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The Larvae of Eastern North American *Eurylophella* Tiensuu (Ephemeroptera: Ephemerellidae)

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ABSTRACT

Fourteen species of *Eurylophella* are recognized in eastern North America based primarily on morphology of full-grown larvae and allozyme frequencies in imagos. *Eurylophella temporalis* (McDunnough) and *E. verisimilis* (McDunnough) are redefined and two species that had previously been synonymized, *E. bicoloroides* (McDunnough) and *E. doris* (Traver), are reinstated. Three species are described as new: *E. enoensis* Funk, *E. poconoensis* Funk, and *E. macdunnoughi* Funk. Four species groups are defined on the basis of morphological characters in the larvae: the *temporalis* group, including *E. doris* (Traver), *E. poconoensis* Funk, *E. prudentalis* (McD.) and *E. temporalis* (McD.); the *lutulenta* group, including *E. aestiva* (McD.), *E. enoensis* Funk and *E. lutulenta* (Clemens); the *funeralis* group, including only *E. funeralis* (McD.); the *bicolor* group, including *E. bicolor* (Clemens), *E. bicoloroides* (McD.), *E. macdunnoughi* Funk, *E. minimella* (McD.) and *E. verisimilis* (McD.). *Eurylophella coxalis* (McD.), whose larva is unknown, is unassigned to group. A morphological key is provided for full-grown larvae.

INTRODUCTION

Eurylophella species are common and conspicuous members of the mayfly fauna in streams, rivers, and some lakes of eastern North America. As a group, the species of *Eurylophella* are quite uniform morphologically and male imagos and larvae are easily recognized at the generic level. However, identification of species has generally been difficult for larvae, and is often impossible for adults (Allen and Edmunds 1963, McDunnough 1931a). This difficulty results from the combination of two factors: morphological differences among species are often quite subtle, and a large amount of intraspecific variation exists. Allen (1980) recognized 15 species of *Eurylophella* worldwide, eleven of which occur in eastern North America. Berner (1984) synonymized two of these, *E. doris* (Traver 1934) and *E. trilineata* (Berner 1946), with *E. temporalis* (McD.), leaving a total of nine eastern species.

Funk et al. (1988) reported the results of an electrophoretic survey of eastern North American species indicating the presence of at least fifteen eastern species, including some that appeared to be morphologically cryptic. The results of that study have enabled us to more easily distinguish intraspecific from interspecific variation in morphology of eastern North American species of *Eurylophella*. Based on additional electrophoretic data and a detailed morphological study of larvae, we here recognize fourteen eastern species, including two that had been synonymized (*E. bicoloroides* McDunnough and *E. doris* Traver), and three that are de-

scribed as new (*E. enoensis*, *E. macdunnoughi*, and *E. poconoensis*).

We have not found reliable morphological characters to separate adults of most species, and therefore provide no key. However, descriptions of male and female imagos are provided for new species. Full-grown larvae of most species can be distinguished morphologically with the key provided.

The larva of *E. coxalis* (McDunnough, 1926) is presently unknown. Larvae tentatively assigned to this species by McDunnough (1931a) are here considered *E. enoensis* Funk.

The only known western North American species of *Eurylophella*, *lodi* Mayo (1952), was not included in the present study because our efforts to aquire larval material for study were largely unsuccessful (we have seen only a single female larva).

McCafferty (1978) suggested that characters used in his earlier phylogenetic study (McCafferty 1977) show that *Dannella bartoni* (Allen 1977) should be included in *Eurylophella*. Allen (1980) provided evidence to the contrary, and erected a new subgenus, *Dannella* (*Dentatella*), to accommodate *bartoni*. We feel the placement of *bartoni* will remain tentative until the adult is known. For the present treatment, we follow Allen (1980) in excluding *D. bartoni* from the *Eurylophella*. However, since existing generic keys will not clearly place *bartoni* in either *Eurylophella* or *Dannella*, we include a couplet (number 1) in our morphological key to accommodate this distinctive species.

METHODS

Electrophoretic work

Initially, mayfly larvae were collected from 40 localities in eastern North America [see Table 1 and Figure 1 in Funk et al. (1988)]. These original collections have been supplemented with additional material from Maine, Pennsylvania, Virginia, West Virginia and Ohio (see species descriptions for locality data). Larvae were returned alive to our laboratory and reared to subimagos in flow-through polypropylene trays (23 x 45 x 22 cm deep) which were checked several times per day during the emergence period. Subimagos were then reared to imagos in small (1 L) freezer containers with screening on top. Reared adults were stored individually at –80°C until electrophoresed. All associated larval exuviae were preserved in 80% ETOH and referenced individually (where possible) to frozen adults. Genitalia were removed from many of the males and preserved with exuviae. When two or more individuals emerged together, exuviae were referenced by groups. Where mixtures of species were present, only adults individually associated with exuviae were electrophoresed.

Allozymes were separated by horizontal starch gel electrophoresis using methods described in Sweeney et al. (1986, 1987). Thirty-four enzyme systems were screened. Of these, 24 were scorable in at least one species, yielding data on 32 presumptive gene loci [see Table 5 in Sweeney et al. (1987) for full enzyme names, enzyme commission numbers, and buffer systems used].

Representative larval exuviae from most site/species combinations (at least two males and two females from each) were mounted on slides in neutral Canada balsam for detailed morphological study. These were photographed for the illustrations provided herein. Most of the measurements given in the descriptions and graphs (Figs. 73–76) were taken from these slide-mounted specimens.

Quantitative morphological characters

Body length (=size in Figure 74a) is measured from the anterior margin of the frons of the hypognathous head to the tip of segment 10, exclusive of tails. All measurements given in the descriptions and figures are in millimeters.

Several other characters useful for distinguishing *Eurylophella* species are quantifiable. With one exception (FWL1), these are abdominal characters. We refer to these characters with abbreviations consisting of two or three capital letters followed by a numerical subscript (e.g., "SMT_7"). The letters are an abbreviated description of the character. The subscripts refer to the segment number or numbers for abdominal characters, or leg number in the case of FWL_1. The methods used for the measurement of these characters are illustrated in Figure 1. All measurements are of sclerotized areas only, unsclerotized cuticle between scerites is ignored.

FWL1 ("femur width to length", fore leg) is a measure of the width of the fore femur at its widest point expressed as a proportion to its length. Measurement is made in dorsal view.

SMT ("submedian tubercle") is a measure of the distance between the submedian tubercles for a particular segment as a proportion of the length of the tergite. For example, SMT_2 is equal to the distance between tubercles on abdominal segment 2 divided by the length of tergite 2 measured at midline (a/b in Figure 1). SMT is measured similarly for other segments; for example, SMT_7 = e/f in Fig. 1. The distance between tubercles on a particular segment is measured center to center at the base of each tubercle (see Fig. 1). When tubercles are directed straight back, this is equivalent to, and more easily measured as, the distance between apices. However, in some species the tubercles on the more anterior segments often diverge from the bases to the apices (e.g., *E. temporalis* in Fig. 60); for these individuals measurement must be made from center to center at the bases of the tubercles, and it is good practice to measure this way for all species.

ITD ("inter-tubercle distance") is the ratio of the distance between tubercles for two segments. For example, $ITD_{2:7}$ is the ratio of the distance between tubercles on segment 2 to that between tubercles on segment 7 (a/e in Fig. 1).

TL ("tubercle length") is a measure of the length of the submedian tubercles as a proportion of the length of the tergite they arise from. For example, TL_7 is equal to the length of the submedian tubercles on segment 7 divided by the length of the tergite at midline (measured in dorsal view). It practice this parameter is best determined by measuring the distance from the anterior margin of tergite 7 to the tip of a tubercle (dimension g; Figure 1), then from the anterior to the posterior margin at midline for that tergite (dimension f; Figure 1). TL_7 is then calculated as (g–f)/f.

MLT ("median length of tergite") is a ratio of the lengths of two tergites, measured at their midlines. For example, $MLT_{2:7}$ is the ratio of the length of tergite 2 to that of tergite 7 (b/f in Fig. 1).

PLP ("posterolateral projection") is the length of a posterolateral projection as a proportion of the length of the tergite exclusive of that projection. This is determined for segment 2, for example, by measuring from the anterolateral margin of the tergite to the posterior tip of the projection (dimension c in Fig. 1) and from the anterolateral margin of the tergite to the posterior margin at the base of the projection (dimension d in Fig. 1). PLP_2 is then calculated as (c–d)/d. Special care must be used for segments 2 and 3 because the posterolateral projections on these segments are often quite small and minor errors in their measure will result in

rather major errors in the PLP values thus derived. These measurements are best made on slide-mounted exuviae under a compound microscope. The measures illustrated in Fig. 1 are of the tergal sclerite only; unsclerotized cuticle must be ignored.

During the course of our study, data collected for the above parameters were plotted by species to facilitate viewing (see Figs. 73–77). Individuals of known genetic composition (i.e., larval vouchers whose imagos have been electrophoresed) are represented in these graphs by open circles. Specimens of unknown genetic composition are represented by horizontal lines. The latter were chosen (mostly from material borrowed from other collections) either because they were from geographically marginal localities or they represented outliers for one or more parameters. Some of these may eventually prove to have been misidentified or represent undescribed species, but graphically, they help to illustrate possible extremes in values.

Listings of material examined are partitioned into five groups. "Type series" is self explanatory. "Larval exuviae vouchers from electrophoretic survey" includes larval exuviae whose imagos were electrophoresed: only the total number of specimens and a list of states and provinces represented are given here. Detailed locality data for these are presented in Funk et al. (1988). For some species we collected and electrophoresed additional material subsequent to that listed in Funk et al. (1988); in all cases, locality data for these are included under "Slide mounts of larval exuviae" (see below). "Additional reared material" includes specimens reared for electrophoresis, but whose imagos have not been electrophoresed. Larval exuviae are in alcohol and associated imagos are currently frozen. "Slide mounts of larval exuviae" includes balsam-mounted exuviae used for illustrations and measurements. "Other larval material" lists preserved material examined from localities not included under the other headings.

The following abbreviations are used for sex and stage of specimens: M—male imago (and/or male exuviae, as noted); F—female imago (and/or female exuviae, as noted); L—Larva.

The most frequently reported collectors are abbreviated as follows: DHF—D.H. Funk; DIR—D.I. Rebuck; ACG—A.C. Graham; BWS—B.W. Sweeney; JWP—J.W. Pierson; RLV—R.L. Vannote; PJD—P.J. Dodds; CED—C.E. Dunn; MKB—M.K. Butcher; DTM—D.T. Mulvey; CFB—C.F. Burgoon; LSD—L.S. Dryden; WLH—W.L. Hendrix; MBG—M.B. Griffith; SKB—S.K. Burian; RBS—R.B. Shamblin; JAG—J.A. Gustin; KNPC—Kentuck Nature Preserve Commission.

Type specimens of new species have been deposited at the Academy of Natural Sciences of Philadelphia (ANSP). All other preserved material is being curated at the Stroud Water Research Center (SWRC) of the Academy of Natural Sciences of Philadelphia unless otherwise designated. Other material examined resides in the following institutions:

CAS	California Academy of Sciences
CNC	Canadian National Collection
CUIC	Cornell University
FAMU	Florida A&M University
INHS	Illinois Natural History Survey
PERC	Purdue University
UAAM	University of Arkansas
UMDE	University of Maine, Orono
UMRM	University of Missouri, Columbia
WIRC	University of Wisconsin, Madison

SYSTEMATIC ACCOUNTS AND KEYS

Genus **EURYLOPHELLA** Tiensuu

Ephemerella bicolor-lutulenta group McDunnough 1930: 55; Traver 1932: 143.
Ephemerella bicolor group McDunnough 1931a: 30; Traver 1935: 564; Berner 1950: 153; Burks 1953: 72.
?*Melanameletus* Tiensuu 1935: 15.
Eurylophella Tiensuu 1935: 20 (as genus); Edmunds and Traver 1954: 238 (as subgenus) (?=*Melanameletus*); Demoulin 1958: 10; Edmunds 1959: 546; Allen and Edmunds 1963: 597; Allen 1980: 84 (as genus); type *karelica* Tiensuu by monotypy.

General Features of *Eurylophella*

Eurylophella can be distinguished from all other ephemerellid genera in the larval stage by the following combination of characters: (1) lamellate tracheal gills on abdominal segments 4–7 (Fig. 2), with the gill on segment 4 semi-operculate, covering most of gills 5–7; (2) gills on segment 1 consist of a single filament, and gills absent from segments 2 and 3; (3) abdominal segment 9 elongate, at least 20% longer than segment 8 at midline; (4) tarsal claws with denticles; (5) maxillary palpi absent[1]; and (6) paired submedian tubercles on segments 1–10 (usually quite small on 8–10, sometimes completely reduced on one or more of these segments), with those on 1–4 blunt and those on 5–10 sharp (Figs. 8, 11). Tubercles on segment 4 are often transitional with regard to sharpness but are rarely as sharp as those on segments 5–7.

Adult male *Eurylophella* can be distinguished from other ephemerellids by the following combination of characters: (1) cerci subequal to terminal filament in length; (2) terminal segment of forceps slightly less than twice as long as broad; (3) second segment of forceps stout; and (4) penes united, broad at base and narrow at apex, and without subapical projections or spines. Adult females cannot be identified to genus except by association.

The species of *Eurylophella* are quite uniform morphologically and specific identifications are difficult with existing keys (Allen and Edmunds 1963, McDunnough 1931a). The following discussion is therefore limited to characters of taxonomic value.

Specific characters in larvae

The length of full-grown larvae of *Eurylophella* species ranges from 6–12 mm. Although variable, body length is useful for the identification of some species. All figures given herein for body length are exclusive of tails.

Occipital tubercles on the head of males range from being almost nonexistent (Fig. 44) to large (Fig. 19), and on females from small (Fig. 35) to large (Fig. 62). The size of occipital tubercles is quite consistent within a species (except for *E. poconoensis*) and is of considerable taxonomic value.

The shape and vestiture of the legs is distinctive for some species. The ratio of

[1]Edmunds' (1959) statement that the type species, *Eurylophella karelica* Tiensuu, has maxillary palpi was erroneous (Edmunds, personal correspondence). Material from Poland provided to us by M. Keffermüller, as well as her correspondence to us and her published description of the larva (Keffermüller 1960), confirms the absence of maxillary palpi in *karelica*.

the width to the length of the fore femur varies predictably (Fig. 74b; see Fig. 1 for method of measurement). Differences in the shape and length of spines on the hind margin of the fore femur are useful only for separating *E. bicoloroides* from *E. macdunnoughi* (Figs. 70–71).

Conspicuous, paired, submedian tubercles are always present on abdominal segments 1–7 and, although considerable intraspecific variation exists, differences in the shape and size of these structures are important taxonomically (e.g., Fig 72a–m). The distance between paired tubercles relative to the length of the tergite they arise from (SMT; see Fig. 1) and to the distance between tubercles on other segments (ITD; same figure) is particularly important for distinguishing species groups.

The relative length of the submedian tubercles is sometimes helpful in identifications, but is difficult to quantify for segments 1–4 and 8–10. For segments 5–7 this character can be quantified (e.g., TL_7; see Fig. 1) and we have found this measure for segment 7 to be useful for the separation of some species.

Submedian tubercles are usually present on tergites 8–10, but these are considerably smaller than those on anterior segments, and are sometimes missing completely. Their degree of development is fairly consistent within species, but due to their variability and the difficulty of quantifying their size, they are generally of little practical taxonomic value.

The length of abdominal segments 5 to 7 is reduced in all *Eurylophella*. However, this reduction varies somewhat between species groups: in the *temporalis* group, segments 5 to 7 are slightly longer, and the anterior segments are slightly shorter than in the other groups. A good indicator for this difference the parameter $MLT_{2:7}$ (equal to b/f in Fig. 1).

The vestiture of the submedian tubercles is sometimes distinctive, but exhibits considerable intraspecific variation. Generally two types of setae may be present on the tubercles (as on the rest of the tergal surface): fine, acute hair-like setae, and coarse, flattened scale-like setae which may be terminally rounded or subacute. The coarser vestiture of the tubercles is sometimes visible under magnifications typical of the stereomicroscope, but the finer setae can only be observed on slide-mounted exuviae under a compound microsope. The presence or absence of either type is somewhat specific and is described for each species. However, these characters are not used in the key.

Abdominal segments 2–9 have variously developed posterolateral projections. The relative size of these is important taxonomically for segments 2, 3 and 9 (as indicated by the paramenters PLP_2, PLP_3, and PLP_9, respectively). Measurements on segments 2 and 3 must be made very carefully—even small errors can have a large effect on PLP values (see Methods section). The shape of the posterolateral projections on segment 9 is distinctive for some species.

In ephemerellids the gills on segments 3 or 4 to 7 are bilamellate, with the ventral lamella further subdivided. In the genera we have examined (*Ephemerella, Drunella, Serratella, Caudatella, Attenella, Dannella, Eurylophella,* and *Timpanoga*) the ventral lamella is laterally bifurcate, and each side is further subdivided dorsally and ventrally. In some species of *Eurylophella*, the dorsal subdivisions are absent or reduced (best seen in side view of gill 4). This character is consistent within species, and we have grouped them into three categories on this basis (see Fig. 2). Note that only the lateral fork of the ventral lamella is illustrated in Figure 2.

Larval coloration is quite variable in most species and, with few exceptions, is of little or no taxonomic value. Colors range from plain brown to gray, often with pale speckling, and sometimes with extensive pale or dark areas giving a general

mottled appearance. A distinct pale median stripe bordered by the submedian tubercles on the abdomen may or may not be present. Although some degree of correlation exists between certain dorsal color patterns and species, it is generally best to ignore these patterns when attempting to identify *Eurylophella* larvae. For example, at least eight species are polymorphic for a pale, dorsal median stripe, so sorting specimens on this basis would be quite misleading. Ventrally, the abdomen may have paired submedian dots, oblique paramedian dashes, and longitudinal sublateral maculae. These markings may be present or absent in various combinations in most species. There are some general trends which can be helpful in sorting species groups (see discussions under respective groups), but these must be used cautiously. Members of the *bicolor* group always have black- or dark brown-tipped posterolateral projections which are most noticeable on segments 4–9 (as in Fig. 38). This condition is never found in members of the *temporalis* or *funeralis* groups, but may be found in certain members of the *lutulenta* group.

Phenology and geographic distribution

Seasonality and adult emergence periods are distinctive for all species. Figure 78 illustrates the sequence of emergence for eastern North American species of *Eurylophella* for approximately 40° north latitude, elevation ~100 m. The absolute times will shift with latitude and altitude, but the sequence remains consistent. Often as many as seven species can be found in one stream reach, and in such cases seasonality can be important evidence for the identification of specimens, especially small larvae.

Eurylophella larvae are usually collected in areas of low current velocity in streams, particularly along the margins, with submerged root masses, woody snags and other organic debris often yielding large numbers of specimens. When present in lakes, *Eurylophella* is most often found in the shallow areas near the margins, on rocks or woody debris, especially in areas that receive at least some wave activity.

In medium-sized (4th to 6th order) streams in eastern North America it is not unusual to find as many as seven *Eurylophella* species coexisting, often with no discernable difference in habitat preference among species. For example, *E. verisimilis* is commonly found with any or all of the following: *E. aestiva, E. prudentalis, E. funeralis, E. bicoloroides, E. macdunnoughi, E. bicolor,* and *E. minimella* in the northeast U.S. and adjacent Canada. Large samples from various times of the year are often needed to adequately assess the species richness of *Eurylophella* at a particular site.

Geographic ranges given in this paper should be regarded as conservative and identifications should not be based solely thereon. Because of the historic difficulty of accurate species identification in this genus, many published records are unreliable. We have incorporated some reports from the literature in our distributional data, including the following: Allen and Edmunds (1963), Berner (1977), Berner and Pescador (1988), Burian and Gibbs (1991), Burks (1953), Daggy (1941), Daniels and Morse (1992), Edmunds et al. (1976), Funk et al. (1988), Hall (1985), Harper and Harper (1981), Harper (1989), Hilsenhoff (1981), Howell (1941), Kondratieff and Harris (1986), Kondratieff and Voshell (1983), Lager et al. (1982), Lauzon and Harper (1988), Lyman (1955), McCafferty and Provonsha (1978), McDunnough (1931a), Neave (1934), Peterson (1989), Peterson et al. (1985), Simpson et al. (1985), Smock (1988), Smock and Roeding (1986), Sprules (1947), Sweeney and Vannote (1987), Traver (1932, 1934, 1935, 1937), Whiting (1992), Wright and Berner

(1949). We believe our range estimates to be reasonably accurate in the area east of the Appalachian mountains, but our knowledge of species distributions west of the Appalachians is less complete.

Determination of species boundaries

We base our concept of species primarily on genetic evidence for reproductive isolation deduced from electrophoretic data, with support from morphological observations of larval exuviae directly associated with the adults examined electrophoretically. In the absence of distinct morphological differences, we considered two populations worthy of specific status if either of the following criteria were met: 1) one or more fixed allelic differences were observed among individuals occurring in the same stream reach (i.e., sympatry in the narrowest sense) in two or more separate drainage basins, or 2) two groups of three or more populations exhibited two or more fixed allelic differences from each other (the two groups occurring in either parapatry or allopatry). These criteria are similar to but slightly more conservative than those suggested by Adams et al. (1987) and Richardson et al. (1986). Two pairs of species from our earlier study (Funk et al. 1988) satisfied the first criterion: *E. verisimilis-A* and *E. verisimilis-B*, herein referred to as *E. bicoloroides* and *E. macdunnoughi*, respectively; *E. temporalis-A* and *E. temporalis-C*, herein *E. poconoensis* and *E. temporalis*, respectively. One pair satisfied the second criterion: *E. temporalis-C* and *E. temporalis-B*, herein *E. temporalis* and *E. doris*, respectively. Two other pairs failed to meet either criterion: *E. verisimilis-B* and *E. verisimilis-C*, both of which we now include in *E. macdunnoughi*; *E. aestiva* and *E. aestiva-A*, together considered *E. aestiva*. Further information is provided in the discussion section for these species.

Eurylophella Species Groups

Morphological differences among *Eurylophella* species are generally relative, with structures differing in size or shape (as opposed to presence or absence). As a result phylogenetic relationships among species remain rather obscure. Both McDunnough (1931a) and Allen and Edmunds (1963) made some inferences based on overall similarities, but neither addressed the question of relationships among species directly or comprehensively.

Funk et al. (1988) presented a phenogram derived from allozyme data. However, this phenogram cannot be interpreted as an accurate representation of phylogeny, especially for the larger groupings, unless we assume constant evolutionary rates and the lack of convergences [a very risky proposition; see Richardson et al. (1986) for discussion]. We have reexamined our allozyme data, including several new populations, using Hennigian techniques (using loci as characters), with both *Dannella simplex* and *Attenella attenuata* as outgroups (unpublished). Unfortunately, the outgroups shared almost no alleles with any of the ingroup, making the determination of ancestral states impossible for most loci. Although allozyme electrophoresis has proven to be an excellent technique for elucidating species boundaries in *Eurylophella* (under the biological species concept), we have found it to be of very limited value for examining phylogenetic relationships.

We have examined the larvae of all known species of *Eurylophella* as well as representatives of the other ephemerellid genera sharing the apomorphic (McCafferty 1977, 1978) loss of gill 3 (i.e., *Dannella, Timpanoga, Attenella*) for

morphological characters that could be used to construct a phylogeny of *Eurylophella* species. These efforts have met with limited success—only two characters were found whose states could be unambiguously polarized (see below). These characters are insufficient for a complete phylogenetic reconstruction.

Despite the inadequacy of our phylogenetic knowledge, we herein propose four species groups: the *temporalis* group, including *E. doris* (Traver), *E. poconoensis* NEW SPECIES, *E. prudentalis* (McD.) and *E. temporalis* (McD.); the *lutulenta* group, including *E. aestiva* (McD.), *E. enoensis* NEW SPECIES and *E. lutulenta* (Clemens); the *funeralis* group, including only *E. funeralis* (McD.); and the *bicolor* group, including *E. bicolor* (Clemens), *E. bicoloroides* (McD.), *E. macdunnoughi* NEW SPECIES, *E. minimella* (McD.) and *E. verisimilis* (McD.). *Eurylophella coxalis* (McD.), whose larva is unknown, is unassigned to group. Since these groups are defined partly by characters whose polarities are unknown, they remain tentative pending a thorough phylogenetic analysis.

One character whose polarity could be determined is the reduction of the dorsal subdivisions of the ventral lamella of gill 4 visible in some *Eurylophella* species (Fig. 2). We consider the condition illustrated in Figure 2a to be the ancestral state based on its presence in other ephemerellids with no gill on segment 3 [*Timpanoga hecuba, Attenella attenuata, A. margarita, Dannella simplex* and *D. lita*], as well as all other ephemerellids we have examined: *Ephemerella* (9 spp.), *Drunella* (9 spp.), *Caudatella* (3 spp.), *Serratella* (4 spp.). Members of our *temporalis* group are plesiomorphic in this regard and therefore constitute a sister group to the remaining eastern North American species of *Eurylophella*. Members of our *lutulenta* group show a reduction in the dorsal subdivisions, both in number (2-5 dorsal, compared with about 9 ventral subdivisions) and size (dorsal ones about half the size of the ventral subdivisions; see Fig. 2b), and these are confined to the lateral edge of the lamella. For members of our *funeralis* and *bicolor* groups the dorsal subdivisions are further reduced in size (1/4 or less the size of the ventral subdivisions, and often difficult to see at all; see Fig. 2c) and number (2-4). On this basis our *lutulenta* group can be considered a sister group to the *funeralis* plus *bicolor* groups.

The characteristic lengthening of abdominal segment 9 and reduction of segments 5 to 7 *Eurylophella* larvae are considered apomorphic by McCafferty (1977, 1978). Although our *temporalis* group species show the same degree of elongation of segment 9 as other *Eurylophella*, the reduction of 5-7 is less pronounced than in other species groups. The best way to measure the degree of reduction in segments 5-7 is in relation to segments 1-4, whose length appears to be unmodified; we use the ratio of the length of segment 2 to that of 7 (measured at midline; $MLT_{2:7}$, Fig. 1) for this purpose. Figure 77a illustrates the distribution of character states for $MLT_{2:7}$ among eastern North American *Eurylophella* species. Although there is some overlap between groups, members of the *temporalis* group all show a value of about 1.2 or lower, while $MLT_{2:7}$ for the other species is consistently higher. This character confirms the *temporalis* group as a sister group to the remaining species of *Eurylophella*.

The polarity of other characters used to define our species groups has not been clearly established. The most important of these is the relative spacing of abdominal tubercles. The *temporalis* group is characterized by rows of tubercles which appear to converge from segment 2-7. In the *lutulenta* group the rows are subparallel. In the *bicolor* group they are divergent. In *E. funeralis* (which we consider as its own group herein) the rows diverge from segment 1 to 4, then converge somewhat toward segment 7.

Other characters used to distinguish species groups are discussed below in Group Designations and Species Descriptions.

The structure of gill 4 in the western North American species *E. lodi* (Mayo 1952) and the European species *E. iberica* (Keffermüller and da Terra 1978) is similar to that shown in Figure 2a, and on this basis would be included in our *temporalis* group. The other European species, *E. karelica* Tiensuu, shows a reduction in the dorsal subdivisions of the lower lamella of gill 4 similar to our Fig. 2b, as in our *lutulenta* group. *Eurylophella lithuanica* Kazlauskas (1959), a presumed synonym of *E. karelica* (Puthz 1978), was unavailable for study. Other characters used to define our species groups are statistical, requiring data from many individuals, preferably from several populations. Since we have seen only one *E. lodi*, two *E. karelica*, and six *E. iberica* (in each case representing a single population), we cannot place these species to group with certainty. For example, in all three species the reduction of segments 5-7 in the specimens we have is borderline with regard to the dichotomy between the *temporalis* group and the other *Eurylophella* (MLT_{2-7} between 1.18 and 1.19). Further study of these species may require a modification of our species groupings.

Morphological Key

This key is intended for use with full-grown (final instar) larvae. Relative sizes of important characters such as tubercles on the abdominal tergites and occiput change during early larval development, and the direction of change is not consistent among species. When the fauna at a particular site is known, and adequate samples from all periods of larval development are available, it is usually possible to identify larvae as small as about 2 millimeters in length (Funk and Sweeney, unpublished), especially for some distinctive species such as *E. funeralis*. For most species larvae that are at least half grown should be identifiable using our key, but final size is an important character for a few.

Single larval specimens, especially partially grown larvae, may not be identifiable with certainty because of the high degree of intraspecific variation commonly encountered in *Eurylophella* larvae. The most accurate identifications will be possible when a large series of full-grown larval specimens from a particular site is available. However, one must be aware that such collections are likely to include two or more species, and in extreme cases as many as seven. A preliminary sorting into groups based on overall size, relative maturity, size of occipital tubercles, conspicuous differences in the spacing of submedian tubercles on the abdomen, shape of the ninth abdominal segment, and color pattern (especially ventral coloration) should facilitate identifications.

Eurylophella larvae are often covered with silt and organic detritus in their natural habitat. This material must be removed to adequately view structures used in the key, especially the posterolateral projections on the second and third abdominal segments and the submedian tubercles on the tergites. Often this material can be removed adequately with a fine paint brush. We have found an ultrasonic cleaner of the type often used to clean technical drawing pens to be particularly valuable, especially for larval exuviae, which may be torn apart with brushing. Most characters used here can be adequately observed under a good stereomicroscope, although for the higher magnification photos we used a compound microscope at 100X.

