

TAXONOMIC STATUS AND PHYLOGENY OF *HABROPHLEBIA* AND *HABROLEPTOIDES*
(LEPTOPHLEBIIDAE: EPHEMEROPTERA)

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Habrophlebia was established by EATON (1881) for the European species *H. fusca* (Curtis). Three other European species of *Habrophlebia* are now recognized. *Habroleptoides* was established by SCHOENEMUND (1929) for the European species *H. modesta* (Hagen). Seven other species of *Habroleptoides* are now recognized and the genus is restricted to Europe. BIANCHERI (1953) considered *Habroleptoides* a subgenus of *Habrophlebia*, while GRANDI (1955) considered *Habroleptoides* synonymous with *Habrophlebia*. I here reconfirm that *Habrophlebia* and *Habroleptoides* are separate genera as indicated by PETERS and EDMUNDS (1970). The imagos of *Habroleptoides* can be distinguished from those of *Habrophlebia* in the male by the inner margin of the genital forceps which has a pointed or blunt projection (Fig. 2) and in the female by the absence of a well developed ovipositor or egg guide. The nymphs of *Habroleptoides* can be distinguished from those of *Habrophlebia* by abdominal gills 1-7 being deeply forked with tracheae unbranched (Fig. 6), by having extremely small posterolateral spines on abdominal segment 8 (Fig. 12), and by the superlingua of the hypopharynx with lateral margins which are blunt and rounded (Fig. 9).

Habrophlebia is represented in Eastern North America by two recognized species. The genus occurs in mountain streams from Eastern Canada to the lowland streams of Northern Florida. PETERS and EDMUNDS (1970) indicated that the Eastern North American representatives of *Habrophlebia* are separable from the European members of *Habrophlebia*, but they did not recognize the North American species as a separate taxonomic entity. Herein I establish a new subgenus, *Hesperaphlebia*, for the North American species of *Habrophlebia*. I further discuss the phylogeny and historical zoogeography of daughter line IA2 as given by PETERS and EDMUNDS (1970).

Subgenus *Habrophlebia* s. s. EATON, 1881

Fig. 3, 4, 7, 10, 13-15

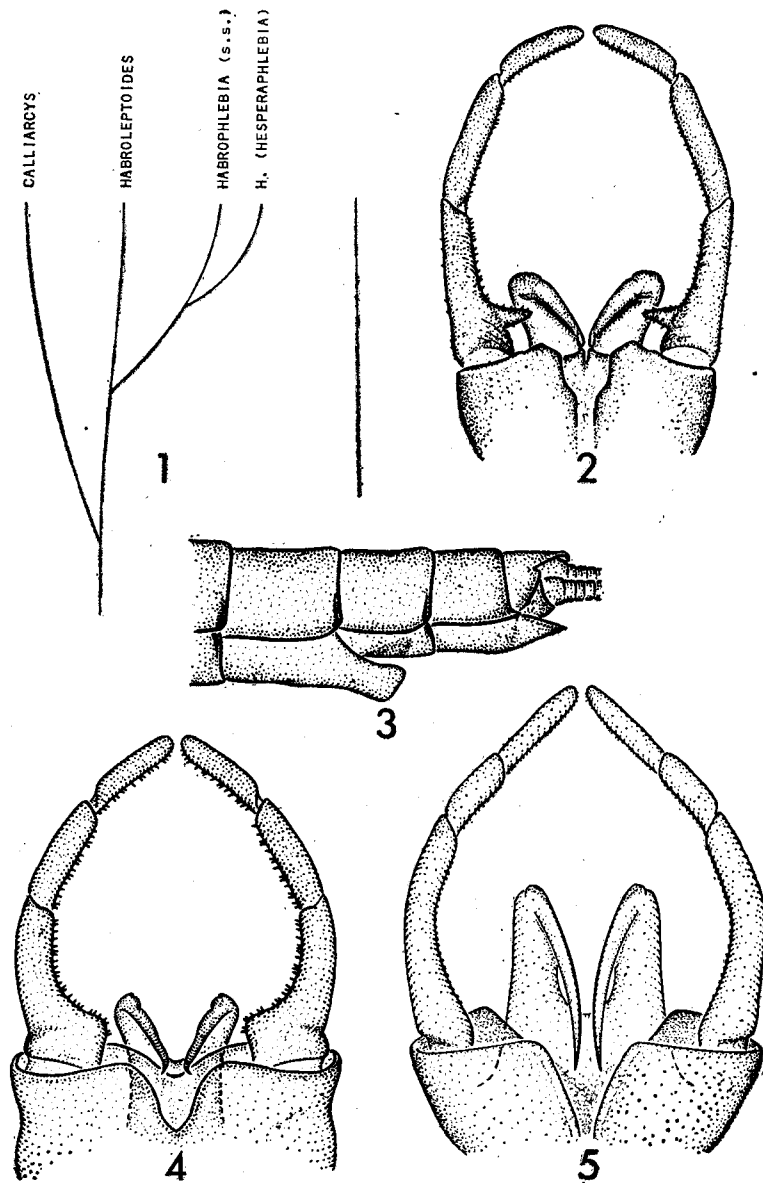
Habrophlebia partim EATON, 1881:195; EATON, 1884 (1883-88):114; ULMER, 1920:117; LESTAGE, 1921:225; GRANDI, 1960:224.

