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Wing evolution within Miroculis and related genera
(Ephemeroptera: Leptophlebiidae) from northern South America

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Introduction

Wing evolution and flight aerodynamics have been little investigated within the order Ephemeroptera. EDMUNDS and TRAVER (1954) discussed the structure, evolution and aerodynamic implications of the archetypical ephemeropteran wing and its diversification within the order, while BRODSKIY (1971, 1975) investigated flight aerodynamics of a single species of mayfly, *Ephemera vulgata* Linnaeus. Wing shape and vein structure are a function of aerodynamic principles, size and the phylogenetic history of the species. The interpretation of wing shape and structure and the relative influence of the above 3 components are often speculative, particularly as the phylogenetic relationships of many insects are unknown and the aerodynamic principles of insect flight, particularly among the Ephemeroptera, are poorly known. Herein, I discuss wing character state evolution, the effect of size on wing shape and structure, and the possible aerodynamic implications within a group of closely related leptophlebiid mayflies from the warm lowland areas of northern South America. The taxonomy and phylogeny of this group, which includes *Miroculis* Edmunds, *Miroculitus* Savage & Peters, *Hermanellopsis* Demoulin and *Microphlebia* Savage & Peters, have recently been treated by SAVAGE and PETERS (1982). While this analysis only treats members of the above taxa, certain conclusions are generally valid within the Leptophlebiidae and other mayfly families.

Methods: Regression analyses and graphs

Selected wing and body characters were measured using an ocular micrometer. Values used to represent groups of specimens in correlation and regression analyses (Figs. 25–29, 34–37) are midpoints of the range of variation measured for each character. Males and females of species of *Miroculis* were treated as separate groups because members of the 3 derived subgenera of *Miroculis* (lineage 4b, Fig. 24), *M. (Atroari)* Savage & Peters, *M. (Yaruma)* Savage & Peters and *M. (Miroculis)* Edmunds, display sexual differences in wing shape (Figs. 30–33). In certain analyses between 2 characters, for example Fig. 30, males of the 3 derived subgenera of *Miroculis* differ from females of these taxa and males and females of all other taxa. To shorten the discussion the term “others” is employed to refer to all groups studied except for males of the 3 derived subgenera of *Miroculis*, or lineage 4b (Fig. 24). Values for males of *Miroculis (Ommaethus) mourei* Savage & Peters were excluded from calculations and graphs that include body length because available specimens were damaged and body length measurements were unreliable. The reduced major axis regression equation (TEISSIER 1948; KERMAK 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.

Least squares and reduced major axis regression lines were calculated for the original data and log transformed data. The 2 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). Statistically, it would be preferable to use log transformed data (KERMACK and HALDANE 1950; HILLS 1978); however, I have used the original data in graphs as they are easier for the reader to interpret, and because the log transformed and original data produced very similar results.

The standard errors of the estimated slopes and intercepts for reduced major axis regression lines were calculated as in KERMACK and HALDANE (1950) and IMBRIE (1956). Tests of differences between these statistics for reduced major axis regression lines follow IMBRIE (1956) and MILLER and KAHN (1962). T-tests (SOKAL and ROHLF 1969) were also employed for tests of both the original and log transformed least squares regression statistics. When 2 statistics are reported as significantly different, the statistics of all methods were significantly different for all tests at the 0.05 level, although only the test statistics of IMBRIE (1956) are provided.

The use of ratios has been subject to much criticism (PEARSON 1897; KENDALL and STUART 1969; BLACKITH and REYMENT 1971; ATCHLEY, GASKINS and ANDERSON 1976), but this criticism has generally been ignored by systematists. In order to circumvent the major statistical problem of ratio data, a nonnormal distribution, I have used both the original ratios and log transformed ratios as recommended by SOKAL and ROHLF (1969) and HILLS (1978). Results of regression analyses on the original ratios and log transformed ratios were very similar, which is consistent with DODSON's (1978) and ALBRECHT's (1978) contention that the statistical criticisms will not effect qualitative results over the range of values in most systematic investigations. Also in each case where a ratio, x/y , is used as a variable in a regression analysis with a third variable z , separate regression analyses of x with z , and y with z were also conducted. Thus all conclusions derived from ratios were checked against analyses of the original variables.

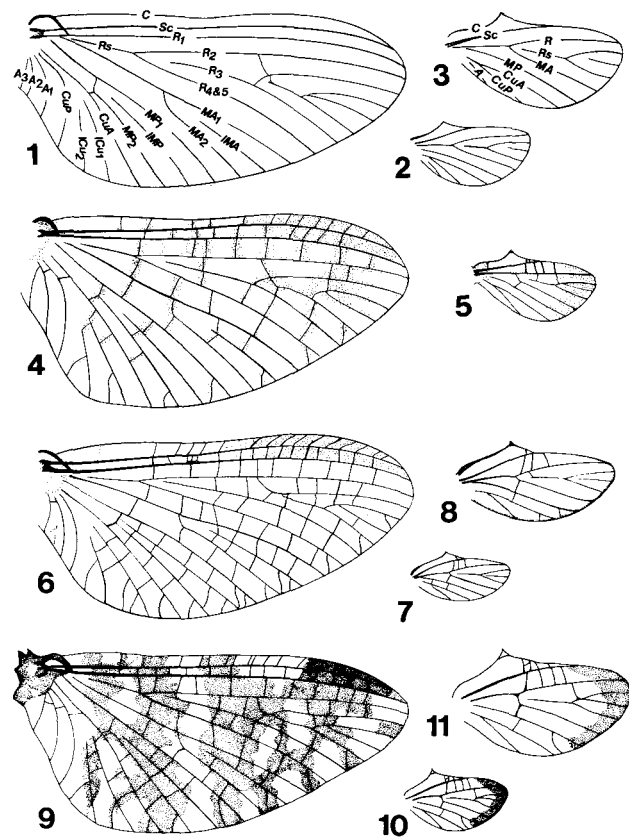
Wing character evolution and terminology

The wing venation 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. All veins of the fore and hind wings of schematic *Miroculis* wings are labeled in Figs. 1–3. Homologies are based upon the corrugation pattern of convex and concave veins (EDMUNDS and TRAVER 1954; KUKALOVA-PECK 1978) and on comparative study of wings in the families Heptageniidae, Ephemeriidae, Siphonuridae, and primitive Leptophlebiidae such as *Leptophlebia* Westwood and *Paraleptophlebia* Lestage.

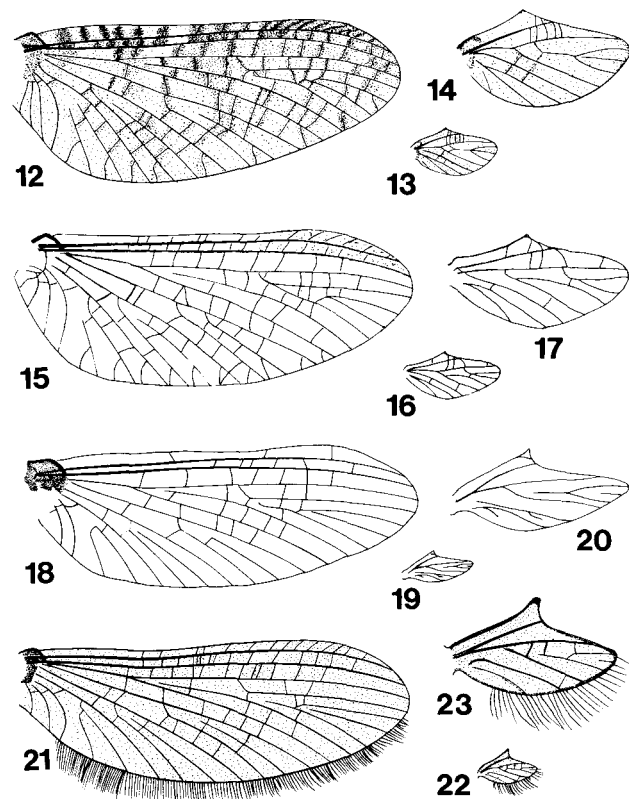
Each of the wing characters listed in Table 1 was analyzed by determining its states and their distributions within *Miroculis* and closely related genera, and among other more distantly related genera of Leptophlebiidae. The probable evolutionary history of the states for each character was delineated, and the probable ancestral and derived states determined. In general, the ancestral character state may be recognized by being the more widely and irregularly distributed state. However, particular importance was placed on character state distributions within other generic complexes that are believed to share a common ancestry with *Miroculis* and related genera based upon previous study of all available characters (see SAVAGE and PETERS 1982, for further discussion).