Eurylophella species collected in Canada, the Great Lakes region of the U.S., and

all areas east of the Appalachian mountains generally show a high degree of uniformity in larval morphology. However, specimens collected from southern Ohio, Indiana, and Illinois, southwest to Missouri and Arkansas often appear aberrant when compared to conspecific material from northern and eastern areas, and some are difficult to identify with certainty. *Eurylophella* seem to be less common and more patchily distributed in this region (judging from the paucity of specimens in most collections from the region). It seems likely that there has been very little gene flow between some of these populations and their northern and eastern counterparts, leading in some cases to significant local differentiation. Limited electrophoretic data (unpublished) from some populations in southern Ohio and western West Virginia support this hypothesis.

For the most part, measurements used in the descriptions and keys are from genetically known populations from eastern and northern areas. However, we have incorporated measurements from some museum specimens, especially those from geographically marginal areas, into our descriptions and keys in order to account for as much variation as possible. Figures 73 to 77 illustrate the distribution of character states for the quantitative measures we have found most useful for species identification.

In an effort to make the key as useful as possible for all of eastern North America some of the couplets are rather long. For maximum accuracy of identifications, we recommend careful use of couplets in their entirety. Because of the reliance on quantitative characters (see Fig. 1) users may find it helpful to make a table of these measurements for the specimen(s) in question before using the key.

Problem Couplets

Couplet 2. The form of the ventral lamella of gill 4 in full-grown larvae will always enable the members of the *temporalis* group to be distinguished with certainty. However, in smaller larvae this structure may be difficult to discern. For these specimens the secondary characters should enable separation. For example, any larva whose rows of submedian abdominal tubercles appear to converge from segment 2 to 7 belongs in the *temporalis* group. The parameter $ITD_{2:7}$ provides an objective measure of this convergence: for members of the *temporalis* group $ITD_{2:7} > 1$, for other groups $ITD_{2:7} < 1$. The only exception to this rule is *E. aestiva* (*lutulenta* group), some specimens of which have $ITD_{2:7}$ values as high as 1.14. However, the rows of tubercles on *E. aestiva* never appear to converge from segment 1 to 7, and all *E. aestiva* have SMT_7 greater than 0.79, a condition only rarely found in members of the *temporalis* group (see discussion under *temporalis*).

Couplets 4 and 5. *Eurylophella poconoensis*, *E. temporalis* and *E. doris* cannot always be reliably distinguished solely on the basis of mophology, necessitating a reliance on known distributions (see discussions in species descriptions).

Couplet 7. When it can be adequately observed, the form of the dorsal subdivisions of the ventral lamella of gill 4 will always distiguish the *lutulenta* group from the *bicolor* group. However, for smaller (half-grown or less) larvae resolution of these structures pushes the limits of even the best stereomicroscopes, and compound microscopes are impractical for observing this structure because of the required angle of view. Careful use of the secondary characters provided in this couplet should enable most individuals to be distinguished reliably.

Couplet 12. The primary characters, the relative length of the posterolateral projections on segments 2 and 3, have the potential to cause problems. In an attempt

to miminize ambiguity we have quantified these characters with the parameters PLP_2 and PLP_3. Measurements must be made very carefully (especially on smaller specimens), preferably under magnifications of 50 to 100X (i.e., higher than those available on most stereomicroscopes). Since there is some overlap between the two groups separated in this couplet (*E. minimella* from *E. bicoloroides* and *E. macdunnoughi*; see Figs. 76a and 76b), we suggest specimens whose PLP_2 and PLP_3 values fall within region of overlap be taken both ways in the key, then checked with the descriptions and discussions under each species.

Couplet 13. The spines on the hind margin of the fore femora are often obscured by silt and detritus clinging to them and specimens usually must be cleaned for adequate viewing. Also, one must not confuse these spines with the fine setae surrounding them (see arrows in Figs. 70 and 71). The structures are best seen in slide-mounted material under a compound microscope, but use of a high quality stereomicroscope at its highest magnification will usually suffice if the specimen is viewed under bright field illumination or against a light background.

Morphological Key to Full-grown Larvae

(*E. coxalis* unknown)

1. Paired submedian tubercles present on at least abdominal segments 1 to 7 ..... *Eurylophella* **2**
— Paired submedian tubercles present only on segments 5 to 7 ..... ***Dannella (Dentatella) bartoni***
2. Dorsal subdivisions of ventral lamella of gill 4 well developed, subequal to ventral subdivisions (Fig. 2a); rows of paired submedian tubercles appearing evenly convergent from abdominal segment 2 to 7 (Figs. 18, 48, 55 and 60), $ITD_{2:7}$ (=a/e in Fig. 1) greater than one; submedian tubercles on segment 7 narrowly spaced (Figs. 21, 53, 58 and 63), SMT_7 (=e/f in Fig. 1) usually less than 0.75 ..... *temporalis* group **3**
— Dorsal subdivisions of ventral lamella of gill 4 reduced or absent (Figs. 2b and 2c); rows of paired submedian tubercles from abdominal segment 2 to 7 appearing subparallel (as in Fig. 23), divergent (as in Fig. 65) or divergent to segment 3 or 4 and parallel or slightly convergent from 4 to 7 (Fig. 28), $ITD_{2:7}$ less than one (except in some *E. aestiva*); submedian tubercles on 7 more widely spaced, SMT_7 greater than 0.75 ..... **6**
3. Occipital tubercles small in both sexes (Figs. 56 and 57), sometimes barely perceptible in males; body length of full-grown larva 6.5 to 8.0 mm; submedian tubercles on 1-3 thin, often pointed, and relatively straight in side view (Fig. 72a); $ITD_{2:7}$ usually 1.3-1.5 (average = 1.39, range 1.10-1.86); average SMT_7 = 0.58 (range 0.49-0.81) ..... ***prudentalis***
— Occipital tubercles usually large in both sexes (Figs. 19, 20, 50, 52, 61 and 62) (occasionally small in *E. poconoensis*; Figs. 49 and 51); body length of full-grown larva usually 8.0-12.0 mm, always greater than 7.5 mm; submedian tubercles on 1-3 thicker, distinctly arched in side view (Fig. 72b-d).; $ITD_{2:7}$ less than 1.4; average SMT_7 = 0.67-0.71 (range 0.57-0.86) **4***
4. Size smaller, average full-grown larval body length in males = 8.2 mm (range 7.8-8.8), females = 9.0 mm (range 8.8-9.3); length of occipital tubercles variable (Figs. 49-52 show extremes); submedian tubercles on segments 1-3 shorter and straighter (Fig. 72c); known only from lakes in the Pocono region of northeastern Pennsylvania ... ***poconoensis***

**poconoensis, temporalis* and *doris* often cannot be reliably distinguished on the basis of morphology.

— Size larger, average full-grown larval body length in males = 9.0 mm (range 8.0-10.0), females = 9.5 mm (range 8.0-12.0); occipital tubercles always large (Figs. 19, 20, 61, and 62); submedian tubercles on segments 1-3 long and dorsally arched (Figs. 72b and 72d); widespread 5

5. Range restricted to the southeastern coastal plain from Delaware to Florida and west to Alabama, to the eastern slope of the southern Appalachians; fore femora broader, ratio of width to length usually greater than 0.38; posterolateral projections on segments 2 and 3 usually longer (average $PLP_2 = 0.16$, $PLP_3 = 0.32$) ..... ***doris***

— Northeastern and midwestern, from Quebec to Pennsylvania, west to Saskatchewan (with one record from the Northwest Territories; see discussion under *E. temporalis*), and west of the Appalachians south to Illinois, Indiana and Ohio; fore femora more slender, ratio of width to length usually less than 0.38; posterolateral projections on segments 2 and 3 usually shorter (average $PLP_2 = 0.11$, $PLP_3 = 0.22$) ..... ***temporalis***

6. Shape of segment 9 distinctive (Fig. 28): posterolateral projections short ($PLP_9 < 0.60$), their inner margins distinctly sinuate, with tips very acute and often slightly incurved, outer margins of segment usually rather straight, often subparallel, and segment with well developed submedian tubercles; submedian tubercles on 1 to 4 long, thin and semi-acute (Fig. 28), dorsally arched in lateral view (Fig 72h); posterolateral projections on 2 and 3 long (Fig. 32; shorter on midwestern specimens); submedian tubercles widely separated on segments 4 to 7 (Fig. 31), the distance between them distinctly greater than length of tergite at midline (average $SMT_7 = 1.17$, range = 1.00-1.43); gill 4 as in Fig. 2c; size large, body length of full-grown larva > 8.0 mm ..... ***funeralis* group, *funeralis***

— Segment 9 variable, not fitting the above description in one or more respects: if posterolateral projections short with sinuate inner margins, their outer margins distinctly convergent (as in Fig. 65) and submedian tubercles poorly developed or absent; submedian tubercles on 1 to 4 shorter, stouter and blunt (as in Fig. 65), straighter in lateral view (Figs. 72e-g, i-m); posterolateral projections on 2 and 3 short (Fig. 47) to long (Fig. 37); submedian tubercles not as widely separated on segments 4 to 7 (Figs. 6, 11, 16, 26, 41, 46, 68), at their widest subequal to or only slightly wider than length of tergite at midline (average $SMT_7 = 0.88$-1.12, range 0.77-1.33; usually less than 1.15); gill 4 as in Fig. 2b or 2c; size variable 7

7. Ventral lamella of gill 4 with two to five small dorsal subdivisions (Fig. 2b); posterolateral projections on segment 9 long, their inner margins relatively straight (Figs. 3, 23, and 33), with PLP_9 usually greater than 0.60 (range = 0.58-0.80); submedian tubercles on segments 1 and 2 more widely separated, range $SMT_1 = 0.50$-0.85, $SMT_2 = 0.58$-0.85, rows of submedian tubercles on abdominal segments 2 to 5 subparallel or slightly divergent posteriorly (Figs. 3, 23, and 33); medium-sized to large species (see Fig. 74a) ..... *lutulenta* group **8**

— Ventral lamella of gill 4 either with no dorsal subdivisions, or with one or two minute dorsal subdivisions on the outer margin of the lamella (Fig. 2c); posterolateral projections on segment 9 shorter, their inner margins slightly sinuate (Figs. 8, 13, 38, 43 and 65), with PLP_9 usually less than 0.60 (range = 0.41-0.63; sometimes greater in *E. minimella*; see Fig. 75a); submedian tubercles on segments 1 and 2 more narrowly separated, range $SMT_1 = 0.26$-0.63, $SMT_2 = 0.38$-0.72, rows of submedian tubercles on abdominal segments 2 to 5 evenly divergent posteriorly (sometimes widening abruptly from 4 to 5; *E. bicolor*) (Figs. 8, 13, 38, 43 and 65); small to medium-sized species (see Fig. 74a) ..... *bicolor* group **10**

8. Large species (body length of full-grown larva 8.7-11.2 mm); occipital tubercles small (Figs. 34 and 35) or medium (Figs. 24 and 25); posterolateral projections on segments 2 and 3 long (Figs. 27 and 37), PLP_3 always greater than 0.25; early season species, with adult emergence in early spring (Fig.78; *E. lutulenta, E. enoensis*) 9

— Medium-sized species (body length of full-grown larva 6.4-8.0 mm); occipital tubercles always well developed (Figs. 4 and 5); posterolateral projections on segments 2 and

3 shorter (Fig. 7), PLP_3 usually less than 0.25 (average = 0.21, range 0.12-0.32); late season species, with adult emergence in summer (Fig.78; *E. aestiva*) ..... ***aestiva***

9. Tergites 6 and 7 with distinct ridges forming the bases of submedian tubercles (Fig. 36); occipital tubercles small (Fig. 34) to nonexistent in male, very small in female (Fig. 35) ..... ***lutulenta***

— Tergites 6 and 7 without distinct ridges forming the bases of submedian tubercles (Fig. 26); occipital tubercles larger (Figs. 24 and 25) ..... ***enoensis***

10. Occipital tubercles distinct and well developed in both sexes (Figs. 66 and 67); common from the Appalachians eastward, from Quebec to Georgia; size medium, body length of full-grown larva 6.8-9.2 mm ..... ***verisimilis***

— Occipital tubercles small and inconspicuous in males (often appearing only as a roughened area; Figs. 9, 14, 39 and 44), small but distinct in females (Figs. 10, 15, 40 and 45); range from Canadian Maritimes south to North Carolina, west to Ontario and Arkansas; size small to medium, body length of full-grown larva 5.1-8.9 mm **11**

11. Space between submedian tubercles on segment 5 distinctly greater than that on segment 4, so that rows of tubercles appear to diverge abruptly from segment 4 to segment 5 (Figs. 8, 11); tubercles on segments 1 to 4 blunt and erect, those on 5 to 7 short (average TL_7 = 0.24, range 0.18-0.31), sharp and low-lying (Fig. 11), protruding only slightly beyond level of tergite in lateral view (Fig. 72 l); posterolateral projections on segment 2 barely perceptable, those on 3 small (Fig. 12); spacing of tubercles on segments 1 and 2 always narrow (SMT_1 = 0.26-0.53, SMT_2 = 0.38-0.56) ..... ***bicolor***

— Rows of submedian tubercles evenly divergent from segment 1 to 5 or 6, without abrupt change from 4 to 5 (Figs. 13, 38, 43); tubercles on segments 1 to 4 blunt to semi-acute and erect, those on 5 to 7 long (average TL_7 = 0.31-0.42, range 0.19-0.54), sharp and erect (Figs. 16, 41, 46), protruding conspicuously beyond tergite in lateral view (Figs. 72 j, k, and m); posterolateral projections on segment 2 barely perceptable (Fig. 47) to small but distinct (Figs. 17, 42), those on 3 small to medium-sized; spacing of tubercles on segment 1 and 2 often wider (SMT_1 = 0.27-0.65, SMT_2 = 0.38-0.73) .. **12**

12. Posterolateral projections on segment 2 very small, barely perceptible (Fig. 47), PLP_2 = 0-0.07; posterolateral projections on segment 3 small (average PLP_3 = 0.12, range 0.05-0.17); submedian tubercles on segments 1 to 4 thinner, semi-acute and erect, those on 5 to 7 long (TL_7 = 0.31-0.54), sharp and semi-erect, the transition in form of submedian tubercles from segments 4 to 5 less distinct (Fig. 46 and 72m); small species, length of full-grown larva 5.1-7.2 mm; late season species, with adult emergence in summer (Fig. 78; *E. minimella*) ..... ***minimella***

— Posterolateral projections on segment 2 small but distinct (Figs. 17 and 42), PLP_2 = 0.04-0.15; posterolateral projections on segment 3 medium sized (average PLP_3 = 0.15-0.19, range 0.07-0.35); submedian tubercles on segments 1 to 4 thicker, blunt and erect, those on 5 to 7 not as long (TL_7 = 0.19-0.41), the transition in form of submedian tubercles from 4 to 5 more distinct (Fig. 16, 41 and 72 j and k); larger species, length of full-grown larva 6.4-8.9 mm; mid-season species, with adult emergence in spring (Fig. 78; *E. bicoloroides, E. macdunnoughi*) **13**

13. Spines on hind margin of fore femora long, thin and acute (Fig. 71); submedian tubercles on segment 2 more widely spaced (normal range of SMT_2 = 0.51-0.66); submedian tubercles on 1 to 4 slightly longer in side view (Fig. 72j) and laterally compressed; distribution from Nova Scotia southwest to north-central Pennsylvania ..... ***bicoloroides***

— Spines on hind margin of fore femora short, stout and blunt (Fig. 70); submedian tubercles on segment 2 more narrowly spaced (normal range of SMT_2 = 0.38-0.58); submedian tubercles on 1 to 4 usually shorter in side view (Fig. 72k), not laterally compressed; distribution Maine to Pennsylvania east of the Appalachians, west of the Appalachians south to Tennessee and west to the Ozarks ..... ***macdunnoughi***

GROUP DESIGNATIONS AND SPECIES DESCRIPTIONS

Temporalis Species Group

Four eastern North American species, *E. prudentalis* (McDunnough), *E. temporalis* (McDunnough), *E. doris* (Traver), and *E. poconoensis* NEW SPECIES, constitute a distinctive group on the basis of gill structure and abdominal tubercle characters in the larvae. These species retain the plesiomorphic state for the ventral lamella of the gill on segment 4 (i.e., with no reduction in the number or size of dorsal subdivisions; Fig. 2a). The reduction in length of abdominal segments 5 to 7 is less pronounced and the anterior segments are slightly longer than in the other species groups, as indicated by the ratio of the lengths of tergite 2 to 7, measured at midline, (see Fig. 77a). The separation of the submedian tubercles on segment 7 is relatively narrow (SMT_7 usually less than 0.75; see Fig. 73b), while the distance between those on segment 2 distinctly wider than those on segment 7 ($ITD_{2,7}$ greater than 1.0; Fig. 73a), so that the rows of tubercles appear to converge from segment 2 to 7. Tergites 5 to 7 have longitudinal ridges which form the bases of the submedian tubercles (Figs. 21, 53, 58 and 63). The fore femora are relatively slender (FWL_1; Fig. 74b). Markings on the larval sterna (submedian dots, oblique paramedian dashes, and longitudinal sublateral maculae) are, when present, usually conspicuous and blackish, contrasting sharply with the pale ground color. The tips of the posterolateral projections of the abdomen are concolorous with the basal portions or slightly darkened (never black-tipped, as is typical of species in the *bicolor* group). Species of the *temporalis* group are medium or large in size (Fig. 74a).

Electrophoretic data from our earlier study (Funk et al. 1988), confirmed by more recent (unpublished) data from populations in Maine, strongly indicate the presence of three genetically distinct species within Berner's (1984) concept of *E. temporalis*. We now consider the species referred to in our earlier work as *E. temporalis-C* to represent McDunnough's *E. temporalis*. Our *E. temporalis-A* is herein described as new (*E. poconoensis* Funk) and *E. temporalis-B* is considered *E. doris* Traver. For *E. doris* we were able to include a population from the type locality in our genetic study. Our decision regarding which of the other two represented McDunnough's *E. temporalis* was based on the fact that all of our *E. temporalis-C* had long occipital tubercles and were large (generally 9-10 mm), consistent with McDunnough's description of *E. temporalis* as well as our own study of his material. In contrast, our *E. temporalis-A* had tubercles of varying length, mostly shorter than McDunnough's specimens, and were of consistently smaller size (generally 8-9 mm). Also, this form appears to be restricted geographically to the Pocono region of northeastern Pennsylvania whereas McDunnough's material was from New England and eastern Canada (but see discussion under *E. poconoensis* below).

Eurylophella doris (Traver) New Combination

Figures 18-22, 72b

Ephemerella doris Traver 1934: 208; Traver 1935: 592, 2 figs; Allen and Edmunds 1963: 616.
Ephemerella trilineata Berner 1946: 67; Berner 1950: 154, 3 figs. **NEW SYNONYM**
Eurylophella temporalis (McDunnough), Berner 1984: 567 (in part); Berner and Pescador 1988: 303.

Larva.—Length: 8.0-10.1. Head: occipital tubercles large and prominent in male (Fig. 19), and female (Fig. 20). Thorax: fore femora slender, average ratio of width to length (FWL_1) = 0.40, range 0.37-0.44. Abdomen: Rows of submedian tubercles evenly convergent from 2-7. Average $ITD_{2:7}$ = 1.21, range 1.05-1.39. Average $ITD_{4:7}$ = 1.26, range 1.13-1.48. Tubercles on segment 2 widely spaced (average SMT_2 = 0.75, range 0.68-0.83). Those on segment 1 variable, but often slightly narrower than on 2 (average SMT_1 = 0.74, range 0.62-0.88; Fig. 18). Spacing of tubercles on segment 7 always distinctly narrower than length of segment at midline (average SMT_7 = 0.69, range 0.57-0.86). Tubercles on 1-4 long and arched (Fig. 72b), with no scale-like setae and with few or no fine setae. Tubercles on 5-7 medium sized, sharp, with no scale-like setae and few or no fine setae. Average TL_7 = 0.23, range 0.16-0.30. Tubercles on 8 and 9 usually small and inconspicuous. Tergites 5-7 with distinct ridges ending in the submedian tubercles (Fig 21). Average $MLT_{2:7}$ = 1.10, range 0.97-1.19. Posterolateral projections on 2 and 3 rather long (Fig. 22). Average PLP_2 = 0.16, range 0.12-0.25; PLP_3 = 0.32, range 0.23-0.44. Posterolateral projections on 9 medium to long, PLP_9 = 0.68, range 0.57-0.73. Dorsal subdivisions of lower lamella of gill 4 subequal to ventral subdivisions in both sized and number (as in Fig. 2a).

Material Examined.—Type series: Holotype male (CU # 1292), reared from larva, **NORTH CAROLINA**: Randolph Co., Uwharrie River, near Farmer, (elev. 450 ft., 35°38'30"N, 79°58'00"W), 6.V.1929, J.R. Traver; 5 male and 4 female paratypes, larvae, **GEORGIA**: Withlacoochee River near Macon, 21-22.III.1931, P.W. Fattig; 1 male and 1 female paratype, larvae, **NORTH CAROLINA**: outlet of Lake Waccamaw, 11.IV.1929, J.G. Needham.

Larval exuviae vouchers from electrophoretic survey [see Table 1 in Funk et al. (1988; as *E. temporalis-B*)]: 113 from Delaware, North Carolina, South Carolina, and Georgia.

Additional reared material (larval exuviae in alcohol, imagos frozen): 71 M, 112 F, from Delaware, Virginia, North Carolina, South Carolina, and Georgia.

Slide mounts of larval exuviae: **DELAWARE**: 2 M, 2 F, New Castle Co., Blackbird Cr., 1.5 mi SW of Blackbird, 39°21'18"N, 75°40'55"W, 20-25.V.1985, DHF; **NORTH CAROLINA**: 2 M, 2 F, Randolph Co., Uwharrie River, near Farmer, 35°38'30"N, 79°58'00"W, 9-14.V.1985, DIR & DHF; **SOUTH CAROLINA**: 2 M, 2 F, Newberry Co., Indian Cr., 5 mi SSE Whitmire, 34°25'29"N, 81°36'18"W, 11-14.V.1985, DIR & DHF; **GEORGIA**: 1 M, 2 F, Habersham Co., Panther Cr. ~7 mi NNW Toccoa, 34°40'24"N, 83°21'17"W, 17.VI to 3.VII.1985, DIR & DHF.

Other larval material: **DELAWARE**: KENT CO., Pratt Branch, Spring Cr., 2.5 mi E of Felton at Rd388, 39°00'37"N, 75°31'47"W, various dates—1980-1985, DHF & R.W. Lake, 8 L, 8 M, 13 F, with exuviae; **FLORIDA**: various localities and dates, L. Berner, 42 L (FAMU); OKALOOSA CO., Blackwater River below Bone Cr, 3.1 mi NW Holt, 30°44'27"N, 86°47'13"W, various dates—1981-1982, MKB, LSD & WLH, 9 L; **GEORGIA**: GRADY CO., Wolf Cr, 2.1 mi ENE of Whigham at US Rt 84, 30°46'09"N, 84°17'28"W, various dates—1981-1982, MKB, LSD & WLH, 48 L; trib of Wolf Cr, 2.7 mi NNE of Whigham, 30°55'08"N, 84°18'19"W, various dates—1981-1982, MKB, LSD & WLH, 29 L, 1 M with exuviae; Black Cr, 4.9 mi NE of Whigham, 30°56'13"N, 84°16'19"W, various dates—1981-1982, MKB, LSD & WLH, 18 L; **NORTH CAROLINA**: DURHAM CO., Eno River at Rd. 1401, 30.IV.1980, BWS & RLV, 3 L; ORANGE CO., tributary of W. Fk. Eno River at Rd1004, 2.6 mi SSW of Cedar Grove, 36°07'49"N, 79°10'33"W, various dates—1980-1981, ACG, JWP, DIR & RBS, 13L; West Fork Eno River at Rd1004, 2.1 mi SSW of Cedar Grove, 36°06'21"N, 79°10'13"W, various dates—1980-1981, ACG, JWP, DIR & RBS, 32 L; same, 25.V to 10.VI.1988, DHF &

DIR, 3 M with exuviae; Eno River at Rt 70, 1.3 mi NNE of Efland, 36°04'58"N, 79°06'34"W, various dates—1980-1981, ACG, JWP, DIR & RBS, 28 L, 1 M, 4 F, with exuviae; RANDOLPH CO., Uwharrie River at Rt. 1316 bridge, ~7 mi W of Ashboro, 11.III.1980, DHF & BWS, 4 L; **SOUTH CAROLINA**: AIKEN CO., Upper Three Runs, at Rd C 1.9 mi E of Jct Rd 2, 33°17'08"N, 81°41'42"W, various dates—1980-1982, MKB, LSD & WLH, 115 L, 3 M, 5 F, with exuviae; EDGEFIELD CO., Turkey Cr., 9.5 mi NW of Edgefield, Sumter Natl. For., 33°47'44"N, 82°03'56"W, various dates—1980-1982, MKB, LSD & WLH, 15L, 5 M, 2 F, with exuviae; MCCORMICK CO., Horton Branch, Long Cane Cr., 5.2 mi ENE of Willington, 33°59'55"N, 82°23'01"W, various dates—1980-1982, MKB, LSD & WLH, 20 L; NEWBERRY CO., Long Branch Indian Cr, 8.7 mi SSW of Whitmire, 34°23'15"N, 81°41'50"W, various dates—1980-1982, MKB, LSD & WLH, 27 L; Indian Cr, 6.5 mi SE of Whitmire, Sumter Natl. For., 34°25'40"N, 81°42'45"W, various dates—1980-1982, MKB, LSD & WLH, 53 L, 2 M with exuviae; small trib of Indian Cr, 1 mi from Rt. 36, 29.IV.1980, BWS & RLV, 11 L, 1 F with exuviae; **VIRGINIA**: GREENVILLE CO., trib of Meherrin River ~2 mi above Emporia, 28.IV.1986, DHF, reared in lab 8-19.V.1986, 2 M, 3 F, with exuviae.

Range.—East of the Appalachians from Virginia, Maryland, and Delaware south to Georgia, continuing south to central Florida. *Eurylophella doris* is not currently known west of the Appalachians.

Discussion.—Traver (1934) described *E. doris* from male and female imagos and larvae collected in North Carolina and Georgia. Berner (1946) described *E. trilineata* from male and female imagos and larvae from Florida. Allen and Edmunds (1963) suggested that both *E. doris* and *E. trilineata* might be synonymous with *E. temporalis*, but declined to take such action. Berner later (1984) synonymized them. Funk et al. (1988) found that southeastern populations (including one from the type locality of *E. doris*) constituted a group that was genetically distinct from northern *E. temporalis* populations. We therefore reinstate *doris* here. Berner (1946) could find nothing to distinguish *E. trilineata* from *E. doris*. Although we have no genetic data from the type locality of *E. trilineata*, morphological and geographic data indicate that *E. trilineata* is conspecific with *E. doris*, and we thus retain its status as a junior synonym.

In the absence of electrophoretic data, the best way to distinguish *E. doris* from its northern relatives is on the basis of geography. Due to the lack of genetic data from south of the Great Lakes and west of the Appalachians, we cannot be sure of the identity of individuals collected in that region. Some specimens from that region (herein presumed to be *E. temporalis*) have broader femora and longer posterolateral projections on segments 2 and 3 than typical northern *E. temporalis*. Additional study may reveal that some of these are *doris*, but for the present, we consider *E. doris* to be restricted to the southeast.

Eurylophella doris is typically found in small to large streams, but may occasionally be found in lentic habitats, especially in impounded reaches of rivers whose unimpounded reaches sustain *E. doris* populations. It has been collected with *E. verisimilis*, *E. enoensis*, *E. bicolor* and *E. aestiva* as far south as northern Georgia and South Carolina. *Eurylophella doris* is the only member of the genus found in southern Georgia and Florida.

Eurylophella poconoensis Funk New Species

Figures 48-54, 72c

Larva.—Length: 7.8-9.3. Head: occipital tubercles small to large in male (Fig. 49, 50), and female (Fig. 51, 12). Thorax: fore femora slender, average ratio of width to

length (FWL_1) = 0.40, range 0.38-0.43. Abdomen: Rows of submedian tubercles evenly convergent from 2-7. Average $ITD_{2:7}$ = 1.22, range 1.09-1.32. Average $ITD_{4:7}$ = 1.28, range 1.21-1.44. Tubercles on segment 2 widely spaced (average SMT_2 = 0.74, range 0.67-0.83). Those on segment 1 variable, but often slightly narrower than on 2 (average SMT_1 = 0.69, range 0.56-0.79; Fig. 48). Spacing of tubercles on segment 7 always distinctly narrower than length of segment at midline (average SMT_7 = 0.67, range 0.65-0.71). Tubercles on 1-4 long and arched (Fig. 72c), with scale-like setae and with few or no fine setae. Tubercles on 5-7 medium sized, sharp, with few scale-like setae and few or no fine setae. Average TL_7 = 0.20, range 0.15-0.24. Tubercles on 8 and 9 usually small and inconspicuous. Tergites 5-7 with distinct ridges ending in the submedian tubercles (Fig 53). Average $MLT_{2:7}$ = 1.11, range 1.00-1.21. Posterolateral projections on 2 and 3 medium length (Fig. 54). Average PLP_2 = 0.14, range 0.09-0.17; PLP_3 = 0.27, range 0.23-0.35. Posterolateral projections on 9 medium to long, PLP_9 = 0.64, range 0.54-0.70. Dorsal subdivisions of lower lamella of gill 4 subequal to ventral subdivisions in both sized and number (as in Fig. 2a).

