculis*. Setae appear randomly distributed over the caudal filament segments and are not marked by clustering at the margins. The comparative study of the caudal filaments of the Leptophlebiidae has not reached the level where this data could help distinguish taxa.

### MICROPHLEBIA NEW GENUS

Figs. 28-31, 40-43, 73-76, 95, 110-111, 120, 133-136, 148-155, 168

IMAGO: Unknown.

MALE SUBIMAGO. Length of male: body, 3.6-5.0 mm; fore wings 3.4-3.9 mm. Eyes (Figs. 40-43): eyes of male separated on meson of head by a length  $1/6$  to  $1/3$  width of an upper portion; dorsally upper portion of eyes circular with medium-sized facets, 17-30 facets in longest row, upper portion set on dorsum of head by a

short, wide stalk as in Figs. 40, 42; diameter of lower portion of eyes approximately equal to height of stalk. Head with posteromedian projection between turbinate portion of eyes (Figs. 41, 43). Antennae subequal to slightly longer than length of prothoracic femora. Wings (Figs. 28-31): maximum width of fore wings slightly greater than  $1/3$  maximum length of fore wings; maximum width of hind wings a little greater than  $1/2$  to less than  $3/5$  length of hind wings; maximum length of hind wings  $1/7$  to slightly less than  $1/6$  maximum length of fore wings; long, thin, branched hair on apical and anal margins of fore and hind wings (Figs. 28-31); vein Rs of fore wings forked  $1/7$  to a little less than  $1/5$  distance from base of vein to margin; vein MA of fore wings forked  $2/5$  to a little greater than  $2/5$  distance from base of vein MA to margin, fork asymmetrical; vein MP of fore wings forked  $1/3$  to a little greater than  $1/3$  distance from base of vein MP to margin, fork asymmetrical; a cross vein connects veins MP and CuA basal to the fusion of MP, and MP<sub>2</sub>; vein ICu<sub>1</sub> attached at base to vein CuA, cubital area reduced as in Fig. 28; marginal intercalaries reduced in number, cross veins few. Hind wings with costal projection well developed, apex rounded, base of projection wide, apex located  $1/2$  to  $3/5$  distance from base to margin of wings; length of vein Sc slightly greater than  $1/2$  to  $3/5$  length of hind wings; apex of wings acute; cross veins few (Figs. 29-30). Claws of a pair dissimilar; one apically hooked as in Fig. 95, other pad-like, blunt. Genitalia (Figs. 73-76): forceps segment 3 from  $3/5$  to  $4/5$  length of segment 2, forceps segment 2 greater than  $2/5$  to less than  $1/2$  length of segment 1, segment 1 with basal  $1/3$ - $1/2$  expanded, with spines on inner basal margin, segments 2 and 3 cylindrical (Figs. 73, 75); styliger plate with anterolateral margins developed anteriorly to form arms which articulate with posterior margin of sternum 9, maximum length of styliger plate along lateral margin from  $2/5$  to  $4/5$  maximum width, maximum length of styliger plate along median line slightly greater than  $1/3$  to  $4/5$  maximum width, posteromedian margin as in Figs. 73, 75; penes tubular, short, divided, sculptured, without appendages (Figs. 73-76). Caudal filaments [broken off specimens apically and missing].

FEMALE IMAGO: Unknown.

MATURE NYMPH. Head prognathous. Antennae [broken off specimens apically and missing]. Mouthparts (Figs. 148-153): lateral margins of clypeus with basal  $1/2$  strongly tapered, apical  $1/2$  slightly tapered; anteromedian margin of clypeus very slightly concave as in Fig. 148. Maximum width of labrum subequal to width of distal portion of clypeus; anterolateral margins of labrum gently rounded as in Fig. 148; dorsal hair on labrum as in Fig. 148, short setae on basal  $2/3$  of lateral margins, submedian areas of hair ventrally; anteromedian emargination with 5 small, subequal-sized denticles (Figs. 148-149). Outer margin of mandibles curved as in Fig. 153, with scattered hair on median area of outer margin; inner basal margin of mandibles smoothly curved as in Fig. 153; incisors of left mandible each with 3 apical projections, and prosthema as in Fig. 153. Lingua of hypopharynx with well developed lateral processes, anterior margin of lingua with median cleft, rounded submedian lobes and short hair as in Fig. 150; superlingua of hypopharynx as in Fig. 150, with hair along anterior margin. Galea-lacinia of maxillae with a subapical row of 18-20 pectinate setae (Fig. 152), apical setae as in Fig. 152, dense; cardo of max-

illae with large setae on outer margin; segment 2 of maxillary palpi 1 to 1-1/3 length of segment 1; segment 3 of palpi 2/5 to slightly less than 3/5 length of segment 2; setae on maxillae as in Fig. 152. Segment 2 of labial palpi 1 to 1-1/4 length of segment 1, outer margin with 3-6 long, thick setae basally and long thin hairs on apical 2/3, width at base and apex of segment 2 approximately equal; segment 3 of palpi 2/5 to 1/2 length of segment 2, inner margin with widely spaced hair-like setae and apex with dense peg-like setae, meson of segment 3 with a diagonal row of 4-6 large setae as in Fig. 151; glossae curved over ventrally, ventral portion of glossae long, straight; paraglossae wide as in Fig. 151; lateral margins of submentum with setae as in Fig. 151; posteromedian margin of submentum with small lobe. Legs (Figs. 120, 154-155): maximum width of tibiae 1-1/4 to 1-1/2 maximum width of tarsi, tibiae in cross section circular, tibiae with a row of dense thick spines on inner lateral margin (Fig. 154); outer margin of femora indented near apex so tibiae can draw partially into femora (Fig. 154); apex of claws hooked and narrow, denticles progressively larger apically, except apical denticle much larger (Fig. 155). Gills (Figs. 133-136): gills on segments 1-7 similar, except apex of dorsal portion variable; dorsal and ventral portions of gills on segments 1-7 dissimilar; gills 1-6 longer than gill 7; dorsal and ventral portions plate-like; dorsal portions approximately 3/4 length and 1/2 width of ventral portions; apex of dorsal portion of gill 1 as in Fig. 133, of gills 2-6 as in Figs. 134-135, of gill 7 as in Fig. 136; apex of ventral portion rounded (Figs. 133-136); tracheae unbranched. Posterolateral spines on abdominal segments 5-6 to 9, spines developed beyond posterior margin of terga on segments 7-8 to 9, spines well developed, acute, on segments 8 and 9 (Fig. 120). Caudal filaments [broken off specimens apically and missing].

ETYMOLOGY: mikros, Gr., meaning small, little; phlebo, Gr., meaning vein, a common ending in the Leptophlebiidae; feminine.

TYPE SPECIES: *Microphlebia surinamensis* NEW SPECIES.

SPECIES INCLUDED: *M. surinamensis* NEW SPECIES; *M. pallida* NEW SPECIES.

DISTRIBUTION: Surinam and the Amazonas State, Brazil (Fig. 168; localities d, i).

DISCUSSION. *Microphlebia* can be distinguished from all other genera of Leptophlebiidae by the following combination of characters. In imagos: (1) upper portion of male eyes are on a short, wide stalk (Figs. 40-43); (2) vein MA of fore wings is forked from 2/5 to a little greater than 2/5 distance from base of vein to margin, fork asymmetrical (Fig. 28); (3) vein MP of fore wings is forked from 1/3 to a little greater than 1/3 distance from base of vein to margin, fork asymmetrical; (4) a cross vein connects veins MP and CuA basal to the fusion of MP, and MP; (5) vein ICu, of fore wings is attached at base to vein CuA; cubital area is reduced as in Fig. 28; (6) marginal intercalaries of fore wings are reduced in number (Fig. 28); (7) hind wings are shaped as in Figs. 29-30; costal projection is well developed, apex rounded, apex located 1/2 to 3/5 distance from base to apex of wings; (8) claws of a pair are dissimilar, one apically hooked as in Fig. 95, other pad-like; (9) anterolateral margins of male styliiger plate are developed anteriorly to form arms which articulate with the posterior margin of sternum 9; and (10) penes are tubular, divided, sculptured and without appendages (Figs. 73-76), and the male genital forceps are shaped as in Figs. 73-75. In nymphs: (1) gills on segments 1-7 are similar,

except apex of dorsal portion variable as in Figs. 133-136; dorsal and ventral portions are plate-like; dorsal portions are approximately  $3/4$  length and  $1/2$  width of ventral portions; ventral portions are rounded apically (Figs. 133-136); (2) basal  $1/2$  of lateral margins of clypeus is strongly tapered; apical  $1/2$  is slightly tapered (Fig. 148); (3) maximum width of labrum is subequal to width of distal portion of clypeus; labrum with short setae on basal  $2/3$  of lateral margins (Fig. 148); (4) outer margin of mandibles is curved with scattered hair on median area as in Fig. 153; (5) lingua of hypopharynx has well developed lateral processes; anterior margin has a median cleft and submedian lobes as in Fig. 150; (6) galea-lacinia of maxillae has a subapical row of 18-20 pectinate setae (Fig. 152); (7) glossae of labium are curved over ventrally; ventral portion of glossae is long and straight (Fig. 151); (8) apex of claws is hooked and narrow; denticles are progressively larger apically, except apical denticle much larger (Fig. 155); and (9) posterolateral spines occur on abdominal segments 5-6 to 9; spines are well developed, acute on segments 8 and 9 (Fig. 120).