Evolution has proceeded in 2 directions from the ancestral state within several of the wing characters discussed herein. To represent this divergent evolution the ancestral state is scored 0, while derived states are scored with negative or positive whole numbers (–1, +1, +2, etc.). Character state transformations in the same direction are assigned progressively larger numbers such as +1, +2, etc. The assignment of positive (+) or negative (–) values is arbitrary and indicates only a difference in direction from the ancestral state, therefore, a –1 and a +1 state would be equally derived.

The evolutionary history of wing character states observed within *Miroculis* and related genera (Table 1) is reviewed below.



Figs. 1-11. Male imaginal fore and hind wings. Schematic wings with abbreviations of venational terminology. 1: fore wing; 2: hind wing; 3: hind wing enlarged. *Miroculis (Miroculis) fittkaui*: 4: fore wing; 5: hind wing. *Miroculis (Yaruma) sp.*: 6: fore wing; 7: hind wing; 8: hind wing enlarged. *Miroculis (Atroari) amazonicus*: 9: fore wing; 10: hind wing; 11: hind wing enlarged



Figs. 12-23. Male fore and hind wings. *Miroculis (Ommaethus) mourei*, imago: 12: fore wing; 13: hind wing; 14: hind wing enlarged. *Miroculitus emersoni*, imago: 15: fore wing; 16: hind wing; 17: hind wing enlarged. *Hermanellopsis incertans*, imago: 18: fore wing; 19: hind wing; 20: hind wing enlarged. *Microphlebia surinamensis*, subimago: 21: fore wing; 22: hind wing; 23: hind wing enlarged

Table 1

Wing character states observed within *Miroculis* and related genera

1. ratio: maximum width of fore wings/maximum length of fore wings in male imagos
 - 1) from 0.43 to 0.51
 - 0) from 0.41 to 0.43 (ancestral)
 - +1) from 0.33 to 0.40
2. presence or absence of a cross vein connecting veins MP and CuA basal to the fusion of MP₁ and MP₂ in fore wings
 - 0) present (ancestral)
 - +1) absent
3. vein MP of fore wings forked to vein MP₂ attached at base to MP₁ by a cross vein
 - 0) slightly less than 0.25 to 0.33 distance from base of vein MP₁ to margin (ancestral)
 - +1) 0.33 to a little less than 0.40 distance from base of vein MP₁ to margin
4. vein MP₂ of fore wings is attached
 - 0) by cross veins to MP₁ and CuA (ancestral)
 - +1) at base to vein MP₁
5. vein ICu₁ of fore wings is
 - 0) free basally or attached to vein CuA by a cross vein (ancestral)
 - +1) attached at base to vein CuA
6. cubital area of fore wings is
 - 0) not reduced (ancestral)
 - +1) greatly reduced
7. marginal intercalaries along posterior margin of fore wings
 - 0) are numerous as in Figs. 4, 6, 9, 12, 15 (ancestral)
 - +1) are greatly reduced in number, Figs. 18, 21
8. ratio: maximum length of hind wings/maximum length of fore wings in male imagos
 - 1) from 0.24 to 0.32
 - 0) from 0.18 to 0.24 (ancestral)
 - +1) from 0.16 to 0.18
 - +2) from 0.14 to 0.16
9. location of terminus of vein Sc in hind wings and shape of costal projection
 - 0) vein Sc ends distad to apex of costal projection; distal margin of costal projection gradually tapers as in Figs. 5, 8, 11, 14, 17 (ancestral)
 - +1) vein Sc ends approximately at location of costal projection; distal margin of costal projection is abrupt as in Figs. 20, 23
10. ratio: length from hind wing base to apex of costal projection/length from base to margin of hind wing in male imagos
 - 1) from 0.27 to 0.36
 - 0) from 0.34 to 0.50 (ancestral)
 - +1) from 0.50 to 0.60
11. veins Sc and R of hind wings
 - 0) do not intersect before reaching base of wings (ancestral)
 - +1) intersect before reaching base of wings (Figs. 20, 23)
12. veins CuA and CuP of hind wings
 - 1) fuse 0.16 to 0.33 distance from base of vein CuA to margin
 - 0) are unfused or fused at base to 0.16 distance from base of vein CuA to margin (ancestral)
 - +1) vein CuP absent
13. membrane of fore and hind wings in imagos
 - 0) with brown pigment (ancestral)
 - +1) hyaline

Character 1. Fore wing width/fore wing length (FWW/FWL) ratios in male imagos have evolved in 2 directions from the ancestral state displayed by *Miroculis* (*Ommaethus*) Savage & Peters (Fig. 12). The 3 derived subgenera of *Miroculis*, *M. (Atroari)*, *M. (Yaruma)* and *M. (Miroculis)*, are unusual in being sexually dimorphic for character 1, and males display the -1 derived state of increased ratio values (Figs. 4, 6, 9). The FWW/FWL ratio dimorphism results from a general body size dimorphism, combined with relatively shorter fore wing lengths and perhaps greater fore wing widths in males. *Miroculitus*, *Hermanellopsis* and *Microphlebia* share the +1 state of reduced ratios (Figs. 15, 18, 21). However, character 1 is size correlated and the +1 derived state has evolved independently in *Miroculitus* (lineage 3a, Fig. 24), and in lineage 1b (Fig. 24) which includes both *Microphlebia* and *Hermanellopsis*. Character state assignment is based upon correlation and regression analyses of body size and wing dimensions within *Miroculis* and related genera.

Character 2. The 4 subgenera of *Miroculis* lack cross veins between veins MP and CuA basal to the fusion of MP₁ and MP₂ in the fore wings (Figs. 4, 6, 9, 12). *Miroculitus*, *Hermanellopsis* and *Microphlebia* retain at least 1 cross vein in this area (Figs. 15, 18, 21) as do the majority of Leptophlebiidae and hence the retention of a cross vein is scored ancestral.

Some genera of Leptophlebiidae such as *Penaphebia* Peters & Edmunds and *Massartella* Lestage from South America are sexually dimorphic for character 2, with larger females displaying basal cross veins and smaller males lacking them. However, no evidence of a sexual dimorphism for character 2 was detected within *Miroculis* and related genera. Indeed the opposite pattern occurs, as genera with smaller body sizes, *Miroculitus*, *Hermanellopsis* and *Microphlebia*, retain basal cross veins, while larger bodied *Miroculis* does not.

Character 3. Fore wing veins MP₁ and MP₂ fuse less than 0.33 the distance from base of vein MP₁ to margin in *Miroculis* and *Miroculitus* (Figs. 4, 6, 9, 12, 15). In *Hermanellopsis* and *Microphlebia* these veins fuse at 0.33 or greater the length of vein MP₁ (Figs. 18, 21). The more basal fusion of veins MP₁ and MP₂ is the probable ancestral state as this state is observed in other families of Ephemeroptera such as the Ephemeroidea, Siphonuridae and Heptageniidae, as well as in many Leptophlebiidae including the South American genera *Penaphebia*, *Massartella* and *Hapsiphebia* Peters & Edmunds.

Character 4. Vein MP₂ of fore wings is attached at base to veins MP₁ and CuA by cross veins (Figs. 4, 6, 9, 12, 18) in *Miroculis* and *Hermanellopsis incertans* (Spieth). Vein MP₂ attaches at base to vein MP₁ in *Miroculitus* (Fig. 15), *Microphlebia* (Fig. 21) and in *Hermanellopsis arsia* Savage & Peters. The attachment of vein MP₂ to MP₁ and CuA by cross veins probably represents the ancestral state as this state is widespread within the Leptophlebiidae, occurs in primitive genera of the Leptophlebiinae e. g., *Paraleptophlebia* and *Habrophlebiodes* Ulmer, and in genera of Atalophlebiinae believed to share a common ancestry with *Miroculis* and related genera such as *Penaphebia*, *Rhigotopus* Pescador & Peters and *Massartella*.

Character 5. Fore wing cubital intercalary veins are highly variable within the Leptophlebiidae. Generally, the base of vein ICu₁ may be free, attached to vein CuA, or attached to vein CuP; however, a number of variations upon these typical states results from the plastic nature of the cubital intercalaries and cross veins. Vein ICu₁ is usually free basally in *Hermanellopsis* and the 4 subgenera of *Miroculis* (Figs. 4, 6, 9, 12). However, on rare occasions vein ICu₁ may be attached at base by a cross vein to CuA in *Miroculis* and *Hermanellopsis*, and in some specimens of *H. incertans* ICu₂ may attach to the "normally free" base of ICu₁ (Fig. 18). Vein ICu₁ is attached at base to vein CuA in *Miroculitus* (Fig. 15) and *Microphlebia* (Fig. 21). The probable ancestral state within *Miroculis* and related genera is vein ICu₁ with the base free. Character state assignment follows from the ancestral state's common distribution within *Miroculis* and related taxa, and its irregular distribution throughout the Leptophlebiidae.

