

Systematics of the *propinquus* Group of *Baetis* Species (Ephemeroptera: Baetidae)¹

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ABSTRACT

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The *Baetis propinquus* group of species is a monophyletic grouping which includes *B. dardanus* McDunnough (= *B. elachistis* Burks, NEW SYNONYM); *B. longipalpus* NEW SPECIES; *B. ephippiatus* Traver; *B. frondalis* McDunnough (= *B. australis* Traver, NEW SYNONYM); *B. atrebatinus* Eaton; *B. tricolor* Tshernova; and *B. propinquus* (Walsh) (= *B. spinosus* McDunnough, NEW SYNONYM). The bases of nomenclatorial revisions are presented along with a key to the adult males of North America. A phylogeny for the species is theorized and a discussion of the evolution of larval and adult characters among the species and hypothetical ancestors is included.

In the course of a comprehensive morphological study of the *Baetis* larvae of North America, nomenclatorial confirmations necessitated the examination of reared adults and the comparison of adult type specimens. As a result, we herein revise certain species and describe a new species. All species involved belong to a monophyletic group within the genus which we call the "*Baetis propinquus* group." In addition, we give a key to the adult males of North American species of the group and present a phylogeny for the entire group. Larvae will be treated in detail in a future paper dealing with all species of *Baetis* in North America.

The *Baetis propinquus* group is defined by a combination of character states: Larvae have a distal lobe on the antennal scapes (Fig. 1) and an indentation on the maxillary palpi (Fig. 4, 5). Adults possess hind wings with 2 longitudinal veins and a weak or absent costal projection (Fig. 19), and have a short, apically rounded, terminal segment on the male forceps (Fig. 12-18). These character states are derived within *Baetis*; however, reductional characteristics of the adults are apparently evolutionarily convergent with some other *Baetis* species.

We include the following nominal species in the *propinquus* group: *B. dardanus* McDunnough (central and western North America), *B. longipalpus* n. sp. (central North America), *B. ephippiatus* Traver (southeastern North America), *B. atrebatinus* Eaton (Eurasian), *B. frondalis* McDunnough (eastern North America), *B. tricolor* Tshernova (Eurasian), and *B. propinquus* (Walsh) (central and western North America).

McDunnough (1925) first recognized the close relationship of *B. propinquus*, *dardanus*, *frondalis*, and *spinosus* based on general appearances and characteristic hind wings. Traver (1935) recognized a "*propinquus* group", but apparently included only *B. propinquus* and *B. dardanus*. Müller-Liebenau (1969) based her *atrebatinus* group on *B. atrebatinus* and *B. tricolor*; and these species fall within our concept of the *propinquus* group.

A taxonomic review of the *propinquus* group follows:

Baetis propinquus (Walsh)

(Fig. 4, 11, 18, 19)

Cloe vicina Walsh, 1862: 380 (not Hagen).

Cloe propinqua Walsh, 1863: 207.

Baetis propinquus (Walsh) Eaton, 1871: 121.

Baetis spinosus McDunnough, 1925: 174. NEW SYNONYM.

Examination of the male lectotype of *B. propinquus* (McDunnough 1925) from the Museum of Comparative Zoology, Harvard University, revealed that the name, *B. spinosus*, commonly and incorrectly applied to this species in the past, must be regarded as a junior synonym. The incorrect usage is a result of the male genitalia of *B. propinquus* never having been described or figured. McDunnough had not been able to examine the genitalia of the lectotype in detail since they were shriveled on the dry specimen, and therefore apparently did not recognize its relationship to his *spinosus*. We were able to restore the genitalia and examine them in detail as a slide preparation. The only other material labeled *propinquus* in the M.C.Z. (a female identified by Walsh) is actually *B. pygmaeus* (Hagen).

The male genitalia of *B. propinquus* possesses a distinct, medially directed projection of the basal enlargement of the forceps (Fig. 18), which readily distinguishes *B. propinquus* from any other North American *Baetis*. *B. tricolor* of Eurasia is very similar to *B. propinquus*.

B. propinquus larvae can be identified by the submarginal row of simple setae on the labrum. These setae are often arranged in aggregates of 2 or 3, and usually the 1st 2 setae nearest the submedial setae are paired (Fig. 11).

Baetis dardanus McDunnough

(Fig. 12)

Baetis dardanus McDunnough 1923: 41.

Baetis propinquus, Burks, 1953: 126, (not McDunnough).