Habrophlebia ULMER, 1929:11; SCHOENEMUND, 1930:53; ULMER, 1932:203; UJHELYI, 1959:42; PETERS, EDMUNDS, 1970:182.

Imago. Length of male fore wings, 5.4–8.5 mm. Base of male genital forceps broad, its inner margin forms an extreme angular bend (Fig. 4). Female with a well developed ovipositor or egg guide extended to middle of abdominal segment 8 (Fig. 3).

Mature nymph. Outer portion of middle abdominal gills terminated in 6 to 9 filamentous processes, inner portion terminated in 3 to 6 filamentous processes (Fig. 7). Small to large posterolateral spines on abdominal segment 8, large posterolateral spines on abdominal segment 9; spines on segments 8 and 9 straight (Fig. 13–15).

The above nymphal characters are based on specimens of *H. fusca*, *H. lauta* EATON, and the possible undescribed nymphs of *H. nervulosa* EATON collected by Dr. TERRA in Portugal.



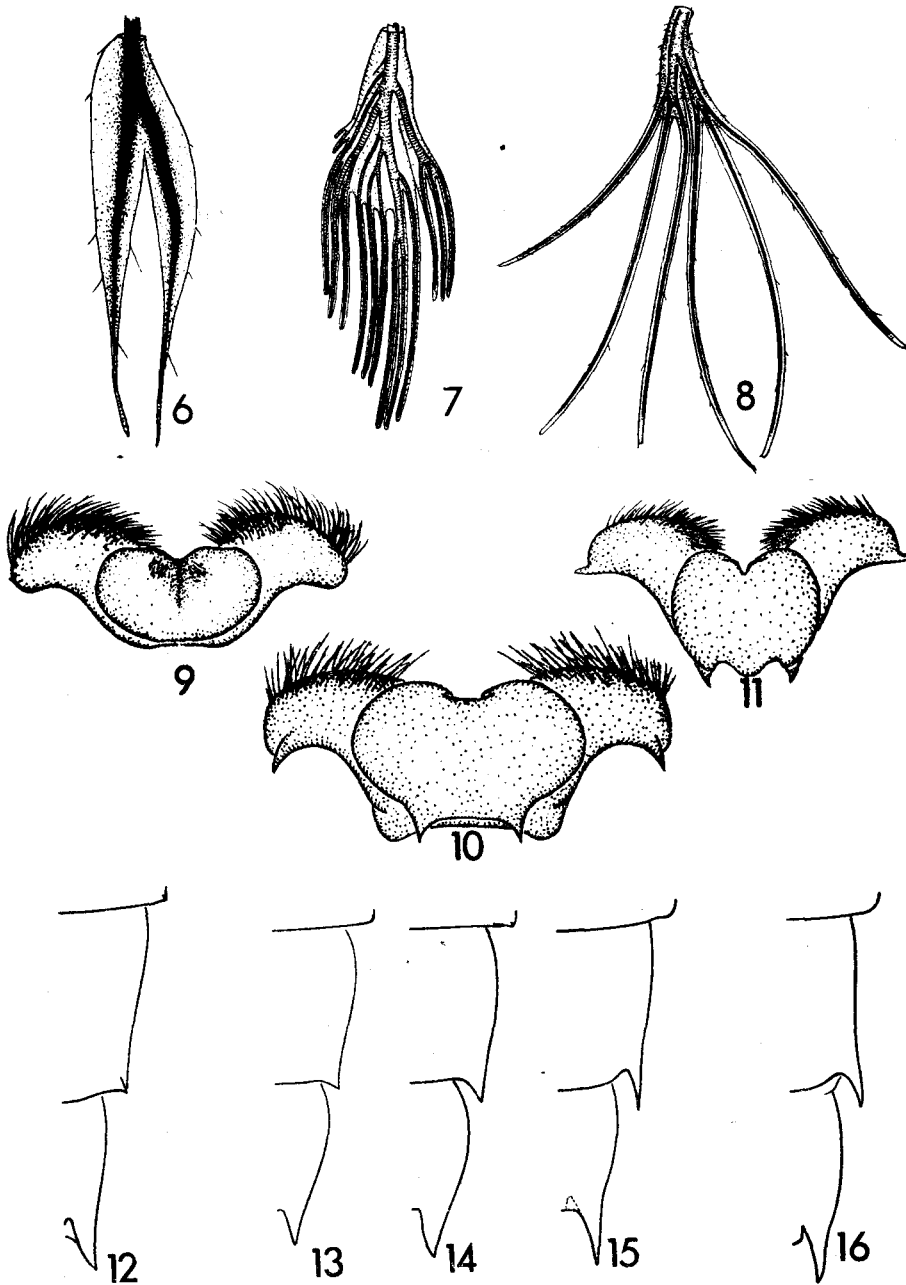
Figs. 1–5. 1. Phylogeny diagram of daughter line IA2 (PETERS, EDMUNDS, 1970) of the Leptophlebiidae, 2. *Habroleptoides modesta* (HAGEN), ventral view of male genitalia. 3–4, *Habrophlebia* (s.s.) *fusca* (CURTIS): 3. lateral view of female ovipositor or egg guide; C, ventral view of male genitalia. 5, *H. (Hesperaphlebia) vibrans* NEEDHAM, ventral view of male genitalia