Character 6. *Miroculis* (Figs. 4, 6, 9, 12), *Miroculitus* (Fig. 15), and *Hermanellopsis* (Fig. 18) retain the ancestral state of an unreduced cubital area, as do the vast majority of

Leptophlebiidae. *Microphlebia* (Fig. 21) displays the derived state of a reduced cubital area. Fore wing width and hence width of the cubital area are correlated with body size within *Miroculis* and related genera (Fig. 26); however, the greater reduction in the cubital area observed in *Microphlebia* is not a simple result of body size reduction. *Microphlebia*, *Hermanellopsis*, *Miroculitus* and *Miroculis* have body length ranges of 3.6–5.0 mm, 3.5–5.0 mm, 4.0–5.0 mm, and 3.8–7.8 mm, respectively. Even though *Hermanellopsis* and *Microphlebia* body lengths completely overlap, and *Miroculitus*, *Miroculis* and *Microphlebia* body lengths partially overlap, no species of *Hermanellopsis*, *Miroculitus* or *Miroculis* has a greatly reduced cubital area, while taxa with larger body sizes such as *Fittkaulus* Savage & Peters (body length, 5.0–6.8 mm) may have reduced cubital areas (SAVAGE and PETERS 1978).

Character 7. Marginal intercalaries along the fore wing posterior margin are numerous in *Miroculis* (Figs. 4, 6, 9, 12) and *Miroculitus* (Fig. 15), while the number of marginal intercalaries is greatly reduced in *Hermanellopsis* (Fig. 18) and *Microphlebia* (Fig. 21). The ancestral state of numerous marginal intercalaries is common and widespread within the Leptophlebiidae and many other families of Ephemeroptera. The derived state of reduced marginal intercalaries has evolved independently on numerous occasions within the Leptophlebiidae and is often associated with reduced fore wing surface areas that may result from reduced body size and/or reduced FWW/FWL ratios. The reduction of fore wing surface areas presumably reduces need for internal strengthening ridges such as marginal intercalaries and cross veins. This phenomenon is observed in other taxa with large size variation such as *Paraleptophlebia* in North America, and could also explain the reduction of marginal intercalaries in *Hermanellopsis* and *Microphlebia*. However, *Miroculitus* which has body lengths and FWW/FWL ratios falling within the range of *Microphlebia* and *Hermanellopsis* retains the ancestral number of marginal intercalaries.

Character 8. Hind wing length/fore wing length (HWL/FWL) ratios have evolved in 2 directions from the ancestral state displayed by *Miroculis* (*Ommaethus*) and *Miroculitus* (Fig. 24). The 3 derived subgenera of *Miroculis*, *M. (Atroari)*, *M. (Yaruma)*, and *M. (Miroculis)* are unusual in being sexually dimorphic for character 8, and males display the -1 derived state of increased ratio values. This dimorphism results primarily from relatively shorter fore wings in male imagos (Fig. 26) and a general body size dimorphism. *Hermanellopsis* (+1) and *Microphlebia* (+2) display positive derived states of reduced ratios. While correlation between character 8 and body size may explain the reduced +1 ratios observed in these taxa, the greatly reduced ratios observed in *Microphlebia* are a combined result of small size and a non-size correlated reduction in the distal development of the hind wings (Figs. 22–23).

Character 9. Hind wing vein Sc terminates distad to apex of costal projection, and the costal projection's distal margin is gradually tapered in *Miroculis* (Figs. 5, 7–8, 10–11, 13–14) and *Miroculitus* (Figs. 16–17). In *Hermanellopsis* (Figs. 19–20) and *Microphlebia* (Figs. 22–23), vein Sc ends approximately at location of the costal projection and accordingly the margin of the costal projection is abrupt. The more distal termination of vein Sc in *Miroculis* and *Miroculitus* represents the ancestral state as vein Sc terminates very near the hind wing apex in most families of Ephemeroptera and in many genera of Leptophlebiidae including those genera considered to be among the most primitive e. g., *Paraleptophlebia*, *Leptophlebia* and *Hapsiphlebia*. Thus, the most ancestral state observed among the Leptophlebiidae would be that of vein Sc terminating near the wing apex and the absence of a costal projection e. g., *Leptophlebia*, *Hapsiphlebia* and *Penaphlebia*; as vein Sc becomes progressively shorter, or progressively derived, an associated costal projection develops e. g., *Miroculis*, and *Miroculitus*; and as the terminus of vein Sc approaches the apex of the costal projection the distal margin of the costal projection becomes increasingly abrupt e. g., *Hermanellopsis*, and *Microphlebia*. The transformation series described above has evolved independently in several phyletic lineages of Leptophlebiidae.

Character 10. The ratio, length from hind wing base to apex of costal projection/length from base to margin of hind wing in male imagos, has evolved in 2 directions within *Miroculis* and related genera from the ancestral state (Figs. 14, 17, 20) retained by *Miroculis* (*Ommaethus*), *Miroculitus* and *Hermanellopsis*. Males of the 3 derived subgenera of *Miroculis* (Figs. 5, 8, 11), *M. (Atroari)*, *M. (Yaruma)* and *M. (Miroculis)*, display the -1 derived state of reduced values for character 10. This -1 derived state results from combination of a slight basal shift in location of the costal projection's apex, plus a distal enlargement of the hind wings that appears to be associated (Fig. 34) with the increased fore wing widths (Fig. 30) observed among males of these taxa. In *Microphlebia*, the distal portion of the hind wings is reduced (Fig. 23), resulting in a relatively more apical location of the costal projection with respect to hind wing length (+1 state).

Character 11. Veins Sc and R of hind wings do not intersect before reaching the wing base in *Miroculis* (Figs. 5, 8, 11, 14) and *Miroculitus* (Fig. 17), while these veins intersect before reaching the wing base in *Hermanellopsis* (Fig. 20) and *Microphlebia* (Fig. 23). The basal intersection of veins Sc and R is the probable ancestral state as it reflects the independent origins of these veins.

Character 12. Veins CuA and CuP of hind wings fuse 0.16 to 0.33 distance from base of vein CuA to margin in *Miroculis* (Figs. 5, 8, 11, 14), and from base to 0.16 the length of vein CuA in *Miroculitus* (Fig. 17). *Microphlebia* lacks vein CuP in the hind wings (Fig. 23). The condition observed in *Miroculitus* (Fig. 17), in which veins CuA and CuP fuse at base to 0.16 distance from base of vein CuA to margin, represents the ancestral state within *Miroculis* and related taxa. The more distal fusion in *Miroculis* is assigned the -1 derived state, while loss of vein CuP in *Microphlebia* represents the +1 derived state. The condition of veins CuA and CuP in hind wings within *Hermanellopsis* is quite variable and nearly includes the range of variation between the total loss of vein CuP in *Microphlebia* (Fig. 23) and the ancestral state of CuA and CuP fusing basally as observed in *Miroculitus* (Fig. 17). Veins CuA and CuP remain unfused in *Hermanellopsis arsia*, however, in some specimens vein CuP is very weakly developed and often broken. In specimens with weak or broken vein CuP, *H. arsia* approaches the +1 derived state observed in *Microphlebia* in which CuP is absent. In *H. incertans* (Fig. 20), CuA and CuP are fused at base to 0.16 the length of vein CuA, which is the ancestral state as observed in *Miroculitus* (Fig. 17). However in available specimens of *H. incertans* vein CuP is incomplete apically and does not reach the wing margin (Fig. 20). Rather than divide the condition of the cubital veins into several more states, I have broadened the definition of the ancestral state to include all variation from the basally fused state of *Miroculitus* to the unfused condition of the cubitals in *Hermanellopsis arsia*.