Male Imago.—(description based on specimens freshly preserved in alcohol) Length: body 7.2-8.1, forewing 7.3-8.2. Head light yellowish-brown with variable dark maculations. Upper portion of compound eye reddish-orange in life. Thorax pale orange-brown, with some dark mottling on pronotum. Legs pale with a dark macula on each coxa. Forelegs with apical macula on tibia. Wings hyaline with faint amber tint on basal areas of primary veins. Abdominal terga light brown with variable markings, often with pale median or paired submedian stripes. Most terga with two black sublateral maculae on each side. Sterna 1-3 yellowish-brown, fading to pale posteriorly. Sometimes with reddish mottling superimposed on both terga and sterna. Penes typical for the genus, and indistinguishable from *E. temporalis*. Tails pale with orange-brown annulations.

Female Imago.—(in alcohol) Length: body 7.6-8.1, forewing 8.3-8.8. Similar to male except for the usual sexual differences.

Material Examined.—

Holotype: Reared male imago (SWRC no. ET LAC 172), **PENNSYLVANIA**: Wayne Co., Lake Lacawac (elev. 1450 ft., 41°22'46"N, 75°17'43"W), collected as larva 22.V.1986, DIR & DHF, reared at SWRC (tray 500), emerged 25.VI.1986. Imago and larval exuviae in alcohol. Deposited at the Academy of Natural Sciences of Philadelphia.

Paratypes: 8 males, 3 females, all reared male imagos with larval exuviae (SWRC no. ET LAC 33-38, 93, 95, 96, 114, 126, 148, 167, 168, 177), same data as holotype, emerged 13.VI to 6.VIII.1986, one male (148) pinned (exuviae in alcohol), remaining specimens in alcohol. Two males and two females deposited at ANSP.

Larval exuviae vouchers from electrophoretic survey [see Table 1 in Funk et al. (1988; *E. temporalis-A*)]: 78 from Pennsylvania.

Additional reared material (larval exuviae in alcohol, imagos frozen): 88 M, 107 F, from Pennsylvania.

Slide mounts of larval exuviae: **PENNSYLVANIA**: 5 M, 2 F, Wayne Co., Lake Lacawac, 41°22'46"N, 75°17'43"W, 15.VI to 11.VII.1986, DIR & DHF; 3 M, 2 F, Wayne Co., Starlight Lake, 41°54'23"N, 75°20'00"W, 9-19.VI.1986, DIR & DHF.

Range.—This species is presently known only from lakes in northeastern Pennsylvania.

Discussion.—This species was discovered during our electrophoretic study (Funk et al. 1988). Were it not for the fact that *E. poconoensis* coexists with *E.*

temporalis with no evidence of interbreeding at all three localities where we collected it, we would have been hesitant to consider it a distinct species. Unfortunately, distinguishing these two solely on the basis of morphology is not always possible. Although there are clear differences in the average values for some parameters (body length, shape of the fore femora, and length of the posterolateral projections on segments 2 and 3; see descriptions and Figs. 74 and 76), there is enough overlap that not all individuals can be identified with certainty. Unlike most populations of *E. temporalis* (or any other *Eurylophella* in eastern North America), *E. poconoensis* exhibits considerable variation in the length of occipital tubercles (Figs. 49-52), and the collections of individuals with small occipital tubercles should indicate its presence. *Eurylophella poconoensis* emerges distinctly later in the season than *E. temporalis* (Fig. 78).

On the basis of morphology, *E. poconoensis* and *E. doris* show an even greater degree of overlap (see descriptions and Figs. 73-76). However, as far as we know these two are allopatric, so geographical distribution is probably a reliable way to distinguish them.

Eurylophella poconoensis with very small occipital tubercles could be confused with *E. prudentalis*. With these specimens couplet 3 must be used carefully, utilizing all the characters given. The combination of more widely spaced submedian tubercles on segment 7 (Fig.73b), larger size (Fig. 74a), and longer posterolateral projections on segment 2 and 3 (Fig. 76a and b) should enable *E. poconoensis* to be distinguished from *E. prudentalis*. Also, *E. poconoensis* has only been found in lakes, whereas *E. prudentalis* has only been found in streams (at least in the region of overlap). When adult males are available, *E. prudentalis* can be easily distinguished by the distinctive ventral protuberance on the penes (see Figs. 2-3 in McDunnough, 1931a; Fig. 4 in Allen, 1963), which is absent in *E. poconoensis*.

Etymology. Eurylophella poconoensis is named for the Pocono Mountains in northeastern Pennsylvania, the only region where the species has been collected to date.

Eurylophella prudentalis (McDunnough)

Figures 55-59, 72a

Ephemerella prudentalis McDunnough, 1931a: 40, 6 figs.; Traver 1935: 616; Burks 1953: 72, 1 fig.; Allen and Edmunds 1963: 611, 4 figs.

Larva.—Length: 7.3-8.2. Head: occipital tubercles small but distinct in male (Fig. 56) and female (Fig. 57). Thorax: fore femora slender, average ratio of width to length (FWL_1) = 0.39, range 0.35-0.43. Abdomen: Rows of submedian tubercles evenly convergent from segment 2-7 (Fig. 55, 58). Average $ITD_{2:7}$ = 1.39, range 1.10-1.86. Average $ITD_{4:7}$ = 1.34, range 1.05-1.50. Distance between tubercles on segment 1 may be equal to or slightly narrower than that on segment 2 (average SMT_1 = 0.70, range 0.55-0.85; Fig. 55). Tubercles on segment 2 widely spaced (average SMT_2 = 0.74, range 0.64-0.84). Spacing of tubercles on segment 7 always distinctly narrower than length of segment at midline (average SMT_7 = 0.58, range 0.49-0.81). Tubercles on 1-4 rather long and somewhat pointed, and directed posteriorly (not strongly arched dorsally; Fig. 72a), without scale-like setae, but with scattered fine setae. Tubercles on 5-7 long, very sharp, usually without scale-like setae and with few fine setae. Average TL_7 = 0.23, range 0.17-0.29. Tubercles on 8 and 9 usually present. Average $MLT_{2:7}$ = 1.09, range 0.93-1.19. Posterolateral

projections on 2 and 3 of medium size (Fig. 59). Average PLP_2 = 0.08, range 0.05-0.13; PLP_3 = 0.20, range 0.12-0.30. Posterolateral projections on 9 of medium length, PLP_9 = 0.61, range 0.54-0.70. Dorsal subdivisions of lower lamella of gill 4 subequal to ventral subdivisions in both sized and number (as in Fig. 2a).

Material Examined.—Type series: Paratype male with exuviae (CNC # 3190), **QUEBEC**: Knowlton (45°13'05"N, 72°30'34"W), 22-26.VI.1929, Walley, Milne, and McDunnough; Paratype female larval exuviae, Foster, Mid-Yamaska River, 11.VI.1930.

Larval exuviae vouchers from electrophoretic survey [Table 1 in Funk et al. (1988), and subsequent unpublished data]: 119 from Quebec, Maine, Vermont, Pennsylvania, Delaware, Virginia, and South Carolina.

Additional reared material (larval exuviae in alcohol, imagos frozen): 94 M, 49 F, from Vermont, Pennsylvania, Delaware, and Virginia.

Slide mounts of larval exuviae: **QUEBEC**: 1 F, Saguenay Co., Rivière Pigou above Rt. 138, 50°16'57"N, 65°38'31"W, 23.VII.1984, DHF; **VERMONT**: 4 M, 2 F, Bennington Co., Batten Kill R., 1.9 mi N of Arlington on Rt. 7, 43°05'52"N, 73°08'31"W, 31.V-7.VI.1985, DIR & DHF; **DELAWARE**: 2 M, 2 F, Sussex Co., Famy's Branch (Sheep Pen Ditch) 1.9 mi NW of Millsboro, 38°33'06"N, 75°19'18"W, 12-17.V.1985, DHF; **VIRGINIA**: 2 M, 2 F, Buckingham Co., Slate River at Rt 24, 5 mi SW of Mt. Rush, 37°28'28"N, 78°39'27"W, 18.V-5.VI.1985, DIR & DHF; **SOUTH CAROLINA**: 2 M, 2 F, Newberry Co., Indian Cr., 5 mi SSE Whitmire, 34°25'29"N, 81°36'18"W, 3-17.V.1985, DIR & DHF.

Other larval material: **MAINE**: Franklin Co., Flagstaff Lake at Rt 27 west of Stratton, 20.VI.1986, SKB, 1 L (UMDE); North Branch Dead River at Rt 27 bridge, Eustis, 20.VI.1986, SKB, 3 L (UMDE); Hancock Co., Mount Desert Island, Duck Brook (upper), 13.VI.1987, SKB, 1 L (UMDE); Mount Desert Island, stream along road near Sunken Heath, 17.V.1987, SKB, 1 L (UMDE); Penobscot Co., Sandbank Stream, trib of Penobscot R., 30.IX.1981, ACG & DHF, 5 L; Swift Brook, 0.8 mi W of Stacyville, 45°51'50"N, 68°31'23"W, 22.X.1981, DHF, DIR, MBG & JWP, 7 L; Piscataquis Co., Piscataquis River, 3.7 mi SW of Monson, 45°14'30"N, 69°32'43"W, 17.VI.1982, ACG, 1 L; Nesowadnehunk Stream in Baxter State Park, 45°54'02"N, 69°02'22"W, 8.XII.1982, DHF & DIR, 4 L; same, 30.VI.1982, ACG, 1 L; **PENNSYLVANIA**: Susquehanna Co., Meshoppen Cr., 1.3 mi SE of Dimock on Rd 57010, 41°43'02"N, 75°52'17"W, 23 to 31.V.1979, DHF, BWS & RLV, 14 L; same 25.V.1982, DIR, 10 L; same, 8.VI.1981, DIR, 1 M with exuviae; tributary of Meshoppen Cr., 2.0 mi E of Dimock, RdT508 at jct RdT518, 41°44'13"N, 75°51'36"W, XI.14.1979, ACG & DTM, 2 L; Montour Co., Chillisquaque Cr. above Montour Power Plant, 41°04'50"N, 76°40'09"W, various dates—1987, DIR, 28 L; Chillisquaque Cr. below Montour Power Plant, 41°04'00"N, 76°40'35"W, various dates—1987, DIR, 72 L; Chillisquaque Cr., near Washingtonville, 41°03'24"N, 76°40'48"W, various dates—1987, DIR, 39 L; Northumberland Co., Chillisquaque Cr. near Potts Grove, 40°57'30"N, 76°46'44"W, various dates—1987, DIR, 12 L; **QUEBEC**: Saguenay Co., Rivière Matamec below Beaver Cr., 50°18'21"N, 65°56'11"W, 10.VII.1981, DHF, 1 L; same, 18.VI.1981, JAG, 1 L; Rivière aux Loups Marins, above Rt. 138, 50°16'44"N, 65°43'12"W, 9.VI.1982, JAG, 2 L; same, 29.V.1982, DHF, 1 L; Ruisseau du Cran Carré, above Rt 138, 50°17'35"N, 65°55'30"W, 2.VII.1982, JAG, 1 L; **SOUTH CAROLINA**: Aiken Co., Upper Three Runs, at Rd C 1.9 mi E of Jct Rd 2, 33°17'08"N, 81°41'42"W, 29.V.1981, MKB, 1 L; Lexington Co., Cat. No. 4-20055-1, 20.IV.1955, L. Berner No. 3706.12, 1 L, (FAMU); Cat. No. 4-20055-2, 20.IV.1955, L. Berner No. 3707.0, 3 L, (FAMU); **VERMONT**: Bennington Co., Batten Kill R. 1.6 mi W of West Arlington on Rt 313,

43°06'04"N, 73°14'31"W, 1.VI.1985, DIR & DHF, 1 L; **VIRGINIA**: GREENVILLE CO., trib of Meherrin River, ~2 mi above Emporia, 28.IV.1986, DHF, 2 M, 3 F, with exuviae.

Range.—Eurylophella prudentalis has been reported from Minnesota, the eastern James Bay region in Ontario, the north shore of the St. Lawrence in Quebec, east to Nova Scotia in the north, and from the Appalachians eastward south to South Carolina. It is apparently absent west of the Appalachians south of the Great Lakes region.

Discussion.—McDunnough (1931a) described *E. prudentalis* from adults and larvae collected in southern Quebec. This is perhaps the only eastern North American species that can be reliably identified as a male imago; there is a distinctive ventral protuberance on the penes about midway out from the base, best seen from a lateral view (see Figs. 2-3 in McDunnough, 1931a; Fig. 4 in Allen and Edmunds, 1963). The larva of this species is most easily distinguished from other members of the *temporalis* group by its smaller occipital tubercles. The form of the submedian tubercles on abdominal segments 1-4 is also distinctive—these tend to be thinner, and less strongly arched in side view than other members of the *temporalis* group (see Fig. 72a-d). *Eurylophella prudentalis* is generally considerably smaller than the other members of this group (see Fig. 74a) and has shorter posterolateral projections on segments 2 and 3 (Fig. 76a and b). It has, on average, the most closely spaced tubercles on segment 7, and highest $SMT_{2:7}$ of any member of the genus (Fig. 73a and b), although there is some overlap with other species of the *temporalis* group in these parameters. The only species it is likely to be confused with is *E. poconoensis*, some specimens of which have head tubercles as small as those found in *E. prudentalis*. In most areas this is not likely to be a problem, as *E. poconoensis* appears to be restricted to the Pocono region of Pennsylvania. In areas of overlap, accurate identification may require the use of adult males. However, *E. prudentalis* larvae usually have more narrowly spaced submedian tubercles on segment 7 (Fig. 73b), are smaller (Fig. 74a), and have shorter posterolateral projections on segment 2 and 3 (Fig. 76a and b). As far as we know, *E. poconoensis* is found only in lakes; we have found *E. prudentalis* only in streams (although there are reports of its occurrence in lakes in the north).

Eurylophella prudentalis is most often found with *E. verisimilis* and *E. macdunnoughi*, all three of which mature at about the same time (see Fig. 78). In the southern part of its range *E. prudentalis* is often found with *doris*.

On a fine scale, *E. prudentalis* seems to be quite patchy in its distribution. It is typically found in in quiet reaches of small streams and rivers (~2nd to 5th order), and is often associated with beaver activity, but can be conspicuously absent from many streams which appear to have suitable habitat. The species is typically not found in lakes, at least from the Appalachian, Piedmont, and Coastal Plain regions of the eastern U.S.

Eurylophella temporalis (McDunnough)

Figures 2a, 60-64, 72d

Ephemerella lutulenta Clemens, 1913: 335 (in part); Clemens 1915: 121 (in part).
Ephemerella lineata Clemens, 1913:336 (in part); Clemens 1915: 122 (in part).
Ephemerella temporalis McDunnough, 1924: 73, 1 fig.; McDunnough 1925: 212; McDunnough 1930: 58, 1 fig.; McDunnough 1931a: 35, 4 figs.; Traver 1935: 623; Burks 1953: 72, 6 figs.; Allen and Edmunds 1963: 614, 6 figs.
Eurylophella temporalis (McDunnough), Berner 1984: 567 (in part).

Larva.—Length: 8.9-12.0. Head: occipital tubercles large and prominent in male (Fig. 61), and female (Fig. 62). Thorax: fore femora very slender, average ratio of width to length (FWL_1) = 0.37, range 0.32-0.39. Abdomen: Rows of submedian tubercles evenly convergent from 2-7. Average $ITD_{2:7}$ = 1.17, range 1.00-1.41. Average $ITD_{4:7}$ = 1.25, range 1.07-1.44. Tubercles on segment 2 widely spaced (average SMT_2 = 0.79, range 0.64-1.11). Those on segment 1 variable, but often slightly narrower than on 2 (average SMT_1 = 0.68, range 0.50-0.85; Fig. 60). Spacing of tubercles on segment 7 usually distinctly narrower than length of segment at midline (average SMT_7 = 0.71, range 0.58-1.05). Tubercles on 1-4 long and arched (Fig. 72d), usually no scale-like setae and with only scattered fine setae. Tubercles on 5-7 medium sized, sharp, with few or no scale-like setae and scattered fine setae. Average TL_7 = 0.24, range 0.16-0.36. Tubercles on 8 and 9 usually small and inconspicuous. Tergites 5-7 with distinct ridges ending in the submedian tubercles (Fig 63). Average $MLT_{2:7}$ = 1.07, range 0.89-1.22. Posterolateral projections on 2 and 3 medium length (Fig. 64). Average PLP_2 = 0.14, range 0.06-0.26; PLP_3 = 0.26, range 0.16-0.38. Posterolateral projections on 9 medium to long, PLP_9 = 0.64, range 0.51-0.82. Dorsal subdivisions of lower lamella of gill 4 subequal to ventral subdivisions in both sized and number (Fig. 2a).

Material Examined.—Type series: Holotype male (CNC # 778), **ONTARIO**: Ottawa (elev. ~150', 45°25'N, 75°40'W), July 4, C.H. Curran; 1 male paratype, same data.

Larval exuviae vouchers from electrophoretic survey [Table 1 in Funk et al. (1988; as *E. temporalis*-C), and subsequent unpublished data]: 55 from Maine and Pennsylvania.

Additional reared material (larval exuviae in alcohol, imagos frozen): 15 M, 28 F, from Maine.

Slide mounts of larval exuviae: **MAINE**: 3 M, 3 F, Piscataquis Co., Moosehead Lake at West Outlet, near Rockwood, 45°39'28"N, 69°44'25"W, 1 to 3.VII.1988, DIR & DHF; **PENNSYLVANIA**: 1 F, Pike Co., Lake Wallenpaupack near Ledgedale (trib. of Lackawaxen River), 41°21'54"N, 75°18'02"W, 10.VI.1986, DIR & DHF; 1 F, Wayne Co., Lake Lacawac, 41°22'46"N, 75°17'43"W, 4.VI.1986, DIR & DHF; 4 F, Wayne Co., Starlight Lake, 41°54'23"N, 75°20'00"W, 30.V to 6.VI.1986, DIR & DHF.

Other larval material: **ILLINOIS**: Lake Co., Sand Lake, 17.VI.1892, Hart & Shiga, Ac.# 18443, 1 L (INHS); Sand Lake, along shore & in pond, 18.VI.1892, Hart & Shiga, Ac. # 18444, 2 L (INHS); same, along shore, 15.VI.1892, Hart & Shiga, Ac. # 18437, 2 L (INHS); Fourth Lake, along shore, 18.VI.1892, Hart & Shiga, Ac.# 18442a, 2 L (INHS); same, 16.VI.1892, Hart & Shiga, Ac.# 18442, 2 L (INHS); Cedar Lake along shore, 16.VI.1892, Hart & Shiga, Ac. # 18449, 4 L, (INHS); same, 20.VI.1892, Hart & Shiga, Ac. # 18450, 6 L (INHS); Mason Co., Sta. H, river below Havana, 21.V.1895, C.A. Hart, Ac.# 13304, 1 L (INHS); nr. Havana, Quiver Chute, 1.VI.1895, C.A. Hart, Ac.# 13335, 1 F exuviae (INHS); Havana, Sta. D, east shore river on Coopers Id., 8.V.1894, C.A. Hart, et al., 1 L, (INHS); **INDIANA**: Harrison Co., Buck Cr., 1 mi S. New Middletown, 11.V.1973, A.V. Provonsha & K. Black, ACC-484 P-54, 1 L (PERC); Little Indian Cr. 3 mi E. Corydon, 10.V.1973, A.V. Provonsha & K. Black, P-53 ACC-48, 32 L (PERC); LaGrange Co., outlet creek 100 yds N. Fish Lake, 20.V.1972, 1 L (PERC); Martin Co., White R. at Hindostan Falls Pub. Fishing Sight, 6.V.1974, A.V. Provonsha & L. Dersch, P136 ACC-475, 10 L (PERC); **KENTUCKY**: Wayne Co., Little South Fork Cumberland River 1.8 km SE Pisgah at bridge on KY 167, KC02WAY, 7.VI.1978, KNPC, 2L (PERC); **MAINE**: Franklin Co., North Branch Dead River at Rt 27, Eustis, 20.VI.1986, SKB, 6 L (UMDE); Hancock Co., Mount

Desert Island, Seal Cove Pond, 28.V.1987, SKB, 3 L (UMDE); Hancock Co., Mount Desert Island, Aunt Betty Pond, 25.V.1987, SKB, 3 L (UMDE); PENOBSCOT CO., St. Poshaw Lake at Cooks Landing, 25.V.1986, SKB, 4 L (UMDE); Sandbank Stream, trib of Penobscot R., 30.IX.1981, ACG & DHF, 1 L; WALDO CO., St. George River at Rts. 220 & 173, , below spillway, 18.VI.1986, SKB, 1 L (UMDE); **NORTHWEST TERRITORIES**: McLean's Bay, adjacent to Great Slave Lake, 24.VII.1990, G.F. Edmunds, Jr., 1 Fexuviae (G.F. Edmunds' personal collection); **QUEBEC**: Wakefield, Gauvreau Lake, 13.VI.1930, J. McDunnough, 2 M exuviae (CNC); Montreal, Grand Lac Jacques-Cartier, B.G. #121, 13.VII.1938, C.G., 2L (INHS); **WISCONSIN**: LaGrange, 21.V.1938, Ross & Burks, 5 L (INHS); same, 31.V.1938, 1 L (INHS).

Range.—Eurylophella temporalis, as recognized herein, has a very broad range in the north. It has been collected from New Brunswick and Quebec in the east. Exuviae from a female larva collected by Dr. G.F. Edmunds, Jr. from the vicinity of Great Slave Lake, N.W.T. represents the westernmost record for the species, and the northernmost record for the genus. East of the Appalachians, the species is probably not found south of Pennsylvania. The southern limit of its range west of the Appalachians is unclear (see discussion below).

Discussion.—Eurylophella temporalis was described by McDunnough (1924) from male and female imagos collected in Ontario and Massachusetts. He later (McDunnough 1931a) described the larva from reared material collected in Ontario and Quebec.

Eurylophella temporalis, *E. poconoensis*, and *E. doris* are genetically distinct (Funk et al. 1988), but difficult to distinguish with certainty on the basis of morphology. *Eurylophella temporalis* larvae from the northern and eastern parts of its range always have long occipital tubercles. This condition, combined with its larger size and more slender fore femora, should aid in distinguishing *E. temporalis* from *E. poconoensis*, which is sympatric (at least in northeastern Pennsylvania). *Eurylophella doris* is also large and has long occipital tubercles, and is therefore is only separable by minor differences in the shape of the fore femora and the length of the posterolateral projections on segments 2 and 3 (see key). However, *E. temporalis* and *E. doris* are apparently parapatric, with *E. doris* replacing *E. temporalis* in the area east and south of the Appalachians, from Virginia, Maryland and Delaware south. Unfortunately, we have no electrophoretic data for populations west of the Appalachians, so we cannot be certain about the identity of specimens from the southwestern extremes of the range as reported by Allen and Edmunds (1963) (i.e., Missouri, southern Illinois and Indiana). We have examined specimens from southern Indiana and Illinois, presumed to be *E. temporalis*, which are quite different from northern and eastern specimens. As compared with typical northern specimens many of these have small occipital tubercles, broad fore femora (see Fig. 74b), widely spaced submedian tubercles on abdominal segments (see Fig. 75b, Fig. 73b) with those on 7 being unusually long (TL_7 as high as 0.35), and long posterolateral projections on segments 2 and 3 (see Fig. 76a and b). Although the submedian tubercles are more widely spaced than typical *E. temporalis*, the ratio of spacing on segment 2 to that on 7 (Fig. 73a) is similar to that found in northern and eastern populations. It is presently unclear whether these specimens represent aberrant (and presumably isolated) populations of *E. temporalis*, or an undescribed species. For the present, we consider them *E. temporalis*.

Like *E. doris*, both *E. temporalis* and *E. poconoensis* larvae are typically dark brown dorsally with pale speckling (see Figs. 18, 48, 60). However, most *E. doris* populations contain individuals with a distinctive, contrasting pattern, with bands

of alternating dark and light coloration. In these individuals the mesonotum is dark anteriorly, light in the middle, and dark again posteriorly, and abdominal terga 2, 3, 5-7, and 9 have extensive dark mottling, the other segments remaining mostly pale, as in Plate 38 of Traver (1935). We have not seen this pattern in *E. temporalis* or *E. poconoensis*, but like *E. doris*, populations of these two often contain some individuals with a prominent pattern of longitudinal stripes, consisting of a pale median stripe, sometimes bordered by a dark stripe on either side.

Eurylophella temporalis is commonly found in the shallow margins of lakes and in slow-flowing or impounded reaches of rivers in the northern part of its range. In the southern part of its range it tends to be restricted to lentic habitats.

Lutulenta Species Group

This group includes three eastern North American species, *E. lutulenta* (Clemens), *E. aestiva* (McDunnough), and *E. enoensis* NEW SPECIES. In these species the dorsal subdivisions of the ventral lamella of the gill on segment 4 are reduced in number (usually to two to four, sometimes as many as five) and size (to about half the size of the ventral subdivisions; see Fig. 2b), but are always clearly visible under moderate magnifications (50X) in full-grown larvae. The spacing between submedian tubercles on segment 2 is rather wide (as in the *temporalis* and *funeralis* groups, but in contradistinction to the *bicolor* group; see Fig. 75b). Unlike members of the *temporalis* group, the spacing of the tubercles remains rather wide toward segment 7 (see Fig. 73b), so that the rows of submedian tubercles usually appear subparallel (in *E. aestiva* and *E. enoensis*) or slightly divergent (*E. lutulenta*). The ratio of the distance between tubercles on segment 2 to that on segment 7 is usually about 1.0 in *E. aestiva*, and somewhat less in *E. lutulenta* and *E. enoensis* (see Fig. 73a). In *E. lutulenta* longitudinal ridges on tergites 5 to 7 form the bases of the submedian tubercles (similar to the *temporalis* group), but these are absent in *E. aestiva* and *E. enoensis*. The posterolateral projections on segment 9 are long (especially in *E. aestiva*) compared to the *funeralis* and *bicolor* groups (Fig. 75a). The fore femora are on average broader than those of other groups, especially members of the *temporalis* group (Fig. 74b). Markings on the larval sterna (submedian dots, oblique paramedian dashes, and longitudinal sublateral maculae) are, when present, usually inconspicuous, brown, and not contrasting sharply with the pale ground color. The tips of the posterolateral projections of the abdomen are often brown-tipped in *E. lutulenta* and *E. enoensis*, as is typical of species in the *bicolor* group. Species of the *lutulenta* group are medium or large-sized (Fig. 74a).

Eurylophella aestiva (McDunnough)

Figures 2b, 3-7, 72e

Ephemerella aestiva McDunnough, 1931a: 64, 6 figs.; Traver 1935: 580; Burks 1953: 75; Allen and Edmunds 1963: 607, 5 figs.

Larva.—Length: 6.4-8.1. Head: occipital tubercles well developed in both sexes (Fig. 4-5). Thorax: fore femora broad, average ratio of width to length (FWL_1) = 0.50, range 0.45-0.55. Abdomen: Rows of submedian tubercles subparallel on 2-7 (Fig. 3). Average $ITD_{2:7}$ = 0.98, range 0.82-1.14. Average $ITD_{4:7}$ = 0.99, range 0.85-1.13. Tubercles on segment 2 rather widely spaced (average SMT_2 = 0.70, range 0.58-0.97). Spacing on tubercles of segment 1 variable, but often slightly narrower on segment

2 (average SMT_1 = 0.60, range 0.43-0.76; Fig. 3). Space between tubercles on segment 7 slightly less than length of segment at midline (average SMT_7 = 0.89, range 0.79-1.12). Tubercles on 1-4 rather long, straight and often somewhat pointed (Fig. 72e), with sparse fine setae, sometimes mixed with coarse, flattened scale-like setae. Tubercles on 5-7 long and sharp, with conspicuous flattened scale-like setae. Average TL_7 = 0.32, range 0.22-0.43. Tubercles on 8 and 9 short and sharp. Average MLT_{2-7} = 1.27, range 1.17-1.44. Posterolateral projections on 2 and 3 small but distinct (Fig. 7). Average PLP 2 = 0.09, range 0.02-0.14; PLP_3 = 0.21, range 0.12-0.32. Posterolateral projections on 9 long, PLP_9 = 0.73, range 0.64-0.83. Gill 4 with dorsal subdivisions of the lower lamella somewhat smaller than ventral subdivisions, and reduced in number (usually to two; see Fig. 2b).

Material Examined.—Type series: Holotype male with larval exuviae (CNC # 3213), **QUEBEC**: Vaudreuil (elev. 71 ft., 45°24'02"N, 74°01'20"W), 12.VII.1930, G.S. Walley; 4 paratypes, male larval exuviae, same data as holotype, 10.VII.1930.

Larval exuviae vouchers from electrophoretic survey [see Table 1 in Funk et al. (1988; *E. aestiva* and *E. aestiva-A*)]: 155 from New York, Pennsylvania, Delaware, Virginia, and North Carolina.