#### KEY TO KNOWN IMAGOS OF MICROPHLEBIA

1. Upper portion of male eyes with 23-30 facets in longest row (Figs. 40-41); femora uniformly brownish-yellow; body length 4.4-5.0 mm; genitalia as in Figs. 75-76 ..... *M. pallida* NEW SPECIES
- Upper portion of male eyes with 17-24 facets in longest row (Figs. 42-43); femora brownish-yellow, apical  $1/3$  washed with brownish-black; body length 3.6-4.4 mm; genitalia as in Figs. 73-74 .....  
..... *M. surinamensis* NEW SPECIES

#### KEY TO KNOWN NYMPHS OF MICROPHLEBIA

1. Femora uniformly brownish-yellow; membrane of abdominal gills light gray; vertex and frons of head washed very lightly with brownish-black; segment 2 of maxillary palpi 1.00-1.20 length of segment 1 .....  
..... *M. pallida* NEW SPECIES
- Femora brownish-yellow, apical  $1/5$ - $1/3$  washed with brownish-black (Figs. 120, 154); membrane of abdominal gills blackish-gray; vertex and frons of head washed heavily with brownish-black; segment 2 of maxillary palpi 1.15-1.30 length of segment 1 .....  
..... *M. surinamensis* NEW SPECIES

#### *Microphlebia surinamensis* NEW SPECIES

Figs. 28-31, 42-43, 73-74, 95, 110-111, 120, 133-136, 148-155, 168

MALE IMAGO: Unknown.

MALE SUBIMAGO (in alcohol). Length: body, 3.6-4.4 mm; fore wings, 3.4-3.9 mm. Eyes (Figs. 42-43): stalked turbinate portion brownish-black; 17-24 facets in

longest row of upper portion, facets light gray; facets of lower portion black, small. Head with posteromedian projection as in Fig. 43; head brownish-yellow, washed heavily with brownish-black. Antennae pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum brownish-yellow, submedian carinae and outer margins washed with brownish-black; mesonotum and metanotum light brown, carinae brownish-black; sterna light brown, lateral margins of sclerites dark brown to brownish-black, prosternum washed with brownish-black; pleura light brown, washed with brownish-black, margins of sclerites and carinae brownish-black. Wings (Figs. 28-31): vein Rs of fore wings forked 0.16-0.18 (n=2) distance from base of vein to margin; length of vein Sc of hind wings 0.55-0.57 (n=2) length of hind wings; longitudinal and cross veins very light brown, with C, Sc and R<sub>1</sub> of fore wings and C and Sc of hind wings brownish-black; membrane whitish, translucent. Legs (Fig. 95): brownish-yellow, apical 1/3 of femora washed with brownish-black, metathoracic femora with median brownish-black macula; prothoracic claws as in Fig. 95. Abdomen (Figs. 110-111): terga 1-10 semihyaline, brownish-yellow with posterior margins brownish-black; terga 1-9 washed with brownish-black, except wash absent on anterior margin and median area of each tergum, terga 1-3 heavily washed and median pale area obscured, terga 4-9 as in Figs. 110-111; tergum 10 with posterior submedian brownish-black maculae; spiracles dark brown, tracheae smoky; sterna 1-8 brownish-yellow, sternum 9 light brown, posterior margins of sterna 1-9 washed lightly with brownish-black. Forceps (Figs. 73-74): segment 3 approximately 0.7 (n=1) length of segment 2; segment 2 approximately 0.6 (n=1) length of segment 1; pale yellow. Styliger plate (Figs. 73-74): maximum length along lateral margin approximately 0.5 (n=1) maximum width; maximum length along median line approximately 0.4 (n=1) maximum width; posteromedian margin as in Fig. 73; brownish-yellow. Penes (Figs. 73-74): length approximately 1.3 (n=1) length of forceps segment 1, sculptured as in Figs. 73-74; dark brown. Caudal filaments brownish-yellow.

FEMALE IMAGO: Unknown.

MATURE NYMPHS (in alcohol). Body length, 3.2-4.4 mm. Eyes: eyes of female black; upper portion of eyes of male black, lower portion black. Head light brown, frons, genae, vertex and posterolateral corners of labrum washed heavily with brownish-black as in Fig. 120. Basal 2/3 of ocelli black, apical 1/3 white. Antennae pale yellow. Mouthparts (Figs. 148-153): segment 2 of maxillary palpi 1.16-1.29 (n=3) length of segment 1, segment 3 of maxillary palpi 0.44-0.53 (n=3) length of segment 1; segment 2 of labial palpi 1.00-1.21 (n=3) length of segment 1, segment 3 of labial palpi 0.44-0.53 (n=3) length of segment 2, labium light yellow, submentum and base of mentum washed with black. Thorax: nota light brown, washed lightly with brownish-black, anterior margin of pronotum and anterolateral corners of mesonotum brownish-black; sterna light brown; pleura light brown, washed lightly with black. Legs (Figs. 154-155): brownish-yellow, apical 1/5-1/3 of femora washed with brownish-black, wash darker on metathoracic femora, metathoracic femora with to without median brownish-black macula. Abdomen (Fig. 120): brownish-yellow, brownish-black wash as in male imago. Gills (Figs. 133-136): membrane blackish-gray, translucent; tracheae black. Caudal filaments brownish-yellow.



SPECIMENS EXAMINED (Fig. 168; locality i): Holotype male subimago, SURINAM: *Suriname Dist.*, Kreek, Powaka, 200', 30-XII-1968, W. L. and J. G. Peters. Paratypes: 1 male subimago, same data as holotype; 2 mature nymphs, same locality as holotype, date of collection 20-XII-1968; 5 nymphs, SURINAM: *Brokopondo Dist.*, Kreek N. W. of Phedra on Kraka-Phedra road, 200', 20-XII-1968, W. L. and J. G. Peters; 1 nymph, SURINAM: *Suriname Dist.*, 1st creek crossing road to Hanover, downstream culvert 500-1000 m, 7-VIII-1969, wet mud at edge of SNOG 4, N. Nieser.

Holotype and 5 nymphal paratypes are deposited in collections of FAMU. One male subimaginal and 3 nymphal paratypes are deposited in UU collections.

LIFE CYCLE ASSOCIATIONS: Nymphs and subimagos are associated by shared color patterns on the legs and abdomen. All specimens except for one nymph were collected in the same area over a period of 10 days.

ETYMOLOGY: Species is named for the country Surinam, type locality.

DISCUSSION: *M. surinamensis* can be distinguished from all other species of *Microphlebia* by the following combination of characters. In male subimagos: (1) body length is 3.6-4.4 mm; (2) upper portion of male eyes has 17-24 facets in longest row (Figs. 42-43); (3) vein Rs of fore wings is forked 0.16-0.18 ( $n=2$ ) distance from base of vein to margin; (4) vein Sc of hind wings ends from 0.55-0.57 ( $n=2$ ) length of hind wings; (5) femora are brownish-yellow, apical 1/3 washed with brownish-black, metathoracic femora with median brownish-black macula; (6) abdominal terga are heavily washed with brownish-black; and (7) genitalia are as in Figs. 73-74. In nymphs: (1) head and abdominal terga are heavily washed with brownish-black (Fig. 120); (2) femora are brownish-yellow, apical 1/5-1/3 washed with brownish-black (Fig. 154); (3) membrane of gills is blackish-gray; and (4) submentum and mentum of labium are washed with brownish-black.

The nymph collected by Dr. Nieser lacks the median brownish-black macula on the metathoracic femora, which is present on other nymphal paratypes.

BIOLOGY: Subimagos were collected at light near a small forest stream at an altitude of 200 feet in mid and late December. Two nymphs were also collected from the same stream which was less than 2 meters wide and roughly 1 meter deep (W. L. and J. G. Peters, pers. comm.).

### ***Microphlebia pallida* NEW SPECIES**

Figs. 40-41, 75-76, 168

MALE IMAGO: Unknown.

MALE SUBIMAGO (in alcohol). Length: body, 4.4-5.0 mm; fore wings, 3.6-4.0 mm. Eyes (Figs. 40-41): stalked turbinate portion brownish-black; 23-30 facets in longest row of upper portion, facets light gray; facets of lower portion black, small. Head with posteromedian projection as in Fig. 41; head brownish-yellow, washed with brownish-black. Antennae pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum brownish-yellow, submedian carinae and outer margins washed with brownish-black; mesonotum and metanotum light brown, carinae

darker; sterna light brown, lateral margins of sclerites darker; pleura brownish-yellow, margins of sclerites and carinae brownish-black. Wings: vein Rs of fore wings forked 0.14-0.16 ( $n=2$ ) distance from base of vein to margin; length of vein Sc of hind wings 0.59-0.60 ( $n=2$ ) length of hind wings; longitudinal and cross veins very light brown, with base of C, Sc and R, dark brown; membrane whitish, translucent. Legs: uniformly brownish-yellow. Abdomen: terga 1-10 light yellow, posterior margins washed with brownish-black; terga 1-9 washed lightly with brownish-black except wash absent on anterior margins and median areas of terga 4-9; tergum 10 with posterior submedian brownish-black maculae; spiracles dark brown, tracheae smoky; sterna 1-8 light yellow, sternum 9 brownish-yellow, posterior margins of sterna 1-9 washed lightly with brownish-black. Forceps (Figs. 75-76): segment 3 approximately 0.6 ( $n=1$ ) length of segment 2; segment 2 of forceps approximately 0.4 ( $n=1$ ) length of segment 1; pale yellow. Styli-plate (Figs. 75-76): maximum length along lateral margin approximately 0.7 ( $n=1$ ) maximum width; maximum length along median line 0.8 ( $n=1$ ) maximum width; brownish-yellow. Penes (Figs. 75-76): length approximately 1.3 ( $n=1$ ) length of forceps segment 1, sculptured as in Figs. 75-76; dark brown. Caudal filaments brownish-yellow.