Character 13. The wing membrane is hyaline (Figs. 15-23) in imagos of *Miroculitus*, *Hermanellopsis* and *Microphlebia*. The intensity and distribution of brown pigment on the wing membrane within *Miroculis* is variable. *Miroculis* (*Ommaethus*) and *M. (Atroari)* share submedian irregular broken transverse bands of brown pigment on the fore wings. This pattern is well developed in *M. (Atroari) amazonicus* Savage & Peters (Fig. 9), but is lighter in both *M. (Ommaethus) froehlichii* Savage & Peters and *M. (Atroari) duckensis* Savage & Peters, and it is obscured due to an entirely light brown membrane in *M. (Ommaethus) mourei* (Fig. 12). Members of *M. (Miroculis)*, except *M. (M.) fittkawi* Savage & Peters (Figs. 4), lack dark pigment on the fore wings, while membrane color within *M. (Yaruma)* ranges from hyaline to the presence of a very light brown tinge. The presence of dark brown pigment is the probable ancestral state within *Miroculis* and related genera. Imagos with pigmented wings are scattered throughout the Leptophlebiidae, being observed in all phyletic lineages. Subimagos of many genera including *Penapplebia* and *Massartella* often have pigmented wings, while pigment is lost in imagos. The common occurrence of darkly pigmented wings in subimagos, and their scattered distribution in imagos reflect the ancestral state of this character. Evolution of the hyaline state has evolved independently on numerous occasions within the Southern Hemisphere Leptophlebiidae (TOWNS and PETERS 1980).

Character state assignment for wing color may be more complex for other Ephemeroptera than that presented herein due to the influence of sexual selection and other aspects of behavioral ecology on wing color.

Phylogeny and wing character state distributions

The distribution of wing character states in Table 1 among the subgenera of *Miroculis* and related genera is superimposed on the branching diagram (Fig. 24) previously developed from study of all available characters by SAVAGE and PETERS (1982) employing the principles of HENNIG (1966) and ROSS (1974). Character state distributions from Table 1 are depicted in Fig. 24 as explained in the figure legend. On rare occasions e. g., character 5 for *Hermanellopsis* and character 13 for *Miroculis* (*Miroculis*), species within a single genus or subgenus display 2 different states for a character. This phenomenon is indicated in Fig. 24 by providing symbols representing the 2 states on different sides of the rectangle.

The basal furcation in Fig. 24 represents evolution of lineage 1b, which includes *Microphlebia* and *Hermanellopsis*, from a common ancestor shared with lineage 1a, which includes *Miroculitus* and the subgenera of *Miroculis*. Members of lineage 1b are distinguished by the following +1 derived wing character states (Fig. 24; Table 1): No. 7 – reduced marginal intercalaries along the posterior margin of the fore wings (Figs. 18, 21); No. 3 – a more distal fusion of veins MP_1 and MP_2 in the fore wings; No. 8 – reduced HWL/FWL ratios; No. 9 – termination of vein Sc in hind wings at location of the costal projection (Figs. 20, 23); and No. 11 – intersection of veins Sc and R in hind wings before reaching the wing base.

Lineage 1a displays the following ancestral (0) states: No. 7 – numerous marginal intercalaries along the posterior margin of fore wings (Figs. 4, 6, 9, 12, 15); No. 3 – a more basal fusion of veins MP_1 and MP_2 in the fore wings; No. 9 – termination of vein Sc in the hind wings beyond costal projection's apex and associated gradual taper of the costal projection's distal margin (Figs. 5, 8, 11, 14, 17); and No. 11 – hind wing veins Sc and R do not intersect before reaching the base of the wings. Members of lineage 1a also display either the ancestral (0) state of character 8 or the –1 derived state of increased HWL/FWL ratios (No. 8).

Furcation 2 represents evolution of *Microphlebia* from a common ancestor shared with *Hermanellopsis*. Lineage 2b, or *Microphlebia*, possesses the following +1 derived wing character states: No. 5 – vein ICu_1 of fore wings is attached at base to vein CuA (Fig. 21); No. 6 – cubital area of fore wings is greatly reduced; No. 10 – hind wings with apex of costal projection located greater than 0.50 distance from base to margin of wings (Fig. 23); and No. 12 – loss of vein CuP from the hind wings. Additionally, *Microphlebia* displays the +2 derived state of No. 8

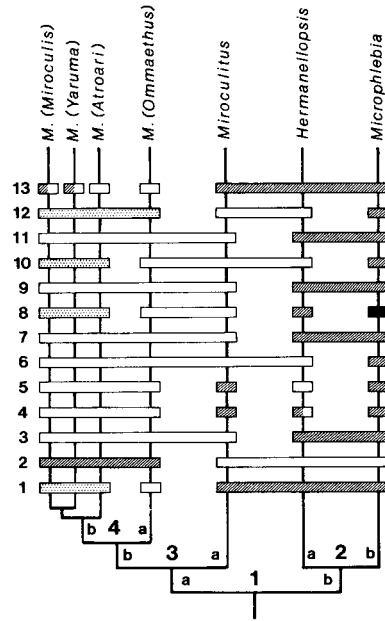


Fig. 24. Branching diagram based upon previous study of all available characters for the subgenera of *Miroculis* and related genera (SAVAGE and PETERS 1982) with wing character states from Table 1 superimposed. Character numbers corresponding to characters in Table 1 are provided along the left margin. Distribution of character states is indicated as follows: –1 states by dots; 0 or ancestral states by empty rectangles; +1 states by diagonal lines; and +2 states by solid rectangles

– greatly reduced HWL/FWL ratios. The derived state of character 5 (Table 1) has evolved twice (Fig. 24) within *Miroculis* and related genera, and appears in both *Miroculitus* (Fig. 15) and *Microphlebia* (Fig. 21).

Hermanellopsis, or lineage 2 a, retains the following ancestral (0) states: No. 5 – vein ICu₁ of fore wings is not attached at base to vein CuA (Fig. 18); No. 6 – cubital area of fore wings is not reduced; No. 10 – hind wings with apex of costal projection located from 0.40–0.50 distance base to margin of wings (Fig. 20); No. 12 – vein CuP of the hind wings is present and veins CuA and CuP may be unfused or fused at base to 0.16 distance from base to margin. *Hermanellopsis* retains the +1 state of character 8 – reduced HWL/FWL ratios, which is indicative of lineage 1 b. The ancestral state of an unreduced cubital area (No. 6) observed in *Hermanellopsis* is shared with all members of lineage 1 a, while the remaining ancestral states (No. 5, 10, 12) are shared with various members of lineage 1 a as indicated in Fig. 24.

Furcation 3 separates *Miroculitus* from a common ancestor shared with *Miroculis*. Lineage 3 b, which includes the 4 subgenera of *Miroculis*, displays the derived +1 state of No. 2 – absence of cross veins between veins MP and CuA basal to the fusion of MP₁ and MP₂ in the fore wings (Figs. 4, 6, 9, 12), and the derived –1 state of No. 12 – veins CuA and CuP of the hind wings fuse 0.16 to 0.33 distance from base to margin (Figs. 5, 8, 11, 14). *Miroculis* retains the ancestral states of No. 4 – vein MP₂ is connected to MP₁ and CuA by cross veins, and of No. 5 – vein ICu₁ of fore wings is free basally or attached at base to vein CuA by a cross vein (Figs. 4, 6, 9, 12). Members of *Miroculis* display either the ancestral (0) or the –1 state of character 1 – increased FWW/FWL ratios in male imagos.

Miroculitus, or lineage 3 a, is distinguished by the following +1 derived states: No. 1 – reduced FWW/FWL ratios; No. 4 – vein MP₂ of fore wings attached at base to vein MP₁ (Fig. 15); and No. 5 – the basal attachment of vein ICu₁ to CuA in the fore wings. FWW/FWL ratios (No. 1) are size correlated (Fig. 27) and the +1 state evolved independently in lineages 1 b and 3 a (Fig. 24). The +1 state of vein ICu₁ (No. 5) has evolved independently in *Miroculitus* and *Microphlebia* (lineage 2 b), while *Hermanellopsis* and *Miroculis* retain the ancestral state. *Miroculitus* retains ancestral states of No. 2 – presence of a cross vein connecting veins MP and CuA basal to fusion of MP₁ and MP₂ in fore wings (Fig. 15), and No. 12 – CuA and CuP of hind wings fuse at base to 0.16 distance from base to margin (Fig. 17). The ancestral state of character 3 observed in *Miroculitus* is shared with members of lineage 1 b, and the ancestral state of character 12 with *Hermanellopsis* (lineage 2 a).

Evolution of the 3 derived subgenera of *Miroculis*, *M. (Atroari)*, *M. (Yaruma)* and *M. (Miroculis)*, from a common ancestor shared with *M. (Ommaethus)* is represented by furcation 4 (Fig. 24). Males of the 3 derived subgenera (lineage 4 b, Fig. 24) share –1 derived character states of No. 1 – increased FWW/FWL ratios, No. 8 – increased HWL/FWL ratios, and No. 10 – decreased ratios of length from hind wing base to apex of costal projection/length of hind wing. *M. (Ommaethus)* retains the ancestral state for these (No. 1, 8, 10) characters. The –1 derived states displayed by males of lineage 4 b are a product of different allometric relationships among some wing dimensions and body size, and a general sexual dimorphism in body size.