Baetis elachistus Burks, 1953: 127. NEW SYNONYM.

The correct application of *B. propinquus* allows the re-establishment of *B. dardanus* as a valid species. Burks (1953) believed *B. dardanus* to be synonymous

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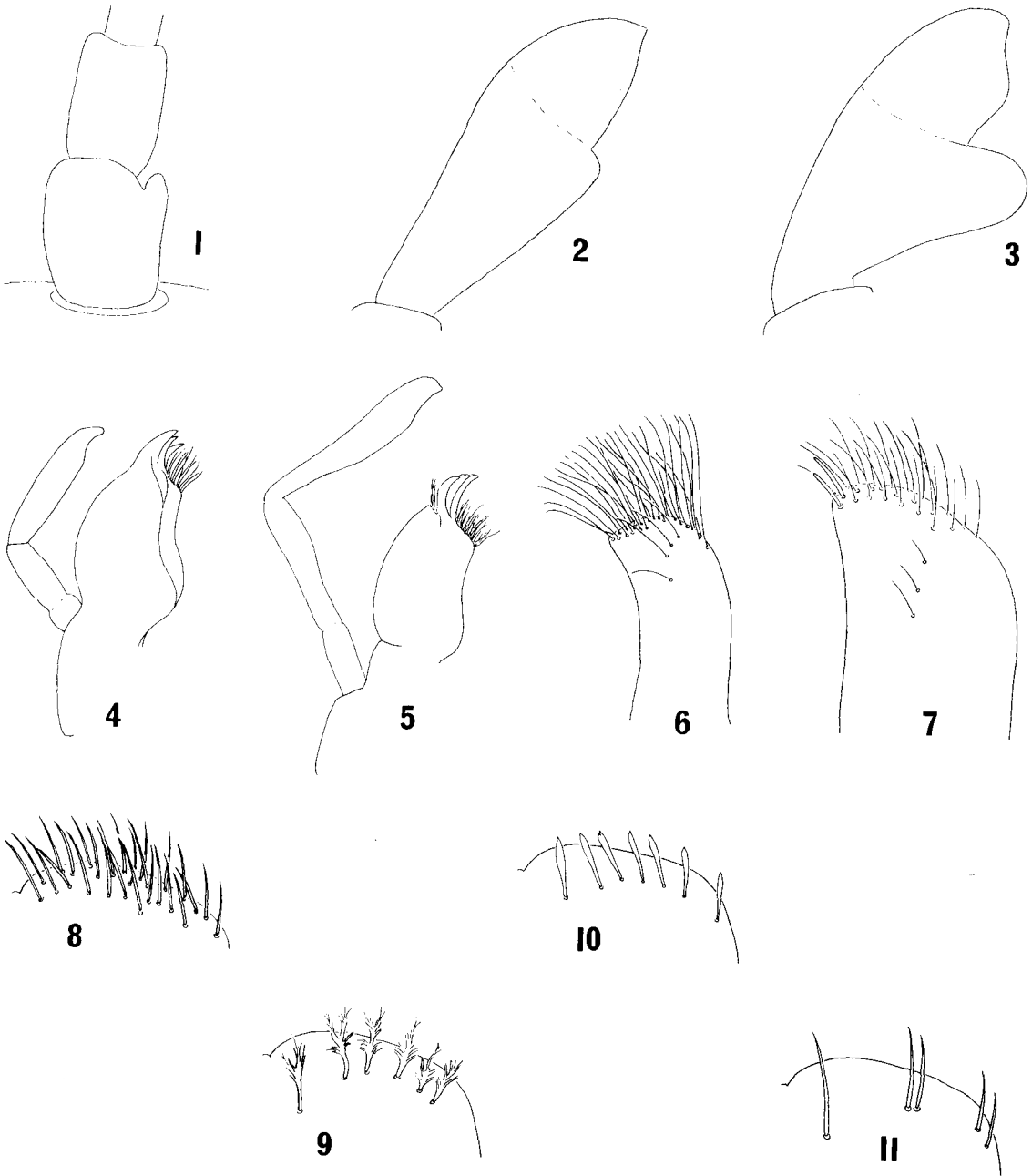


FIG. 1-11.—1. Antenna and pedicel of *B. propinquus* group. 2-3. Labial palpus. 2. *B. longipalpus*. 3. *B. ephippiatus*. 4-5. Maxilla. 4. *B. propinquus*. 5. *B. longipalpus*. 6-7. Paraglossa. 6. *B. longipalpus*. 7. *B. ephippiatus*. 8-11. Right anterior marginal area of labrum. 8. *B. longipalpus*. 9. *B. ephippiatus*. 10. *B. frondalis*. 11. *B. propinquus*.

with *B. propinquus*; however, he would not, at that time, have been able to recognize the fundamental genitalic differences for reasons discussed under *B. propinquus*, above. Burks (1953) described *B. elachistus* and distinguished it from *B. dardanus* (as *B. propinquus*) by the darker abdominal terga. Our examination of the type series of *B. elachistus* has indicated that they are structurally identical to *B. dardanus*, and we therefore place *B. elachistus* as a junior synonym of *B. dardanus*.