FEMALE IMAGO: Unknown.

MATURE NYMPH (in alcohol). Body length, 3.2-5.0 mm. Eyes: eyes of female black; upper portion of eyes of male black, lower portion black. Head brownish-yellow, genae washed with black. Basal 2/3 of ocelli black, apical 1/3 white. Antennae pale yellow. Mouthparts: segment 2 of maxillary palpi 1.05-1.18 ( $n=2$ ) length of segment 1, segment 3 of maxillary palpi 0.50-0.52 ( $n=2$ ) length of segment 2; segment 2 of labial palpi 1.04-1.07 ( $n=2$ ) length of segment 1, segment 3 of labial palpi 0.46-0.48 ( $n=2$ ) length of segment 2, labium light yellow. Thorax: nota brownish-yellow, margins of pronotum washed with brownish-black; sterna brownish-yellow; pleura brownish-yellow, washed lightly with black. Legs: uniformly brownish-yellow. Abdomen: color and marks as in male subimago. Gills: membrane light gray, translucent; tracheae black. Caudal filaments pale yellow.

SPECIMENS EXAMINED (Fig. 168; locality d): Holotype male subimago, BRAZIL: *Amazonas State*, Rio Branquinho, near junction with Rio Cuieiras, N. of Manaus, at light, 19-VII-1961, E. J. Fittkau. Paratypes: 1 male subimago, BRAZIL: *Amazonas State*, Rio Branquinho, near Rio Cuieiras, N. of Manaus, 22-IV-1961, E. J. Fittkau; 4 nymphs, BRAZIL: *Amazonas State*, Aracu Creek, 15 km from Manaus, road to Rio Branco, 8-VI-1962, E. J. Fittkau.

Holotype and 2 nymphal paratypes are deposited in collections of INPA. One male subimaginal and 2 nymphal paratypes are deposited in FAMU collections.

LIFE CYCLE ASSOCIATIONS: Nymphs and male subimagos were associated by shared abdominal color patterns.

ETYMOLOGY: *pallida*, L., meaning pale.

DISCUSSION: *M. pallida* can be distinguished from all other species of *Microphlebia* by the following combination of characters. In male subimagos: (1) body length is 4.4-5.0 mm; (2) upper portion of male eye has 23-30 facets in longest row (Figs. 40-41); (3) vein Rs of fore wings is forked 0.14-0.16 ( $n=2$ ) distance from base of vein to margin; (4) vein Sc of hind wings ends 0.59-0.60 ( $n=2$ ) length of hind

wings; (5) femora are uniformly brownish-yellow; (6) abdominal terga are washed lightly with brownish-black; and (7) genitalia are as in Figs. 75-76. In nymphs: (1) head and abdominal terga are lightly washed with brownish-black; (2) femora are uniformly brownish-yellow; (3) membrane of gills is light gray; and (4) submentum and mentum of labium are uniformly light yellow.

**BIOLOGY:** The holotype male subimago was collected at light near the mouth of the Rio Branquinho between 1830 and 1915 hours, in mid-July. The paratype subimago was collected at light under a dense Igapó forest in mid April. One nymph collected in early July had wing pads which were beginning to turn black. Thus, *M. pallida* emerges at least as early as April and probably into August.

Nymphs were collected in weak current on fine detritus. (Translated from Dr. E. J. Fittkau's field notes).

### Genus **HERMANELLOPSIS** Demoulin, 1955

Figs. 32-39, 77-80, 85-86, 89, 94, 168

*Hermanella* (*Hermanellopsis*) Demoulin, 1955, 31(20):8

*Hermanella* Spieth, 1943, 1244:9 (partim); Traver, 1947, 18:159-160 (partim)

*Hermanellopsis*: Edmunds, Jensen and Berner, 1976:222.

**IMAGO.** Length of male: body, 3.5-5.0 mm; fore wings, 4.0-4.9 mm; prothoracic legs [broken from specimens and missing]. Length of female: body, 3.1 mm; fore wings, 3.2-3.3 mm. Eyes: eyes of male contiguous to separated on meson of head by a length  $1/8$  width of an upper portion; dorsally upper portion of male eyes circular with medium-sized facets, 25-38 facets in longest row, upper portion set on dorsum of head by a short, wide stalk; width of lower portion of male eyes approximately equal to height of stalk; eyes of female separated on meson of head by a length approximately 5 times maximum width of an eye. Lateral ocelli enlarged. Wings (Figs. 32-39): maximum width of fore wings  $1/3$  to a little less than  $2/5$  maximum length of fore wings; maximum width of hind wings a little less than to a little greater than  $1/2$  length of hind wings; maximum length of hind wings  $1/6$  to slightly greater than  $1/6$  length of fore wings; vein Rs of fore wings forked slightly less than  $1/6$  to a little less than  $1/5$  distance from base of vein to margin; vein MA of fore wings forked a little greater than  $2/5$  to a little less than  $1/2$  distance from base of vein to margin, fork asymmetrical; vein MP of fore wings forked (Fig. 35) to  $MP_2$  attached at base to  $MP_1$  and CuA by a cross vein (Fig. 32) from slightly greater than  $1/3$  to a little less than  $2/5$  distance from base of vein MP to margin, fork asymmetrical; a cross vein connects veins MP and CuA basal to the fusion or attachment of veins  $MP_1$  and  $MP_2$ ; vein ICu<sub>1</sub> of fore wings attached to CuA by a cross vein, cubital area as in Figs. 32, 35; cross veins numerous in anterior  $2/3$  of fore wings, reduced in posterior  $1/3$  of fore wings; marginal intercalaries reduced in number (Figs. 32, 35). Hind wings with costal projection well developed, apex acute, pointed to slightly rounded as in Figs. 34, 36-39, base of projection wide, apex located a little greater than  $2/5$  to a little less than  $1/2$  distance from base to margin of wings; length of vein Sc a little

less than  $1/2$  length of hind wings; apex of wings acute, pointed to slightly rounded; cross veins few. Claws of a pair dissimilar; one apically hooked as in Fig. 94, other pad-like, blunt. Male genitalia (Figs. 77-80): forceps segment 3 approximately  $3/4$  length of segment 2, forceps segment 2 from  $2/5$  to  $1/2$  length of segment 1, segment 1 with basal  $1/3$ - $1/2$  expanded, with spines on inner basal margin (Figs. 77-78), segments 2 and 3 cylindrical, segment 3 rounded apically; styliger plate with anterolateral margins developed to form arms which articulate with posterior margin of sternum 9, maximum length of styliger plate along lateral margin from  $4/5$  to a little less than equal to maximum width, maximum length of styliger plate along median line a little greater than  $2/5$  to less than  $1/2$  maximum width, posterior margin of styliger plate with two submedian projections as in Figs. 77-80; penes long, tubular, narrow, divided, acute apically, without appendages. Sternum 7 of female with small posteromedian genital extension as in Figs. 85-86. Sternum 9 of female with posteromedian cleft as in Fig. 89. Caudal filaments [broken off specimens and missing].

**SUBIMAGO.** Characters similar to imagos except upper portion of eyes, prothoracic legs and genital forceps of males not fully extended. Male head with posteromedian projection between turbinate portion of eyes. Upper portion of eyes of male smaller, eyes of male contiguous to separated on meson of head by a length  $1/6$  width of an upper portion; height of stalk of upper portion from  $1/4$  to  $1/3$  width of lower portion. Wings: membrane translucent, whitish; long, thin hair on apical and anal margins of fore and hind wings with short branches (Figs. 35-39).

**MATURE NYMPH:** Unknown [see discussion].

**TYPE SPECIES:** *Hermanellopsis incertans* (Spieth).

**SPECIES INCLUDED:** *H. incertans* (Spieth); *H. arsia* NEW SPECIES.

**DISTRIBUTION:** Surinam and Amazonas State, Brazil (Fig. 168; localities d, h).

**DISCUSSION.** *Hermanellopsis* can be distinguished from all other genera of Lep-toptlebiidae by the following combination of characters. In imagos: (1) upper portion of male eyes are on a short, wide stalk; (2) eyes of female are separated on meson of head by a length approximately 5 times maximum width of an eye; (3) vein MA of fore wings is forked a little greater than  $2/5$  to a little less than  $1/2$  distance from base of vein to margin, fork asymmetrical as in Figs. 32, 35; (4) vein MP of fore wings is forked asymmetrically as in Fig. 35, to vein  $MP_2$  attached at base to  $MP_1$  and CuA by a cross vein as in Fig. 32; a cross vein connects veins MP and CuA basal to the fusion or attachment of veins  $MP_1$  and  $MP_2$ ; (5) marginal intercalaries of fore wings are reduced in number as in Figs. 32, 35; (6) hind wings are shaped as in Figs. 33-34, 36-39; costal projection is developed, apex located a little greater than  $2/5$  to a little less than  $1/2$  distance from base to margin of wings; (7) claws of a pair are dissimilar, one apically hooked as in Fig. 94, other pad-like; (8) anterolateral margins of male styliger plate are developed anteriorly to form arms which articulate with the posterior margin of sternum 9 (Figs. 77-80); (9) posterior margin of male styliger plate has submedian well developed projections as in Figs. 77-80; penes are tubular, narrow, divided and without appendages (Figs. 77-80); genital forceps are shaped as in Figs. 77-80; and (10) sternum 9 of female has a posteromedian cleft as in Fig. 89.