Size and wing character evolution

Even though the vast majority of characters in Table 1 are not directly size related, size has played an important role in determining wing shape within *Miroculis* and related genera, and possibly some of the derived wing character states shared by *Hermanellopsis* and *Microphlebia*, and to a lesser extent *Miroculitus*, are an artifact of small size and may have evolved independently. For example, reduced FWW/FWL ratios (No. 1), reduced

HWL/FWL ratios (No. 8), and reduction of marginal intercalaries (No. 7) are likely associated with an overall size reduction.

Within *Miroculis* and related genera, 32 percent ($r = 0.57$, $r^2 = 0.32$, $P = 0.02$, $n = 16$) of the variation in FWW/FWL ratio (No. 1) can be explained by body length alone. However, when males and females of lineage 4b and all remaining taxa are treated separately, body length explains 72 percent ($r = 0.85$, $P = 0.004$, Fig. 27) of the FWW/FWL ratio variation within lineage 4b and 59 percent ($r = 0.77$, $P = 0.043$, Fig. 27) of the variation within the remaining taxa. The dichotomy in FWW/FWL ratios (Fig. 27) with respect to size between members of lineage 4b and the remaining related taxa, is primarily a result of a lack of correlation between body length ($r = 0.30$, $P = 0.436$, Fig. 25) and fore wing length in males of lineage 4b and positive correlation between body length and fore wing length in females of lineage 4b and all remaining taxa, or the "others" group ($r = 0.84$, $P = 0.005$, Fig. 25), combined with a positive correlation between body length and fore wing width common to all taxa ($r = 0.78$, $P < 0.001$, Fig. 26). Thus, increasing body size results in larger FWW/FWL ratios in members, particularly the larger males, of lineage 4b than in the remaining taxa. However, as is apparent from Fig. 27, it will not be possible to assign very small species to phyletic line based on FWW/FWL ratios, or character 1.

Males of lineage 4b (Fig. 24) share the -1 derived state of character 1 - increased FWW/FWL ratios (Figs. 28-30). Midpoints of fore wing length are plotted against midpoints of fore wing width for 17 groups within *Miroculis* and related taxa in Fig. 28. Points representing males of the 3 derived subgenera (lineage 4b, Fig. 24) all fall below the line of best fit for the remaining groups. A similar pattern is observed when fore wing lengths are plotted against FWW/FWL ratios (Fig. 29): males of lineage 4b form a cluster below the line of best fit for the other groups. As mentioned previously, due to size correlation it will not be possible to place small species phyletically based on character 1. Curiously, within *Miroculis*, the opposite and less obvious situation actually occurs. Very large species of *M. (Ommaethus)*, or lineage 4a (Fig. 24), also attain ratios typical of small members of lineage 4b. When FWW/FWL ratios are plotted against fore wing length this becomes apparent (Fig. 29). In the graph (Fig. 29), it appears that overlap does not occur; however, values plotted are midpoints. Inspection of ranges reveals that males of a small species of lineage 4b, *M. (Miroculis) maraniae* Savage & Peters, have ratios ranging from 0.43-0.45, while the largest species of lineage 4a, *M. (Ommaethus) froeblichii*, has a known range of 0.41-0.43. Thus, as suggested by Fig. 29, very large species in the "others" category may have ratios similar to much smaller males of lineage 4b, and use of FWW/FWL ratio as a phyletic or taxonomic character will present problems at both ends of the size spectrum unless the body size of the specimen is taken into consideration.

The 3 derived subgenera of *Miroculis* (lineage 4b) are unusual in being sexually dimorphic for FWW/FWL ratio (Figs. 29-30). Knowledge that body length is correlated with FWW/FWL ratio within lineage 4b ($r = 0.85$, $P = 0.004$, Fig. 27) suggests the following question: does the sexual dimorphism in fore wing shape correspond to a sexual dimorphism in body length? Comparisons are tenuous, as female imagoes are known for only 2 species of the 3 derived subgenera. However, the vast majority of female specimens of both species are smaller than their corresponding males. For 16 females and 11 males of *M. (Miroculis) fittkai*, character 1 is significantly correlated ($r = 0.42$, $P = 0.029$, $n = 27$) with pterothorax length and females are generally smaller. (Pterothorax length was used to estimate size because abdomens of some specimens were damaged.) However, when males and females of *M. (M.) fittkai* are examined separately, character 1 and pterothorax length are significantly correlated for males ($r = 0.61$, $P = 0.048$, Fig. 33), but not for females ($r = 0.36$, $P = 0.17$, $n = 16$). Inspection of the data reveals that 4 large female specimens do have wide fore wings (Fig. 32), but they also have very long fore wings (Fig. 31) such that small ratios are maintained (Fig. 33). When fore wing length is plotted against fore wing width, slopes of regression lines for males and females of *M. (M.) fittkai* (Fig. 30) are significantly different

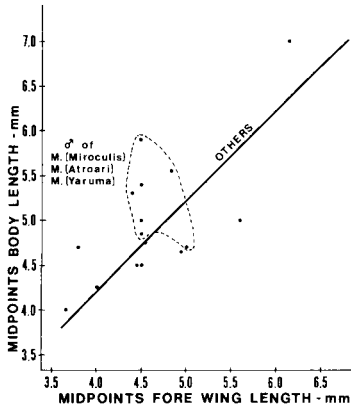


Fig. 25. Relationship between midpoints of body length (mm) and fore wing length (mm) for 16 groups within *Miroculis* and related genera. Values for male imagos of lineage 4b (Fig. 24) are enclosed by dashes. Regression line: others, $Y = 1.02x + 0.12$, $r = 0.84$, $P = 0.005$, $n = 9$

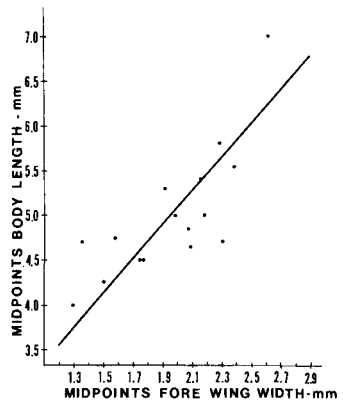


Fig. 26. Relationship between midpoints of body length (mm) and fore wing width (mm) for 16 groups within *Miroculis* and related genera. Regression line: all, $Y = 1.89x + 1.32$, $r = 0.78$, $P < 0.001$, $n = 16$

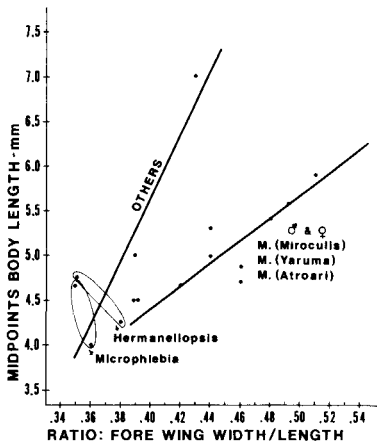


Fig. 27. Relationship between midpoints of body length (mm) and fore wing width/length ratio for 16 groups within *Miroculis* and related genera. Values for *Microphlebia* and *Hermanellopsis* are enclosed by solid lines. Regression lines: others, $Y = 34.72x - 8.26$, $r = 0.77$, $P = 0.043$, $n = 7$; male and female imagos of lineage 4b (Fig. 24), $Y = 12.77x - 0.71$, $r = 0.85$, $P = 0.004$, $n = 9$

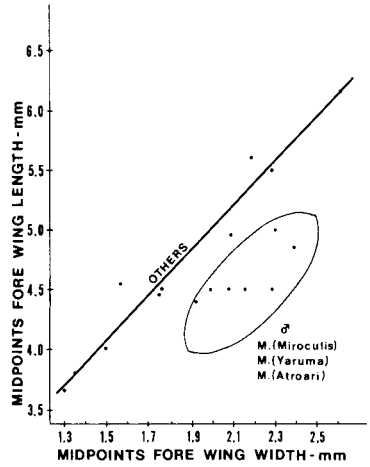


Fig. 28. Relationship between midpoints of fore wing length (mm) and fore wing width (mm) for 17 groups within *Miroculis* and related genera. Values for male imagos of lineage 4b (Fig. 24) are enclosed by an ellipse. Regression line: others, $Y = 1.90x + 1.22$, $r = 0.98$, $P < 0.001$, $n = 10$