Males of this species are characterized by the unsclerotized, ventral posteromedian projection between the

forceps bases which is covered with short setae and which is broadly rounded to truncate in shape (Fig. 12). The larvae are unknown.

***Baetis longipalpus* n. sp.**

(Fig. 2, 5, 6, 8, 13)

Adult Male

Length of body 4-6 mm, fore wing 4-6 mm, hind wing 0.7-1.0 mm. Head brown; antennae paler; shaft of turbinate eyes darker than dorsal surface. Thorax and coxae brown; remaining leg segments and claws creamy

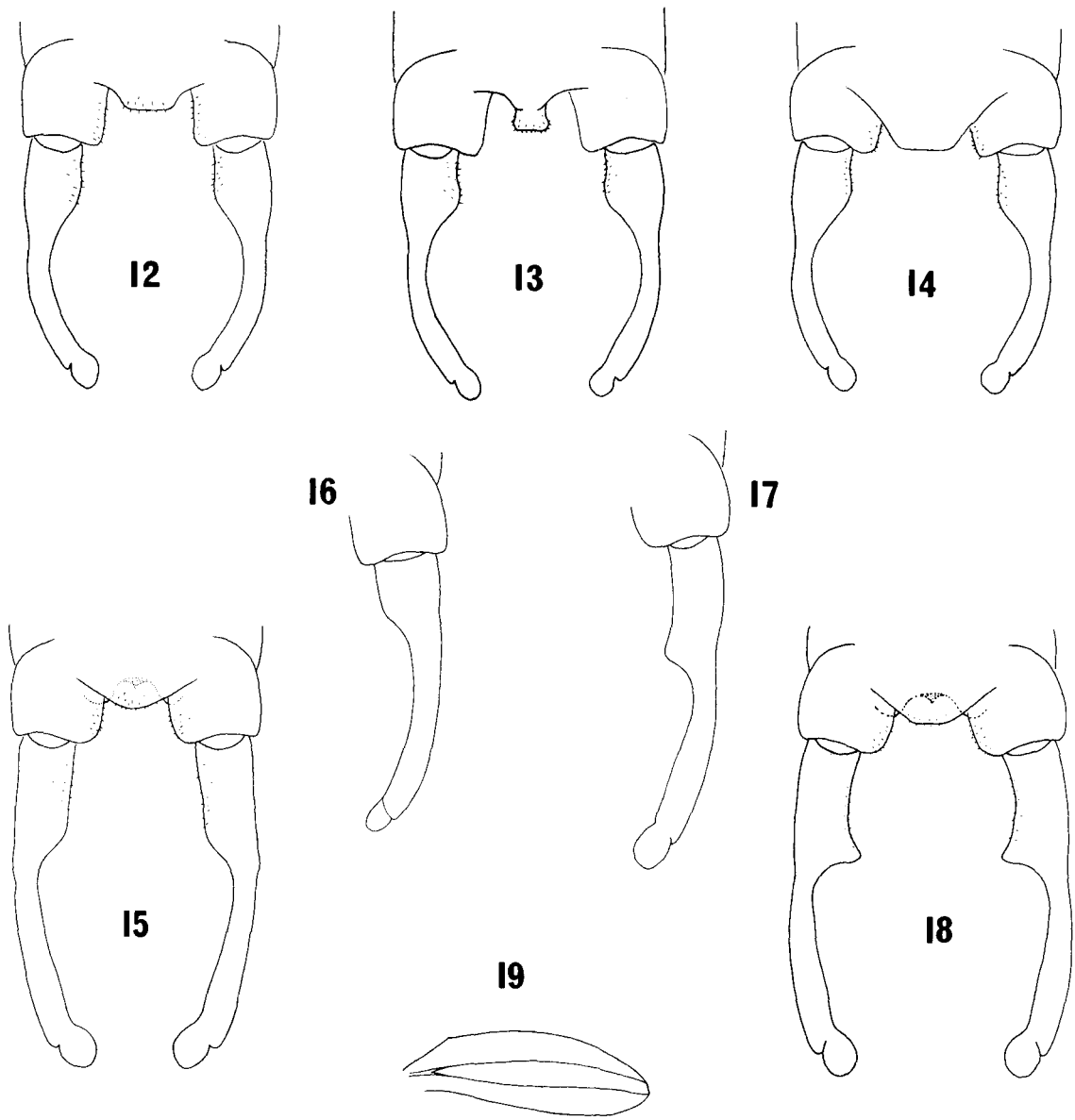


FIG. 12-19.—12-18. genitalia, ventral view. 12. *B. dardanus*. 13. *B. longipalpus*. 14. *B. ehippiatus*. 15. *B. frondalis*. 16. *B. atrebatinus*. 17. *B. frondalis*. 18. *B. propinquus*. 19. Hind wing of *B. propinquus*. (16 and 17 drawn from photographs, Müller-Liebenaу 1969: Fig. 110a and 111a).

white. Wings hyaline; marginal intercalaries absent from first interspace; hind wing with costal projection absent and with 2 longitudinal veins. Abdominal segments 2-6 translucent white; spiracles pigmented black; segments 7-10 opaque, darker brown dorsally; forceps and cerci white. Genitalia in ventral view (Fig. 13) with basal enlargement of forceps bulging, tapering apically; elongate portion very slender basally, increasing in width apically, and with distal third parallel sided; terminal segment as long as wide.

Adult Female

Length of body 4-6 mm, fore wing 4-6, hind wing 0.7-1.0 mm. Head brown; antennae paler; eyes black. Thorax and coxae brown; legs paler. Wings hyaline with veins faintly tinted with brown; fore wings with mar-

ginal intercalaries absent from 1st interspace, and paired, single, or absent in 2nd interspace; hind wing without costal projection and with 2 longitudinal veins. Abdominal terga darker than sterna, with black shading; spiracles and tracheal trunks pigmented; cerci faint translucent brown.

Larva