Spieth (1943) referred the species *incertans* to *Hermanella*, a genus established by Needham and Murphy (1924) for nymphs of *H. thelma*. Spieth's description was based upon 3 male imagos and he provided good figures of the male genitalia, fore and hind wings (Spieth 1943). Spieth listed 2 female imagos as paratypes but did not describe them. We have examined 1 female paratype and a description is provided herein.

Traver (1947) pointed out differences in wing venation between imagos of *incertans* and nymphal wing pads of *Hermanella thelma* Needham and Murphy. On the basis of Traver's comment Demoulin (1955) placed *H. incertans* as the type species of a new subgenus, *Hermanellopsis*. Demoulin (1955) also associated 4 nymphs from Santa Catarina State, Brazil as *Hermanella (Hermanellopsis)* sp. From study of the literature (Needham and Murphy 1924; Traver 1947; Demoulin 1955) and specimens of *Hermanella* reared by W.L. and J.G. Peters (unpublished data) it is obvious that the species *thelma* and *incertans* belong neither to the same genus nor to allied genera (Edmunds et al. 1976), and that Demoulin's *Hermanella (Hermanellopsis)* sp. is an undescribed species of true *Hermanella*, and not the unknown nymph of *Hermanellopsis*.

The hind wing of *Hermanellopsis incertans* figured by Edmunds et al. (1976, Fig. 332) differs from Spieth's (1943, Fig. 14) figure. Edmunds et al. (1976) do not show vein CuP while Spieth (1943) figures vein CuP attached at base to CuA with dashed lines. In specimens of Spieth's paratypes available to us (Figs. 33-34), vein CuP is attached at base to vein CuA but vein CuP terminates before reaching the wing margin. In *Hermanellopsis arsia* vein CuP is free basally (Figs. 36-39).

Edmunds et al. (1976) provide generic characters of the supposed nymph of *Hermanellopsis* based upon an undescribed species represented by a single nymph from the highlands of Panama. This nymph was associated with *Hermanellopsis* based upon shape of the hind wing pads (Edmunds et al. 1976; Edmunds, pers. comm.), and consequently the identity of the nymph is uncertain (Edmunds et al. 1976). As characters given to distinguish the nymph of *Hermanellopsis* by Edmunds et al. (1976) are not sufficient to distinguish *Hermanellopsis* from undescribed genera in collections available to us, nor from unrelated described genera, and the characters listed are not linked to any described taxon at the species level, we have restricted *Hermanellopsis* to the species *H. incertans* and *H. arsia*.

#### KEY TO KNOWN MALE IMAGOS OF HERMANELLOPSIS

1. Hind wings with apex of costal projection and apex of wings pointed as in Figs. 33-34; vein MP<sub>2</sub> of fore wings attached at base to MP<sub>1</sub> and CuA by a cross vein as in Fig. 32; genitalia as in Fig. 77 . . . . *H. incertans* (Spieth)
- Hind wings with apex of costal projection and apex of wings as in Figs. 36-39; vein MP<sub>2</sub> of fore wings attached to MP<sub>1</sub> as in Fig. 35; genitalia [subimago] as in Figs. 78-80 . . . . . *H. arsia* NEW SPECIES

***Hermanellopsis incertans* (Spieth)**

Figs. 32-34, 77, 85-86, 89, 168

*Hermanella incertans* Spieth, 1943, 1244:9*Hermanella (Hermanellopsis) incertans*: Demoulin, 1955, 31(20):8*Hermanellopsis incertans*: Edmunds, Jensen and Berner, 1976:222

MALE IMAGO (in alcohol). Length: body, 3.5-5.0 mm; fore wings, 4.0 mm; prothoracic legs [broken off specimens and missing]. Eyes: stalked turbinate portion brownish-yellow apically, brownish-black basally; 25-31 facets in longest row of upper portion, facets orangish-yellow; facets of lower portion black, small. Head brownish-yellow, washed lightly with brownish-black. Scape and pedicel brownish-yellow, flagellum pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum brownish-yellow, washed with brownish-black, carinae and sutures brownish-black, remainder of nota dark brown, carinae darker; sterna brownish-yellow; pleura light brown. Wings (Figs. 32-34): maximum width of fore wings 0.37-0.38 (n = 1) maximum length of fore wings; maximum width of hind wings 0.46-0.48 (n = 1) maximum length of hind wings; vein MP<sub>2</sub> of fore wings attached at base to vein MP<sub>1</sub> and vein CuA by a cross vein as in Fig. 32; hind wings with costal projection well developed, apex acute, pointed, apex located 0.46-0.48 (n = 1) distance from base to margin of wings; apex of hind wings acute, pointed (Figs. 33-34); longitudinal and cross veins very light brown, with C, Sc and R<sub>1</sub> of fore wings, and C and base of Sc of hind wings darker; membrane hyaline, apical 1/3 of cells of C and Sc of fore wings whitish, translucent. Legs: [prothoracic legs broken off specimens and missing]; remainder of legs pale yellow. Abdomen: terga and sterna semihyaline, light brownish-yellow; terga washed lightly with brownish-black, wash darker posterolaterally; spiracles smoky, tracheae semihyaline. Forceps (Fig. 77): segment 3 approximately 0.75 (n = 1) length of segment 2; segment 2 approximately 0.45 (n = 1) length of segment 1; light brown. Styli (Fig. 77): maximum length along lateral margin approximately 0.85 (n = 1) maximum width; maximum length along median line 0.48 (n = 1) maximum width; posteromedian margin gently rounded with median notch and submedian, narrow, pointed projections as in Fig. 77; light brown. Penes (Fig. 77): length approximately 1.75 (n = 1) length of forceps segment 1, base of penes bulbous as in Fig. 77; brown. Caudal filaments pale yellow.

FEMALE IMAGO: Unknown.

FEMALE SUBIMAGO (in alcohol). Length: body, 3.1 mm; fore wings, 3.2-3.3 mm. Eyes black. Head brownish-yellow, washed with brownish-black, brownish-black Y shaped mark on vertex, with v portion of Y directed anteriorly. Antennae, ocelli and thorax with color and marks as in male imago. Wings: as in male imago except membrane whitish, translucent. Abdomen (Figs. 85-86, 89): terga and sterna semihyaline, light brownish-yellow; terga 1-10 washed lightly with brownish-black, tergum 1 with wash heavy medially and laterally, terga 2-8 with wash heavy laterally, tergum 10 with submedian brownish-black bars; spiracles smoky, tracheae semihyaline. Caudal filaments pale yellow.

MATURE NYMPH: Unknown.

TYPE LOCALITY: SURINAM: Zandry I (Fig. 168; locality h).

DEPOSITION OF TYPE: Holotype male imago deposited in AMNH collections.

SPECIMENS EXAMINED: 1 male imaginal and 1 female subimaginal paratype, SURINAM: *Marowijne Dist.*, Marowijne River, Pedrosoenqoe Falls, Bonapark Placer, July 1, 1939, Geijskes.

DISCUSSION: Imagos of *H. incertans* can be distinguished from imagos of all other species of *Hermanellopsis* by the following combination of characters: (1) upper portion of male eyes has 25-31 facets; (2) hind wings are shaped as in Figs. 33-34; apex of costal projection and apex of hind wings are pointed; (3) vein  $MP_2$  of fore wings is attached at base to vein  $MP_1$  and vein CuA by cross veins as in Fig. 32; (4) posteromedian margin of male styliger plate is gently rounded with a median notch and submedian projections as in Fig. 77; and (5) penes are long and narrow as in Fig. 77.

BIOLOGY. Collection records indicate that imagos of *H. incertans* emerge in June and July.

### ***Hermanellopsis arsia* NEW SPECIES**

Figs. 35-39, 78-80, 94, 168

MALE IMAGO: Unknown.

MALE SUBIMAGO (in alcohol). Length: body, 4.5-5.0 mm; fore wings, 4.2-4.9 mm. Eyes: stalked turbinate portion brownish-black; 32-38 facets in longest row of upper portion, facets grayish-yellow to grayish-white; facets of lower portion black, small. Head light brownish-yellow, dorsal surface washed lightly with brownish-black, ventral surface washed with brownish-black. Antennae pale yellow. Basal 1/2 of ocelli black, apical 1/2 white. Thorax: pronotum light brownish-yellow, washed very lightly with brownish-black, median carinae, submedian sutures and outer margins washed heavily with brownish-black; remainder of nota light brown, carinae dark brown; sterna brownish-yellow, outer margins of sclerites dark brown; pleura brownish-yellow, washed with brownish-black. Wings (Figs. 35-39): maximum width of fore wings 0.33-0.36 (n=4) maximum length of fore wings; maximum width of hind wings 0.49-0.57 (n=4) maximum length of hind wings; vein  $MP_2$  of fore wings attached at base to vein  $MP_1$  as in Fig. 35; hind wings with costal projection well developed, apex acute, rounded to pointed, apex located 0.44-0.48 (n=4) distance from base to margin of wings (Figs. 36-39); apex of hind wings acute, pointed to slightly rounded; longitudinal and cross veins very light brown to hyaline except C, Sc and R<sub>1</sub> of fore wings and C and base of Sc of hind wings darker brown, with to without brownish-black wash; membrane whitish, translucent. Legs (Fig. 94): pale yellow, prothoracic claws as Fig. 94. Abdomen: terga light brownish-yellow with posterior margins brownish-black; terga 1-10 washed lightly with brownish-black, tergum 1 with wash heavy, terga 2-10 with wash lighter, terga 2-9 with wash darker posterolaterally, terga 6-10 with wash darker submedially; spiracles brownish-black, tracheae washed lightly with brownish-black; sterna 1-8

very light brownish-yellow; sternum 9 with anterior margin rounded and developed anteriorly as in Fig. 79, brownish-yellow, margins dark brown. Forceps (Figs. 78-80): segment 3 from 0.57-0.66 ( $n=2$ ) length of segment 2; segment 2 from 0.52-0.70 ( $n=2$ ) length of segment 1; pale yellow. Styli (Figs. 78-80): maximum length along lateral margin 0.57-0.60 ( $n=2$ ) maximum width; maximum length along median line 0.44-0.47 ( $n=2$ ) maximum width; posteromedian margin with shallow, wide emargination and submedian projections as in Figs. 78-80; pale yellow. Penes (Figs. 78-80): length approximately 1.7-2.1 ( $n=2$ ) length of forceps segment 1, with base as in Fig. 78; dark brown. Caudal filaments pale yellow.