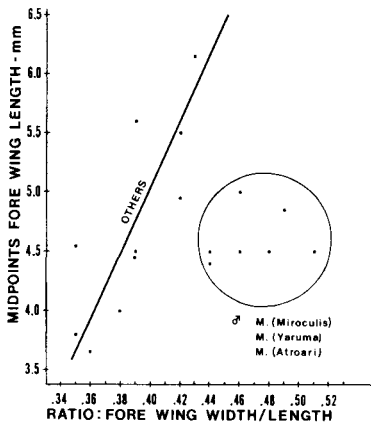


Fig. 29. Relationship between midpoints of fore wing length (mm) and fore wing width/length ratio for 17 groups within *Miroculis* and related genera. Values for male imagos of lineage 4b (Fig. 24) are enclosed by a circle. Regression line: others, $Y = 28.48x - 6.34$, $r = 0.79$, $P = 0.006$, $n = 10$

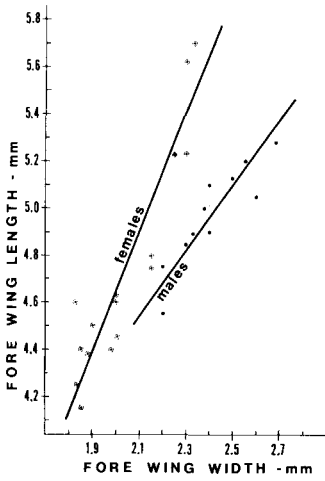


Fig. 30. Relationship between fore wing length (mm) and fore wing width (mm) for 16 female and 11 male specimens of *Miroculis (M.) fittkai*. Regression lines: females, $Y = 2.58x - 0.52$, $r = 0.91$, $p < 0.001$, $n = 16$; males, $Y = 1.36x + 1.70$, $r = 0.90$, $P < 0.001$, $n = 11$

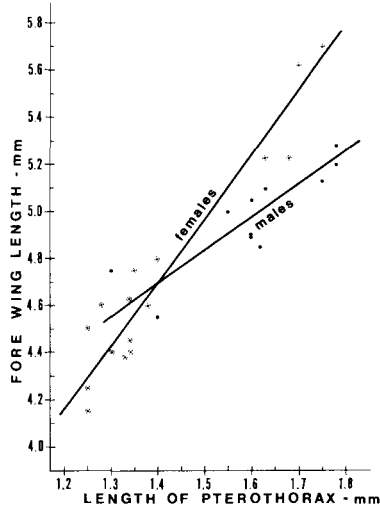


Fig. 31. Relationship between fore wing length (mm) and pterothorax length (mm) for 16 female and 11 male specimens of *Miroculis (M.) fittkai*. Regression lines: females, $Y = 2.71x + 0.91$, $r = 0.96$, $P < 0.001$, $n = 16$; males, $Y = 1.43x + 2.69$, $r = 0.85$, $P = 0.001$, $n = 11$

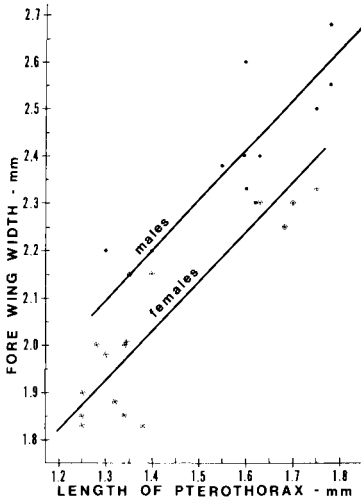


Fig. 32. Relationship between fore wing width (mm) and pterothorax length (mm) for 16 female and 11 male specimens of *Miroculis (M.) fittkai*. Regression lines: females, $Y = 1.05x + 0.56$, $r = 0.87$, $P < 0.001$, $n = 16$; males, $Y = 1.05x + 0.73$, $r = 0.82$, $P = 0.002$, $n = 11$

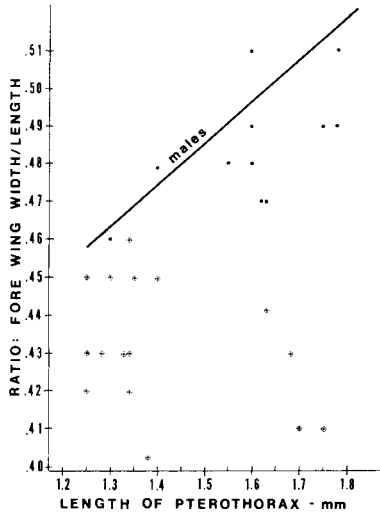


Fig. 33. Relationship between fore wing width/length ratio and pterothorax length (mm) for 16 female and 11 male specimens of *Miroculis (M.) fittkai*. Regression line: males, $Y = 0.11x + 0.32$, $r = 0.61$, $P = 0.048$, $n = 11$

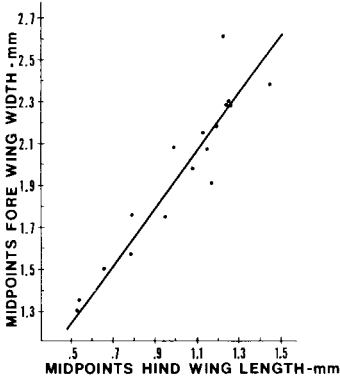


Fig. 34. Relationship between midpoints of fore wing width (mm) and hind wing length (mm) for 17 groups within *Miroculis* and related genera. Regression line: all, $Y = 1.39x + 0.54$, $r = 0.93$, $P < 0.001$, $n = 17$

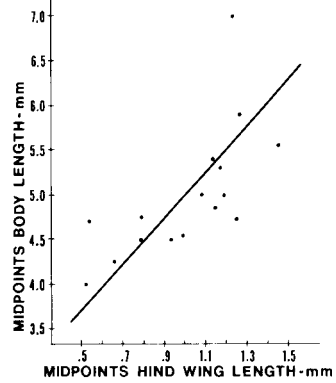


Fig. 35. Relationship between midpoints of body length (mm) and hind wing length (mm) for 16 groups within *Miroculis* and related genera. Regression line: all, $Y = 2.63x + 2.35$, $r = 0.67$, $P = 0.004$, $n = 16$

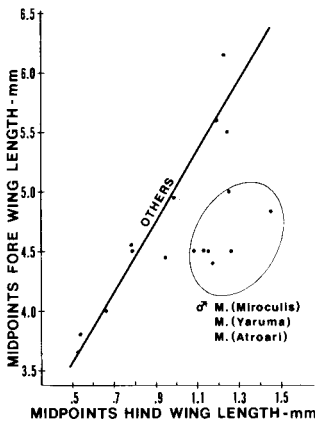


Fig. 36. Relationship between midpoints of fore wing length (mm) and hind wing length (mm) for 17 groups within *Miroculis* and related genera. Values for male imagos of lineage 4b (Fig. 24) are enclosed by an ellipse. Regression line: others, $Y = 3.03x + 2.02$, $r = 0.96$, $P < 0.001$, $n = 10$

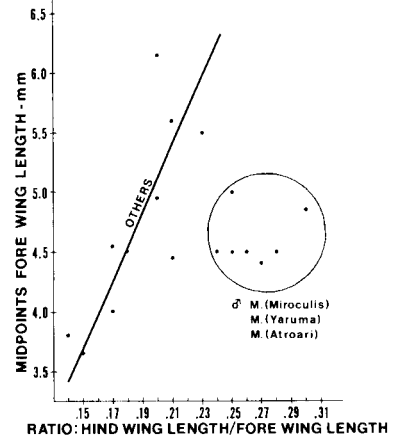


Fig. 37. Relationship between midpoints of fore wing length (mm) and hind wing length/fore wing length ratio for 17 groups within *Miroculis* and related genera. Values for male imagos of lineage 4b (Fig. 24) are enclosed by a circle. Regression line: others, $Y = 28.68x - 0.62$, $r = 0.79$, $P = 0.007$, $n = 10$

($z = 3.86$, $P < 0.01$). From Figs. 30, 33, it is obviously not possible to separate very small males from females based on FWW/FWL ratios. If the 4 large females accurately reflect conditions in large females then large males will be easily separated from both large and small females, and the sexual dimorphism in FWW/FWL ratio will be apparent without a sexual dimorphism in body length when both sexes are large (Fig. 30, 33).