Additional reared material (larval exuviae in alcohol, imagos frozen): 85 M, 69 F, from New York, Pennsylvania.

Slide mounts of larval exuviae: **PENNSYLVANIA**: 2 M, 1 F, Delaware Co. Delaware R. at Dillontown, 41°52'02"N, 75°15'50"W, 25.VI.1985 to 2.VII.1985, DIR & DHF; 2 M, 1 F, Wyoming Co. Meshoppen Cr., 41°36'45"N, 76°00'58"W, 1-24.VII.1985, DIR & DHF; 1 M, 3 F, Chester Co., White Clay Creek, 39°51'47"N, 75°47'07"W, 2-6.VII.1985, DHF; **DELAWARE**: 2 M, 1 F, New Castle Co., Blackbird Cr., 39°21'18"N, 75°40'55"W, 18.VI.1985 to 10.VII.1985, DHF; **VIRGINIA**: 1 M, 1 F, Rappahannock Co., Jordan R., 38°45'51"N, 78°02'04"W, 4-12.VII.1985, DIR & DHF; **NORTH CAROLINA**: 1 M, 2 F, Randolph Co., Uwharrie R., 35°38'30"N, 79°58'00"W, 4-14.VII.1985, DIR & DHF.

Other larval material: **DELAWARE**: Kent Co., Pratt Branch, Spring Cr., 2.5 mi E of Felton at Rd388, 39°00'37"N, 75°31'47"W, 3.VI.1981, DHF, 5 L; New Castle Co., West Cr., near Newark, 7.VI.1951, T. Dolan, 1 L; **INDIANA**: Harrison Co., Blue R. 1 mi E White Cloud, MP-74, 21.VI.1972, A.V. Provonsha, E. Levine, 1 L (PERC); **KENTUCKY**: Breathitt Co., Buckhorn Cr. 0.4 mi NE KY 470 at bridge over creek, KK02BRE, 19.VI.1978, KNPC, 5L (PERC); Jackson Co., Horse Lick Cr., 2.2 km NE Rockcastle/Jackson Co. line at bridge on KY 1955, KC01JAC, 3.VII.1978, KNPC, 14L (PERC); Lee Co., Sturgeon Cr. 1.1 mi N of Lee/Owsley Co. line at KY 587 bridge, KK01LEE, 3.VII.1978, KNPC, 6L (PERC); McCreary Co., Beaver Cr. at US Forest Service Rd. #51, Beaver Cr. Wilderness Area, KC03MCY, 4.VII.1978, KNPC, 6L (PERC); Perry Co., Troublesome Cr. at Home Place Community Center on KY 476, 1.0 mi NE of jct of KY 476 and KY 28, KK01PER, 20.VI.1978, KNPC, 3L (PERC); Pulaski Co., Buck Cr. 3.3 km N of US 80 on KY 1667, KC01PUL, 13.VI.1978, KNPC, 1L (PERC); Rockcastle Co., Trace Branch off US 490 at 1st bridge W Lamera on Wattle Road, KC01ROC, 5.VII.1978, KNPC, 3L (PERC); Rowan Co., N. Fk. Triplett Cr., 5.7 mi NNE on KY 377 from jct. with KY 32, KL01ROW, 2.VI.1978, KNPC, 1L (PERC); Wayne Co., Little South Fork Cumberland River, Ford at Ritner, KC01WAY, 9.VI.1978, KNPC, 2L (PERC); **MAINE**: Penobscot Co., Swift Brook, 0.8 mi W of Stacyville, 45°51'50"N, 68°31'23"W, 28.VI.1982, ACG, 2 L; **MISSOURI**: Iron Co., Strother Cr., T33N R1W S35, BMS-2, 13.VI.1979, L. Trial, 1 L (UMRM); same, BMS-3, 13.VI.1979, L. Trial, 3 L, (UMRM); Carver Cr., T32N R3E S34, 17.V.1979, L. Trial, 1 L; Shannon Co., Mahans Cr., T29 R4W S27 SW1/4, JFM-1, 29.VI.1981, L. Trial, 1

L (UMRM); **NEW YORK**: DELAWARE CO., Beaver Kill, 1 mi W of Horton, 41°58'18"N, 75°02'23"W, 26.VII.1983, PJD & JWP, 1 L; **PENNSYLVANIA**: CHESTER CO., E. Br. White Clay Cr. at New Garden Station Rd., below Avondale, 2.VI.1989, DHF, 2 L; Pickering Cr., 1.3 mi WNW of Charlestown below Rd15046, 40°06'09"N, 75°34'39"W, various dates—1980-1981, PJD, CED, CFB & DIR, 15 L, 19 M, 21 F, with exuviae; MONTOUR CO., Chillisquaque Cr. above Montour Power Plant, 41°04'50"N, 76°40'09"W, various dates—1987, DIR, 7 L; Chillisquaque Cr. below Montour Power Plant, 41°04'00"N, 76°40'35"W, various dates—1987, DIR, 7 L; Chillisquaque Cr., near Washingtonville, 41°03'24"N, 76°40'48"W, various dates—1987, DIR, 23 L; NORTHUMBERLAND CO., Chillisquaque Cr. near Potts Grove, 40°57'30"N, 76°46'44"W, various dates—1987, DIR, 44 L; PIKE CO., Lake Wallenpaupack near Ledgedale (trib. of Lackawaxen River), 41°21'54"N, 75°18'02"W, 16.VI.1985, DHF & DIR, 5L; WAYNE CO., Delaware River at Dillontown, 41°52'02"N, 75°15'50"W, various dates—1982-1983, DHF, DIR & JWP, 7 L; West Branch Delaware River 1.3 mi NE of Deposit, 42°04'38"N, 75°24'21"W, 28.VIII.1984, DIR, 1 L; **TENNESSEE**: HARDIN CO., Cat. No. 6-956-2, 9.VI.1956, L. Berner No. 3896.2, 1 L (FAMU); **VIRGINIA**: BEDFORD CO., Big Otter River, on CR670, 0.4 mi N jct Hwy 221, 37°22'14"N, 79°25'14"W, 2.VII.1980, S. Parrish, 1 L; BUCKINGHAM CO., Slate River at Rt 24, 5 mi SW of Mt. Rush, 37°28'28"N, 78°39'27"W, various dates—1981-1983, ACG, JWP & MBG, 27 L; FAUQUIER CO., Thumb Run at Rd770, 1.15 mi NW of Orlean, 38°45'47"N, 77°58'51"W, 12.VI.1981, JWP, 3 L; RAPPAHANOCK CO., Thornton River, 6.2 mi S of Ben Venue, above Rt 729, 38°37'45"N, 78°04'00"W, various dates—1980-1981, CED, 9 L, 1 M with exuviae; WASHINGTON CO., S. Fk. Holston River at Wright Bridge on Rt. 91, Damascus, 9.VII.1980, J.W. Richardson, 10 L.

Range.—*Eurylophella aestiva* is common and widespread from southern Quebec and Ontario to North Carolina east of the Appalachians (Funk et al. 1988; Fig. 1). West of the Appalachians we have seen material from Tennessee, Indiana and Missouri.

Discussion.—McDunnough (1931a) described this species from reared material collected in Quebec. Although he was unable to reliably distinguish the adults from those of *E. bicolor*, the larvae were distinct. He remarked that a distinctive feature of *E. aestiva's* biology was its late (seasonal) emergence period. We have confirmed McDunnough's observations on *E. aestiva's* seasonality throughout its range (see Fig. 78).

Funk et al. (1988) found evidence for the existence of morphologically cryptic species within what we here consider *E. aestiva*. One population (referred to as *"E. aestiva-A"*, from White Clay Creek, Chester Co.,Pennsylvania, USA; 39°51'47"N, 75°47'07"W) exhibited fixed allelic differences at two enzyme loci and significant differences at two others. We have found no morphological features with which this form may be distinguished from the other populations of *E. aestiva*. As it is only known from a single population that was not sympatric (i.e., not occurring in the same stream) with typical *E. aestiva*, by the criteria outlined above (see *Basis for determination of species boundaries* in Methods section) we conservatively consider these to be conspecific with *E. aestiva* for the present treatment. However, the six populations of typical *E. aestiva* included in our electrophoretic survey, ranging from New York to North Carolina, were quite uniform genetically, and should additional populations of *"E. aestiva-A"* be discovered, especially if found in the same stream with typical *E. aestiva*, this form would be considered worthy of specific status.

The larvae of *E. aestiva* are easily distinguished from all other *Eurylophella*

species by characters given in the key. In combination, the subparallel rows of submedian tubercles on the abdomen, long posterolateral projections on segment 9, well developed occipital tubercles, and the broad femora, as well as the conspicuously late seasonal nature of this species make it one of the most distinctive species in the genus. The suggestion by earlier authors (Allen and Edmunds 1963, McDunnough 1931a) that *E. aestiva* is closely related to *E. bicolor* or *E. verisimilis* seems to have been based primarily on similarity in size. On the basis of characters of the 4th gill, the spacing of abdominal tubercles and the shape of segment 9, we believe the species more properly belongs with *E. lutulenta* and *E. enoensis.*

Eurylophella aestiva is characteristically found in small or medium-sized streams (~3rd order) to large rivers (~8th order). In the northern part of its range *E. aestiva* often coexists with *E. verisimilis, E. macdunnoughi, E. bicolor,* and *E. minimella,* and sometimes *E. bicoloroides.* In the southern part of its range it may be found with *E. doris* or *E. enoensis.* Its larvae do not appear until late spring or early summer, and it is always the last *Eurylophella* species to begin adult emergence (see Fig. 78). It is apparently not found in lakes.

Eurylophella enoensis Funk New Species

Figures 23-27, 72g

Ephemerella coxalis McDunnough, 1931a: 37, 3 figs. (in part); Traver 1935: 589 (in part); Burks 1953: 73, 1 fig. (in part); Allen and Edmunds 1963: 617, 1 fig. (in part).

Larva.—Length: 8.3-10.5. Head: occipital tubercles medium-sized and conspicuous in both sexes (Figs. 24-25). Thorax: fore femora broad, average ratio of width to length (FWL_1) = 0.46, range 0.38-0.49. Abdomen: Rows of submedian tubercles subparallel or slightly divergent from segment 2-7 (Fig. 23). Average $ITD_{2:7}$ = 0.88, range 0.71-1.07. Average $ITD_{4:7}$ = 1.00, range 0.82-1.14. Tubercles on segment 2 rather widely spaced (average SMT_2 = 0.73, range 0.59-1.00). Spacing of tubercles on segment 1 slightly narrower than on segment 2 (average SMT_1 = 0.67, range 0.54-0.86; Fig. 23). Distance between tubercles on segment 7 subequal to or greater than the length of segment at midline (average SMT_7 = 1.05, range 0.92-1.31). Tubercles on 1-4 short to medium in length, very blunt, and erect (Fig. 72g), with sparse fine setae and usually without coarse, flattened scale-like setae. Tubercles on 5-7 sharp, with numerous fine setae and a few coarse, flattened scale-like setae, the latter restricted to the bases of the tubercles. Tergites 5-7 without distinct ridges forming the base of the tubercles (Fig. 26), but with abundant and conspicuous flattened scale-like setae scattered evenly in submedian areas to the bases of tubercles. Average TL_7 = 0.29, range 0.21-0.36. Tubercles on 8 and 9 small, often inconspicuous. Average $MLT_{2:7}$ = 1.29, range 1.11-1.50. Posterolateral projections on 2 and 3 rather large (Fig. 27). Average PLP_2 = 0.16, range 0.09-0.25; PLP_3 = 0.32, range 0.27-0.38. Posterolateral projections on 9 long, PLP_9 = 0.62, range 0.49-0.71. Gill 4 with dorsal subdivisions of the lower lamella smaller than ventral subdivisions, and reduced in number (usually from two to five, compared with about nine ventral subdivisions; see Fig. 2b).

Male Imago. (in alcohol) Length: body 7.5-10.2, forewing 8.2-11.0. Head light brown with variable black maculations. Upper portion of compound eye reddish-orange in life. Two general patterns of body coloration are found: one is light brown covered with black speckling, the other is light to dark brown without speckling. The presence or visibility of other maculation depends on whether or not there is

speckling. In speckled individuals the thorax is light brown with speckling, the legs are pale yellow with speckling, and with faint indications of dark apical banding. The terga are light brown with extensive black speckling, and with large submedian black maculations on 6 and 7. The sterna are paler, with dense black speckling. In non-speckled individuals the thorax is uniform brown to dark brown, the legs are pale yellow with faint dark apical bands on the femora and also on each tarsomere of the middle and hind legs. The terga are light to dark brown with blackish submedian stripes (delineating a paler median area), often with another very thin or broken dark median stripe, and with variable sublateral dark maculation, especially on segments 2-4. The sterna are pale with black submedian dots and paramedian dashes. Genitalia typical for the genus, with a rather narrow subapical median excavation and a conspicuous median tubercle on the subgenital plate, but generally not distinguishable from other species. The tails of both speckled and non-speckled individuals are pale with conspicuous dark annulation at the apex of each segment.

Female Imago. (in alcohol) Length: body 8.6-10.3, forewing 9.8-10.8. Otherwise similar to male except for the usual sexual differences.

Material Examined.—

Holotype: Reared male imago (SWRC no. EL A 01), **NORTH CAROLINA**: Orange Co., West Fork Eno River at Rd 1004, 2.1 miles south of Cedar Grove (elev. 580 ft., 36°08'21"N, 79°10'13"W), collected as larva 10.III.1986, DHF, reared at SWRC (tray 502), emerged 12.IV.1986. Larval exuviae and imaginal segments 9 and 10 on slide (balsam). Remainder of imaginal abdomen in alcohol (head and thorax were used for electrophoresis). Deposited at the Academy of Natural Sciences of Philadelphia.

Paratypes: Reared male imago (SWRC no. EL TUR 01), **SOUTH CAROLINA**: Edgefield Co., Turkey Creek, 9.5 miles northwest of Edgefield, Sumter National Forest (elev. 265 ft., 33°47'44"N, 82°03'56"W), collected as larva by WLH, LSD, and MKB, emerged in laboratory (SWRC tray SC124) on 9.IV.1981. Larval exuviae and imaginal segment 9 on slide (balsam), remainder in alcohol; Three males, one female, reared, same data, emerged (SWRC tray SC115) on 14.IV.1981, in alcohol, including larval exuviae (deposited at ANSP); Three larvae, 1 male, 2 female, same data, MKB, 16.III.1981.

Larval exuviae vouchers from electrophoretic survey [see Table 1 in Funk et al. (1988; as *E. sp. 1*)]: 1 from North Carolina (Holotype).

Slide mounts of larval exuviae: **NORTH CAROLINA**: 1 M (Holotype); **SOUTH CAROLINA**: 1 M (Paratype), 1 F, same data.

Other larval material: **KENTUCKY**: Bell Co., Clear Cr. at US Hwy 25E below Falls, M-335, 3.V.1982, W.P. McCafferty & A.V. Provonsha, 1L (PERC); Carter Co., Tygarts Cr. at jct KY 1662 and US 60, KT01CAR, 17.IV.1978, KNPC, 2L (PERC); Clay Co., Goose Cr. at confl. with Mud Lick Cr. at Lipps, KK01CLA, 17.X.1978, KNPC, 1L (PERC); Lee Co., Sturgeon Cr. 1.1 mi N of Lee/Owsley Co. line at KY 587 bridge, KK01LEE, 19.X.1978, KNPC, 1L (PERC); Lewis Co., Indian Cr. 67m upstream from Kinniconick Cr. confluence, 0.6 km SE KY 344/377 jct., KO01LEW, 6.X.1983, KNPC, 1L (PERC); **MISSOURI**: Franklin Co., Bourbeuse River, near Union, 30.IV.1963, D. Ramsey, 1L (UMRM); Iron Co., Big Cr., SFB-2A, T33N R3E S.35, 30.XI.1979, L. Trial, 2L (UMRM); **NORTH CAROLINA**: Orange Co., Eno River at end of Rd 1568, 6.5 mi east-southeast of Hillsboro (elev. 365 ft., 36°02'42"N, 78°59"23"W), 11.XI.1981, ACG, 2 L; West Fork Eno River at Rd1004, 2.1 mi SSW of Cedar Grove, 36°06'21"N, 79°10'13"W, 22.III.1988, DHF & DIR, 1 L; **ONTARIO**: Rideau River, Ottawa,

17.V.1928, Adams & Brown, 1L (CNC); **SOUTH CAROLINA**: EDGEFIELD CO., Turkey Creek, 9.5 miles northwest of Edgefield, Sumter National Forest, 33°47'44"N, 82°03'56"W, 9.IV.1981, WLH, LSD, & MKB, 2 M subimagos with exuviae, 3 F subimagos with exuviae; same, 14.IV.1981, 1 M subimago, 2 F imagos, all reared; same, 9.IV.1981, 1 L; same, 19.X.1981, 13 L; same, 18.XII.1980, 1 L; same, 6.II.1981, 1 L; same, 30.I.1981, 1 L; same, 23.II.1981, 4 L; same, 17.II.1981, 2L; same, 3.XII.1981, 2 L; same, 5.XI.1981, 3 L; same, 15.I.1982, 2 L; same, 23.II.1981, 3 L; same, 5.XII.1980, DHF, 11 L.; **TENNESSEE**: DAVIDSON CO., Buffalo Creek, Newsome Sta., 24.V.1945, M. Wright, 11L, (FAMU; L. Berner No. 2059.0).

Range.—Eurylophella enoensis is apparently wide-ranging, though infrequently collected. McDunnough's (1931a) "*E. ?coxalis*" was from southeastern Ontario, and subsequent reports include Quebec, Maine, Nova Scotia, Indiana, Tennessee, Georgia and North Carolina. In addition to the type locality in North Carolina, we have specimens from South Carolina, and have seen specimens from Tennessee and Missouri.

Discussion.—The larva of *E. enoensis* is morphologically indistinguishable from the larva referred to as "*E. ?coxalis*" by McDunnough (1931a). *Eurylophella coxalis* (McDunnough) was originally described in 1926 from adult males and females collected in Quebec. McDunnough later (1931a) described a single partially grown larva which he tentatively associated with *E. coxalis*. The basis for this association was circumstantial; *E. coxalis* was the only species of McDunnough's *bicolor* group (= *Eurylophella*) whose larva was still unknown, and had been collected near where the larva in question was found. We have examined this larva as well as the adult types of *E. coxalis*. It appears from the developmental stage of the larva (about 7.5 mm long when killed) that when full-grown its length would be at least 9 millimeters, considerably larger than the adult size of *E. coxalis*, whose larvae we predict would be only about 7 millimeters when full-grown. On the basis of size and structural similarity, we believe McDunnough's *E. ?coxalis* larva is conspecific with our *E. enoensis*. However, we feel justified in considering the species as new because the adults of *E. enoensis* that we have reared are quite distinct morphologically from McDunnough's *E. coxalis*.

Eurylophella enoensis is similar to *E. lutulenta* in many respects, including the presence of black speckling in some specimens, both larval and adult. Such speckling had previously been thought to be unique to *E. lutulenta*. Larval *E. enoensis* can be distinguished from *E. lutulenta* by the absence of ridges forming the bases of the submedian tubercles on segments 5-7 and the distinctly larger occipital tubercles. It also averages slightly smaller in size, and, as mentioned by McDunnough (1931a), the posterolateral projections on segments 4-7 are noticeably longer and thinner than those of *E. lutulenta*. The latter difference is quite apparent when specimens of the two are directly compared (see figures 23 vs. 33), but is difficult to quantify and is not useful as a key character.

A series collected in central Tennessee (see "material examined" above) are aberrant in several respects (see outliers in Figs. 73-77): the posterolateral projections on segment 9 are short, SMT_2 is high, the femora are slender, the submedian tubercles on segments 1 to 4 are long, faint ridges are present at the base of the submedian tubercles on segments 6 and 7 on some specimens, and full-grown larvae were collected at what would appear to be very late in the season for *E. enoensis*. The ridges on 6 and 7 are almost as well developed as in *E. lutulenta* in a few of the specimens, but all other characters are closer to *E. enoensis*. These specimens may eventually prove to be another, perhaps new, species. For now we

consider them *E. enoensis*.

Unlike *E. lutulenta*, whose subimagos have distinctively mottled wings, the *E. enoensis* subimagos that we have seen all have uniform dark slate to black colored wings, like all the other eastern *Eurylophella* species.

In Funk et al. (1988) *E. enoensis* was represented by a single specimen (the holotype), which we referred to as "*E. sp. 1* (near *coxalis*)". Caution must be exercised when basing conclusions on the electrophoresis of a single individual, but this one was so different from all other eastern species that our genetic distance estimates would probably not change significantly had we been able to electrophorese a larger sample (see discussion in Funk et al. 1988). Although from a morphological point of view *E. enoensis* and *E. lutulenta* appear quite similar, our estimate of Nei's (1978) genetic distance between these two was higher (1.25) than for any other pairwise comparison with *E. enoensis*.

In contrast to univoltine populations of other *Eurylophella* species we have studied, both *E. lutulenta* and *E. enoensis* appear to complete a significant portion (often half or more) of their growth in the fall, and subsequently complete their development in early spring (see Fig. 78). Other univoltine populations of *Eurylophella* generally enter winter as very small larvae, completing 90% or more of their growth in spring or summer.

Etymology. This species is named for the type locality, the Eno River in North Carolina.

Eurylophella lutulenta (Clemens)

Figures 33-37, 72f

Allied to *Ephemerella*, Nymph No. 5 Eaton, 1884: 133 pl 40, 64; Lestage 1924: 44; Tiennsuu 1935: 22.

Ephemerella lutulenta Clemens, 1913: 335 (in part); Clemens 1915: 121, 1 fig. (in part); McDunnough 1924: 74; McDunnough 1925: 212; McDunnough 1931a: 32, 6 figs.; McDunnough 1931a: 32 (= *lineata* Clemens); Traver 1935: 609; Burks 1953: 72, 3 figs.; Allen and Edmunds 1963: 618, 6 figs.

Ephemerella lineata Clemens, 1913: 336, 1 fig. (in part); Clemens 1915: 122 (in part).

Larva.—Length: 9.3-11.7. Head: occipital tubercles in males small (Fig. 34) to almost nonexistent, very small in female (Fig. 35). Thorax: fore femora broad, average ratio of width to length (FWL_1) = 0.45, range 0.42-0.49. Abdomen: Rows of submedian tubercles slightly divergent from segment 2-7 (Fig. 33). Average $ITD_{2:7}$ = 0.80, range 0.74-0.84. Average $ITD_{4:7}$ = 0.97, range 0.90-1.02. Tubercles on segment 2 rather widely spaced (average SMT_2 = 0.72, range 0.68-0.81). Spacing of tubercles on segment 1 slightly narrower than on segment 2 (average SMT_1 = 0.72, range 0.56-0.84; Fig. 33). Distance between tubercles on segment 7 always greater than the length of segment at midline (average SMT_7 = 1.12, range 1.04-1.14). Tubercles on 1-4 short and somewhat compressed laterally, appearing quite blunt in side view, and directed posteriad (Fig. 72f), with abundant fine setae mixed with a few coarse, flattened scale-like setae. Tubercles on 5-7 sharp, with distinct ridges on tergites forming the base of the tubercles on 5 or 6-7 (Fig. 36), and with conspicuous flattened scale-like setae and scattered fine setae on ridges and tubercles. Average TL_7 = 0.27, range 0.20-0.31. Tubercles on 8 and 9 usually inconspicuous. Average $MLT_{2:7}$ = 1.24, range 1.14-1.40. Posterolateral projections on 2 and 3 rather large (Fig. 37). Average PLP_2 = 0.14, range 0.08-0.20; PLP_3 = 0.32, range 0.25-0.35. Posterolateral projections on 9 long, PLP_9 = 0.65, range 0.58-0.73. Gill 4 with dorsal subdivi-

sions of the lower lamella smaller than ventral subdivisions, and reduced in number (usually from two to five, compared with about nine ventral subdivisions; see Fig. 2b).

Material Examined.—Type series: Holotype male (CNC #1216), **ONTARIO**: Go Home Bay, Georgian Bay, Lake Huron (elev. 581 ft., 44°59'40"N, 79°56'09"W), 29.V to 19.VI 1912, W.A. Clemens; F larval exuviae, same, 1.VI.1912.

Larval exuviae vouchers from electrophoretic survey [see Table 1 in Funk et al. (1988)]: 37 from Vermont.

Additional reared material (larval exuviae in alcohol, imagos frozen): 15 M,17 F, from Vermont.

Slide mounts of larval exuviae: **VERMONT**: 5 M, 3 F, Bennington Co., Emerald Lake, 0.5 mi north of Dorset (elev. 711 ft, 43°16'35"N, 73°00'16"W), coll 24.IV.1985, DIR & DHF, emerged in laboratory (SWRC tray # 312) 16-22.V.1985.

Other larval material: **MAINE**: Penobscot Co., Swift Brook, 0.8 mi west of Staceyville (elev. 375 ft, 45°51'50"N, 68°31'23"W), 22.X.1981, DHF, 1 L; **MICHIGAN**: Cheyboygan Co., Trout Cr., T.37N.-R.3W.-S.22, 29.V.1938, F.E. Lyman 267.4, 3L (FAMU; L. Berner No. 1263.17); **VERMONT**: Bennington Co., Emerald Lake, 0.5 mi north of Dorset (elev. 711 ft, 43°16'35"N, 73°00'16"W), 24.IV.1985, DIR & DHF, 24 L.

Range.—Eurylophella lutulenta has been reported from Wisconsin to New Brunswick, south to northwestern Arkansas, Tennessee and North Carolina. We have been unable to confirm any records south of about 43° N Latitude. At least some of the southern records represent *E. enoensis*.

Discussion.—Clemens (1913) described *E. lutulenta* from male and female imagos and larvae collected in the Georgian Bay region of Ontario. In the same paper he described *E. lineata* from a female imago and some larvae, distinguished from *E. lutulenta* by the presence of a conspicuous median stripe. McDunnough (1931a) found *E. lineata* to be a color variant of *E. lutulenta*, and synonymized the two. He also found that Clemens' collections of both species from the type locality included some *E. temporalis*.

Eurylophella lutulenta is the largest eastern species. Its large size, long posterolateral projections on 2 and 3, and the distinctive ridges on terga 5-7 forming the bases of the submedian tubercles distinguish *E. lutulenta* from other members of the *lutulenta* group.

There are some discrepancies in the literature regarding the size and shape of the submedian tubercles on abdominal segments 1-4 in *E. lutulenta*. In Burks' (1953) Fig. 158 (p. 63) these structures appear as long, tapering and dorsally arched in side view. McDunnough (1931a) in his key also indicates that the tubercles on 1-4 are "long, finger-like, tapering". However, Allen and Edmunds (1963; Fig. 36a) show the tubercles on segment 1-4 as being relatively short and slender. Clemens' material from the type locality, as well as our material from Maine and Vermont are more like Burks' Fig. 159 (*E. coxalis*) and our Fig. 72f; that is, short and very blunt. The confusion may result from the fact that these tubercles though short, are laterally compressed, so that they appear slender in dorsal view (our fig. 33) but short and blunt in lateral view. The inclusion of some *E. temporalis* (which do have long, arching tubercles on 1-4) in Clemens' original series may also have contributed to this confusion. Further confusion may be the result of inaccurate identifications by subsequent authors; we have seen specimens labeled *E. lutulenta* from several collections that are actually *E. funeralis*—this species does have long, slender, arching submedian tubercles. Specimens we have seen from Michigan

have tubercles that are longer than those we consider typical, but these are still blunt and stout in lateral view, and are laterally compressed. Allen and Edmunds' figure (1963; Fig. 36a) and our Fig. 72f represent the normal range of appearance for these structures in *E. lutulenta*.

As noted by McDunnough (1925, 1931a), the subimaginal wings of *E. lutulenta* are very distinctively colored. The ground color is tan, with most crossveins heavily margined in black, especially toward the outer margin where the marginal intercalaries are also margined with blackish and the blackish color tends to coalesce. The effect is a distinctive mottled appearance, quite different from any other eastern member of the genus (the subimagos of other species have unicolorous slate gray to flat black wings). The larvae of *E. lutulenta* often have a fine blackish speckling superimposed on a pale brown base color over the entire body (as is typically true of the imago).

The species most similar to *E. lutulenta* morphologically is *E. enoensis*. However, the distinct tergal ridges forming the bases of the submedian tubercles found on segments 5 or 6-7 in *E. lutulenta* (Fig. 33, 36) are absent in *E. enoensis*. Also, the occipital tubercles are distinctly smaller in *E. lutulenta*, and the rows of submedian tubercles on 2-7 are usually slightly divergent (rather than subparallel, as in *E. enoensis*).

Eurylophella lutulenta is typically found in lakes. It is the earliest emerging member of the genus in eastern North America (see Fig. 78). In contrast to most other eastern species of *Eurylophella*, *E. lutulenta* larvae appear to complete a large portion of their growth in the fall (sometimes one half or more; personal observation), thereby enabling completion of development in early spring. *Eurylophella enoensis* is similar in this respect, and both species can often be identified easily in the fall, when most other species are too small to be keyed.