FEMALE IMAGO: Unknown.

MATURE NYMPH: Unknown.

SPECIMENS EXAMINED (Fig. 168; locality d): Holotype male subimago, BRAZIL: Amazonas State, Rio Cuieiras, N. of Manaus, 24-IV-1961, E. J. Fittkau. Paratypes: 4 male subimagos, same data as holotype.

Dr. E. J. Fittkau's field notes state that the specimens were collected at light in the settlement (colony) of Caleca do Porco.

Holotype is deposited in the collections of INPA. Two paratypes are deposited in the FAMU collections, and 2 paratypes are deposited in UU collections.

LIFE CYCLE ASSOCIATIONS: Unknown.

ETYMOLOGY: from *arsios*, Gr., meaning fitting, friendly; feminine.

DISCUSSION: Subimagos of *Hermanellopsis arsia* can be distinguished from subimagos of all species of *ermanellopsis* by the following combination of characters: (1) upper portion of male eyes has 30-40 facets in longest row; (2) hind wings are shaped as in Figs. 36-39; apex of costal projection and apex of hind wings are pointed to rounded as in Figs. 36-39; (3) vein  $MP_2$  of fore wings is attached at base to vein  $MP_1$  as in Fig. 35; (4) posteromedian margin of male styli (Figs. 78-80) has a shallow, wide emargination and submedian projections as in Fig. 78; and (5) penes are long, narrow and straight as in Figs. 78-80.

Direct comparisons between *Hermanellopsis arsia* and *H. incertans* for certain characters are not possible as *Hermanellopsis arsia* is known only from male subimagos and *H. incertans* only from male imagos and female subimagos. In addition, the types of *H. incertans* are badly damaged. Shape of the posteromedian margin of the styli (Figs. 78-80) and apex of the costal projection of the hind wings appear to differ between the two taxa. However, shape of the posteromedian margin could change as the styli (Figs. 78-80) expand with the molt to the imaginal stage, and comparisons between costal projections of subimagos and imagos are dubious especially since *Hermanellopsis arsia* displays considerable variation in hind wing shape (Figs. 36-39). The shape of sternum 8 of *Hermanellopsis arsia* is very distinctive (Fig. 79) but abdominal segments of the available specimens of *H. incertans* are badly damaged and comparisons are not possible.

## PHYLOGENY

Reconstruction of probable phylogenetic relationships among taxa treated in this study is based on analysis of the external mor-



phology of imagos, subimagos and nymphs. Each morphological character is analyzed for its probable evolutionary state, ancestral (plesiomorphic) or derived (apomorphic). Character states must be assigned with caution and only after detailed morphological study of the taxa in question and of related taxa. The possibility of character state changes associated with growth, correlations with size, and with other characters or functional groups of characters must be taken into consideration. Generally, a character state is considered to be ancestral when it is found in other families of mayflies, in ancient lineages of the Leptophlebiidae and distributed irregularly or commonly over a wide spectrum of related taxa. Information on functional morphology and behavior, and an understanding of the evolution of the character in unrelated taxa often assist in character state assignment.

Morphological studies for purposes of family level ex-group comparisons were concentrated on the Siphonuridae and members of the Ephemeroidea. This follows from previous phylogenetic studies that suggest the Leptophlebiidae and Ephemeroidea are sister groups, and along with the ephemereleid-tricorythid line evolved from a pre-Oniscigastrine siphonurid (Edmunds 1972, 1973; Landa 1969, 1973).

Genera of Leptophlebiidae representative of most major geographic areas were examined, however, emphasis was placed on study of South American taxa. The generic limits of some northern South American taxa were defined based on undescribed species available in the collections of Florida A&M University, while the generic limits and taxonomic status of the Leptophlebiidae of southern South America follows Pescador (1976) and Pescador and Peters (1980a, b; in press). Six genera of fossil mayflies have been attributed to the Leptophlebiidae (Hubbard and Savage 1981). All fossil records of Leptophlebiidae are Holarctic except for *Atalophlebia culleni*, which is known from Pliocene deposits in Australia (Riek 1954). As the known distribution of the fossil, *Atalophlebia culleni*, falls within the present range of the extant *Atalophlebia*, it provides little additional biogeographic information. Fossil taxonomy is based on only a few characters and generally fossils are not of sufficient quality to provide data for phylogenetic reconstruction. Therefore, only extant taxa have been

considered in construction of the phylogenetic hypotheses, and only those extant genera most closely related to the 4 genera treated taxonomically in the previous section are included in the phylogenetic diagrams and discussion.

The sequence of phyletic branching of taxa and inclusive phyletic lines is determined by uniting lineages that possess the greatest number of shared derived character states (Hennig 1966; Estabrook 1972), while shared ancestral character states may aid in establishment of pregroup relationships (Edmunds 1972). Immediately following each phylogenetic diagram, characters used to determine the furcations are enumerated (see Tables 2-4). Character states for each phyletic line are preceded by an indication of probable evolutionary state as follows: D, derived or apomorphic; A, ancestral or plesiomorphic.

The basal furcation within the Leptophlebiidae (furcation 1, Fig. 1) represents evolution of the Leptophlebiinae from a common ancestor shared with the Atalophlebiinae (Peters 1980). The Leptophlebiinae, or lineage 1a (Fig. 1), corresponds to lineage I, Fig. 1, of Peters and Edmunds (1970) and presently includes the following genera: *Paraleptophlebia* and *Leptophlebia* from North America, Europe and northern Asia; *Habrophlebia* from North America and Europe; *Habroleptoides* and *Calliarcys* from Europe; *Habrophlebiodes* from North America and Asia; and *Dipterophlebiodes* and *Gilliesia* from Asia. No representative of the subfamily Leptophlebiinae is presently known from South America, Africa or Australia. Lineage 1b, or the subfamily Atalophlebiinae, includes all remaining genera of Leptophlebiidae, although, only the *Hapsiphlebia*, *Penaphlebia*, *Miroculis* and *Atalonella* lineages are represented (Fig. 1).

Character state assignment for the basal furcation within the Leptophlebiidae (furcation 1, Fig. 1, Table 2) follows from a sister group relationship between the Leptophlebiidae and the Ephemeroidea as suggested by previous workers (Edmunds 1972; Landa 1969, 1973). However, if the Ephemeroidea evolved from within the Leptophlebiidae as suggested by McCafferty and Edmunds (1979) certain character state assignments would be altered in furcation 1 (Fig. 1). Detailed comparative morphological studies among the families of the Ephemeroidea and the subfamilies of the

Leptophlebiidae are needed to delineate relationships among these taxa and clarify character state assignment for the basal furcation within the Leptophlebiidae. Most nymphal mouthpart character states (2, 4-6) provided for lineage 1a (Table 2) are thought to be ancestral as these states are observed in several other families including the Siphonuridae, Ephemerellidae, Tricorythidae and most members of the Ephemeroidea. The presence of thickened, submedian setae on the labrum's anterior margin (3) may appear specialized (Peters 1980), however, this state is considered ancestral herein as it is observed within the Ephemeridae e.g., *Ephemera*, and the Euthyplociidae e.g., *Campylocia*, and is very similar to states observed in primitive Tricorythidae e.g., *Tricorythus*. The male styliiger plate (1) of lineage 1a is scored ancestral because the deep cleft appears to represent an initial stage of fusion of the gonocoxites (Snodgrass 1935; Matsuda 1976), which have become entirely fused in all other Leptophlebiidae. However, it is possible that gonocoxite fusion occurred prior to the evolution of the Leptophlebiidae and that the deep cleft of the Leptophlebiinae is secondarily derived.

Furcation 2 (Fig. 1) separates the *Hapsiphlebia* lineage from a common ancestor shared by the *Penaphlebia*, *Miroculis* and *Atalonella* lineages. The *Hapsiphlebia* lineage as defined by Pescador and Peters (1980) includes the following genera: *Hapsiphlebia* from South America; *Aprionyx* from Africa; and *Atalomicria*, *Atalophlebia*, *Jappa* and *Ulmerophlebia* from Australia. Towns and Peters (1980) also placed *Zephlebia cruentata* from New Zealand in this lineage. Members of the *Hapsiphlebia* lineage (2a, Table 2) possess derived states of character 3 — large denticles on the outer incisor of the right mandible (Towns and Peters 1980), and character 7 — prominent setae on the lateral margins of the abdominal terga (Pescador and Peters 1980). Members of lineage 2b share derived states of labral shape and size (1, 2), an elongated mandibular prosthecal tuft (4), a narrow maxillary palpal segment 2 (5), and an elongated labial palpal segment 3 that lacks spine-like setae on the inner margin (6).