Length of body 4-6 mm excluding caudal filaments. Head generally pale; genae darker; antennae with scapes darkly shaded and with pedicels and flagella paler; maxillary palpi extending well beyond galea-laciniae (Fig. 5), terminal segment bulging medially; labial palpi slender, acute apically (Fig. 2). Thorax with large medial pale band on pro- and mesonotum; venter paler than dorsum; legs pale; femora with short median dark marks and

slightly darkened basally. Abdomen with dorsal maculation variable, typically with submedian pale dots and anteriorly converging pale dashes, and posterior median pale area; tergum 7 often paler than other terga; sterna paler than terga; sterna 8 and 9 often darker relative to other sterna; gills on segments 1-7, rounded posteriorly; caudal filaments pale with a narrow dark band slightly beyond middle, median terminal filament 0.5-0.8 length of cerci.

Material Examined

HOLOTYPE, ♂.—Indiana: Posey Co. Wabash R. at Old Dam, New Harmony, VIII-12-1974, Provonsha, Dersch. Specimen in alcohol. Deposited in Entomological Research Collection, Purdue University.

PARATYPES.—Same collecting data as for holotype: 13♂, 1♀, in alcohol, wings and genitalia and 4 larvae on slides deposited in Ent. Res. Coll., P. U.; 3♂ and 2 larvae in alcohol deposited in U.S. National Museum of Natural History, Washington, D. C.

Additional Material—Larvae and adults, IN: Martin Co., E. Fork White R. at Hindostan Falls Public Fishing Site, VI-20-1974, VII-17-1975, Provonsha, et al.; Posey Co., Wabash R. at Old Dam, New Harmony, VIII-12-1975, VII-20-1977, Provonsha, McCafferty, et al; WI: Richland Co., Wisconsin R., VIII-22-1975, Bergman (reared).

The adult males of *B. longipalpus* are characterized by the unique shape of the ventral, posteromedian projection between the forceps bases (Fig. 13). In closely related species this projection is either broadly rounded or truncate as in *B. dardanus* (Fig. 12), or sclerotized and devoid of setae as in *B. ephippiatus* (Fig. 14). The larvae are also unique with respect to the unusual size of the maxillary palpi (Fig. 5), and the shape of the labial palpi (Fig. 2). *B. longipalpus* may be misidentified as *B. propinquus* in the keys or by the superficial descriptions of Burks (1953) and Traver (1935).