Funeralis Species Group

Eurylophella funeralis (McDunnough) is so distinctive that we here consider it a group unto itself. Like members of the *bicolor* group, the dorsal subdivisions of the ventral lamella of gill 4 are quite reduced in *E. funeralis* (as in Fig. 2c), and are often difficult to see at all (occasionally larger; see *E. funeralis* description and discussion). However, in other respects *E. funeralis* is quite different from the *bicolor* group. The spacing between submedian tubercles on segments 1 and 2 is wider (see Fig. 75b). The spacing on segment 7 is relatively wide also, usually distinctly wider than the length of the tergite at midline (see Fig. 73b). Unlike any other species of *Eurylophella*, the rows of submedian tubercles usually appear to diverge from segment 1 to segment 4 or 5, then converge slightly toward segment 7 (Fig. 28). This condition is especially apparent in small larvae. The submedian tubercles on segments 1 to 4 are longer than in any other species (especially noticeable on 3 and 4; see Fig. 72h). This combination of tubercle length and spacing makes *E. funeralis* the most easily recognized of the eastern species, and individuals as small as one or two millimeters in length can be easily identified on this basis. There are no longitudinal ridges forming the bases of the submedian tubercles on segments 5 to 7. The shape of the posterolateral projections on segment 9 is unique (Fig. 28), and the posterolateral projections on segments 2 and 3 are the longest of any *Eurylophella*. Submedian dots and oblique paramedian dashes are usually absent from the larval sterna. Longitudinal sublateral maculae are often present, but these are usually not conspicuous, being light to dark brown in color. The tips of the posterolateral

projections of the abdomen are never conspicuously darker than basal areas, as is typical of the *bicolor* group. Conspicuously absent in *E. funeralis* is the array of dorsal color patterns found in most other species of *Eurylophella*; *E. funeralis* larvae are unicolorous brown, without conspicuous maculation aside from some banding on the legs and faint sublateral maculae on the sterna.

Eurylophella funeralis (McDunnough)

Figures 28-32, 72h

Ephemerella funeralis McDunnough, 1925:210, 2 figs.; McDunnough 1931a: 39, 4 figs.; Traver 1935: 599; Burks 1953: 75, 1 fig.; Allen and Edmunds 1963: 612, 4 figs.

Larva.—Length: 8.1-10.3. Head: occipital tubercles medium sized in male (Fig. 29), and female (Fig. 30). Thorax: fore femora of medium width, average ratio of width to length (FWL_1) = 0.41, range 0.38-0.45. Abdomen: Rows of submedian tubercles divergent from 1-5, parallel or slightly convergent from 5-7 (Fig. 28). Average $ITD_{2:7}$ = 0.85, range 0.73-1.00. Average $ITD_{4:7}$ = 1.11, range 0.90-1.33. Tubercles on segment 2 widely spaced (average SMT_2 = 0.72, range 0.63-0.79). Spacing of tubercles on segment 1 slightly narrower than on segment 2 (average SMT_1 = 0.65, range 0.57-0.80; Fig. 28). Distance between tubercles on segment 7 at least as great as length of segment at midline, usually distinctly greater (average SMT_7 = 1.17, range 1.00-1.43). Tubercles on 1-4 very long, arched, and rather thin (Fig. 72h), with a few scale-like setae and scattered fine setae. Tubercles on 5-7 medium sized, sharp, with scale-like setae and with few fine setae. Average TL_7 = 0.27, range 0.21-0.35. Tubercles on 8 and 9 conspicuous, longer than most other species. Average $MLT_{2:7}$ = 1.38, range 1.23-1.60. Posterolateral projections on 2 and 3 longest of the *Eurylophella* (Fig. 32). Average PLP_2 = 0.24, range 0.13-0.36; PLP_3 = 0.41, range 0.29-0.61. Posterolateral projections on 9 relatively short, PLP_9 = 0.54, range 0.40-0.66. Inner margin of posterolateral projections on segment 9 distinctly sinuate, with tips very acute and often slightly incurved (Fig. 28). The outer margins of segment 9 often rather straight and subparallel. Gill 4 with 2 to 5 dorsal subdivisions of the lower lamella, almost completely reduced in size (as in Fig. 2c), sometimes difficult to see. Occasionally, these subdivisions are larger, approaching the degree of development illustrated in Fig. 2b, but still restricted to the lateral margin.

Material Examined.—Type series: 1 female paratype (CNC # 1273), **QUEBEC**: Covey Hill, Allen's Brook, (elev. 56 ft., 45°01'09"N, 73°45'28"W), 23.VI.1924, G.S. Walley.

Larval exuviae vouchers from electrophoretic survey [Table 1 in Funk et al. (1988), with additional unpublished data]: 410 from Quebec, Maine, New Hampshire, Vermont, New York, Pennsylvania, Delaware, Ohio, West Virginia, Virginia, South Carolina, and Georgia.

Additional reared material (larval exuviae in alcohol, imagos frozen): 100 M, 619 F, from Quebec, Maine, Vermont, New Hampshire, New York, Pennsylvania, Delaware, Ohio, West Virginia, Virginia, North Carolina, South Carolina, and Georgia.

Slide mounts of larval exuviae: **QUEBEC**: 1 F, Saguenay Co., Trapper Cabin Cr., Rivière Matamec, 50°19'15"N, 65°57'38"W, 4.VII.1982, DHF; **VERMONT**: 1 M, Bennington Co., South Fork Goodman Brook, W Br. Batten Kill, 43°13'47"N, 73°07'11"W, 19.VI.1984, DHF; 1 F, Bennington Co., Batten Kill R. 1.6 mi W of West

Arlington on Rt 313, 43°06'04"N, 73°14'31"W, 26.V.1985, DIR & DHF; **PENNSYLVANIA**: 2 M, 2 F, Susquehanna Co., tributary of Wyalusing Cr., 3 mi W of Montrose, 41°49'11"N, 75°56'00"W, 3-28.VI.1986, DIR & DHF; 1 F, LSB1, 9.V.1986, DHF **VIRGINIA**: 1 M, 1 F, Tazewell Co., headwaters of Station Spring Cr, MBC Ranch, 37°05'14"N, 81°24'08"W, 24-29.V.1990, DHF; **WEST VIRGINIA**: 1 M, 1 F, Greenbriar Co., Hamrick Run, N. Fk. Cherry R., at Rt 55, 38°13'41"N, 80°24'04"W, 19-27.V.1990, DHF; 1 M, 1 F, Cabell Co., Hisey Fork of Fourpole Cr., 1 mi S of Huntington at Interstate Rt. 64, 38°23'18"N, 82°26'08"W, 9-29.V.1987, DHF.

Other larval material: **CONNECTICUT**: Fairfield Co., Indian Well Cr., Indian Well State Park, 3 mi NW Shetton, 20.V.1979, DHF, 16 L; **DELAWARE**: Kent Co., Pratt Branch, Spring Cr., 2.5 mi E of Felton at Rd388, 39°00'37"N, 75°31'47"W, 20.I.1981, D.H. Funk, 2 L; New Castle Co., Castle Cr, trib of Pike Cr, nr Limeric Circle subdivision, Linden Green II, 4.IV.1978, C.M.A., 7 L; **INDIANA**: Martin Co., Small stream 7 mi SE Shoals on Hwy. 150, P266 ACC-1966, 24.IV.1976, A.V. Provonsha & M. Minno, lab reared 1.V.1976, 1 M, 3 F with exuviae (PERC); Perry Co., Poison Cr., approx 5 mi NW Derby, P-330 ACC-2019, 19.V.1977, M. Minno & S. Yocom, 2 L (PERC); trib of Deer Cr. on St. Hwy. 66, 8 mi N of Brg. on Deer Cr., MP98 ACC-1731, 23.V.1973, W.P. McCafferty, K. Black & A.V. Provonsha, 1 L (PERC); Kraus Cr., CF-27 ACC-450, 6.V.1972, D. Lockwood, 1 L (PERC); **KENTUCKY**: Carter Co., Tygarts Cr. at jct KY 1662 and US 60, KT01CAR, 17.IV.1978, KNPC, 1L (PERC); Elliott Co., Ruin Cr. 0.7 mi N jct KY 556 and 755 at bridge on KY 556, KS01ELL, 4.X.1978, KNPC, 1L (PERC); Harlan Co., small trib of Poor Branch 4 mi W of cumberland at US Hwy 119, M-331, 2.V.1982, W.P. McCafferty & A.V. Provonsha, 2L (PERC); McCreary Co., Marsh Cr. 1.8 km S KY 1470 on Marsh Cr. Rd. at mouth of Privot Branch, KC02MCY, 4.V.1978, KNPC, 6L (PERC); Leslie Co., Greasy Cr. 1.5 mi above Chappell, KY post office on KY 2009, KK01LES, 10.V.1978, KNPC, 1L (PERC); Letcher Co., N. spring inlet to Kingdom Come at Kingdom Come St. Park, M-327, 2.V.1982, W.P. McCafferty & A.V. Provonsha, 5L (PERC); Powell Co., 0.9 mi SE of Bert T. Combs Parkway at bridge on Hatton Branch Rd., KK01POW, 25.V.1978, KNPC, 1L (PERC); **MAINE**: Franklin co., Carrabassett River at rest area on Rt. 16, 5.VIII.1992, 13 L; Penobscot Co., CRY3, various dates—1981-1982, ACG, DHF, JWP, DIR, MBG & MKB, 15 L; Sandbank Stream, Penobscot R., 30.IX.1981, ACG & DHF, 1 L; Piscataquis Co., trib of Abol Stream, Baxter State Park, 45°51'41"N, 68°57'36"W, various dates—1981-1982, ACG & DHF, 6 L, 2 M with exuviae; Nesowadnehunk Stream in Baxter State Park, 45°54'02"N, 69°02'22"W, various dates—1981-1982, ACG, DHF, JWP, DIR, MBG & MKB, 27 L; Piscataquis River, 3.7 mi SW of Monson, 45°14'30"N, 69°32'43"W, various dates—1981-1982, ACG, DHF, JWP, DIR, MBG & MKB, 10 L; Blanchard Plt., Blacksone Brook, 29.IX.1981, ACG & DHF, 12 L; **MARYLAND**: Allegany Co., small stream nr Little Orleans, Green Ridge State Forest, 30.IV.1978, DHF & ACG, 20 L; Frederick Co., small spring seep in Gambrill State Park, 6 mi W of Frederick, 27.IV.1978, DHF & ACG, 32 L; **NEW YORK**: Delaware Co., East Branch Delaware River, 0.8 mi SW of Downsville, 42°04'19"N, 75°00'25"W, various dates—1982, DHF, DIR, JWP & PJD, 8 L; East Branch Delaware River, 2.7 mi WSW of Shinhopple, 42°01'30"N, 75°07'14"W, 9.XI.1982, PJD & DIR, 1 L; Beaver Kill, 1 mi W of Horton, 41°58'18"N, 75°02'23"W, 20.IV.1982, JWP & DHF, 1 L; same, PJD, DIR & JWP, 1 L; West Branch Delaware River at Hale Eddy, 42°00'10"N, 75°23'03"W, 3.V.1982, PJD & JWP, 1 L;, Franklin Co., trib of St. Regis River 7 mi S of Santa Clara, 2.VI.1979, DHF, BWS & RLV, 4 L; Lewis Co., Pringle Cr, trib of Fish Cr. at Michigan Mills Rd, W. Turin Twp, 1.VI.1979, DHF, BWS & RLV, 7 L; St. Lawrence Co., trib of St. Regis River 3 mi SW of Hopkinton on Rt. 72,

2.VI.1979, DHF, BWS & RLV, 4 L; **NORTH CAROLINA**: Newfound Gap, 28.V.1934, T.H. Frison, 1 L (INHS); MACON CO., Big Cr., Cat. No. viii-1748-2, 17.VIII.1948, L. Berner No. 3168.10, 1 L (FAMU); Ashville, Shoapes Cr., Coweeta Hydrologic Area, 27.III.1979, CFB, 1 L; **OHIO**: LAWRENCE CO., 2nd order trib of Storms Cr, 1 mi E of Ellisonville, 38°36'23"N, 82°37'45"W, 29.IV.1978 (then reared 12.V to 25.V.1978), DHF & ACG, 19 M, 20 F with exuviae; same, 9.V.1979, DHF & BWS, 62 L; same, 10.III.1981, DHF, 20 L; WASHINGTON CO., trib of Baker Run, Moss Run, Little Muskingum R., 3.2 mi WSW Dart, 9.V.1979, DHF & BWS, 1 L; **ONTARIO**: MUSKOKA DIST. MUNICIPALITY, Harp Lake inlet 4, near Dorset, 45°23'N, 79°08'W, 11.VI.1985, D. Giberson, 7 L; **PENNSYLVANIA**: CARBON CO., trip of Hickory Run, Hickory Run State Park, 28.IV.1979, DHF & ACG, 26 L; CHESTER CO., W Fk, W Br McCorkles Rock Cr, 3.2 mi NW Unionville, 39°55'22"N, 75°46'43"W, 14.IX.1981, DHF & BWS, 2 L; trib of W Br. Brandywine Cr., 0.5 mi E of Northbrook, 39°55'10"N, 75°40'35"W, 15-24.V.1978, DHF, 8 L, 25 F with exuviae; Spring Cr., Buck Run, 3.5 mi NW Unionville, 39°55'17"N, 75°47'22"W, 24.V.1978, 3 F with exuviae; Pickering Cr., 1.3 mi WNW of Charlestown below Rd15046, 40°06'09"N, 75°34'39"W, 4.II.1980, CED & CFB, 1L; FULTON CO., 2nd order trib of Fortune Teller Cr., trib of Licking Cr., 1.2 mi ESE Hustontown at Pennsylvania Turnpike, 10.V.1979, DHF & BWS, 24 L; LEBANON CO., Haystack Cr., nr Green Point, 19.I.1975, DHF, 1 L; MCKEAN CO., trib of Kinzua Cr. ~10 mi N of Kane on Rt. 321, 17.IV.1979, DHF, 26 L; SUSQUEHANNA CO., tributary of Wyalusing Cr., 3 mi W of Montrose, 41°49'11"N, 75°56'00"W, various dates—1980 to 1982, ACG, DTM, DIR & DHF, 14 L, 2 m, 22 F, with exuviae; trib of Meshoppen Cr, 2 mi E of Dimock, 41°44'13"N, 75°51'36"W, various dates—1979-1980, ACG, DTM, PJD & DHF, 26 L, 2 M with exuviae; headwaters of Meshoppen Cr. at Rd T573, 30.V.1979, DHF, BWS & RLV, 4 L; trib of Meshoppen Cr. at Rd 57010, 31.V.1979, DHF, BWS & RLV, 25 L; Starrucca Cr. at Rt 296, 30.V.1979, DHF, BWS & RLV, 2 L; Butler Cr. at Gibson gauging station on Rt 547, 31.V.1979, DHF, BWS & RLV, 1 L; WAYNE CO., Delaware River at Dillontown, 41°52'02"N, 75°15'50"W, 3.V.1983, MBG, 1 L; WESTMORELAND CO., confl. Roaring Run and Pike Run, tribs of Indian Cr., 0.8 mi SE of Champion, 10.V.1979, DHF & BWS, 5 L; **QUEBEC**: Knowlton, Penney's Branch, 24.VI.1930, G.S. Walley & L.J. Milne, 1 L (CNC); SAGUENAY CO., Ruisseau du Cran Carré, above Rt 138, 50°17'35"N, 65°55'30"W, various dates—1982, JAG & DHF, 10 L; Rivière aux Loups Marins, above Rt. 138, 50°16'44"N, 65°43'12"W, 4.VII.1982, JAG, 3 L; Rivière Pigou above Rt. 138, 50°16'57"N, 65°38'31"W, various dates—1982, JAG & DHF, 5 L; **TENNESSEE**: GREENE CO., Camp Cr. nr. Mercer, 27.III.1946, M. Wright, 1 L, (FAMU; L. Berner No. 2016.1); Putnam Co., Meadow Cr., E. Br. Obey River, E. Monterey, 28.IV.1945, M. Wright, 1 L, (FAMU; L. Berner No. 2067.0); Meigs Co., Decatur Apr, Cat. No. 4-1154-1, 11.IV.1954, J. Pugh, 1 L, (FAMU; L. Berner No. 3419.1); **VERMONT**: BENNINGTON Co., Heinz Spring Brook, Battenkill, 26.XI.1979, CFB & ACG, 28 L; small stream in Hopgood Recreation Area, 2.VI.1979, DHF, BWS & RLV, 26 L; Batten Kill R. 1.6 mi W of West Arlington on Rt 313, 43°06'04"N, 73°14'31"W, 23.V.1980, ACG & DTM, 1 L; HAMILTON CO., small stream along Rt. 30, 100yds S of Franklin Co. line, 2.VI.1979, DHF, BWS & RLV, 24 L; **VIRGINIA**: BEDFORD CO., Hemp Mill Branch of Sheep Cr., CR686 2.5 mi NW jct CR688, 37°24'08"N, 79°39'02"W, various dates—1979-1981, S. Parrish, CED, CFB, PJD & DIR, 9 L; unnamed tributary of Sheep Cr., CR680 0.65 mi NW jct CR614, 37°24'58"N, 79°38'46"W, various dates—1979-1981, PJD, CFB, CED, DIR & DHF, 28 L, 1 F with exuviae; Sheep Cr., on CR614 0.7 mi N jct CR680, 37°25'21"N, 79°38'24"W, various dates—1979-1980, CFB, CED, PJD & DHF 31 L; Big Otter River, on CR670, 0.4 mi N jct Hwy 221, 37°22'14"N, 79°25'14"W,

6.XII.1979, CFB & CED, 2 L; same, 27.III.1980, PJD & DHF, 1L; GILES CO., Little Stony Cr., 2.6 mi S Kire at Rt 613, 37°24'15"N, 80°30'34"W, 11.III.1981, DHF, 1 L; Giles Co., Sinking Cr. 1.6 mi NW of Newport at Rt700, 37°18'41"N, 80°30'59"W, 11.III.1981, DHF, 24 L; FAUQUIER CO., Thumb Run at Rd770, 1.15 mi NW of Orlean, 38°45'47"N, 77°58'51"W, 24.IV.1981, JWP, 1 L; NELSON CO., Mill Cr. at Hwy 686, W of Montebello, 14.VIII.1979, BWS, DHF & CED, 3 L; South Fk Piney Cr., 14.VIII.1979, BWS, DHF & CED, 1 L; PATRICK CO., trib of Smith River, 2.7 mi W Jct 613 & 8, 29.VIII.1979, BWS, CED & B.A. Anderson, 7 L; RAPPAHANNOCK CO., Thornton River, on Rte 211, E of Thornton Gap, 17.VIII.1979, BWS, DHF & CED, 1 L; unnamed tributary of Hittles Mill Stream, on CR663 1.1 mi W jct CR628, 38°46'45"N, 78°08'29"W, 3.VI.1980, CFB & CED, 1 F with exuviae; same, 12.III.1981, DIR, 4 L; JOR2, various dates—1979-1981, CED, CFB, PJD & DIR, 14 L; Jordan River, on CR637 0.9 mi NNW jct CR647, 38°45'51"N, 78°02'04"W, 20.V.1980, 1 F with exuviae; **WEST VIRGINIA**: CABELL CO., Hisey Fork of Fourpole Cr., 1 mi S of Huntington at Interstate Rt. 64, 38°23'18"N, 82°26'08"W, 28.IV.1978 (adults reared 8.V to 1.VI.1978), DHF & ACG, 62 L, 44 M, 47 F with exuviae; MCDOWELL CO., Shannon Branch near Capels, 22.IV.90, DHF, 1 L; TAYLOR CO., small stream in Tygert Lake State Park, 11 mi SE Grafton, 30.IV.1978, DHF & ACG, 3 L; **WISCONSIN**: ASHLAND CO., Deer Cr., 10.X.1980, 1 L (WIRC); BAYFIELD CO., Muskeg Cr., 13.IX.1968, 1 L (WIRC); Redcliff Brook, 25.VIII.1970, 1 L (WIRC); MARINETTE CO., Whiskey Cr., 26.V.1979, 2 L (WIRC); PRICE CO., N. Br. Levitt Cr., 4.IX.1972, 2 L (WIRC); RUSK CO., Soft Maple Cr., 11.IX,1963, 1 L (WIRC); SAUK CO., Otter Cr., 8.IV.1965, 4 L (WIRC); TAYLOR CO., Sheepranch Cr., 28.V.1970, 2 L (WIRC);

Range.—Wisconsin and Ontario east to Nova Scotia, as far north as the upper northern shore of the St. Lawrence in Quebec, south to northwest Arkansas, northern Alabama and Georgia, and South Carolina.

Discussion.—McDunnough (1925) described *E. funeralis* from female imagos collected in southern Quebec. A single male was designated as an allotype because McDunnough was uncertain about its association with the female type. He later (McDunnough 1931a) described the larva from reared females collected in Knowlton, Quebec, and suggested that given the apparent absence of males, his allotype might more likely represent *E. verisimilis*. Traver (1935) reared males from two localities in New York.

In the north and east, *Eurylophella funeralis* is the most easily recognized species in the genus. The distinctive shape of segment 9, the very long posterolateral projections on segment 2 and 3, and the size and spacing of the submedian tubercles are all distinctive (see discussion under *funeralis* group above). Unlike most other species of *Eurylophella*, *E. funeralis* larvae are generally unicolorous brown dorsally, without markings except for some banding on the legs. Ventrally there are usually only faint sublateral maculae on the sterna. The long, conspicuous fine setae covering the body of *E. funeralis* are denser and more conspicuous than those of other *Eurylophella* species.

Specimens from the lower Midwest often have shorter posterolateral projections on 2 and 3 as well as shorter and straighter submedian tubercles on 1 to 4. Also, in these areas $ITD_{4:7}$ is generally greater than 1.1. However, the distinctive shape of segment 9 should enable identification of these specimens.

Typically the dorsal subdivisions of the lower lamella of gill 4 are small to minute, and restricted to the lateral edge of the lamella (as in Fig. 2c). Occasionally specimens are found that have the dorsal subdivisions better developed, sometimes approaching the degree seen in Fig 2b, especially in the southern part of the

range west of the Appalachians. However, compared with members of the *lutulenta* group, the dorsal subdivisions on these specimens more closely confined to the lateral edge of the lamella.

Parthenogenesis is common in *E. funeralis* (see Sweeney and Vannote 1987 and references therein). Many populations consist entirely of females, while others have sex ratios of up to 1:1. Some populations appear to be a mix of bisexuals and parthenogens. Among *Eurylophella*, parthenogenesis appears to be unique to *E. funeralis*, although it is known in other mayflies, including some ephemerellids (e.g., *Ephemerella invaria* and *E. rotunda*; see McDunnough 1931b).

Eurylophella funeralis is generally restricted to small (1st to 3rd order) streams, although individuals are occasionally collected in larger streams and rivers (most commonly in the vicinity of small tributaries). In 1st order streams *E. funeralis* is usually the only *Eurylophella* present, and is commonly found with *E. verisimilis* in 2nd to 3rd order reaches.

Bicolor Species Group

As we recognize it here, the *bicolor* group includes five species, *E. verisimilis* (McDunnough), *E. bicoloroides* (McDunnough), *E. macdunnoughi* NEW SPECIES, *E. bicolor* (Clemens), and *E. minimella* (McDunnough). In these species the dorsal subdivisions of the ventral lamella of the gill on segment 4 are reduced to two very small remnants restricted to the lateral edge of the lower lamella (Fig. 2c). Often they are difficult to see at all (especially in larval exuviae). The spacing between submedian tubercles on segments 1 and 2 is narrower than in other groups (see Fig. 75b). The tubercle spacing on segment 7 is relatively wide, usually subequal to the length of the tergite at midline (see Fig. 73b). Thus, the rows of submedian tubercles are distinctly divergent posteriorly (SMT 2:7 usually less than 0.8; see Fig. 73a). As in *E. funeralis* and some *lutulenta* group species, there are no longitudinal ridges forming the bases of the submedian tubercles on segments 5 to 7. The posterolateral projections on segment 9 are short compared to the *temporalis* and *lutulenta* groups (Fig. 75a). The fore femora are broader than those of the *temporalis* group, but narrower than those of the *lutulenta* group (see Fig. 74b). Markings on the larval sterna (submedian dots, oblique paramedian dashes, and longitudinal sublateral maculae) are, when present, usually rather inconspicuous brown, and do not contrast sharply with the ground color. Dorsally, species of this group are quite variable in coloration, ranging from plain brown to dark brown with pale speckling, sometimes with pale median or submedian stripes, banding on the posterolateral projections, or even a contrasting band pattern similar to that found in *E. doris*. The tips of the posterolateral projections of the abdomen are always brown- or black-tipped. The latter coloration is most evident when viewed against a white background, and can be a useful character for quick sorting of larvae by species group. The *bicolor* group species are small to medium-sized (Fig. 74a).

Eurylophella bicolor (Clemens)

Figures 8-12, 72 l

Ephemerella bicolor Clemens, 1913: 336, 1 fig.; Clemens 1915: 123, 1 fig.; McDunnough 1930: 56, 1 fig.; McDunnough 1931a: 61, 7 figs.; Traver 1935: 584; Burks 1953: 74, 3 figs.; Allen and Edmunds 1963: 603, 19 figs.

Larva.—Length: 6.0-8.3. Head: occipital tubercles minute or absent in male (Fig.

9), small in female (Fig. 10). Thorax: fore femora of medium width, average ratio of width to length (FWL_1) = 0.44, range 0.40-0.46. Abdomen: Rows of submedian tubercles rather evenly divergent from 1-4, widening abruptly from 4-5 , and slightly divergent or subparallel from 5-7 (Fig. 8, 11). Average $ITD_{2:7}$ = 0.63, range 0.50-0.80. Average $ITD_{4:7}$ = 0.80, range 0.66-0.96. Tubercles on segment 2 narrowly spaced (average SMT_2 = 0.49, range 0.38-0.56). Spacing of tubercles on segment 1 narrower (average SMT_1 = 0.39, range 0.26-0.53; Fig. 8). Distance between tubercles on segment 7 about the same as length of segment at midline (average SMT_7 = 1.06, range 0.92-1.22). Tubercles on 1-4 short, stout, blunt, and erect (Fig. 72 l), protruding only slightly above level of tergite in side view, with few or no scale-like setae and only sparse hair setae. Tubercles on 5-7 short, sharp and low, with few scale-like setae and no fine setae. Average TL_7 = 0.24, range 0.18-0.31. Tubercles on 8 and 9 usually present. Average $MLT_{2:7}$ = 1.38, range 1.19-1.56. Posterolateral projections on 2 short, sometimes nonexistent, those on 3 short (Fig. 12). Average PLP_2 = 0.04, range 0.01-0.07; PLP_3 = 0.10, range 0.05-0.14. Posterolateral projections on 9 short, PLP_9 = 0.50, range 0.41-0.59. Gill 4 with dorsal subdivisions of the lower lamella almost completely reduced (as in Fig. 2c), often difficult to see.

Material Examined.—Type series: Holotype male (CNC #1216), **ONTARIO**: Go Home Bay, Georgian Bay, Lake Huron (elev. 581 ft., 44°59'40"N, 79°56'09"W), 1-12.VII.1912, W.A. Clemens.

Larval exuviae vouchers from electrophoretic survey [Table 1 in Funk et al. (1988) with additional unpublished data]: 89 from Maine, Vermont, New York, Pennsylvania, and North Carolina.

Additional reared material (larval exuviae in alcohol, imagos frozen): 60 M, 87 F, from Maine, Vermont, New York, and Pennsylvania.

Slide mounts of larval exuviae: **MAINE**: 1 M, 3 F, Piscataquis Co., Moosehead Lake at West Outlet, near Rockwood, 45°39'28"N, 69°44'25"W, 7-10.VII.1988, DIR & DHF; 2 M, 2 F, Piscataquis Co., Nesowadnehunk Stream in Baxter State Park, 45°54'02"N, 69°02'22"W, 15-29.VII.1988, DIR & DHF; **VERMONT**: 2 M, 1 F, Bennington Co., Batten Kill R. 1.6 mi W of West Arlington on Rt 313, 43°06'04"N, 73°14'31"W, 17-22.VI.1985, DIR & DHF; **PENNSYLVANIA**: 2 M, 2 F, Wyoming Co., Meshoppen Cr., 1.6 mi E of Meshoppen, 41°36'45"N, 76°00'58"W, 8-11.VI.1985, DIR & DHF; **NORTH CAROLINA**: 4 M, 1 F, Randolph Co., Uwharrie River, near Farmer, 35°38'30"N, 79°58'00"W, 4-11.V.1985, DIR & DHF.