The apically broadened maxillary palpal segment 2 (character 5, furcation 2, Table 2) observed in members of the *Hapsiphlebia* lineage is considered to be ancestral. The broadened state may ap-

pear specialized when considering only the Southern Hemisphere Leptophlebiidae (Towns and Peters 1980), however, this state is also observed irregularly in members of the Leptophlebiinae (lineage 1a, Fig. 1) e.g., in some species of *Leptophlebia* and *Paraleptophlebia*, while a slightly broadened condition occurs in several other members of the Leptophlebiinae e.g., *Habroleptoides*, *Habrophlebiodes* and *Habrophlebia*. A slightly broadened to broadened maxillary palpal segment 2 is also observed among the Siphonuridae e.g., *Siphonurus*, and Ephemeroidea e.g., *Rhoenanthus*, *Potamanthus* and *Campylocia*. The slightly broadened condition is the probable ancestral state for the Leptophlebiidae, while the very broad state observed in most members of the *Hapsiphlebia* lineage and in some species of *Leptophlebia* and *Paraleptophlebia*, as well as the narrow, unbroadened maxillary palpi of lineage 2b represent derived states. As it is often difficult to objectively distinguish the slightly broadened and broadened states, these two states were combined and treated as the ancestral state in furcation 2.

Furcation 3 (Fig. 1) represents evolution of the *Penaphlebia* lineage from a common ancestor shared by the *Miroculis* and *Atalonella* lineages. The *Penaphlebia* lineage presently includes *Penaphlebia* and *Massartella* from South America (Pescador and Peters 1980). Members of the *Penaphlebia* lineage (3a) display the derived state of pectinate setae on the inner margin of maxillary palpal segment 2 (7). Data on state distribution for this character (7) are based on light microscopy and further studies employing SEM are needed. The *Atalonella* and *Miroculis* lineages (3b) share derived states (Table 2) of long subimaginal wing setae (1), reduced numbers of fore wing costal cross veins (2), shortened hind wing vein Sc (3), nymphal mouthpart characters 4-6 and 8, and development of denticles on nymphal claws (9).

Shape of the nymphal labrum has long been used as a generic character, however, labral shape (characters 1, and 2 of furcation 2, Table 2) and setation patterns (character 5, furcation 3, Table 2) may also be employed as phyletic characters to separate lineages. The ancestral leptophlebiid labrum as observed in the Leptophlebiinae (lineage 1a) the *Hapsiphlebia* lineage (2a), and most Ephemeroptera other than members of the Heptageniidae and

Oligoneuriidae is characterized by the following: (1) lateral margins are nearly parallel (rectangular shape); (2) maximum width is less than distal width of clypeus (small size); and (3) apical setae are well developed while short, stiff basal setae are absent. Other lineages of Leptophlebiidae, including the *Miroculis* and *Atalonella* lineages (lineage 3b, Fig. 1), have variable labra, but never as above. Usually, the derived condition is a labrum (Figs. 137-142, 148) in which: (1) lateral margins are distally expanded; (2) maximum width is at least equal and usually greater than distal width of clypeus; and (3) basal 2/3 of lateral margins have short, stiff setae with thin, hair-like setae apically. Members of the *Penaphlebia* lineage (3a, Fig. 1) lack stiff basal setae, but the labrum is apically broadened in *Penaphlebia*.

Character states of the nymphal clypeus (4) display a distribution pattern similar to those of labral character 5. The derived state is shared by most genera of Leptophlebiidae, while all members of the *Penaphlebia* (3a, Fig. 1) and *Hapsiphlebia* (2a) lineages and most members of the Leptophlebiinae (lineage 1a) retain the ancestral clypeus with straight margins. This is particularly noticeable in the area of fusion with the frons, which is abrupt and not gently curved (Figs. 137-138, 142, 148) as in members of the *Miroculis* and *Atalonella* lineages and many other genera.

Evolution of the *Miroculis* lineage (4a) from a common ancestor shared with the *Atalonella* lineage is represented by furcation 4 (Fig. 1). The *Miroculis* lineage includes *Miroculis*, *Miroculitus*, *Microphlebia* and *Hermanellopsis* from northern South America. The *Atalonella* lineage (4b) includes *Atalonella* from southern South America and Australia and *Archethraulodes* from southern South America. *Rhigotopus* from southern South America (Pescador and Peters 1980) and *Zephlebia* (*Neozephlebia*) from New Zealand (Towns and Peters 1980) have also been included as members of the *Atalonella* lineage.

The *Miroculis* lineage (4a, Fig. 1) displays derived states for 12 of the 13 characters used to separate lineages of furcation 4. Members of the *Miroculis* lineage may be distinguished by presence of the following derived character states (Table 2): (1) modified male imaginal eyes (Figs. 40-54); (2) dissimilar male imaginal prothoracic claws (Figs. 90-95); (3) the asymmetric fork of vein MA in the fore

wings in which vein  $MA_1$  is relatively straight and vein  $MA_2$  is strongly curved basally (Figs. 7, 13, 16, 22, 25, 28, 32, 35); (4) presence of a well developed hind wing costal projection (Figs. 9, 11, 24, 27, 30, 34, 37); (5) termination of hind wing vein Sc from slightly less than  $1/2$  to  $3/5$  distance from base to wing apex; (6) long, branched subimaginal wing setae (Figs. 28-31); (7) large spines on the inner basal margin of forceps segment 1 (Figs. 55, 58, 63, 65, 71, 73, 77-78); (8) elongated forceps segments 2 and 3 (Figs. 55, 58, 63, 65, 71, 73, 77-78); (9) divided, tubular penes without appendages (Figs. 55-80); (10) length of maxillary palpal segment 3 is less than  $3/5$  length of segment 2 (Figs. 146, 152); (11) length of labial palpal segment 3 is less than  $3/5$  length of segment 2 (Figs. 145, 151); and (12) inner margin of labial palpal segment 3 has a row of widely spaced hair-like setae (Fig. 164). Members of the *Miroculis* lineage retain the ancestral state of the labial glossae (Figs. 145, 151), in which the glossae curve over ventrally (13), as do members of the *Penaphlebia* (3a) and *Hapsiphlebia* (2a) lineages.

Within the Leptophlebiidae size of setae on the inner margin of labial palpal segment 3 progressively decreases from large spine-like setae in members of the Leptophlebiinae (lineage 1a) and *Hapsiphlebia* lineage (2a), to prominent denticle-like setae in the *Penaphlebia* lineage (3a), to thick blade-like setae (Figs. 166-167) in members of the *Atalonella* lineage (4b) and many other genera. Members of the *Miroculis* lineage (4a) are unique in having a row of widely spaced hair-like setae (Fig. 164) on the inner margin of labial palpal segment 3. However, available data are limited as use of scanning electron microscopy is necessary to differentiate between blade-like setae and hair-like setae in many species. *Zephlebia* (*Neozephlebia*) differs from other members of the *Atalonella* lineage in retaining the ancestral spine-like denticles on labial palpal segment 3 (Townsend and Peters 1980).

Branched subimaginal wing setae (Figs. 28-31) are considered derived (6) as all members of the Leptophlebiinae and most genera of Leptophlebiidae have unbranched setae. Subimaginal wing setae were first studied as taxonomic and phyletic characters by Pescador (1976). He reported that branched setae occurred in the *Penaphlebia* lineage, while the remainder of the taxa he studied in-

cluding the *Hapsiphebia*, *Atalonella* and *Atalophlebioides* lineages had unbranched setae. Survey of the Leptophlebiidae revealed branched setae in all members of lineages 3a and 4a (Fig. 1) plus the following genera: *Thraululus*, *Simothraululus*, *Indialis*, *Megaglena*, *Choroterpes*, *Choroterpides*, *Cryptopenella*, *Fulletominus*, *Farrodes*, *Homothraululus*, *Simothraulopsis*, *Borinquena* and *Rhigotopus*. Interestingly, *Nathanella*, *Isca*, *Notophlebia* and *Fullela* have unbranched setae. These 4 genera are grouped phyletically with the first 8 genera listed above (Peters and Edmunds 1970), which suggest that the branched condition may have evolved on several occasions.

Phyletic placement of *Rhigotopus* is speculative as the nymphal stage is unknown. Pescador and Peters (1980) placed *Rhigotopus* as a member of the *Atalonella* lineage (4a), however, *Rhigotopus* shares derived states of branched subimaginal wing setae (6) and divided penes (character 9 in part) with members of the *Miroculis* (4a) and *Penaphlebia* (3a) lineages. Further refinement of the phyletic placement of *Rhigotopus* awaits discovery of the nymphal stage, but we suggest that *Rhigotopus* may be more closely allied to the *Penaphlebia* and *Miroculis* lineages than to the *Atalonella* lineage.

Interpretation of phylogenetic relationships among *Miroculis* and related genera (Figs. 2-3) is hampered by incomplete knowledge of life cycle stages for some taxa. *Miroculis* is represented by both sexes in all life cycle stages, while *Microphebia* is known from nymphal and male subimaginal specimens. *Miroculitus* is known from wings and genitalia of the holotype male imago and 4 poorly preserved male subimagos. *Hermanellopsis* is represented by a single female subimago and 2 badly damaged male imagos of *H. incertans*, and 5 male subimagos of *H. arsia*. The nymphal stages of *Miroculitus* and *Hermanellopsis* remain unknown, and probable phylogenetic relationships of these two taxa are based on adult characters only.