This species has been collected only in riffle areas of large rivers (Indiana and Wisconsin). It appears to be univoltine (Bergman and Hilsenhoff 1978, as *propinquus*) with emergence occurring primarily in Aug.

Baetis frondalis McDunnough

(Fig. 10, 15)

Baetis frondalis McDunnough 1925: 173.

Baetis australis Traver, 1932: 230. NEW SYNONYM.

Traver (1932 and 1935) described *B. australis* and acknowledged its close affinities to *B. frondalis*. Her recognition of 2 species was based on *B. australis* being slightly more slender, its basal abdominal terga having more pale areas, and the excavation between the bases of the forceps being less deeply excavated. On the basis of our examinations of the type series of *B. frondalis*, the holotype slide mount of the male genitalia, and numerous larval and adult material from scattered localities throughout its range in eastern North America, we have found the differences cited by Traver to be inconsistent. We therefore place *B. australis* as a junior synonym of *B. frondalis*.

B. frondalis is characterized by long, cylindrical, basal forceps enlargements in adult males (Fig. 15). This structure differs from the homologous structure in *B.*

propinquus (Fig. 18) in having, from a ventral perspective, a simple quadrate shape rather than an apical medially directed acute projection. *B. frondalis* is most similar to the Eurasian *B. atrebatinus* as larvae and to the Eurasian *B. tricolor* as adults. Its phyletic relationship to these latter species will be discussed below.

Key to the North American Adult Males of the *Baetis propinquus* Group

- Ventral posteromedian projection between forceps bases covered with setae (Figs. 12, 13, 15, 18) 2
Ventral posteromedian projection bare, often well sclerotized and pigmented (Fig. 14) *B. ephippiatus*
- Ventral posteromedian projection between forceps bases broadly rounded to broadly truncate (Fig. 12, 15, 18); abdominal segments 2-6 pale translucent or opaque brown 3
Ventral projection slightly constricted basally (Fig. 13); abdominal segments 2-6 pale translucent *B. longipalpus*
- Basal enlargement of forceps short and robust, about as long as wide (Fig. 12); no chitinous internal spine between forceps bases *B. dardanus*
Basal enlargement of forceps slender, more than twice as long as wide (Figs. 15, 18); chitinous internal spine usually visible 4
- Basal enlargement of forceps simple, subquadrate from a ventral perspective (Fig. 15); abdominal segments 2-6 usually opaque brown *B. frondalis*
Basal enlargement of forceps with distal, medially directed, acute projection (Fig. 18); abdominal segments 2-6 usually pale translucent *B. propinquus*

Phylogeny

The inferred phylogeny of the *propinquus* group species is represented in Fig. 20. Morphological character sources for ascertaining relationships include the adult male genitalia and larval mouthparts. Hypothetical common ancestors are denoted by upper case letters, and character evolution in lineages are depicted on the diagram by reference to corresponding morphological figures.

In addition to the derived characteristics (discussed in the introduction) which distinguish this group as monophyletic within *Baetis*, the earliest Ancestor (A) within the group can be defined in terms of characters which subsequently evolved within the *propinquus* group. These ancestral character states of the hypothetical ancestor have been deduced as follows: In the larval stage, the labrum possessed a row of simple, narrow, submarginal setae in addition to a pair of submedian, simple setae (not figured); the maxillary palpi extended slightly beyond the galea-laciniae (as in Fig. 4); the median lobe of the 2nd segment of the labial palpi was moderately developed in size (as in Fig. 2, although possibly slightly broader); and the paraglossae were relatively slender (as in Fig. 6). In the adult males, the genitalia (as in Fig. 12) possessed forceps with the basal enlargement short and robust and approximately as long as wide; the ventral posteromedian projection between the forceps bases was setose and broadly rounded to broadly truncate; and there was no internal chitinous spine present between the forceps bases.