Slopes of regression lines for fore wing length versus pterothorax length for males and females of *M. (M.) fittkani* are significantly different ($z = 3.86$, $P < 0.01$, Fig. 31) and the

slope of the regression line is shallower for males. Thus males, which are generally larger, have relatively shorter fore wings than females (Figs. 25, 31). However, midpoints of fore wing length and body length are not correlated for males of the 3 derived subgenera (Fig. 25). This suggests that males of different species have separate parallel regression lines such that fore wing length and body length relationships are species-specific for males of lineage 4b. Data on females, particularly large females, are very limited but are consistent with the concept that females of each species are represented by a segment of a common "others" line (Fig. 28–29).

Fore wing width and body length are significantly correlated within *Miroculis* and related taxa (Fig. 26) and the large fore wing widths of males are partly explained ($r^2 = 0.61$, $P < 0.001$, Fig. 26) by their larger size. When fore wing width is plotted against pterothorax length for 27 specimens of *M. (M.) fittkani* (Fig. 32), slopes for males and females are equal and intercepts different such that parallel lines result. While the intercepts are not significantly different at the 0.05 level, the regression line for males lies above that for females as do all data points for a particular pterothorax length. This suggests that with larger sample sizes the intercepts in Fig. 32 may be significantly different.

The limited data suggest that the wing shape sexual dimorphism displayed by members of lineage 4b, while generally associated with a sexual dimorphism in body length, may also occur without a dimorphism in body size when both sexes are large (Figs. 30, 33) due to dimorphic relationships between body size and fore wing width and length (Figs. 31–32).

The greater reduction of wing surface area associated with reduced FWW/FWL ratios observed in *Hermanellopsis* and *Microphlebia* (Fig. 27), or lineage 1b (Fig. 24), presumably reduces need for internal strengthening ridges. Thus, reduced marginal intercalaries (No. 7) and reduction of numbers of cross veins are both likely associated with body size reduction. This phenomenon is observed in other taxa with large size variation such as *Paraleptophlebia* in North America, and could also explain the reduction of marginal intercalaries in *Hermanellopsis* and *Microphlebia*. Small members of lineage 1a, such as females of *Miroculis* (*Miroculis marauiae* and *M. (M.) fittkani* and males of *Miroculitus emersoni* (Needham & Murphy), which have body lengths falling within the range of *Microphlebia* and *Hermanellopsis*, retain the ancestral number of marginal intercalaries. However, retention of marginal intercalaries in small members of lineage 1a could be attributed to their slightly larger FWW/FWL ratios, as well as their common phylogenetic history. As increasingly small members of these 2 groups converge in FWW/FWL ratios, they will likewise converge in other size-associated characters; therefore, small members of lineage 1a should not be expected to retain the ancestral marginal intercalaries.

The distribution of HWL/FWL ratios (Fig. 24), or character 8, parallels that of FWW/FWL ratios (No. 1), except that *Miroculitus* and *Miroculis* (*Ommaethus*) share the ancestral state, and *Microphlebia* displays the +2 derived state of greatly reduced HWL/FWL ratios. The 3 derived subgenera of *Miroculis* are unusual in being sexually dimorphic for character 8 (Figs. 36–37) and males display the -1 derived state of increased ratio values. As in the case of FWW/FWL ratios, this dimorphism results primarily from relatively shorter fore wings in male imagos (Fig. 25), combined with larger hind wings that are associated (Fig. 35) with a general body size dimorphism.

Although body length is correlated with hind wing length within *Miroculis* and related taxa ($r = 0.67$, $P = 0.004$, Fig. 35), interactions among fore wing width and length and hind wing length are also important in understanding hind wing size and shape. In stepwise multiple regression, with hind wing length as the dependent variable and fore wing width and length and body length as independent variables, body length enters the equation last. HWL/FWL ratios (No. 8) are most highly correlated with FWW/FWL ratios ($r = 0.92$, $P = 0.001$, $n = 17$), and within *Miroculis* and related genera the strongest correlation observed is between fore wing width and hind wing length ($r = 0.93$, $P = 0.001$, Fig. 34). Thus, the larger hind wing lengths and HWL/FWL ratios of males of lineage 4b are partially

a result of a size dimorphism but they also correspond to the larger fore wing widths and FWW/FWL ratios observed within this lineage. Interestingly, in species with the largest FWW/FWL ratios such as *M. (Miroculis) fittkaui* (Figs. 4–5) and *M. (Atroari) amazonicus* (Figs. 9–11), the shape of the hind wing is modified by the expansion of the apical area. The expansion of the apical area in conjunction with a basal shift in the hind wing costal projection produces the –1 derived state of character 10 observed in males of lineage 4b.

The reduced HWL/FWL ratios (+1 state) indicative of lineage 1b correspond to the reduced size of these taxa (Figs. 27, 35), and their short (Figs. 36–37), narrow fore wings (Figs. 27, 34). However, the +2 derived state of greatly reduced ratios observed in *Microphlebia* is a combined result of small size and a non-size correlated reduction in the distal portion of the hind wings (Figs. 22–23). The reduction of the distal portion of the hind wings also results in the +1 state of character 10 – increased ratios of length to costal projection's apex/length of hind wing.

The distribution of HWL/FWL (No. 8) and FWW/FWL (No. 1) ratios within *Miroculis* and related taxa differ primarily in that *Miroculitus* shares ancestral ratios for character 8 with *Miroculis (Ommaethus)*. *Miroculitus* has a *Miroculis*-like hind wing, and while the fore wings of *Miroculitus* converge with size reduction in width and length to values typical of members of lineage 1b the hind wings have been less affected. Thus, *Miroculitus* retains HWL/FWL ratios typical of the larger-bodied members of *Miroculis (Ommaethus)*, or lineage 4a.

Aerodynamic implications

Imagos of Ephemeroptera do not feed and the principal selective force on imagos is that of successful reproduction. The vast majority of mayflies (EDMUNDS and TRAVER 1954; BRINK 1957; SAVOLAINEN 1978) and all Leptophlebiidae (BRODSKIY 1973) form mating swarms. Within these swarms individuals, particularly males (BRODSKIY 1973), move vertically. In most cases males fly nearly straight upwards and fall passively or fly slowly downwards (EDMUNDS and TRAVER 1954; BRODSKIY 1973; PESCADOR and PETERS 1974). Although flight aerodynamics of only a single species of mayfly, *Ephemera vulgata*, have been investigated (BRODSKIY 1971, 1975), combination of some general principles of insect flight (WEIS-FOGH and JENSEN 1956; PRINGLE 1957; NACHTIGALL 1976; WEIS-FOGH 1976) with results of EDMUNDS and TRAVER's (1954) comparative study of ephemeropteran wing morphology and swarming behavior provide guide lines by which the wing types observed within *Miroculis* and related genera may be interpreted.

EDMUNDS and TRAVER (1954) suggested that the ancestral vertical flight wing type was characterized by the presence of bullae, fluting, and strong longitudinal, intercalary and cross veins. This wing type is common in many families of Ephemeroptera such as the Siphonuridae, Heptageniidae and among primitive genera of Leptophlebiidae such as *Paraleptophlebia*. Bullae are important in this type of wing as they allow the distal portion of an inflexible wing to bend on the upstroke thereby reducing resistance, while the wing remains rigid on the downstroke (EDMUNDS and TRAVER 1954). Fore wings of *Miroculis* retain the ancestral marginal intercalaries (Figs. 4, 6, 9, 12), and the wings appear to be of the rigid vertical flight type, particularly as exemplified by the subgenus *M. (Ommaethus)* (Fig. 12). However, bullae, which are typical of rigid, primitive, vertical flight wings are not found within *Miroculis* and related genera.

In males of the 3 derived subgenera (lineage 4b, Fig. 24) the fore wings have become relatively shorter and wider, and the cubital area is well developed (Figs. 4, 6, 9). This expansion of the wing allows the longitudinal veins to diverge rearward and hence reduce functional fluting (EDMUNDS and TRAVER 1954). The rearward divergence of the veins combined with a general weakening of the longitudinal veins posterior to Rs allows greater flexibility even though the marginal intercalaries are retained.