Subgenus *Hesperaphlebia*, new subgenus

Fig. 4, 8, 11, 16

Habrophlebia partim ULMER, 1920:117.*Habrophlebia* TRAVER, 1935:549; BERNER, 1950:145; BURKS, 1953:94.

Imago. Length of male fore wings, 4.5–5.0 mm. Base of male genital forceps broad, its inner margin smoothly tapered toward apex of segment (Fig. 5). Female without a well developed ovipositor or egg guide.



Figs. 6–16. 6–8. Abdominal gill 4: 6, *Habroleptoides modesta*; 7, *Habrophlebia* (s.s.) *fusca*; 8, *H. (Hesperaphlebia) vibrans*. Hypopharynx: 9, *Habroleptoides modesta*; 10, *Habrophlebia* (s.s.) *fusca*; 11, *H. (Hesperaphlebia) vibrans*. 12–16. Margin of abdominal segments 8–9: 12, *Habroleptoides modesta*; 13, *Habrophlebia* (s.s.) *lauta* EATON, Czechoslovakia; 14, *H. (s.s.) fusca*, Italy; 15, *Habrophlebia* (s.s.) sp. (possibly *H. nervulosa* EATON), Portugal; 16, *H. (Hesperaphlebia) vibrans*

Mature nymph. Outer portion of middle abdominal gills terminated in 3 filamentous processes, inner portion terminated in 3 filamentous processes (Fig. 8). Large posterolateral spines on abdominal segments 8 and 9, spines curved inwardly (Fig. 16).

Etymology. *hesperos*, G., meaning west; *phlebo*, G., meaning vein.

Type species. *Habrophlebia (Hesperaphlebia) vibrans* NEEDHAM.

The phylogeny of daughter line IA2 was discussed by PETERS and EDMUNDS (1970) and PETERS and TERRA (1974). A summary of our knowledge is given in Fig. 1. This phylogeny diagram is patterned after that given by PETERS and EDMUNDS (1970).