Other larval material: **ARKANSAS**: Carrel Co., Water Wingfield, 1.VIII.1963, 1 L (UAAM); Washington Co., 20.V.1966, Carter, 2 L (UAAM); **INDIANA**: Harrison Co., Blue Riv. 1 mi E. White Cloud, P-52 ACC-449, 10.V.1979, A.V. Provonsha & K. Black, 23 L (PERC); **KENTUCKY**: Pulaski Co., Fishing Cr. 0.5 mi S of St. Rd 635 & 70 junct., M-337, 4.V.1982, W.P. McCafferty & A.V. Provonsha, 43L (PERC); **MAINE**: Franklin Co., Carrabassett River at rest are on Rt. 16, 5.VIII.1992, DHF, 1 L; Penobscot Co., Swift Brook, 0.8 mi W of Stacyville, 45°51'50"N, 68°31'23"W, 21.VII.1982, ACG, 1 F with exuviae; Piscataquis Co., Lucky Pond near Spencer Bay, Moosehead, 16.VI.1939, 1 L (INHS); Piscataquis River, 3.7 mi SW of Monson, 45°14'30"N, 69°32'43"W, 17.VI.1982 through 20.VIII.1982, ACG, 24 L; tributary of Nesowadnehunk Stream, Baxter State Park, 45°54'13"N, 68°02'16"W, 12.VII.1982, ACG, 1 L; **MICHIGAN**: Delta Co., Rapid River at Rapid River, 12.V.1949, Frison & Ross, 2 L (INHS); **MISSOURI**: Carter Co., Big Spring, BS-0, T26N R1E S.6, 11.II.1974, R.M. Duchrow, 2 L (UMRM); Ellington Co., Current River, Rt. 106, 19.V.1986, D. Judd, 1 L (D. Judd); Greene Co., James River-1, BHT-780523-2, 23.V.1978, voucher specimen B.H. Tracey MS thesis, 2 L (UMRM); Reynolds Co.,

Brushy Cr. BM6-1, T33n R1W S16 NWYy, 17.V.1979, L Trial, 2 L (UMRM); same, BM6-2, 11.II.1980, L. Trial, 13 L (UMRM); same, BM6, T33N R1W S25 SE1/4, 17.V.1979, L. Trial, 3 L (UMRM); Bu Fork, T32N R1W S.20, 7.IV.1982, L. Trial, 1 L (UMRM); RIPLEY CO., Current River, C-49, T23N R2E S34, 10.II.1974, R.M. Duchrow, 7 L (UMRM); **NEW YORK**: DELAWARE CO., West Branch Delaware River at Hale Eddy, 42°00'10"N, 75°23'03"W, JWP & PJD, 14.VI.1982, 2 L; East Branch Delaware River, 2.7 mi WSW of Shinhopple, 42°01'30"N, 75°07'14"W, 2.VI.1982, JWP & PJD, 1 L; same, 12.VII.1983, JWP & DIR, 1 L; Beaver Kill, 1 mi W of Horton, 41°58'18"N, 75°02'23"W, 15.VI.1982, JWP & PJD, 6 L; same, 30.VI.1982, DHF & PJD, 13 L; **NORTH CAROLINA**: DURHAM CO., Eno River at Rd. 1401, 30.IV.1980, BWS & RLV, 1 L; **PENNSYLVANIA**: NORTHUMBERLAND CO., Chillisquaque Cr. near Potts Grove, 40°57'30"N, 76°46'44"W, 24.III.1987 through 2.VI.1987, DIR, 19 L; WAYNE CO., Delaware River at Dillontown, 41°52'02"N, 75°15'50"W, 3.VI.1982, PJD & JWP, 8 L; WYOMING CO., Susquehanna River, 0.6 mi S of Meshoppen, 41°36'20"N, 76°02'57"W, 21.V.1979, DHF,1 L; **QUEBEC**: Lachine (elev. 69 ft., 45°26'11"N, 73°42'09"W), 20.VI.1930, L.J.M. & G. S. Walley, 1 M and 1 F exuviae; **VIRGINIA**: RAPPAHANNOCK CO., Jordan River, on CR637 0.9 mi NNW jct CR647, 38°45'51"N, 78°02'04"W, 20.V.1982, MBG, 1 L; **VERMONT**: BENNINGTON CO., Batten Kill R., 1.9 mi N of Arlington on Rt. 7, 43°05'52"N, 73°08'31"W, 3.VI.1979, DHF, BWS & RLV, 1 L; same, 10.VI.1981, DIR, 1 L; same, 16.VI.1981, ACG, 1 L; Batten Kill R. 1.6 mi W of West Arlington on Rt 313, 43°06'04"N, 73°14'31"W, 12.VII.1980, ACG & DTM, 1 M, 1 F, both with exuviae.

Range.—*Eurylophella bicolor* is one of the most wide ranging species of the genus, being found from the Canadian Maritimes west to Saskatchewan, south to the Ozarks and east to the Carolinas.

Discussion.—Clemens (1913) described *E. bicolor* from adult males and females and larvae collected in the Georgian Bay region of Ontario. McDunnough (1931a) described characters for distinguishing *E. bicolor* larvae from other species of *Eurylophella*.

Larvae of *E. bicolor* can be recognized by the distinctively abrupt transition in shape and spacing of the submedian tubercles from segment 4 to 5. Those on 1 to 4 are small, very blunt, erect and rather narrowly spaced. The space between tubercles widens abruptly at segment 5 (see Figs 8 and 11), and these structures are short, sharp and low on 5 to 7.

Although Allen and Edmunds (1963) suggested that *E. bicolor* and *E. minimella* are "near cognate", the two are easily distinguished as larvae. In *E. minimella* the submedian tubercles are longer and more erect, with a rather indistinct transition between segments 4 and 5 (see discussion under that species). There is almost no overlap in the range of TL_7 for the two (see descriptions). The tubercles on segment 2 are narrowly separated in *E. bicolor* (see Fig. 75b) and show almost no overlap with *E. minimella* in this character, and the posterolateral projections on segment 9 are short (Fig. 75a).

Due to variation in the length of the posterolateral projections on abdominal segments 2 and 3 (Fig. 76a and b), this species may occasionally be confused with *E. bicoloroides* or *E. macdunnoughi*. In addition to the distinctive spacing of tubercles on segments 4 to 5 mentioned above, *Eurylophella bicolor* is generally separable from those species by its smaller size (Fig. 74a) and shorter submedian tubercles on segments 1-7 (Fig. 72 l), and lower $ITD_{4:7}$ (Fig.77b). Also, the submedian tubercles on segment 2 are more closely spaced than in *E. bicoloroides* (Fig. 75b).

Eurylophella bicolor is typically found in large streams (~5th order) to large rivers

(~9th order), as well as lakes (in the northern part of its range). In rivers, it often coexists with *E. verisimilis, E. macdunnoughi, E. minimella, E. aestiva* and *E. doris* (within their respective ranges), and in northern lakes it is frequently found with *E. temporalis* and *E. lutulenta*. In the southwestern portion of its range, it is often the only species of *Eurylophella* present.

Eurylophella bicoloroides (McDunnough) New Status
Figures 13-17, 71, 72j

Ephemerella bicoloroides McDunnough, 1938: 23.
Ephemerella verisimilis McDunnough, Allen and Edmunds 1963: 608 (in part).

Larva.—Length: 6.7-8.1. Head: occipital tubercles minute or absent in male (Fig. 14), small in female (Fig. 15). Thorax: fore femora of medium width, average ratio of width to length (FWL_1) = 0.41, range 0.39-0.45. Spines along posterior margin of fore femora long and acute (Fig. 71). Abdomen: Rows of submedian tubercles evenly divergent from 1-4, subparallel on 5-7 (Fig. 13). Average $ITD_{2,7}$ = 0.74, range 0.57-0.90. Average $ITD_{4,7}$ = 0.92, range 0.79-1.14. Tubercles on segment 2 rather narrowly spaced (average SMT_2 = 0.59, range 0.45-0.68). Spacing of tubercles on segment 1 somewhat narrower (average SMT_1 = 0.49, range 0.37-0.63; Fig. 13). Distance between tubercles on segment 7 about the same as length of segment at midline (average SMT_7 = 1.03, range 0.78-1.19). Tubercles on 1-4 of medium length, erect and blunt, especially in side view (Fig. 72j), with a mixture of fine setae and a few (or sometimes no) stout scale-like setae (especially towards the base). Tubercles on 5-7 long and sharp, with some fine and stout scale-like setae. Average TL_7 = 0.31, range 0.23-0.41. Tubercles on 8 and 9 very short, sometimes absent. Average $MLT_{2,7}$ = 1.26, range 1.10-1.43. Posterolateral projections on 2 and 3 small but distinct (Fig. 17). Average PLP_2 = 0.07, range 0.03-0.12; PLP_3 = 0.15, range 0.07-0.24. Posterolateral projections on 9 short, PLP_9 = 0.52, range 0.45-0.57. Gill 4 with dorsal subdivisions of the lower lamella almost completely reduced (Fig. 2c), often difficult to see.

Material Examined.—Type series: Holotype male (reared from nymph) (CNC # 4290), **NOVA SCOTIA**: Cape Breton Island, Victoria Co., Baddeck Forks (elev. 150 ft., 46°10'53"N, 60°46'10"W), 3.VII.1936, J. McDunnough; 12 M, 12 F paratypes, same data, T.N. Freeman.

Larval exuviae vouchers from electrophoretic survey [Table 1 in Funk et al. (1988; as *E. verisimilis-A*),with additional unpublished data]: 75 from Maine, Vermont, New York, and Pennsylvania.

Additional reared material (larval exuviae in alcohol, imagos frozen): 89 M, 106 F, from New York and Pennsylvania.

Slide mounts of larval exuviae: **VERMONT**: 1 M, Bennington Co., Batten Kill R. 1.6 mi W of West Arlington on Rt 313, 43°06'04"N, 73°14'31"W, 14.VI.1985, DIR & DHF; **NEW YORK**: 3 M, 1 F, Schoharie Co., Schoharie Cr. near Esperance at US Rt. 20, 42°45'22"N, 74°15'07"W, 5-8.VI.1986; 2 M, 3 F, Delaware Co., East Branch Delaware River, 0.8 mi SW of Downsville, 42°04'19"N, 75°00'25"W, 18.VII.1983, 7-11.VI.1984, DHF; **PENNSYLVANIA**: 2 M, 2 F, Susquehanna Co., tributary of Wyalusing Cr., 3 mi W of Montrose, 41°49'11"N, 75°56'00"W, 17-24.VI.1986, DIR & DHF.

Other larval material: **NEW YORK**: Oneida Co., East Branch Mohawk Cr. at Rt. 67, 1.VI.1979, DHF, BWS & RLV, 1 L; Mohawk River on Rt. 46, 31.V.1979, DHF, BWS & RLV, 9 L; **PENNSYLVANIA**: Susquehanna Co., trib of Meshoppen Cr. above Rd.

57010, 31.V.1979, DHF, BWS & RLV, 15 L; tributary of Wyalusing Cr., 3 mi W of Montrose, 41°49'11"N, 75°56'00"W, 7.IV.1980, ACG & DTM, 2 L; same, 29.V.1980, 4 L; same, 31.V.1981, DIR, 3 L; Meshoppen Cr., 1.3 mi SE of Dimock on Rd 57010, 41°43'02"N, 75°52'17"W, 2.VI.1980, ACG & DTM, 1 F with exuviae; same, 9-19.VI.1981, DIR, 1 M, 3 F, with exuviae; WYOMING CO., trib of Tunkhannock Cr. 2.5 mi SW of Nicholson on Rt. 92, 29.IV.1979, DHF & ACG, 23 L.

Range.—Nova Scotia to northeastern Pennsylvania.

Discussion.—McDunnough (1938) described *E. bicoloroides* from male and female imagos and larvae, collected on Cape Breton Island, Nova Scotia. McDunnough (1938) compared the larvae to *E. bicolor*, from which the new species could be distinguished by the longer submedian tubercles on segments 1-4 (reported to be twice as long as in *E. bicolor*) and the noticeably longer and sharper tubercles on segments 5-7. Our data confirm McDunnough's observations. However, as pointed out by Allen and Edmunds (1963), both the size of the posterolateral projections on segments 2 and 3 and the size and spacing of submedian tubercles on 1-7 in *E. bicoloroides* suggest a closer similarity to *E. verisimilis*. As the only character Allen and Edmunds (1963) could find to distinguish between them was the size of the occipital tubercles (which they believed to be variable in *E. verisimilis*; see discussion under that species), they synonymized *E. bicoloroides*.

Funk et al. (1988) found evidence suggesting that *E. verisimilis* (*sensu* Allen and Edmunds 1963) actually included at least four genetically distinct species. One of these, *E. verisimilis* (s.s.), always has well developed occipital tubercles, while the other three are distinguished as a group by their much smaller occipital tubercles. What Funk et al. (1988) referred to as *E. verisimilis-A* turned out to be *E. bicoloroides* McDunnough; *E. verisimilis-B* and *E. verisimilis-C* are combined under *E. macdunnoughi* NEW SPECIES.

Although *E. bicoloroides* and *E. macdunnoughi* are quite distinct genetically, they are difficult to tell apart morphologically. The submedian tubercles on segments 1 and 2 are usually more widely spaced in *E. bicoloroides* (see descriptions and Figs. 13, 38, and 75b) and in areas of sympatry at least, the submedian tubercles on 1 to 4 are slightly longer (Fig. 72j) and are usually distinctly compressed laterally (not the case in *E. macdunnoughi*). However, the most reliable character we have found to separate them is length and shape of the spines on the fore femora. In all members of this group, there is a row of spines on the fore femur, beginning on the anterior margin 2/3 to 3/4 out from the base of the femur, running basally and dorsally to about midlength on the dorsal surface of the femur, then apically and posteriorly, to the hind margin, and continuing along that margin to about 3/4 out from the base of the femur. This row of spines delimits a rather flattened apical region on the dorsum of the femur. *Eurylophella bicoloroides* can be distinguished from *E. macdunnoughi* by the shape and length of these spines on the hind margin toward the apex of the femur. In *E. bicoloroides* they are long and acute (Fig. 71), and in *E. macdunnoughi* short and blunt (Fig. 70). Generally, the spines in the dorsal region are similar length and shape to those on the hind margin, but these tend to be more variable; in some *E. macdunnoughi* they may be longer and more acute than those on the hind margin, although still shorter and blunter than those typically seen on *E. bicoloroides*. Other members of the *bicolor* group are similar to *E. macdunnoughi* with regard to these spines. When using this character, one must be careful not to confuse these spines with the long, fine setae present in both species along the hind margin of the femur. On slide-mounted exuviae the spines and setae are easily observed, especially under high magnification (≥100X). They may be difficult to see

on unmounted larvae examined under a stereomicroscope—under these circumstances the highest magnification available should be used and the larvae should be examined using bright field illumination or against a white background. Any silt or detritus clinging to the femur should be carefully removed with a fine paint brush.

Individuals of *E. bicoloroides* having relatively small posterolateral projections on abdominal segments 2 and 3, with $PLP_2 < 0.75$ and/or $PLP_3 < 0.17$, may result in ambiguity or even a wrong turn at couplet 12 of our morphological key. Careful use of the entire couplet should result in accurate identifications for most individuals. However, specimens with PLP_2 and PLP_3 values falling in the region of overlap (see couplet 12 in key and Fig. 76), especially those collected in the northeastern region, should be taken both ways in the key and then carefully checked against the descriptions. *Eurylophella bicoloroides* are usually distinctly larger than *E. minimella* (Fig. 74a) and the posterolateral projections on segment 9 are shorter (Fig. 75a).

At the local level *Eurylophella bicoloroides* has a peculiar distribution. It appears to be very patchy, quite unlike *E. verisimilis*, which is nearly ubiquitous in small and medium-sized streams throughout its range (see discussion above). Everywhere we have collected *E. bicoloroides*, *E. verisimilis* has also been present, and often *E. macdunnoughi*, too. However, all of the specimens in McDunnough's type series are *E. bicoloroides*, so this pattern of co-occurrence may not be universal. We have found *E. bicoloroides* in small (2nd order) streams up to medium sized rivers (~6th or 7th order). In the large streams we have found it in reaches below reservoirs with hypolimnetic release, where it appears to replace *E. macdunnoughi*.

Eurylophella macdunnoughi Funk New Species

Figures 38-42, 70, 72k

Ephemerella verisimilis McDunnough, Allen and Edmunds 1963: 608 (in part).

Larva.—Length: 6.4-8.9. Head: occipital tubercles minute or absent in male (Fig. 39), small in female (Fig. 40). Thorax: fore femora of medium width, average ratio of width to length (FWL_1) = 0.40, range 0.36-0.45. Spines along posterior margin of fore femora short and often blunt (Fig. 70). Abdomen: Rows of submedian tubercles evenly divergent from 1-4, subparallel on 5-7 (Fig. 38). Average $ITD_{2:7} = 0.71$, range 0.54-0.94. Average $ITD_{4:7} = 0.92$, range 0.68-1.11. Tubercles on segment 2 narrowly spaced (average $SMT_2 = 0.49$, range 0.38-0.73). Spacing of tubercles on segment 1 slightly narrower (average $SMT_1 = 0.43$, range 0.27-0.61; Fig. 38). Distance between tubercles on segment 7 about the same as length of segment at midline (average $SMT_7 = 0.97$, range 0.77-1.14). Tubercles on 1-4 of medium length, erect and blunt, especially in side view (Fig. 72k), with a mixture of fine setae and stout scale-like setae (mostly towards the base). Tubercles on 5-7 long and sharp, with some fine and stout scale-like setae. Average $TL_7 = 0.31$, range 0.19-0.43. Tubercles on 8 and 9 very short, sometimes absent. Average $MLT_{2:7} = 1.40$, range 1.07-1.58. Posterolateral projections on 2 and 3 small but distinct (Fig. 42). Average $PLP_2 = 0.09$, range 0.04-0.14; $PLP_3 = 0.19$, range 0.13-0.27. Posterolateral projections on 9 short, $PLP_9 = 0.52$, range 0.42-0.67. Gill 4 with dorsal subdivisions of the lower lamella almost completely reduced (Fig. 2c), often difficult to see.

Male Imago.—(freshly preserved in alcohol) Length: body 5.9-7.6, forewing 6.0-7.7. Head pale brown with only faint maculations. Upper portion of compound eyes reddish-orange in life. Thorax brown, sometimes reddish, with pale speckling

dorsally. Legs pale with a dark macula on each coxa. Forelegs with a faint apical band on tibia. Wings hyaline with a light amber tint on basal areas of primary veins. Abdominal terga chestnut brown with pale speckling and paired submedian pale stripes. Most terga with two black sublateral maculae on each side. Anterior sterna brown with pale speckling. Posterior segments paler. Submedian and paramedian blackish dots present on most sterna. Penes typical for the genus, and indistinguishable from most other species. Tails pale with light brown annulations. All body coloration in specimens preserved in alcohol tends to fade in time to pale brown with blackish maculae (pale speckling disappears).

Female Imago.— (in alcohol) Length: body 5.8-7.8, forewing 6.3-8.6. Otherwise similar to male except for the usual sexual differences.

Material Examined.—

Holotype: Reared male imago (SWRC no. EV DD 153), **PENNSYLVANIA**: Wyoming Co., Meshoppen Cr., 1.6 mi E of Meshoppen, 41°36'45"N, 76°00'58"W, elev. 720 ft., collected as larva 25.IV.1985, DIR & DHF, reared at SWRC (tray 311), emerged 23.V.1985. Imago on pin, except for segment 9 and 10 of abdomen, which is in alcohol with larval exuviae. Deposited at the Academy of Natural Sciences of Philadelphia.

Paratypes: 3 males, 3 females, all reared male imagos with exuviae (SWRC no. EV DD 25, 136-138, 173, 174), same data as holotype, emerged 9.VI.1981, and 22-25.V.1985, specimens in alcohol. One male and one female deposited at ANSP.

Larval exuviae vouchers from electrophoretic survey [Table 1 in Funk et al. (1988; as *E. verisimilis-B* and *E. verisimilis-C*), with additional unpublished data]: 232 from Maine, Vermont, New York, Pennsylvania, Virginia, West Virginia, and Ohio.

Additional reared material (larval exuviae in alcohol, imagos frozen): 215 M, 271 F, from Vermont, New York, Pennsylvania, Virginia, West Virginia, and Ohio.

Slide mounts of larval exuviae: **VERMONT**: 3 M, 3 F, Bennington Co., Batten Kill R. 1.6 mi W of West Arlington on Rt 313, 43°06'04"N, 73°14'31"W, 25.V to 16.VI.1985, DIR & DHF; **NEW YORK**: 2 M, 2 F, Delaware Co., East Branch Delaware River, 0.8 mi SW of Downsville, 42°04'19"N, 75°00'25"W, 17.VI to 3.VII.1985, DIR & DHF; **PENNSYLVANIA**: 3 M, 3 F, Wyoming Co., Meshoppen Cr., 1.6 mi E of Meshoppen, 41°36'45"N, 76°00'58"W, 20-21.V.1985, DIR & DHF; 2 M, 2 F, Montour Co., Chillisquaque Cr. above Montour Power Plant , 41°04'50"N, 76°40'09"W, 22.V to 5.VI.1987, DIR; **WEST VIRGINIA**: 2 M, 2 F, Cabell Co., Hisey Fork of Fourpole Cr., 1 mi S of Huntington at Interstate Rt. 64, 38°23'18"N, 82°26'08"W, 28.V to 3.VI.1987, DHF; **VIRGINIA**: 2 M, 2 F, Giles Co., Sinking Cr. 1.6 mi NW of Newport at Rt700, 37°18'41"N, 80°30'59"W, 20-28.V.1985, DIR & DHF.

Other larval material: **ARKANSAS**: Washington Co., 17.X.1965, D. Gladden, 2 L (UAAM); Clear Cr., 2.V.1969, 1 L (UAAM); **INDIANA**: Franklin Co., Whitewater Riv. between Laurel and Metamura, MP-179 ACC-1696, 23.V.1975, W.P. McCafferty, A.V. Provonsha & B.L. Heath, 1 L (PERC); Harrison Co., Buck Cr. 1 mi S New Middletown, ACC-484 P-54, 11.V.1973, A.V. Provonsha & K. Black, 1 L (PERC); Martin Co., Small stream 7 mi SE Shoals on Hwy. 150, P266 ACC-1966, 24.IV.1976, A.V. Provonsha & M. Minno, 2 L (PERC); Perry co., Poison Cr. approx 5 mi NW Derby, P-330 ACC-2019, 19.V.1977, M. Minno & S. Yocom, 2 L (PERC); **KENTUCKY**: Bell Co., Clear Cr. at US Hwy 25E below Falls, M-335, 3.V.1982, W.P. McCafferty & A.V. Provonsha, 2L (PERC); W. inlet stream at Chenoa Lake, Kentucky Ridge State Forest, M-333, 2.V.1982, W.P. McCafferty & A.V. Provonsha, 1L (PERC); Breathitt Co., Canoe Cr. 3.7 mi S KY 30 at mouth of Canoe Cr., KK01BRE, 1.VI.1978, KNPC, 2L (PERC); same, 19.VI.1978, KNPC, 2L (PERC);

Quicksand, 8.V.1947, POR & MOS, 1 L (INHS); CARTER CO., Tygarts Cr. at jct KY 1662 and US 60, KT01CAR, 17.IV.1978, KNPC, 9L (PERC); same, 31.V.1978, KNPC, 2L (PERC); CLAY CO., Goose Cr. at confl. with Mud Lick Cr. at Lipps, KK01CLA, 9.V.1978, KNPC, 8L (PERC); CLINTON CO., Smith Cr. 2.3 mi SE Albany on KY 696, 13.VI.1978, KNPC, 1L (PERC); ELLIOTT CO., Ruin Cr. 0.7 mi N jct KY 556 and 755 at bridge on KY 556, KS01ELL, 26.VI.1978, KNPC, 4L (PERC); GREENUP CO., White Oak Cr. 3.7 mi E of KY 7 on KY 2070 and 0.1 mi N KY 2070, KT01GUP, 31.V.1978, KNPC, 20L (PERC); HARLAN CO., Poor Branch at US Hwy 119, 2 mi W of Cumberland, M-329, 2.V.1982, W.P. McCafferty & A.V. Provonsha, 2L (PERC); small trib of Poor Fork at US Hwy 119, 2 mi W of Cumberland, M-328, 2.V.1982, W.P. McCafferty & A.V. Provonsha, 1L (PERC); JACKSON CO., War Fork of Station Camp Cr. at Turkey Foot Camp, M-338, 4.V.1982, W.P. McCafferty & A.V. Provonsha, 9L (PERC); KNOTT CO., Laurel Fork 0.9 mi SE on KY 1098 from jct with KY 160, KK01KNO, KNPC, 3L (PERC); KNOX CO., Road Fork Cr. 1.0 km N of DeWitt at bridge on KY 223, KC01KNX, 18.VI.1978, KNPC, 1L (PERC); LESLIE CO., Greasy Cr. 1.5 mi above Chappell, KY post office on KY 2009, KK01LES, 10.V.1978, KNPC, 30L (PERC); LETCHER CO., Colliers Branch 3.17 km E jct US 119 and Colliers Branc Rd., KC01LET, 22.VI.1978, KNPC, 3L (PERC); ROWAN CO., N. Fk. Triplett Cr., 5.7 mi NNE on KY 377 from jct. with KY 32, KL01ROW, 2.VI.1978, KNPC, 5L (PERC); MCCREARY CO., Beaver Cr. at US Forest Service Rd. #51, Beaver Cr. Wilderness Area, KC03MCY, 4.VII.1978, KNPC, 1L (PERC); PERRY CO., Troublesome Cr. at Home Place community Center on KY 476, 1.0 mi NE of jct of KY 476 and KY 28, KK01PER, 20.VI.1978, KNPC, 3L (PERC); POWELL CO., 0.9 mi SE of Bert T. Combs Parkway at bridge on Hatton Branch Rd., KK01POW, 25.V.1978, KNPC, 13L (PERC); WAYNE CO., Little South Fork Cumberland River, Ford at Ritner, KC01WAY, 9.VI.1978, KNPC, 1L (PERC); Little South Fork Cumberland River 1.8 km SE Pisgah at bridge on KY 167, KC02WAY, 7.VI.1978, KNPC, 6L (PERC); WHITLEY CO., S. Fork Cr. on Daniel Boone Forest Rd #193, 4.3 km NE jct with KY 90, KC01WHI, 6.VI.1978, KNPC, 16L (PERC); **MAINE**: PENOBSCOT CO., Swift Brook, 0.8 mi W of Stacyville, 45°51'50"N, 68°31'23"W, 26.V.1982, ACG, 3 L; same, 9.XII.1982, DHF & DIR, 3 L; PISCATAQUIS CO., Piscataquis River, 3.7 mi SW of Monson, 45°14'30"N, 69°32'43"W, 27.V.1982, ACG & MKB, 1 L; **NEW YORK**: LEWIS CO., East Branch Fishing Cr. below Widner Pond, 1.VI.1979, DHF, BWS & RLV, 14 L; **OHIO**: ATHENS CO., Marietta Run 5 mi ESE of Amesville, trib of Federal Cr., Hocking River., elev 630 ft., 9.V.1979, DHF & BWS, 30 L; WASHINGTON CO., 1st order trib of Baker Run, Moss Run, Little Muskingum River, 3.2 mi WSW of Dart, elev. 680 ft., 9.V.1979, DHF & BWS, 20 L; **PENNSYLVANIA**: MONTOUR CO., Chillisquaque Cr. above Montour Power Plant , 41°04'50"N, 76°40'09"W, 20.IV.1987 to 1.VI.1987, DIR, 21 L; Chillisquaque Cr. below Montour Power Plant , 41°04'00"N, 76°40'35"W, 8.IV.1987 to 18.V.1987, DIR, 16 L; Chillisquaque Cr., near Washingtonville, 41°03'24"N, 76°40'48"W, 3.II.1987 to 21.IV.1987, DIR, 6 L; NORTHUMBERLAND CO., Chillisquaque Cr. near Potts Grove, 40°57'30"N, 76°46'44"W, 8.II.1987 and 19.V.1987, DIR, 4 L; SUSQUEHANNA CO., Meshoppen Cr., 1.3 mi SE of Dimock on Rd 57010, 41°43'02"N, 75°52'17"W, 31.V.1979, DHF, BWS & RLV, 2 L; same, 9.VI.1981, 14.VI.1981, 25.V.1982, DIR, 5 L, 1 F with exuviae; WYOMING CO., Meshoppen Cr., 1.6 mi E of Meshoppen, 41°36'45"N, 76°00'58"W, 13.V.1980, ACG & DTM, 1 L; SUS8, 21.V.1979, DHF, 1 L; headwaters Meshoppen Cr. at Rd. T573, 30.V.1979, DHF, BWS & RLV, 2 L; **TENNESSEE**: GREENE CO., Frank's Creek, 13.IV.1947, M. Allen, 2 L (FAMU; L. Berner No. 3065.2); same, 20.IV.1946, M. Allen, 1 L (FAMU; L. Berner No. 3069.0); same, 17.III.1946, M. Wright, 1 L (FAMU; L. Berner No. 2061.0); same, 7.IV.1946, M. Wright, 1 L (FAMU;

L. Berner No. 2048.2); **VERMONT**:, BENNINGTON CO., Batten Kill R., 1.9 mi N of Arlington on Rt. 7, 43°05'52"N, 73°08'31"W, 23.V.1980, ACG & DTM, 1 L; same, 27.V.1981, DIR, 1 L; **VIRGINIA**: BOTETOURT CO., Mill Cr. near Gala between US 220 and RR bridge, 7.IV.1982, MBG, 2 L; GILES CO., Sinking Cr. 1.6 mi N of Newport at Rt 700, 37°18'41:N, 80°30'59"W, elev. 1810 ft., 8.V.1979, DHF & BWS, 38 L; same, 11.III.1981, DHF, 6 L; same, DIR, 21.II.1985, 15 L; same, 28.V.1985, DHF & DIR, 3 F with exuviae; **WEST VIRGINIA**: CABELL CO., Hisey Fork of Fourpole Cr., 1 mi S of Huntington at Interstate Rt. 64, 38°23'18"N, 82°26'08"W, 29.IV.1978, DHF & ACG, 15 L, and 13 M, 7 F, emerged in lab 19.V to 1.VI.1978, all with exuviae; same, 8.V.1979, DHF & BWS, 1 L; MCDOWELL CO., Shannon Branch near Capels, 22.IV.1990, DHF, 14 L.