Based on available specimens, *Hermanellopsis* appears to be most closely related to *Microphebia*, while *Miroculitus* appears to be most closely related to *Miroculis*.

*Hermanellopsis* and *Microphebia* share the following derived character states: (1) reduced fore wing width/length ratios; (2)

reduced hind wing length/fore wing length ratios; (3) reduced numbers of marginal intercalaries in the fore wings; (4) a more distal location of fork of vein MP in fore wings; (5) the termination of vein Sc in hind wings approximately at the costal projection's apex and associated abrupt distal margin of the costal projection; (6) fusion of veins Sc and R in hind wings before reaching wing base; and (7) a lack of wing pigment. *Hermanellopsis* and *Microphlebia* also share several ancestral states including the presence of a cross vein connecting veins MP and CuA basal to fusion of veins MP<sub>1</sub> and MP<sub>2</sub> in fore wings, and condition of the male prothoracic claws. The available data suggest that *Hermanellopsis* is best represented as a member of lineage 1b (Fig. 2). However, the reduced fore wing width/length ratios, reduced marginal intercalaries in fore wings and reduced hind wing length/fore wing length ratios shared by *Hermanellopsis* and *Microphlebia* could be explained as a result of small size and may have evolved independently (Savage, in press).

The basal furcation in Fig. 2 represents evolution of lineage 1b, which includes *Microphlebia* and *Hermanellopsis*, from a common ancestor shared with lineage 1a, which includes *Miroculis* and *Mirocilitus*. In the list of character states provided for lineage 1b (Table 3), the female imaginal eye character state (6) is based on *Hermanellopsis* only and nymphal character states (7-12) are based on *Microphlebia* only, while states of these characters listed for lineage 1a are based on *Miroculis* only. Members of lineage 1b (Fig. 2, Table 3) are distinguished by derived states of fore and hind wing characters 1-5, shape of nymphal gills (11), and reduced abdominal spines (12). Members of lineage 1a retain ancestral states of the above characters, while sharing derived states of female imaginal eyes (6) and nymphal mouthpart characters 7-10.

Nymphs of *Miroculis* have a subapical row of 31-55 pectinate spine-like setae (Figs. 146, 160-161) on the galea-lacinia of the maxillae (character 10, furcation 1, Table 3). Survey of specimens available in collections of Florida A&M University indicate the ancestral state, as observed in the Siphonuridae and in members of the Leptophlebiinae (lineage 1a, Fig. 1), is a subapical row of 4-8 setae. Most other genera of Leptophlebiidae have 9-28 setae with the vast majority having 12-25 setae. *Microphlebia* of lineage 1b



(Fig. 2) has 18-20 pectinate spine-like setae (Fig. 152). *Thraulus hsui*, some members of the *Atalophlebioides* lineage, and an undescribed genus from New Zealand (D.R. Towns, pers. comm.) have as many as 35 setae, while *Miroculis* has 31-55 setae. The subapical row is most developed in *Petersophlebia inequalis* from Madagascar which has 75-90 subapical setae. Other nymphal mouthpart specializations (7-9) observed in *Miroculis* relate to clypeus and labrum shape and are also present in other derived lineages.

Abdominal gills of *Microphlebia* (Figs. 133-136) are considered derived as the dorsal portion is greatly reduced in size, while *Miroculis* gill portions are subequal as in most Leptophlebiidae. However, *Hapsiphlebia* also has a reduced dorsal portion, and gills of *Penaphlebia*, *Hapsiphlebia* and *Microphlebia* are all plate-like, which appears to be an ancestral condition. One could also argue that the 3 apical projections observed in *Miroculis* (Figs. 121-132) are a derived condition as *Miroculis* is the only genus in South America in which this occurs. However, on a worldwide level gills with 3 apical projections are quite common, and gills of *Miroculis* are nearly identical to gills of all members of the *Choroterpes* lineage and *Leptophlebia*. Rather than break the condition of the gills up into numerous characters and score each one separately, we treat gill shape as a single character and score it based on relative size of the dorsal and ventral portions. As the Leptophlebiidae of South America become better known it likely will prove advantageous to divide gill shape into numerous characters.

Furcation 2 (Fig. 2) represents evolution of *Microphlebia* (lineage 2b) from a common ancestor shared with *Hermanellopsis* (lineage 2a). Characters used to distinguish lineages of furcation 2 (Table 3) are based only on adult males. *Microphlebia* (lineage 2b) exhibits derived states of wing shape characters 1-5 (Savage, in press). *Hermanellopsis* (lineage 2a) displays derived states of the styliger plate's posterior margin (6) and penes (7). The well developed, narrow, submedian projections on the posterior margin of the styliger plate (6) and apically acute, narrow penes (7) observed in *Hermanellopsis* (Figs. 77-80) are unique within *Miroculis* and related genera.

The evolution of *Miroculitus* from a common ancestor shared with *Miroculis* is depicted by furcation 3 (Fig. 2). *Miroculis* (lineage 3b) is distinguished by the following derived states: absence of a cross vein between veins MP and CuA basal to the fusion of veins MP<sub>1</sub> and MP<sub>2</sub> in fore wings (2); a more distal fusion of veins CuA and CuP in the hind wings (5); and by the unusual male imaginal claws (6). The derived prothoracic claws displayed by male imagos of *Miroculis* are unique within the Leptophlebiidae. The claws are dissimilar. One claw has a single lateral, long, narrow spike-like projection, while the other is pad-like, and blunt (Figs. 90-92). *Miroculitus* possess the derived states of reduced fore wing width/length ratios (1), the basal attachment of vein MP<sub>2</sub> to MP<sub>1</sub> (3), and vein ICu<sub>1</sub> to CuA (4) in the fore wings. The reduced fore wing width/length ratios observed in *Miroculitus* and members of lineage 1b (Fig. 2) probably result from convergent evolution associated with body size reductions (Savage, in press).

The basal evolutionary split within *Miroculis* is represented by furcation 4 (Figs. 2, Table 3). Lineage 4b includes *M. (Miroculis)*, *M. (Yaruma)* and *M. (Atroari)*, while lineage 4a is represented by *M. (Ommaethus)*. The 3 derived subgenera of *Miroculis* (lineage 4b) share derived states of female imaginal eyes (6), male wings (2-4) and nymphal labrum (7). *Miroculis (Ommaethus)* displays derived states of male imaginal eyes (1) and posteromedian margin of the styliger plate (5).

Data on female imagos within *Miroculis* are limited. Only 1 species, *M. (Ommaethus) mourei*, from lineage 4a (Fig. 2) and 2 species, *M. (Miroculis) fittkai* and *M. (M.) marauiae*, from lineage 6b are known. As female imagos of lineages 5a and 6a (Fig. 2) are unknown, it is possible that female eye character 6 might be moved to a different furcation as further data becomes available.

The upper portion of male imaginal eyes (1) observed in *M. (Ommaethus) mourei* (Figs. 51-52) and *M. (O.) froehlichii* (Figs. 53-54) are unusual among unstalked forms. They have a slightly reduced facet number, and are widely separated on the meson of the head. However, each of the 4 subgenera of *Miroculis* is characterized by a different derived male imaginal eye. *Miroculis* is the only genus of Leptophlebiidae in which all derived types of male imaginal eyes

occur, and at the present time no member of the *Miroculis* lineage displays the ancestral leptophlebiid eye-type such as that found in the *Atalonella*, *Penaphlebia* and most other generic complexes; the only other generic complex, or lineage, which displays the 3 derived eye-types of lineage 4b (Fig. 2) is the *Thraulus* lineage.

The question of which eye-type is ancestral within *Miroculis* is best dealt with by dividing the eye into 2 characters. One is stalked (derived) or unstalked (ancestral), and the other is facet number reduced (derived) or not reduced (ancestral). Male eyes of *M. (Miroculis)* and *M. (Yaruma)* are stalked (Figs. 44-48), while eyes of *M. (Ommaethus)* and *M. (Atroari)* are unstalked (Figs. 49-54). Eyes of *M. (Miroculis)* have greatly reduced facet numbers, *M. (Ommaethus)* slightly reduced facet numbers, while *M. (Yaruma)* and *M. (Atroari)* retain the ancestral 30-40 facets. Thus, eyes of *M. (Miroculis)* display 2 derived states, *M. (Yaruma)* and *M. (Ommaethus)* each display 1 derived state, and *M. (Atroari)* retains 2 ancestral states. From the above, the *M. (Atroari)* eye-type represents the most ancestral type within *Miroculis*. The increased separation on the meson of the head and slightly reduced facet number of *M. (Ommaethus)* are likely associated and evolved from a *M. (Atroari)*-like ancestor, while the stalked eyes of *M. (Miroculis)* and *M. (Yaruma)* represent a separate line of evolution.

The posterior margin of the styliger plate (5) observed in *M. (Ommaethus)*, which has a pronounced U-shaped indentation (Figs. 65, 68), is scored derived. The flat to rounded margin (Figs. 55, 57, 61, 63, 64) of lineage 4b is scored ancestral as this is the most common state within the Letophlebiidae and within *Miroculis* and related genera. However, it is probable that the pre-*Miroculis* ancestor had a styliger plate with a small indentation as observed in *Rhigotopus*, or *Massartella*, and that states observed in the 2 major lineages of *Miroculis* evolved in different directions from such an ancestor. Perhaps, the small notch observed in *M. fittkai* (Fig. 58), which is the most primitive member of *M. (Miroculis)*, (Fig. 3), reflects this ancestry.