DEMOULIN (1965) established *Oligophlebia* for two fossil species from Baltic amber and suggested the genus was most closely related to *Calliarcys*. Later DEMOULIN (1970) synonymized *Oligophlebia* with *Paraleptophlebia*. I have not included *Oligophlebia* in the phylogeny diagram, as I also believe the genus belongs to daughter line IA1 of PETERS and EDMUNDS (1970). While I have not studied the types of these fossil species and do not know if the two species represent *Paraleptophlebia*, DEMOULIN's drawings of the male holotype of *Oligophlebia calliarcys* DEMOULIN show several morphological details common only to extant members of daughter line IA1 — *Paraleptophlebia* and *Leptophlebia*. These characters are: 1) absence of a costal projection on the hind wings; 2) styliger plate of the male genitalia deeply cleft and formed into one smooth sclerite on the ventral surface; and 3) segments 2 and 3 of the male genital forceps short. The drawing of the penes of the male genitalia lacks details and cannot be compared with penes for other genera.

The morphological divergence of the imagos of *Hesperaphlebia* from *Habrophlebia* is as great as the divergence of *Habrophlebia* and *Calliarcys* from *Habroleptoides*. However, the divergence of the nymphs of *Hesperaphlebia* from *Habrophlebia* is small compared to that of *Habrophlebia* and *Calliarcys* from *Habroleptoides*. Based on generic criteria developed by EDMUNDS (1962) and PETERS and EDMUNDS (1970) *Hesperaphlebia* is herein considered a subgenus of *Habrophlebia*. Based on my zoogeographical studies of Leptophlebiidae, daughter line IA2 appears to have originated in the Cretaceous and diversified during the Late Cretaceous and Paleocene. The present distribution of daughter line IA2 in Eastern North America and Europe is apparently similar to the original distribution and compares with the Eastern North American-European landmass in the Late Cretaceous (CRACRAFT, 1974). By Middle Eocene the Eastern North American-European landmass was completely separated (CRACRAFT, 1974) and the ancestor of *Hesperaphlebia* was isolated from the ancestor of *Habrophlebia* s. s. *Hesperaphlebia* is the only living representative of daughter line IA2 in the Nearctic region.

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SUMMARY

Taxonomic status and phylogeny of Habrophlebia and Habroleptoides (Leptophlebiidae: Ephemeroptera)

Habrophlebia occurs in Europe and Eastern North America, while *Habroleptoides* is restricted to Europe. I reconfirm that *Habrophlebia* and *Habroleptoides* are separate genera based on morphological characters of both the nymphs and imagos. In Eastern North America *Habrophlebia*

occurs in mountain streams from Eastern Canada to the lowland streams of Northern Florida. I establish a new subgenus, *Hesperaphlebia*, for the North American species of *Habrophlebia* based on morphological characters of both the nymphs and imagos. The phylogeny of *Habroleptoides*, *Calliarcys*, and *Habrophlebia* is summarized. This phyletic line appears to have originated in the Cretaceous and diversified during the Late Cretaceous and Paleocene. By Middle Eocene the ancestor of *Hesperaphlebia* was completely isolated from the ancestor of *Habrophlebia* s. s.

DISCUSSION

W. P. McCAFFERTY: Bill, is the strong median process that is present on the first segment of the forceps in *Habroleptoides* considered by you to be the ancestral character state among the genera discussed? — Is this the condition found in *Calliarcys*?

W. L. PETERS: Yes, the strong median process on the forceps of *Habroleptoides* is the ancestral character state among the genera discussed. The condition is not found in *Calliarcys*; however, the proposed phylogeny is based on other characters.

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Postscript: Dr. J. FONTAINE indicated to me that the illustrations and discussions of the hypopharynx of *Habroleptoides* are wrong in PETERS and EDMUNDS (1970) and in this paper. The lateral margins of the superlingua are expanded as in *Habrophlebia* and slightly rounded at the apex (Fig. 17) — not blunt and rounded as given in PETERS and EDMUNDS (1970) and in this paper. However, this correction does not alter any taxonomic or phylogenetic conclusions in this paper. A new key to the genera belonging to daughter line I given in PETERS and TERRA (1974 in press) need not be altered. However, reference to [Fig. 198] in the second part of couplet 6 should be deleted and Fig. 17 given herein should be included. This character in the hypopharynx helps to distinguish *Habroleptoides* from *Paraleptophlebia*, and I am very grateful to Dr. FONTAINE for pointing it out to me.

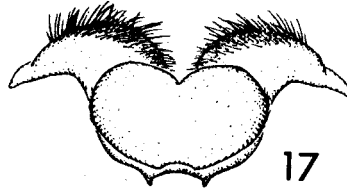


Fig. 17. Hypopharynx of *Habroleptoides* sp. (corrected)