Range.—Maine to Pennsylvania, west to Indiana south to Arkansas and Tennessee. South of Pennsylvania known only from west of the Appalachians, except for the New River drainage in Virginia.

Discussion.—*Eurylophella macdunnoughi* includes both *E. verisimilis-B* and *E. verisimilis-C* of Funk et al.'s (1988) electrophoretic study. In that study, they considered eight populations from Maine, Vermont, New York, and northeastern Pennsylvania to represent the (undescribed) species *E. verisimilis-B*, which appeared to be restricted geographically to the northeast. Their *E. verisimilis-C* was based on a single population from Sinking Creek, part of the New River drainage of southwestern Virginia, which showed what appeared to be fixed or nearly fixed allelic differences at four enzyme loci. For two reasons, we now consider these forms to be conspecific. First, *E. verisimilis-C* failed to meet our criteria for species (see *Basis for determination of species boundaries* in Methods section). Secondly, more recent (unpublished) electrophoretic work on populations from central Pennsylvania, Ohio, and West Virginia has revealed that our *E. verisimilis-B* and *E. verisimilis-C* actually represent opposite ends of a very steep cline in allele frequencies.

Allele frequencies and genetic distance measurements for populations at northern and southern extremes of *E. macdunnoughi's* range (i.e., *E. verisimilis-B* and *E. verisimilis-C* of our electrophoretic study) suggest there has been virtually no recent gene flow between them. For example, the average Nei's (1978) genetic distance between *E. macdunnoughi* in northeastern Pennsylvania and southwestern Virginia was 0.33, about three times as large as the highest value observed among any pairwise conspecific comparison for all other species tested, some of which were separated by nearly four times the geographic distance (Funk et al. 1988). A thorough survey throughout this species' range might reveal the existence of several distinct geographic races, but at present our sampling resolution is too coarse to discern any clear groupings.

Genetically, *E. macdunnoughi* is most similar to *E. verisimilis* (Funk et al. 1988). However, the smaller occipital tubercles in *E. macdunnoughi* allow these two to be rather easily distinguished. From a morphological point of view, *E. macdunnoughi* is more similar to *E. bicoloroides*. The best character for separating these two is the difference in shape and length of the spines on the hind margin of the fore femora (see discussion under *E. bicoloroides*, and Figs. 70-71). This character must be observed carefully to avoid misidentifications (see suggestions under *Problem couplets* before the key). Also, the submedian tubercles on 1 to 4 are usually shorter (Fig. 72k) and not laterally compressed as in *E. bicoloroides*, and those on 2 are more narrowly spaced (see description and Fig. 75b).

There is some overlap in the distributions of lengths of the posterolateral projections on segments 2 and 3 between *E. macdunnoughi* and *E. minimella* (see Fig.

76a and b), so it is possible with some specimens to go the wrong way at couplet 12. For this reason we recommend that specimens which are borderline for these characters be taken both ways in the key and then checked against the descriptions. Specimens of *E. macdunnoughi* are usually larger than *E. minimella* (Fig. 74a), with shorter posterolateral projections on segment 9 and more narrowly spaced tubercles on segment 2 (Fig. 75a and b).

Eurylophella macdunnoughi specimens from the midwest sometimes resemble *E. bicolor* with regard to the posterateral projections on segments 2 and 3 and the shape of the submedian abdominal tubercles. However, the transition in spacing and shape of the tubercles on segments 4 to 5 is less abrupt than that seen in *E. bicolor* (see couplet 11).

In the northeastern U.S., *E. macdunnoughi* is commonly found in large streams (4th or 5th order) to large rivers (7th or 8th order). It usually coexists with *E. verisimilis* in the upper reaches and replaces that species in lower reaches. Other species commonly encountered with *E. macdunnoughi* in this region are *E. prudentalis, E. aestiva, E. bicolor, E. minimella,* and occasionally *E. bicoloroides*. In the southwestern part of its range (west of the Appalachians), *E. macdunnoughi* is common in smaller streams, comparable to those containing *verisimilis* in areas east of the Appalachians.

Etymology.—Eurylophella macdunnoughi is named in honor of James McDunnough, who described most of the species in this genus, wrote the first key (McDunnough 1931a), and noted therein (p. 63):

> "The following four species {*E. bicolor, E. minimella, E. aestiva,* and *E. verisimilis*} are very closely allied and in the adults possess no very definite characters for specific distinction, even the male genitalia failing in this respect. This leads me to believe that we are dealing with a group the individuals of which have split away either from each other or from a parent form at a comparatively recent date and that even now fresh species may be in the act of formation."

Eurylophella minimella (McDunnough)

Figures 43-47, 72m

Ephemerella minimella McDunnough, 1931a: 63, 4 figs.; Traver 1935: 612; Burks 1953: 74, 1 fig.; Allen and Edmunds 1963: 606, 4 figs.

Larva.—Length: 5.9-7.7. Head: occipital tubercles minute or absent in male (Fig. 44), small in female (Fig. 45). Thorax: fore femora of medium width, average ratio of width to length (FWL_1) = 0.42, range 0.38-0.47. Abdomen: Rows of submedian tubercles rather evenly divergent from 1-5, slightly divergent or subparallel from 5-7 (Fig. 43, 46). Average $ITD_{2:7}$ = 0.81, normal range 0.69-0.90. Average $ITD_{4:7}$ = 0.95, range 0.80-1.14. Tubercles on segment 2 rather widely spaced (average SMT_2 = 0.62, range 0.53-0.72). Spacing of tubercles on segment 1 distinctly narrower (average SMT_1 = 0.48, range 0.37-0.65; Fig. 43). Distance between tubercles on segment 7 about the same as length of segment at midline (average SMT_7 = 1.01, range 0.88-1.19). Tubercles on 1-4 rather long, erect and somewhat pointed (Fig. 72m), with scale-like setae and fine setae. Tubercles on 5-7 long, sharp and erect, with scale-like setae and fine setae. Average TL_7 = 0.42, range 0.31-0.54. Tubercles on 8 and 9 present, and relatively well developed. Average $MLT_{2:7}$ = 1.30, range

1.13-1.44. Posterolateral projections on 2 short, sometimes nonexistent, those on 3 short (Fig. 47). Average $PLP_2 = 0.04$, range 0.01-0.07; $PLP_3 = 0.12$, normal range 0.05-0.16. Posterolateral projections on 9 of medium length, $PLP_9 = 0.59$, normal range 0.54-0.70. Gill 4 with dorsal subdivisions of the lower lamella almost completely reduced (as in Fig. 2c), often difficult to see.

Material Examined.—Type series: Holotype male with associated larval exuviae (CNC # 3216), **QUEBEC**: Knowlton, Knowlton Creek (elev. 700 ft., 45°13'05"N, 72°30'34"W), 7.VII.1930, L.J. Milne.

Larval exuviae vouchers from electrophoretic survey [see Table 1 in Funk et al. (1988)]: 14 from New York and Pennsylvania.

Additional reared material (larval exuviae in alcohol, imagos frozen): 2 M, 2 F, from Maine and Pennsylvania.

Slide mounts of larval exuviae: **NEW YORK**: 2 F, Delaware Co., Beaver Kill, 1 mi W of Horton, 41°58'18"N, 75°02'23"W, 25.VI to 10.VII.1985, DIR & DHF; **PENNSYLVANIA**: 1 M, 1 F, Wayne Co., Delaware River at Dillontown, 41°52'02"N, 75°15'50"W, 28.VI to 4.VII.1985, DIR & DHF; 2 M, 2 F, Wyoming Co., Meshoppen Cr., 1.6 mi E of Meshoppen, 41°36'45"N, 76°00'58"W, 27.VI to 6.VII.1985, DIR & DHF.

Other larval material: **MAINE**: Franklin Co., Carrabassett River at Rt. 16 rest area, 5.VIII.1992, DHF, 1 L; Penobscot Co., Swift Brook, 0.8 mi W of Stacyville, 45°51'50"N, 68°31'23"W, 27.VII.1982, ACG, 1 F with exuviae; same, 26.VII.1982, 1 M, 1 F, both with exuviae; same, 25.VII.1982, 1 F with exuviae; same, 10.VIII.1982, 1 M with exuviae; same, 30.VII.1982, 1 F with exuviae; same, 9.VIII.1982, 1 M, 1 F, both with exuviae; same, 28.VI.1982, 6 L; Piscataquis Co., Piscataquis River, 3.7 mi SW of Monson, 45°14'30"N, 69°32'43"W, 30.VII.1982, ACG, 1 L; same, 8.VII.1982, 3 L; same, 17.VI.1982, 1 L; same, 27.V.1982, ACG & MKB, 1 L; **NEW YORK**: Delaware Co., West Branch Delaware River 1.3 mi NE of Deposit, 42°04'38"N, 75°24'21"W, 28.VIII.1984, DIR, 2 L; same, 26.VII.1982, PJD & JWP, 2 L; East Branch Delaware River, 2.7 mi WSW of Shinhopple, 42°01'30"N, 75°07'14"W, 27.VII.1982, PJD & JWP, 3 L; same, 12.VI.1983, JWP & DIR, 3 L; same, 13.VII.1982, DHF & JWP, 3 L; Beaver Kill, 1 mi W of Horton, 41°58'18"N, 75°02'23"W, 27.VII.1982, JWP & PJD, 3 L; same, 12.VII.1983, DIR & JWP, 3 L; same, 30.VI.1982, DHF & PJD, 4 L; same, 15.VI.1982, JWP & PJD, 2 L; same, 30.VI.1982, DHF & PJD, 3 L; same, 13.VII.1982, JWP & DHF, 6 L; **PENNSYLVANIA**: Susquehanna Co., tributary of Partners Cr., 1.9 mi SW of Harford, on Rd 944, 41°45'27"N, 75°44'46"W, 24.VI.1980, BWS, 3 L; Wayne Co., Delaware River at Dillontown, 41°52'02"N, 75°15'50", 14.VII.1982, DHF & JWP, 1 L; **TENNESSEE**: Cheatham Co., Turner Cr., Hwy 70, 26.IV.1945, M. Wright, 2 L (FAMU; L. Berner No. 2053.1); Grainger Co., trib of Cheroxee R., 11.IV.1954, J. Pugh Cat. No. 4-1154-2, 1 L (FAMU; L. Berner No. 3412.4).

Range.—Eurylophella minimella is known from the northern U.S. and southern Canada, from Minnesota to Nova Scotia, and as far south as Pennsylvania. The species has been reported from North Carolina, South Carolina and Tennessee (Berner 1977, Traver 1935, Wright and Berner 1949) but we have only been able to confirm two of these, both from Tennessee.

Discussion.—McDunnough described *E. minimella* from a reared male imago collected in southern Quebec.

The most distinctive feature of *E. minimella* is the size and shape of the submedian tubercles. In other species of the *bicolor* group, the tubercles are typically erect on 1 to 4, while those on 5 to 7 are low-lying and directed posteriorly. For *E. minimella* the normal transition between segments 4 and 5 is much less

distinct: although the tubercles on 5 to 7 are sharper, they are still quite erect. Although their tips are directed posteriorly, these tubercles protrude conspicuously above level tergite, particularly evident in side view (see Fig. 72m).

Eurylophella bicolor and *E. minimella* are similar in size and the degree of development of the occipital tubercles and posterolateral projections on segments 2 and 3, and they both emerge rather late in the season (see Fig. 78). However, they are quite distinct in other aspects of their morphology, and are quite easily distinguished. The difference in the size and shape of the submedian tubercles on 1 to 7 between *E. minimella* and other species of the *bicolor* group mentioned above is especially true for *E. bicolor*. There is essentially no overlap in the distribution of TL_7 between *E. minimella* and *E. bicolor* (see descriptions). Also, in *E. minimella* the submedian tubercles on segment 2 are more widely spaced, with almost no overlap in observed SMT_2 values for the the two species (see Fig. 75b), and the spacing between tubercles never widens abruptly between 4 and 5 in *E. minimella* as it does in *E. bicolor*. Also, the posterolateral projections on segment 9 are usually distinctly longer than in *E. bicolor* (see Fig. 75a). Once seen, the two are not likely to be confused.

Specimens of *E. bicoloroides* or *E. macdunnoughi* with smaller than average posterolateral projections on segments 2 and 3 may sometimes be confused with *E. minimella* (see discussions under those species). However, *E. minimella* can be distinguished by the combination of its small size, distinctively shaped abdominal tubercles (with those on segment 2 widely spaced) and long posterolateral projections on segment 9.

Eurylophella minimella is typically a northern species. We have seen only three specimens from south of Pennsylvania assignable to this species (from two localities in Tennessee; see records above). These specimens are larger than those typically found in the north, and their submedian tubercles are shorter and less erect.

Assuming the Tennessee populations are disjunct, *E. minimella* appears to have a more restricted geographic range than most of its congeners, being common only in medium-sized rivers (~4th to 7th order) in southern Canada and northern U.S. It is a late season species (Fig. 78), and is not often collected.

Eurylophella verisimilis (McDunnough)

Figures 2c, 65-69, 72i

Ephemerella verisimilis McDunnough, 1930: 57, 3 figs.; McDunnough 1931a: 65, 6 figs.; Traver 1935: 626; Burks 1953: 74; Allen and Edmunds 1963: 608, 5 figs. (in part).

Larva.—Length: 6.8-9.2. Head: occipital tubercles well developed in both sexes (Fig. 66-67). Thorax: fore femora slender to medium in width, average ratio of width to length (FWL_1) = 0.40, range 0.37-0.46. Spines along posterior margin of fore femora short and blunt (similar to Fig. 70). Abdomen: Rows of submedian tubercles evenly divergent from 1-4, subparallel on 5-7 (Fig. 65). Average $ITD_{2:7}$ = 0.76, range 0.59-0.90. Average $ITD_{4:7}$ = 0.97, range 0.84-1.25. Tubercles on segment 2 rather narrowly spaced (average SMT_2 = 0.56, range 0.44-0.65). Spacing of tubercles on segment 1 narrower (average SMT_1 = 0.46, range 0.33-0.62; Fig. 65). Distance between tubercles on segment 7 about the same as length of segment at midline (average SMT_7 = 1.02, range 0.83-1.33). Tubercles on 1-4 rather short, erect and usually blunt, especially in side view (Fig. 72i), with a mixture of fine setae and

conspciuous, stout, scale-like setae (especially towards the base). Tubercles on 5-7 long and sharp, with a mixture of fine setae and conspicuous stout scale-like setae. Average $TL_7 = 0.34$, range 0.27-0.43. Tubercles on 8 and 9 very short, sometimes absent. Average $MLT_{2-7} = 1.38$, range 1.23-1.58. Posterolateral projections on 2 and 3 small but distinct (Fig. 69). Average $PLP_2 = 0.12$, range 0.06-0.18; $PLP_3 = 0.23$, range 0.16-0.33. Posterolateral projections on 9 short, $PLP_9 = 0.55$, range 0.45-0.63. Gill 4 with dorsal subdivisions of the lower lamella almost completely reduced (Fig. 2c), often difficult to see.

Material Examined.—Type series: 2 male paratypes, (CNC # 3130), **QUEBEC**: Saguenay co., Bradore Bay, (elev. ~50 ft., 51°27'35"N, 57°14'34"W), 21-26.VII.1929, W.J. Brown.

Larval exuviae vouchers from electrophoretic survey [Table 1 in Funk et al. (1988) with additional unpublished data]: 858 from Quebec, Maine, Vermont, New York, Pennsylvania, Delaware, Virginia, North Carolina, South Carolina, and Georgia.

Additional reared material (larval exuviae in alcohol, imagos frozen): 607 M, 631 F, from Quebec, Maine, Vermont, New York, Pennsylvania, Delaware, Virginia, North Carolina, South Carolina, and Georgia.

Slide mounts of larval exuviae: **QUEBEC**: 3 M, 2 F, Saguenay Co., Rivière Pigou above Rt. 138, 50°16'57"N, 65°38'31"W, 9-12.VII.1982, 19.VII.1984, DHF; **VERMONT**: 2 M, 2 F, Bennington Co., Batten Kill R. 1.6 mi W of West Arlington on Rt 313, 43°06'04"N, 73°14'31"W, 28.V-17.VI.1985, DIR & DHF; **NEW YORK**: 2 M, 2 F, Delaware Co., East Branch Delaware River, 0.8 mi SW of Downsville, 42°04'19"N, 75°00'25"W, 7-28.VI.1985, DIR & DHF; **PENNSYLVANIA**: 2 M, 2 F, Wyoming Co., Meshoppen Cr., 1.6 mi E of Meshoppen, 41°36'45"N, 76°00'58"W, 20-21.V.1985, DIR & DHF; 3 M, 2 F, Susquehanna Co., tributary of Wyalusing Cr., 3 mi W of Montrose, 41°49'11"N, 75°56'00"W, 17-28.VI.1985, DIR & DHF; 2 M, 2 F, Chester Co., E. Fk. E. Br. White Clay Cr., 0.8 mi WSW of London Grove, 39°51'47"N, 75°47'07"W, 13-16.V.1985, DHF; **DELAWARE**: 2 M, 2 F, New Castle Co., Blackbird Cr., 1.5 mi SW of Blackbird, 39°21'18"N, 75°40'55"W, 17-22.V.1985, DHF; **VIRGINIA**: 2 M, 2 F, Bedford Co., Big Otter River at jct Hwy 43 & CR682, 37°23'22"N, 79°33'05"W, 5-14.V.1985, DIR & DHF; **NORTH CAROLINA**: 2 M, 2 F, Randolph Co., Uwharrie River, near Farmer, 35°38'30"N, 79°58'00"W, 4-9.V.1985, DIR & DHF; **SOUTH CAROLINA**: 2 M, 2 F, McCormick Co., Horton Branch, Long Cane Cr., 5.2 mi ENE of Willington, 33°59'55"N, 82°23'01"W, 1-9.V.1985, DIR & DHF.

Other larval material: **DELAWARE**: New Castle Co., West Creek nr. Newark, 7.VI.1951, T. Dolan, 4 L; **MAINE**: Aroostook Co., Mount Chase Twp. Sargent Br. 5 mi N of Patton, 30.IX.1981, ACG & DHF, 18 L; Piscataquis Co., Piscataquis River, 3.7 mi SW of Monson, 45°14'30"N, 69°32'43"W, various dates—1982, ACG, 7 L; Nesowadnehunk Stream in Baxter State Park, 45°54'02"N, 69°02'22"W, various dates—1981-1983, ACG, DHF, JWP, DIR & MKB, 31 L; **NEW YORK**: Adirondack Park, High Rock Pond outlet, near Eagle Bay, 19.VI.1941, Frison & Ross, 1 L (INHS); Franklin Co., trib of St. Regis River ~7 mi S of Santa Clara, 2.VI.1979, DHF, BWS & RLV, 4 L; Lewis Co., East Branch Fishing Cr. below Widner Pond, 1.VI.1979, DHF, BWS & RLV, 18 L; Pringle Cr, Fish Cr., Michigan Mills Rd, West Turin Twp. 1.VI.1979, DHF, BWS & RLV, 4 L; Oneida Co., E. Branch Mohawk Cr. on Rt 67, 1.VI.1979, DHF, BWS & RLV, 12 L; Mohawk River on Rt 46, 31.V.1979, DHF, BWS & RLV, 2 L; St. Lawrence Co., trib of St. Regis River, 3 mi SW of Hopkinton on Rt. 72, 2.VI.1979, DHF, BWS & RLV, 10 L; **NORTH CAROLINA**: Orange Co., West Fork Eno River at Rd1004, 2.1 mi SSW of Cedar Grove, 36°06'21"N, 79°10'13"W, various dates—1981-1982, ACG, JWP, RBS, & DIR, 75 L, 7 M, 3 F, with exuviae; Eno

River at Rt 70, 1.3 mi NNE of Efland, 36°04'58"N, 79°06'34"W, various dates—1981, ACG, JWP & RBS, 9 L; **PENNSYLVANIA**: Chester Co., trib of W Br. Brandywine Cr., 0.5 mi E of Northbrook, 39°55'10"N, 75°40'35"W, 24.V.1978, DHF, 2 M with exuviae; Pickering Cr., 1.3 mi WNW of Charlestown below Rd15046, 40°06'09"N, 75°34'39"W, various dates—1980, PJD, CFB, CED, ACG & DTM, 10 L, 5 M, 8 F, with exuviae; Black Run in Nottingham Park 1.5 mi SW of Nottingham, 39°44'32"N, 76°02'30"W, 9.V.1993, DHF, 43 L; Montour Co., Chillisquaque Cr. above Montour Power Plant , 41°04'50"N, 76°40'09"W, 3.II to 18.V.1987, DIR, 13 L; Chillisquaque Cr. below Montour Power Plant , 41°04'00"N, 76°40'35"W, 3.II to 12.V.1987, DIR, 4 L; Chillisquaque Cr., near Washingtonville, 41°03'24"N, 76°40'48"W, 24.III to 12.V.1987, DIR, 13 L; Chillisquaque Cr. near Potts Grove, 40°57'30"N, 76°46'44"W, 24.III to 19.V.1987, DIR, 10 L; Susquehanna Co., Meshoppen Cr. at Rd T522, 30.V.1979, DHF, BWS & RLV, 30 L; Starrucca Cr. at RT296, DHF, BWS & RLV, 13 L; Tunkhannock Cr. just off Rt. 92 on Rd 57148, 31.V.1979, DHF, BWS & RLV, 23 L; trib of Meshoppen Cr. above Rd. 57010, 31.V.1979, DHF, BWS & RLV, 24 L; Butler cr. at Gibson gauging station on rt. 547, 31.V.1979, DHF, BWS & RLV, 28 L; trib of Meshoppen Cr, 2 mi E of Dimock, 41°44'13"N, 75°51'36"W, various dates—1979-1981, ACG, DTM & DIR, 6 L, 2 M with exuviae; Meshoppen Cr., 1.3 mi SE of Dimock on Rd 57010, 41°43'02"N, 75°52'17"W, various dates—1979-1982, DHF, BWS, RLV, ACG, DTM & DIR, 18 L, 2 M, 2 F, with exuviae; Wyoming Co., trib of Tunkhannock Cr., 2.5 mi S of Nicholson on Rt. 92, 29.IV.1979, DHF & ACG, 10 L; **QUEBEC**: Saguenay Co., Rivière aux Loups Marins, above Rt. 138, 50°16'44"N, 65°43'12"W, various dates—1982, JAG & DHF, 28 L; Ruisseau du Cran Carré, above Rt 138,50°17'35"N, 65°55'30"W, various dates—1982, JAG & DHF, 39 L, 1 M, 1 F, with exuviae; Rivière Matamec below Beaver Cr., 50°18'21"N, 65°56'11"W, various dates—1982, JAG & DHF, 63 L, 4 M, 2 F, with exuviae; Bradore Bay, (elev. ~50 ft., 51°27'35"N, 57°14'34"W), 12.VII.1930, W.J. Brown, 2 M exuviae (CNC); Lac Warren, 1.VIII.1938, O.F. Decharge #298, 1 L (INHS); **VERMONT**: Bennington Co., West Branch Batten Kill R., 2 mi S of Dorset on Rt 30, 43°13'10"N, 73°04'18"W, various dates—1979-1981, ACG, DTM & DIR, 29 L; Batten Kill R., 1.9 mi N of Arlington on Rt. 7, 43°05'52"N, 73°08'31"W, various dates—1980-1981, ACG, DTM & DIR, 15 L; **VIRGINIA**: Botetourt Co., Mill Cr. near Gala between US 220 and RR bridge, 7.IV.1982, MBG, 6 L; Fauquier Co., Thumb Run at Rd770, 1.15 mi NW of Orlean, 38°45'47"N, 77°58'51"W, various dates—1980-1981, ACG, JWP, DIR & CED, 29 L, 7 M, 2 F, all with exuviae; Bedford Co., Big Otter River, on CR670, 0.4 mi N jct Hwy 221, 37°22'14"N, 79°25'14"W, 22.V.1980, CFB & CED, 1 M with exuviae; unnamed tributary of Sheep Cr., CR680 0.65 mi NW jct CR614, 37°24'58"N, 79°38'46"W, 26.III.1980, PJD & DHF, 1 L; same, 6.V.1981, PJD, 4 L; Sheep Cr., on CR614 0.7 mi N jct CR680, 37°25'21"N, 79°38'24"W, 6.XI.1980, CED & DTM, 4 L; same, 5.V.1981, PJD, 3 L; Rappahannock Co., unnamed tributary of Hittles Mill Stream, on CR663 1.1 mi W jct CR628, 38°46'45"N, 78°08'29"W, 2.VI.1980, CFB & CED, 1 M with exuviae; Bearwallow Cr., above bridge on CR630, 2.2 mi W jct Hwy 522, 38°47'07"N, 78°08'54"W, 7.V.1981, PJD, 3 L; same, 22.IV.1982, MBG, 1 L; Hittles Mill Stream at jct CR630 & CR638, 38°47'38"N, 78°07'04"W, various dates—1980-1981, CFB, CED, DIR & DHF, 5 M with exuviae; Thumb Run at Rd770, 1.15 mi NW of Orlean, 38°45'47"N, 77°58'51"W, 12.VI.1981, JWP, 3 L; Rappahanock Co., Thornton River, 6.2 mi S of Ben Venue, above Rt 729, 38°37'45"N, 78°04'00"W, various dates—1979-1980, CFB & CED, 26 L, 3 M, 2 F, with exuviae;

Range.—Eurylophella verisimilis is known from Quebec and Nova Scotia, west to eastern Ontario, south to South Carolina and Georgia, from the Appalachians

eastward. Within this area *E. verisimilis* is nearly ubiquitous in small to medium-sized streams (2nd to 6th order). Although *E. verisimilis* is apparently found in the northern Great Lakes region, in the middle and southern latitudes it does not occur west of the Appalachians.

Discussion.—McDunnough (1930) described *E. verisimilis* from male and female imagos collected in northeastern Quebec. He also described larvae from the type locality that he presumed to be conspecific. The following year specimens from the type locality were reared (McDunnough 1931a), verifying the association.

Although all of McDunnough's larvae from the type locality have well developed occipital tubercles, Allen and Edmunds (1963) found that occipital tubercles in what they considered to be *E. verisimilis* from other areas varied from almost nonexistent (as in our Figs. 14-15) to well developed (our Figs. 66-67). As McDunnough's *E. bicoloroides* (McDunnough 1938) appeared to them to be identical to *E. verisimilis* in all respects except for the poorly developed occipital tubercles, they synonymized the two. Electrophoretic analysis of populations from Quebec to Georgia (Funk et al. 1988) provided clear genetic evidence that individuals with small occipital tubercles were reproductively isolated from the typical *E. verisimilis*, and that *E. verisimilis* (sensu stricto) show remarkably little variation in the size of the occipital tubercles. Allen and Edmunds' concept of *E. verisimilis* included both *E. bicoloroides* McDunnough 1938 and *E. macdunnoughi* NEW SPECIES.

The almost complete reduction of the dorsal subdivisions of the lower lamella on gill 4 and divergent rows of submedian tubercles on abdomen identify *Eurylophella verisimilis* as a member of the *bicolor* group, and the relatively long posterolateral projections on segments 2 and 3 and well developed occipital tubercles distinguish it from other species in this group.

Eurylophella verisimilis is characteristically found in small to medium-sized (~2nd to 6th order) streams and rivers. It often coexists with *E. funeralis* in the smaller streams, and *E. prudentalis, E. macdunnoughi, E. bicolor, E. minimella,* and *E. aestiva* in the medium-sized streams. It is sometimes found with *E. bicoloroides* in the north, and *E. doris* or *E. enoensis* (in the south). It tends to be replaced by *E. macdunnoughi* in the larger (7th to 8th order) reaches of many northeastern rivers. It is generally not found in lakes.

Group Uncertain

Since the larva of *Eurylophella coxalis* (McDunnough, 1926) is unknown we are not able to place it in a species group. Larvae tentatively assigned to this species by McDunnough (1931a) are here considered *enoensis* Funk.

Eurylophella coxalis (McDunnough)

Ephemerella coxalis McDunnough, 1926: 186; McDunnough 1931a: 37 (in part); Traver 1935: 589 (in part); Burks 1953: 73, 2 figs. (in part); Allen and Edmunds 1963: 617, 4 figs. (in part)

Larva.—Unknown.

Material Examined.—Type series: Holotype male (CNC # 2070), **QUEBEC**: Dorval, (elev. 69 ft., 45°26'28"N, 73°46'20"W), 20.VI.1925, F.P. Ide; 1 male paratype, same data; 1 female paratype, **QUEBEC**: Ste. Annes, 24.VI.1925, F.P. Ide.

Discussion.—McDunnough (1926) described *E. coxalis* from male and female imagos collected in Quebec. He later (1931a) tentatively assigned a single partly grown larva to this species. We consider this larva to be *E. enoensis* Funk (see discussion under *E. enoensis*, above). We have not collected *E. coxalis*.