Wing evolution within *Miroculis* and related genera has proceeded in two directions from a *Miroculis (Ommaethus)*-like or lineage 4a-type ancestor. In general, lineage 1b and to a lesser ex-

tent lineage 3a are characterized by smaller body sizes and associated reductions in fore wing width/length ratios, fore wing marginal intercalaries, and hind wing length/fore wing length ratios, while males of lineage 4b are characterized by a complex interaction of body size and wing dimensions that result in increased fore wing width/length and hind wing length/fore wing length ratios (Savage, in press). The dichotomy in fore wing width/length (Fig. 169) and hind wing length/fore wing length ratios (Fig. 170) between males of lineage 4b and the remaining taxa, or others, is primarily a result of positive correlation between body size and fore wing length in the "others" group ( $r = 0.86$ ,  $P = 0.012$ , Fig. 171) and a lack of correlation between body size and fore wing length ( $r = 0.30$ ,  $P = 0.436$ , Fig. 171) in males of lineage 4b, combined with positive correlation among body size and fore wing width ( $r = 0.78$ ,  $P < 0.001$ , Fig. 172), and hind wing length ( $r = 0.67$ ,  $P = 0.004$ , Fig. 173) common to all taxa.

Furcation 5 represents evolution of lineage 5b, which includes *M. (Miroculis)* and *M. (Yaruma)*, from a common ancestor shared with *M. (Atroari)*. Members of lineage 5b (Fig. 2, Table 3) possess derived states of stalked male imaginal eyes (1) and fore wing membrane color (2). *M. (Atroari)*, or lineage 4a, displays derived male imaginal prothoracic femora/tibiae ratios (3).

Members of lineage 5b (Fig. 2) have stalked male imaginal eyes (Figs. 44-46), which are considered derived following the argument presented in discussion of furcation 4, while eyes of *M. (Atroari)* retain the ancestral unstalked (Figs. 49-50) condition as does *M. (Ommaethus)*.

The color, intensity and distribution of pigment on the fore wing membrane (2) within *Miroculis* is variable. *Miroculis (Ommaethus)* and *M. (Atroari)* share submedian irregular broken transverse bands of brown pigment. This pattern is well developed in *M. (Atroari) amazonicus* (Fig. 19), but is lighter in both *M. (Ommaethus) froehlichii* and *M. (Atroari) duckensis*, and it is partially obscured due to an entirely light brown membrane in *M. (Ommaethus) mourei* (Fig. 22). Members of *M. (Miroculis)* and *M. (Yaruma)*, except *M. (Miroculis) fittkai* (Fig. 10), lack dark pigment on the fore wings. While the pigment pattern observed in *M.*

(*Ommaethus*) and *M. (Atroari)* may be specialized, the presence of dark brown pigment is the probable ancestral state within *Miroculis*. Imagos with pigmented wings are scattered throughout the Leptophlebiidae, being observed in all generic lineages. Subimagos of many genera including *Penaphlebia* and *Massartella* (lineage 3a, Fig. 1) often have darkly pigmented wings, while pigment is lost in imagos. We believe the common occurrence of darkly pigmented wings in subimagos, and their scattered distribution in imagos reflect the ancestral state of this character.

Derived male imaginal prothoracic femora/tibiae ratios (3) easily separate *M. (Atroari)* from the remaining subgenera of *Miroculis* (Fig. 174). Prothoracic tibiae and femora lengths are highly correlated for males of *M. (Miroculis)* and *M. (Ommaethus)*, ( $r = 0.96$ ,  $P < 0.05$ ,  $n = 4$ , Fig. 174). However, prothoracic tibiae and femora lengths are not significantly correlated if *M. (Atroari) duckensis* is included in the calculations, and the point representing *M. (A.) duckensis* lies considerably above the regression line for other males of *Miroculis* (Fig. 174). While data are limited, the reduced ratios of *M. (A.) duckensis* are a combined result of longer tibiae and shorter femora than would be expected based upon body lengths (Savage 1979).

We have placed *M. (Yaruma)* as a member of lineage 5b (Fig. 2). Data on *M. (Yaruma)* are extremely limited, as nymphs, female imagos, and male imaginal prothoracic legs are unknown. As a result only the first 2 characters listed for furcation 5 (Table 3) associate *M. (Yaruma)* with lineage 5b. These character states are: (1) stalked imaginal eyes (Figs. 47-48); and (2) lack of dark pigment on the fore wings. *M. (Yaruma)* and *M. (Atroari)* share several character states not observed in *M. (Miroculis)*. These are: 1) antennae with scape and pedicel pale yellow; 2) forceps segments without brownish-black wash; and 3) posteromedian margin of the styliger plate rounded (Figs. 61-64).

Pale yellow antennae probably represent the ancestral state as they are also observed in all members of *Miroculitus*, *Hermanellosis*, and *Microphlebia*, and half the species of *Miroculis (Ommaethus)*. Lack of brownish-black wash on the apical forceps segments could also be an ancestral state as *Miroculitus*, *Her-*

*manellopsis*, *Microphlebia*, and most other Leptophlebiidae possess this character state. However, forceps of *Miroculis* (*Ommaethus*) are washed with brownish-black so character state assignment is subject to debate. The posteromedian margin of the styliger plate is difficult to analyze. Three basic types of posterior margins are observed within *Miroculis*. *M. (Ommaethus)* has a large median indentation (Figs. 65-68). *M. (Miroculis)* has a flat to gently rounded posterior margin (Figs. 55, 57-58), while *M. (Atroari)* and *M. (Yaruma)* have rounded margins (Figs. 61, 63-64). *M. (Miroculis)*, especially *M. (M.) fittkaui* (Fig. 58), appears to possess the most ancestral state, while *M. (Ommaethus)*, *M. (Yaruma)* and *M. (Atroari)* possess derived states. However, all states observed within lineage 4b (Fig. 2) are seen in other Leptophlebiidae, and rounded margins appear common in groups with long penes. Within *M. (Atroari)*, the rounded posterior margin of *M. (A.) amazonicus* (Fig. 63) is well developed, while that of *M. (A.) duckensis* (Fig. 64) is not well developed. Thus, what appears to be 3 character states may actually be 2, as flat to rounded may be best understood as 1 highly variable character state. Of 3 character states that conflict with our placement of *M. (Yaruma)*, 2 are probably ancestral states, and the 3rd character may represent a single highly variable character state shared by lineage 4b (Fig. 2). Until more data become available, we feel *M. (Yaruma)* is best placed in lineage 5b (Fig. 2) based on characters listed for that furcation (Table 3).

Furcation 6 (Fig. 2) represents evolution of *M. (Miroculis)* from a common ancestor shared with *M. (Yaruma)*. *M. (Miroculis)*, or lineage 6b (Fig. 2, Table 3), is distinguished by the probable derived states of antennae color (2), male imaginal eyes (1), and genital forceps color (3), while *M. (Yaruma)* retains the ancestral states of these characters. The highly derived male imaginal eyes (1) of *M. (Miroculis)* are characterized by reduced facet number, and associated increased stalk length and facet size (Figs. 44-46). Eyes of *M. (Yaruma)* retain the ancestral facet number and size (Figs. 47-48).

Discussion of phylogenetic relationships between species is restricted to members of *M. (Miroculis)*, or lineage 6b (Fig. 2), as

this is the only lineage for which imagos of 3 species are known. *M. (Miroculis)* is currently represented by 4 species. *Miroculis (M.) fittkai* and *M. (M.) marauiae* are known from all life cycle stages, *M. (M.) rossi* from male imagos, and *M. (M.) brasiliaensis* from mature nymphs. Probable phylogenetic relationships between the 3 species known from the imaginal stage are represented in Fig. 3. Phylogenetic placement of *M. brasiliaensis* is uncertain and awaits association with the imaginal stage.

Furcation 1 (Fig. 3) represents evolution of lineage 1b, which includes *M. (M.) marauiae* and *M. (M.) rossi*, from a common ancestor shared with *M. (M.) fittkai* (lineage 1a). *Miroculis (M.) fittkai* (lineage 1a, Table 4) is distinguished by derived states of the male genitalia (2, 3), while members of lineage 1b share derived wing membrane color (1), and shape of the styliiger plate's posterior margin (4).

Hyaline wings (1) are considered derived following the argument presented in the discussion of furcation 5, Fig. 2. Ratios of forceps segments 2/1 observed in *M. (M.) fittkai* (Fig. 58) are unique within lineage 4b (Fig. 2) and shape of the inner margin of forceps segment 1 is unique within *Miroculis* and related genera. Character state assignment for shape of the styliiger plate's posterior margin (4) is speculative. Herein, the notched condition of *M. (M.) fittkai* (Fig. 58) is scored ancestral following the argument in discussion of furcation 4, Fig. 2. However, as this condition is unique within *Miroculis*, this state may actually represent a derived state.

Evolution of *M. (M.) rossi* from a common ancestor shared with *M. (M.) marauiae* is represented by furcation 2, Fig. 3. *M. (M.) rossi* has derived male imaginal eyes (1) and penes (3, 4), whereas *M. (M.) marauiae* retains ancestral states for all characters except caudal filament color (2). However, caudal filament color is variable within *Miroculis* and character state assignment is highly speculative. Penes of *M. (M.) rossi* (Figs. 55-56) have a row of 15 stout spines on a ventral ridge. Presence of stout spines is unique within *Miroculis*, but the ventral ridge is also observed in *M. (Atroari) amazonicus* (Fig. 63). Penes of *M. (M.) rossi* lack an apical notch or excavation which is unique within *Miroculis*.

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