While increased flexibility associated with the greatly developed cubital area in males of lineage 4b could increase thrust (EDMUNDS and TRAVER 1954; NACHTIGALL 1976), ordinary steady state aerofoil action (WEIS-FOGH 1976) and Walker's flight theory (WEIS-FOGH and JENSEN 1956) suggest that the well developed cubital area is most important in lift production. Ordinary steady state aerofoil action (WEIS-FOGH 1976) states that lift/unit length is directly proportional to wing width (cord). Thus, wider wings produce more lift. Application of Walker's theory (WALKER 1925, 1927; WEIS-FOGH and JENSEN 1956; PRINGLE 1957) which is compatible with data on the flight of some locusts (WEIS-FOGH and JENSEN 1956), hawk moths and birds (WEIS-FOGH 1972) suggest that the inner $\frac{2}{3}$ of the wing produces $\frac{3}{4}$ of the lift, while thrust entirely depends on the outer $\frac{1}{3}$ of the wing. That the well developed cubital area results in lift production is further supported by its occurrence only in males and by the relatively shorter wings of males, which suggest the male wing of lineage 4b is "designed" for lift and not thrust production.

Similarly shaped fore wings, with greatly developed cubital areas, also occur in the Caenidae and Tricorythidae (EDMUNDS and TRAVER 1954). *Miroculis* differs from these 2 families, however, in the condition of the hind wings. All Caenidae lack hind wings, while hind wings are extremely reduced or absent in the Tricorythidae. In the 3 derived subgenera of *Miroculis*, the hind wings are large and very flexible with only the C and Sc veins heavily sclerotized. Thus, if the hind wings move in close association with the fore wings it would increase the effective sculling surface. Interestingly, the strongest correlation among the wing characters studied within *Miroculis* and related genera is between fore wing width and hind wing length ($r = 0.93, P < 0.001$, Fig. 34).

In the narrow fore wings of *Microphlebia*, cross veins are numerous and relatively strong anteriorly and medially, while cross veins and marginal intercalaries are entirely absent from the posterior and distal wing margins (Fig. 21). Wings of *Microphlebia* resemble the sculling wings of some Diptera and Hymenoptera. Sculling wings are characterized by an anterior wing margin that is rigid due to the presence of heavily sclerotized longitudinal veins, and by a posterior wing portion that is flexible as longitudinal and cross veins are reduced or absent. The rigid anterior margin leads the membrane in the direction of the wing stroke (PRINGLE 1957), and as the wing moves downward, the membrane is inclined upward. This drives air backward producing forward thrust (EDMUNDS and TRAVER 1954; NACHTIGALL 1976). Increased thrust resulting from flexibility of the posterior wing margin has been demonstrated in models of bee wings by FREUND (NACHTIGALL 1976). The role of the small hind wings (Figs. 22–23) of *Microphlebia* in flight is highly speculative. I suggest that due to their very heavily sclerotized C, Sc and R_1 veins, the costal projection of the hind wings could add support to the cubital-anal area of the fore wings during vertical flight movements in the swarm.

Aerodynamic principles, size and phylogeny have each played an important role in determining wing shape and vein structure within *Miroculis* and related genera; however, it is often impossible to assess the relative roles of these 3 components quantitatively due to interaction between components and our limited understanding of insect flight. Some conclusions of this study are generally valid throughout the Ephemeroptera such as that the number of cross veins, number of marginal intercalaries, and wing dimensions (length, width, and various ratios) are associated with body size. Generally, wing shape characters such as FWW/FWL and HWL/FWL ratios appear to be more strongly correlated with size and aerodynamic principles than the structure or arrangement of the veins within the wings, which appear to be most strongly correlated with the species' phylogenetic history. However, the role of size must be evaluated separately for each character or correlated set of characters and each group of related taxa. For example, the hind wings and HWL/FWL ratios of *Miroculitus* have remained *M. (Ommaethus)*-like, while the FWW/FWL ratios of *Miroculitus* have converged with size reduction to approach values typical of members of lineage 1b (Fig. 24), or *Hermanellopsis* and *Microphlebia*.

Data on the wing shape sexual dimorphism within members of the 3 derived subgenera of *Miroculis* (lineage 4b, Fig. 24) suggest wing shape and aerodynamics may be influenced by sexual selection and behavioral ecology. The greater FWW/FWL and HWL/FWL ratios displayed by males of lineage 4b are generally associated with a sexual dimorphism in body length, but the wing shape dimorphism may also occur without a dimorphism in body size when both sexes are large due to dimorphic relationships between body size and fore wing width and length (Figs. 30–33). Perhaps females display less flexibility of wing shape because of the restraint that they carry a “load of eggs” to the oviposition site. The female role in the swarm is generally to move horizontally through the swarm, while males are usually required to perform successive vertical movements in the swarm as well as potentially complicated attachment and copulatory movements during flight. The status of wing evolution and the relative roles of various factors will remain speculative until detailed data become available on the phylogeny and flight aerodynamics for several closely related groups of Ephemeroptera and/or other insects.

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Summary

Wing character state evolution, the effect of size on wing shape and structure, and the possible aerodynamic implications within a group of closely related leptophlebiid mayflies from the warm lowland areas of northern South America are treated. Wing shape and vein structure are a function of aerodynamic constraints, size, and the phylogenetic history of the taxa. Generally, wing shape characters such as fore wing width/length and hind wing length/fore wing length ratios appear to be more strongly correlated with size and aerodynamic principles than the structure, or arrangement of the veins within the wings, which appears to be most strongly correlated with the species' phylogenetic history. However, size need not influence all characters or correlated sets of characters equally as demonstrated by the convergence between the fore wings of *Miroculitus* and *Hermanellopsis* with size reduction, and the lack of size-associated changes in the hind wings of *Miroculitus*. Data on the wing shape sexual dimorphism within members of 3 subgenera of *Miroculis*, *M. (Atroari)*, *M. (Yaruma)* and *M. (Miroculis)*, suggest that wing shape and aerodynamics may be influenced by sexual selection and behavioral ecology. The greater fore wing width/length and hind wing length/fore wing length ratios displayed by males of these 3 subgenera are generally associated with a sexual dimorphism in body length. However, the wing shape sexual dimorphism may also occur without a dimorphism in body size when both sexes are large due to dimorphic relationships between body size and fore wing width and length.

Some conclusions of this study, such as that the number of cross veins, number of marginal intercalaries, and wing dimensions (length, width and various ratios) are associated with body size, are generally valid throughout the Ephemeroptera.

Zusammenfassung

Zur Evolution der Flügel bei Miroculis und verwandten Gattungen (Ephemeroptera: Leptophlebiidae) aus dem nördlichen Südamerika

Die Entwicklung der Merkmalsausprägung von Flügeln, der Einfluß der Größe auf Flügelform und Struktur und die aerodynamischen Möglichkeiten in einer Gruppe engverwandter leptophlebiider Eintagsfliegen aus den wärmeren tiefliegenden Gebieten des Nordens von Südamerika sind hier behandelt. Flügelform und Aderstruktur sind eine Funktion der aerodynamischen Zwänge, der Größe, und der phylogenetischen Geschichte der Taxa. Im allgemeinen erscheinen die Flügelmerkmale, wie z. B. Breite/Länge des Vorderflügels und das Verhältnis der Hinter-/Vorderflügelänge wohl stärker mit Größe und aerodynamischen Prinzipien verbunden, während die Struktur oder die Anordnung der Flügeladern mit der phylogenetischen Geschichte stärker verknüpft scheint. Aber die Größe beeinflusst

nicht alle Merkmale oder entsprechende Merkmalsgruppen gleich, dies zeigt z. B. die Konvergenz zwischen den Vorderflügeln von *Miroculitus* und *Hermanellopsis* mit der Größenreduktion und der Mangel an Veränderungen in den Hinterflügeln des *Miroculitus* im Zusammenhang mit Größenwandel. Daten für den Sexualdimorphismus der Flügelform in den drei *Miroculis*-Untergattungen *M. (Atroari)*, *M. (Yaruma)*, und *M. (Miroculis)*, weisen darauf hin, daß die Flügelform und Aerodynamik durch sexuelle Zuchtwahl und behavioristische Ökologie beeinflusst werden dürften. Die höheren Werte für das Verhältnis Vorderflügelbreite/-länge und Hinter-/Vorderflügelänge bei den Männchen dieser drei Untergattungen sind im allgemeinen mit einem Sexualdimorphismus in der Körperlänge verbunden. Aber ein Sexualdimorphismus in der Flügelform kann wegen der dimorphischen Verbindungen zwischen Körpergröße und Vorderflügelbreite und -länge auch ohne Körpergrößendimorphismus vorkommen, wenn beide Geschlechter groß sind.

Einige Erkenntnisse dieser Untersuchung, z. B. Queraderzahl, Interkalaraderzahl, und Flügeldimension (Länge, Breite, und verschiedene Verhältnisse), die mit der Körpergröße verbunden sind, sind für die Ephemeroptera allgemein gültig.

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