All the above adult ancestral states are present in *B. dardanus*. Also, since *B. dardanus* larvae are unknown,

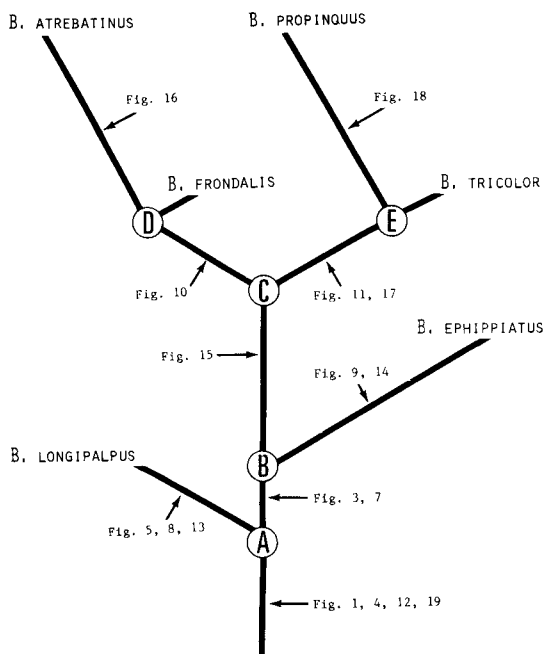


FIG. 20.—Phylogeny of the *propinquus* group of *Baetis* species (*B. dardanus* not included).

it cannot be exactly placed within the phylogeny at this time (see further discussion below).

B. longipalpus represents a lineage independently evolved from ancestor A as demonstrated by the lack of synapomorphy with other species and at least three exclusive character shifts: (1) the development of numerous labral setae obscuring the ordered row of submarginal setae (Fig. 8); (2) the distinct increase in size of the maxillary palpi (Fig. 5); and (3) the basal constriction of the ventral posteromedian projection of the male genitalia (Fig. 13).

All other species and their common Ancestor (B) are characterized by striking developments in the larval labium. The median lobe of the second segment of the labial palpi is approximately as large as segment 3 (as in Fig. 3), a condition unique within the genus *Baetis*. In addition, the paraglossae are expanded laterally resulting in a uniquely robust structure (as in Fig. 7).

B. ephippiatus represents an independent lineage originating from Ancestor B. Its larvae developed branched submarginal setae on the labrum (Fig. 9), and the ventral posteromedian projection of the adult male genitalia lost all setae and became well sclerotized and pigmented (Fig. 14). These character states are unique to this species.

In a second lineage originating from Ancestor B extensive changes in the male genitalia occurred (represented by Ancestor C and its daughter lineages). A unique, chitinized, internal spine arose (seen from a ventral perspective) between the forceps bases. There was also a general elongation of the forceps, particularly of the basal enlargements (as in Fig. 15 and 18). This latter condition has apparently been subject to convergence within *Baetis*, although within the *propinquus* group it was singly derived.

As mentioned earlier, *B. dardanus*, whose larvae remain unknown, cannot be accurately placed within the phylogeny. However, it can be excluded as a possible descendant of Ancestor C since it possesses the more ancestral type of genitalia (Fig. 12).

Ancestor C gave rise to 2 lineages. In that leading to Ancestor D, the submarginal labral setae became apically expanded and spatulate (Fig. 10), a character state found only in *B. frondalis* and *B. atrebatinus*.

Ancestor D gave rise to the sibling species, *B. frondalis* and *B. atrebatinus*. *B. frondalis* changed little from Ancestor D, being identical to it in terms of the phyletic characters under discussion. Although we have not seen specimens of *B. atrebatinus*, the basal enlargement of its forceps (Müller-Liebenau 1969) (Fig. 16) appears to represent a condition superficially similar to the more ancestral state. Besides the exclusively derived states of the labral setae and genitalic spine which would clearly place the species as discussed above, this conclusion that the forceps shape is secondarily derived is supported by the fact that the slender elongate portion of the forceps of *B. atrebatinus* is not constricted basally as in the more ancestral species. In addition, the terminal segment of the forceps is dome-shaped rather than bulbous.

Ancestor E also arose from Ancestor C, and the labral setae became reduced in number and arranged in small aggregates of 2 or 3, as seen in *B. tricolor* and *B. propinquus* (Fig. 11). Similar conditions are common in some other *Baetis* but within the *propinquus* group this condition apparently represents an independent derivation. Also in Ancestor E a slight protrusion of the apicomedial corner of the enlarged basal portion of the forceps developed (as in Fig. 17).

Ancestor E gave rise to the sibling species, *B. tricolor* and *B. propinquus*. *B. tricolor* represents a lineage that has changed little, being similar to Ancestor E in terms of the phyletic characters under discussion. In *B. propinquus*, on the other hand, the apicomedial corner of the enlarged basal portion of the forceps became more amplified and acute (Fig. 18), thus representing the most advanced state in the phenocline of this character (follow Fig. 12–14 to 15 to 17 to 18).

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