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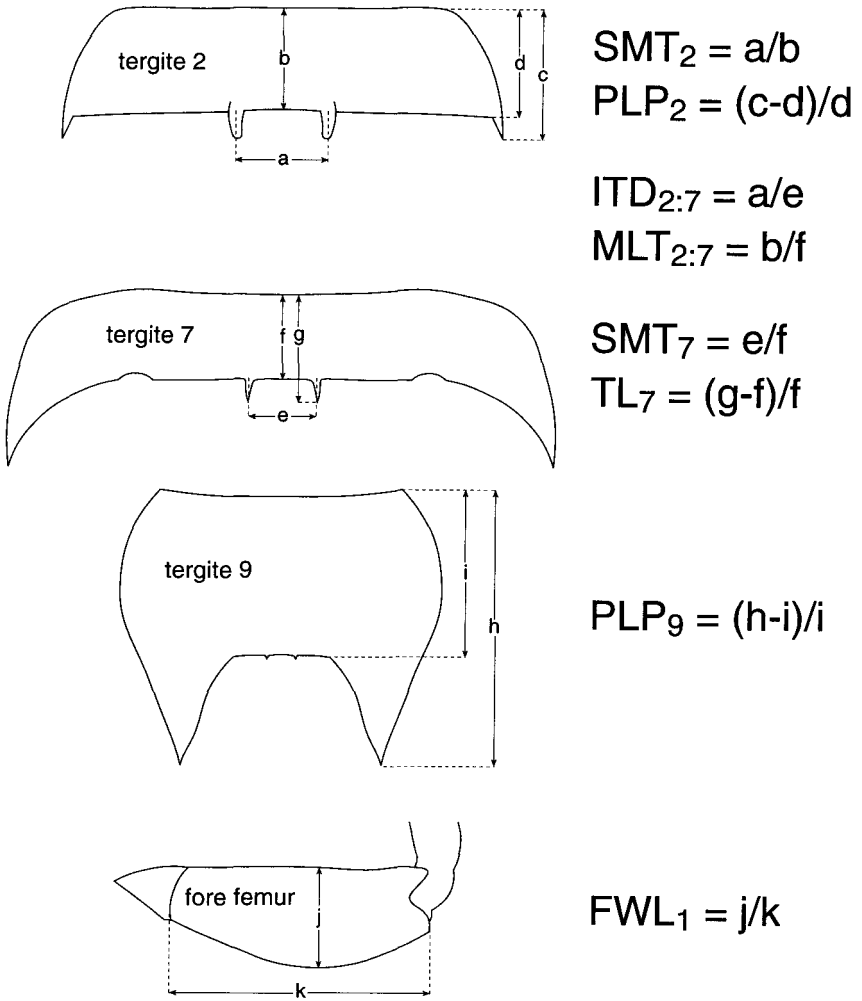
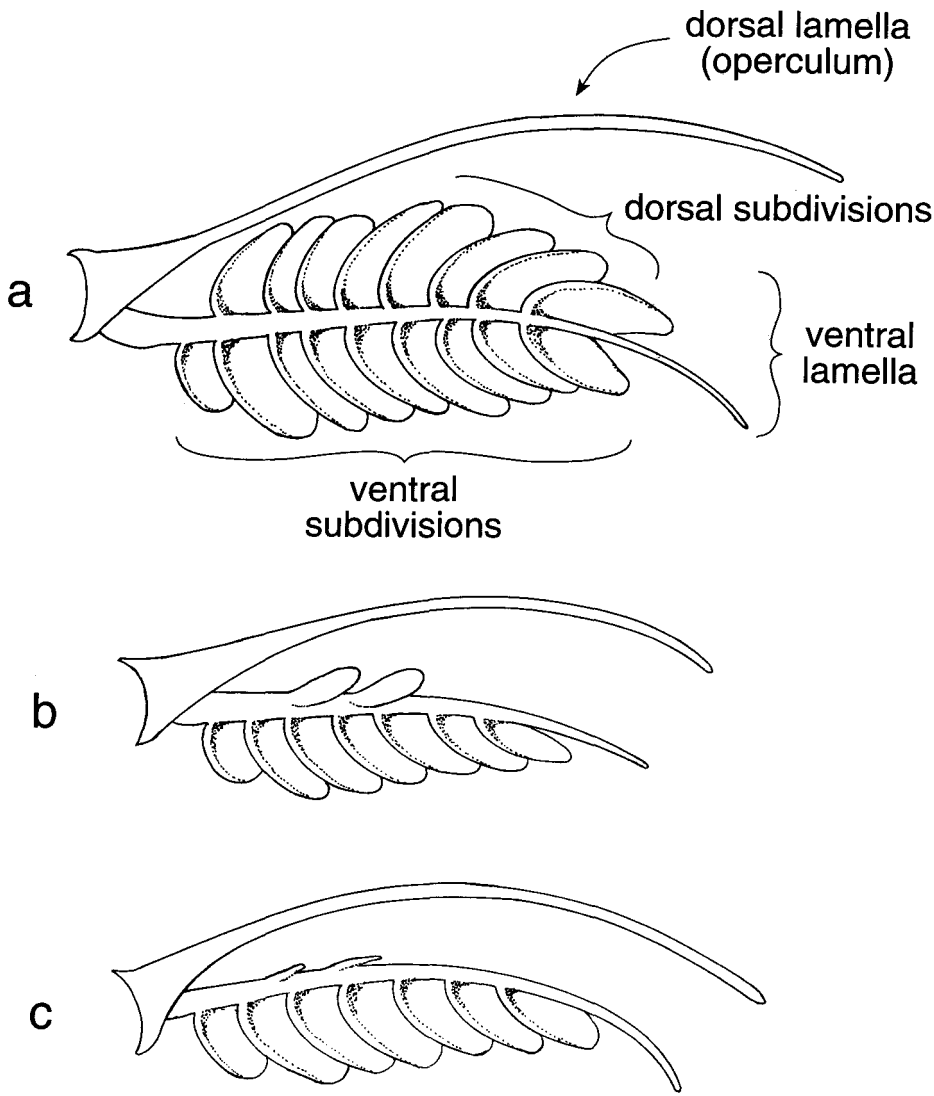
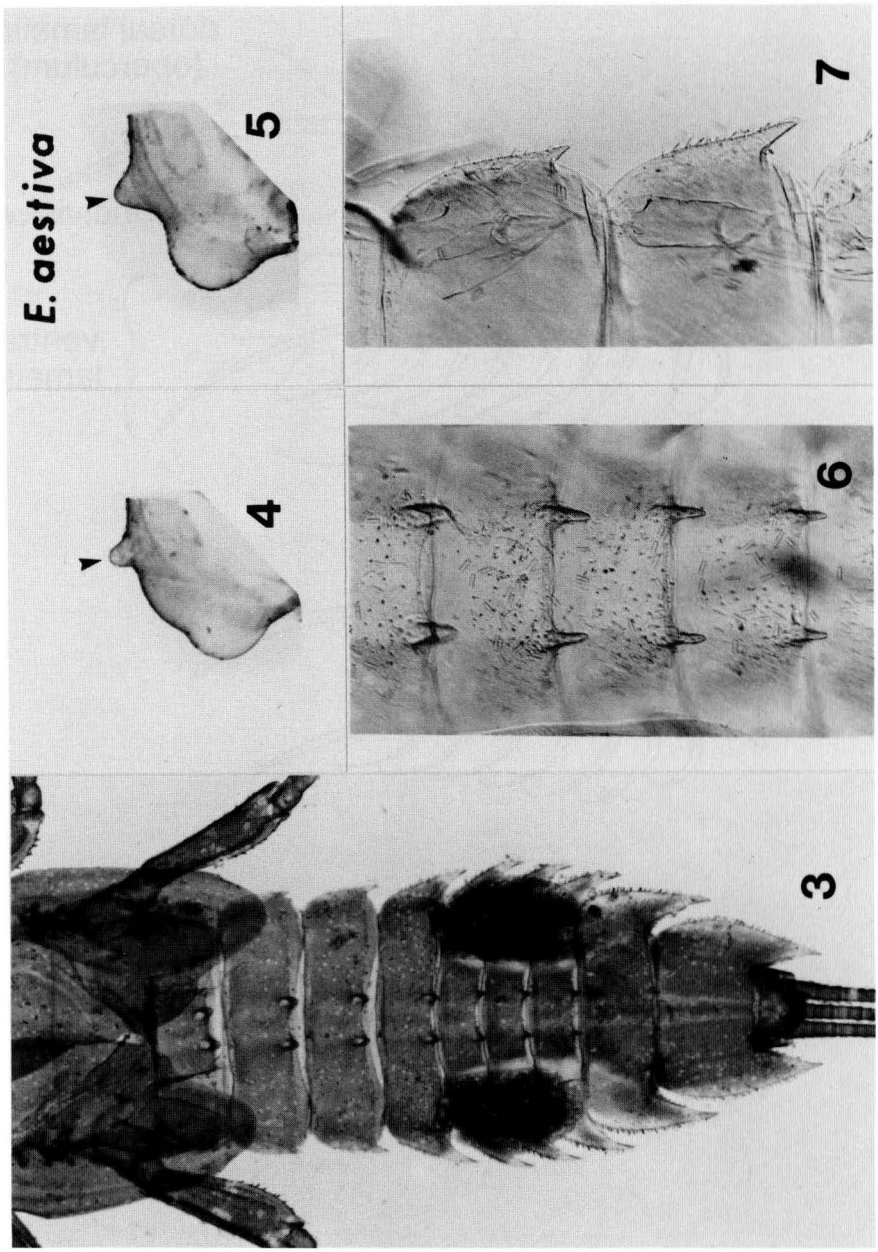


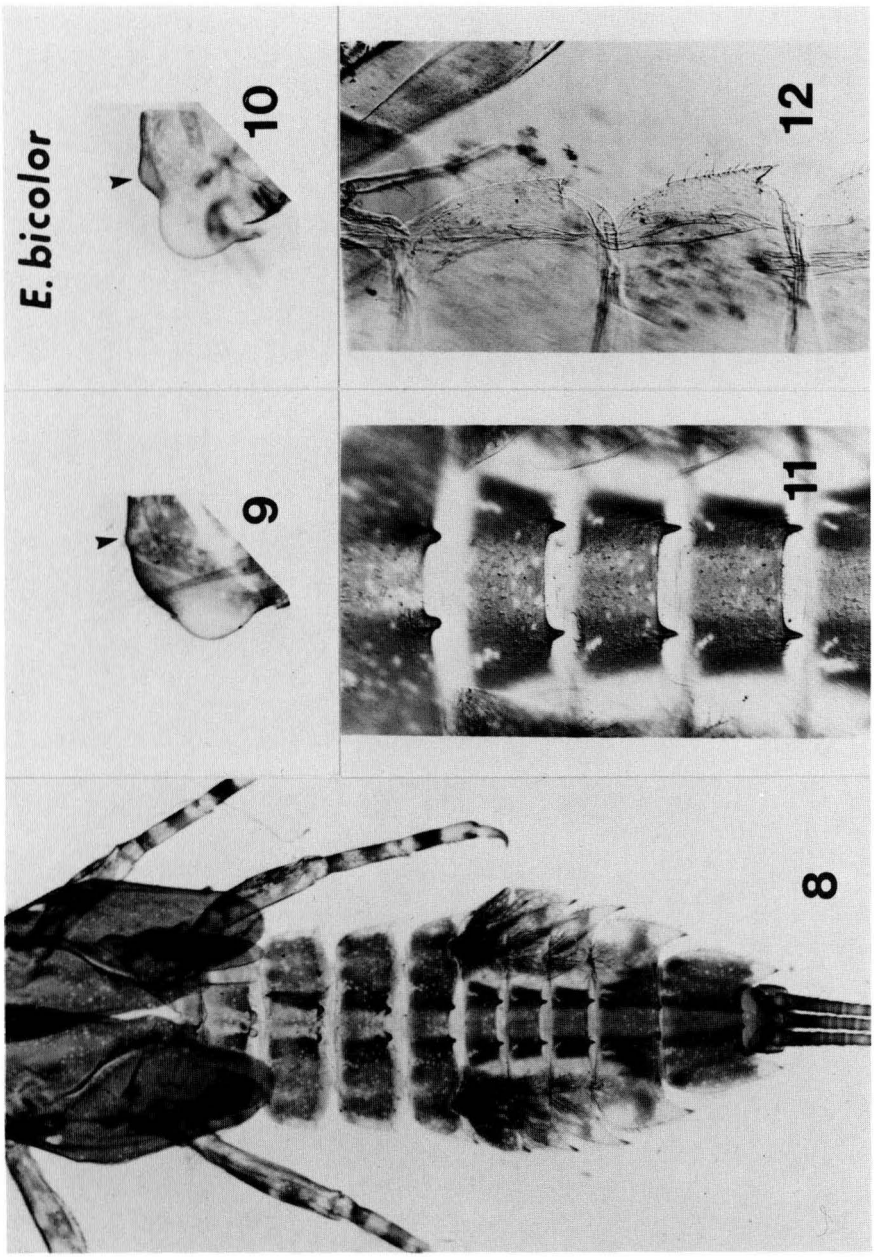
FIGURE 1. Diagramatic representation of larval abdominal tergites 2, 7 and 9 and the right fore femur illustrating the methods used for measurement of the parameters SMT, PLP, ITD, MLT, TL and FWL used in the key and descriptions. The parameter SMT_j is a measure of the distance between the paired submedian tubercles (measured center to center at their bases) for a particular segment (*j*) expressed as a proportion of the tergal length (measured at midline) for that segment. Examples of SMT are illustrated in the figure for segment 2 (SMT_2) and segment 7 (SMT_7); SMT_2 = a/b and SMT_7 = e/f. PLP_j is a measure of the length of a posterolateral projection for a particular segment (*j*) expressed as a proportion to the length of the tergite exclusive of that projection, illustrated here for segments 2 (PLP_2) and 9 (PLP_9). $ITD_{j:k}$ is the ratio of the distance between paired submedian tubercles for two segments (*j* and *k*), illustrated here for segments 2:7 ($ITD_{2:7}$). $MLT_{j:k}$ is the ratio of the lengths of two tergites (*j* and *k*) measured at midline, illustrated here for segments 2:7 ($MLT_{2:7}$). TL_j is a measure of the length of a submedian tubercle for a particular segment (*j*) expressed as a proportion of the median tergal length for that segment, shown here for sgment 7 (TL_7). FWL_j is a measure of the width of a femur (*j*) at its widest point expressed as a proportion to its length (both measured in dorsal view), shown here for the fore leg (FWL_1). Note that all measurements are of sclerites only (unsclerotized cuticle between tergites is ignored).



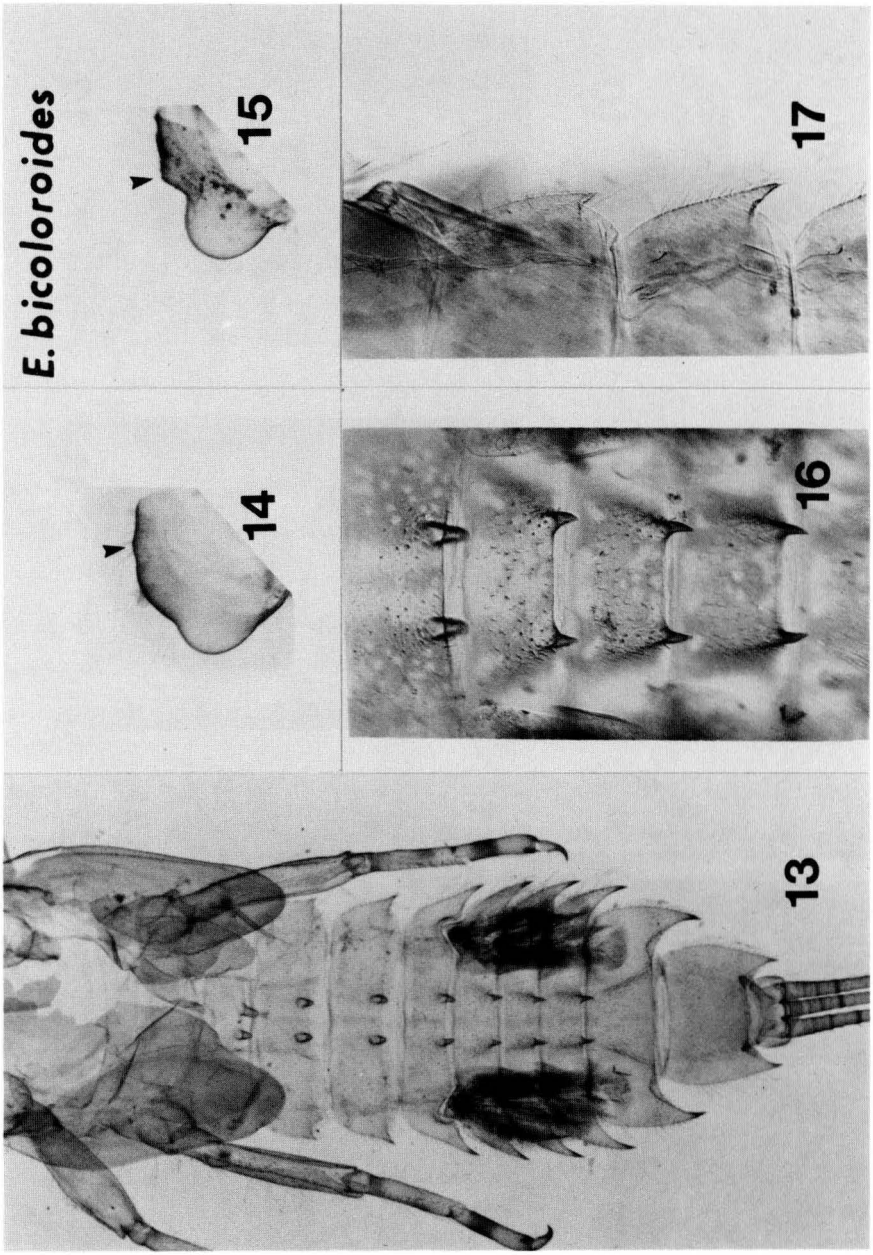
FIGURES 2a-c. Lateral view of the left gill on segment 4 in *Eurylophella* larvae showing varying degrees of reduction of the dorsal subdivisions of the ventral lamella. Gill 4 in *Eurylophella* is divided into a dorsal lamella (operculum) and a laterally bifurcate ventral lamella. Each fork of the ventral lamella is further subdivided dorsally and ventrally. Only the lateral fork is illustrated in this figure; **a**, *E. temporalis* (*temporalis* group); **b**, *E. aestiva* (*lutulenta* group); **c**, *E. verisimilis* (*bicolor* group).



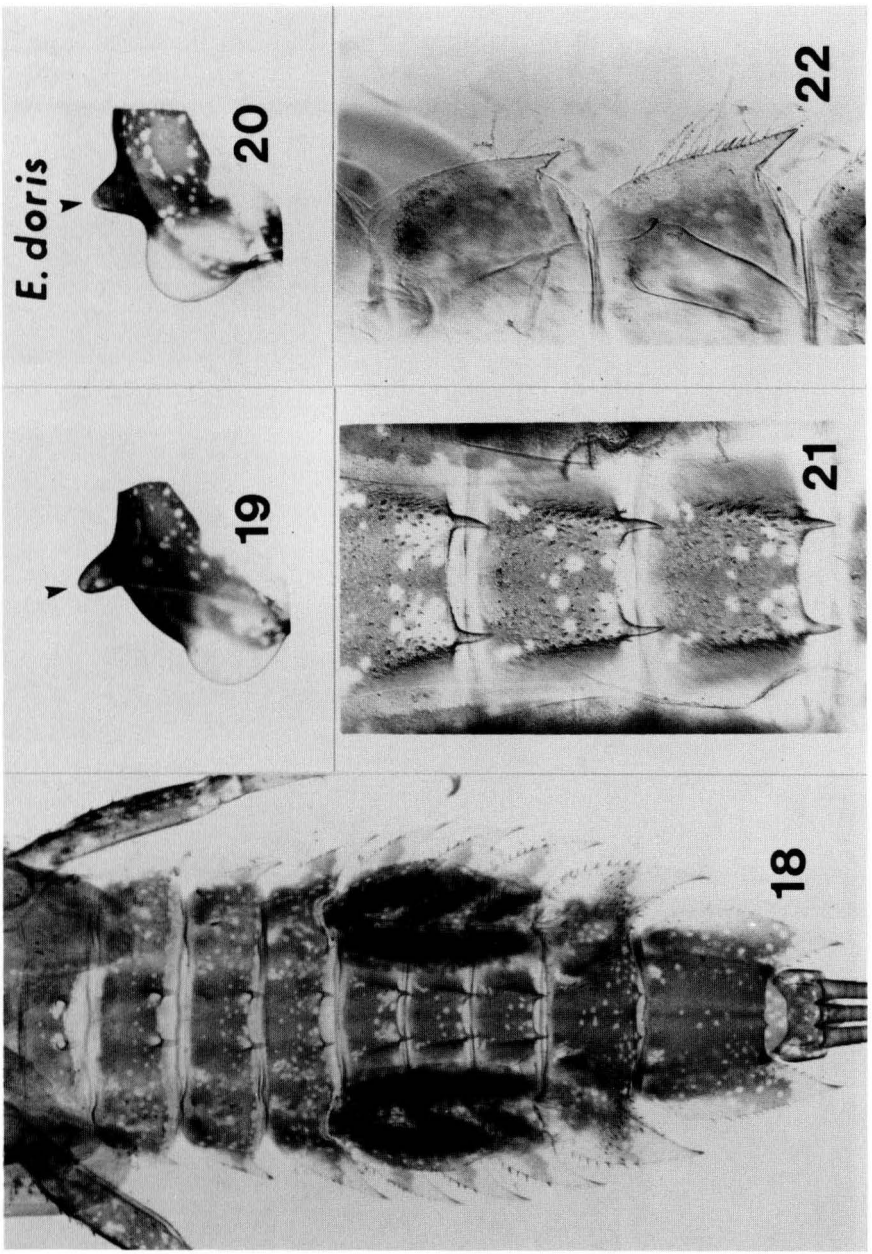
FIGURES 3-7. *Eurylophella aestiva*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **3**, dorsal view of abdomen; **4**, anterior view of right side of head, male; **5**, anterior view of right side of head, female; **6**, dorsal view of terga 4-7; **7**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



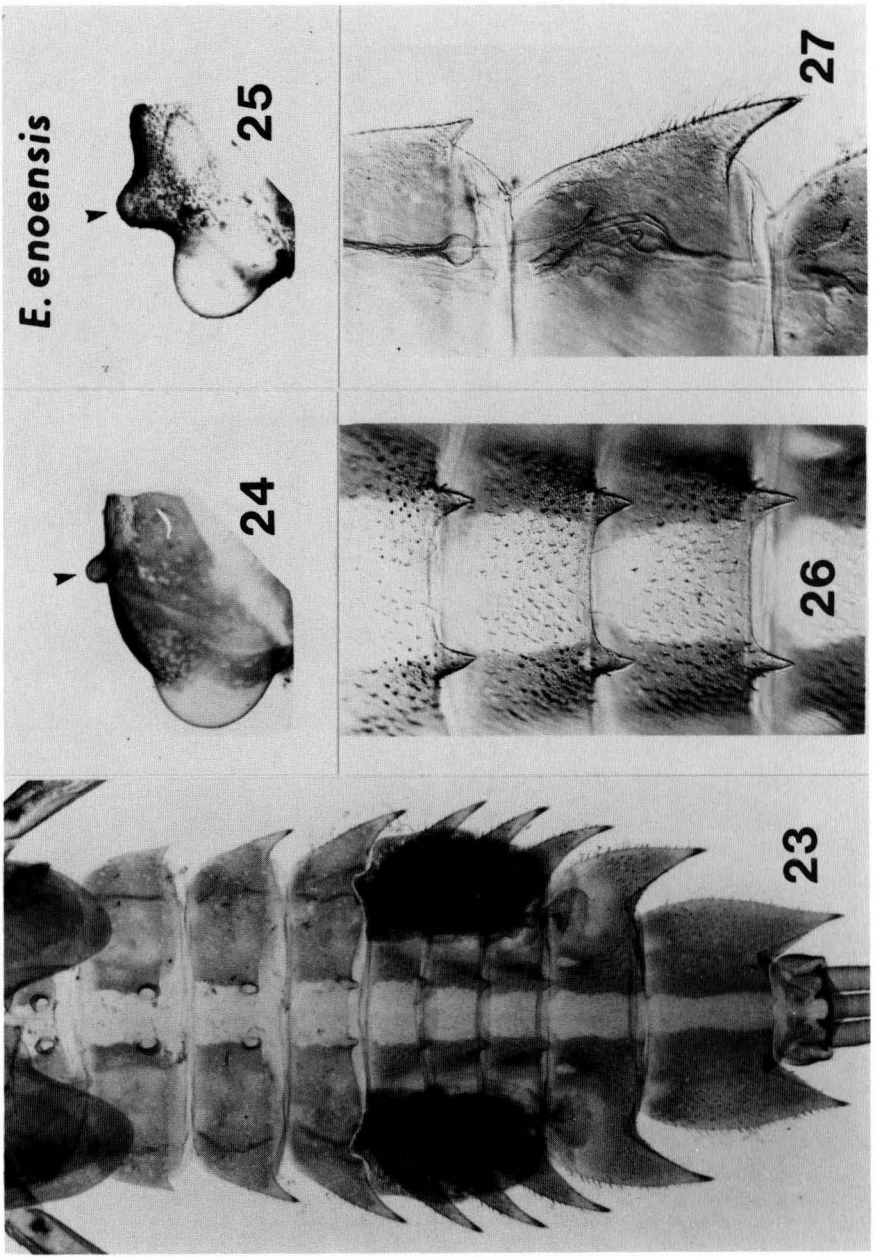
FIGURES 8-12. *Eurylophella bicolor*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **8**, dorsal view of abdomen; **9**, anterior view of right side of head, male; **10**, anterior view of right side of head, female; **11**, dorsal view of terga 4-7; **12**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



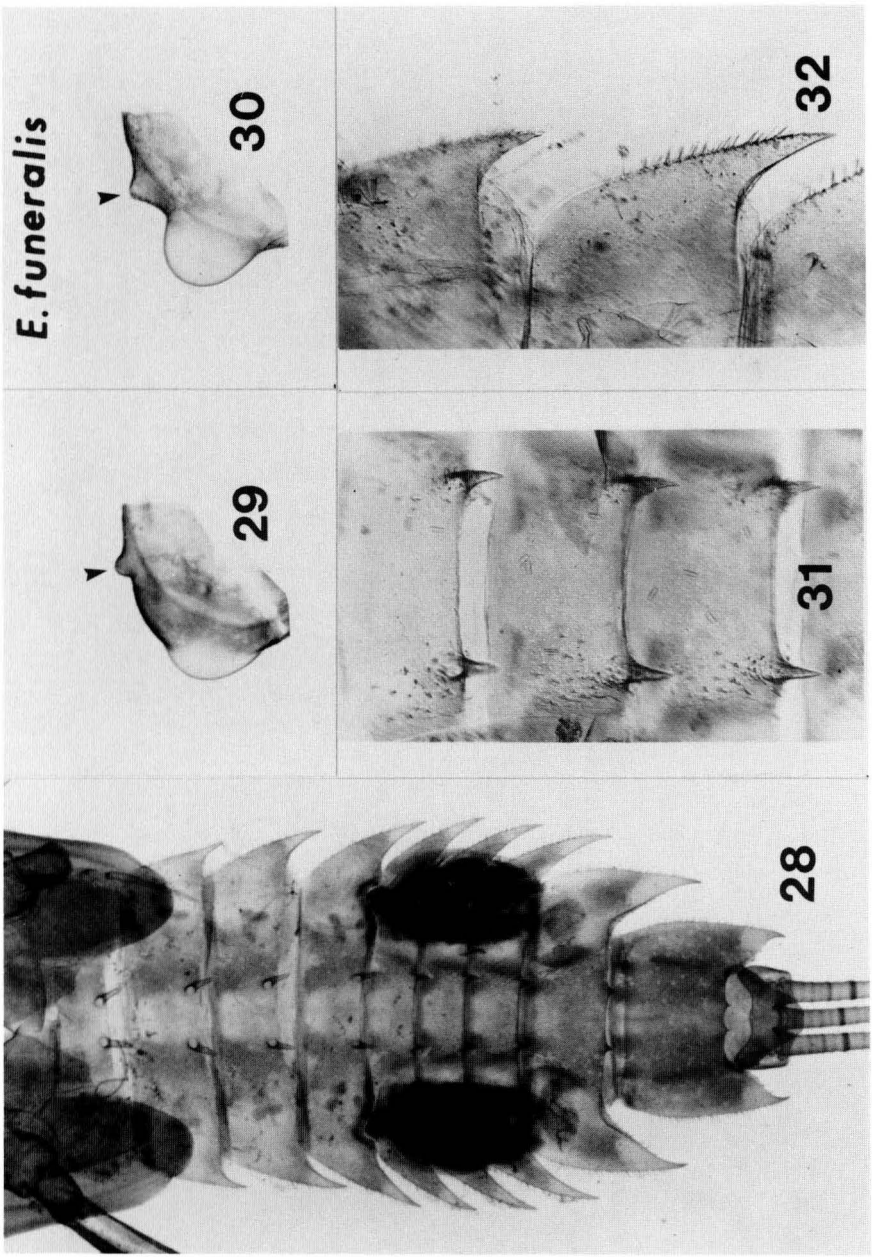
FIGURES 13-17. *Eurylophella bicoloroides*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **13**, dorsal view of abdomen; **14**, anterior view of right side of head, male; **15**, anterior view of right side of head, female; **16**, dorsal view of terga 4-7; **17**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



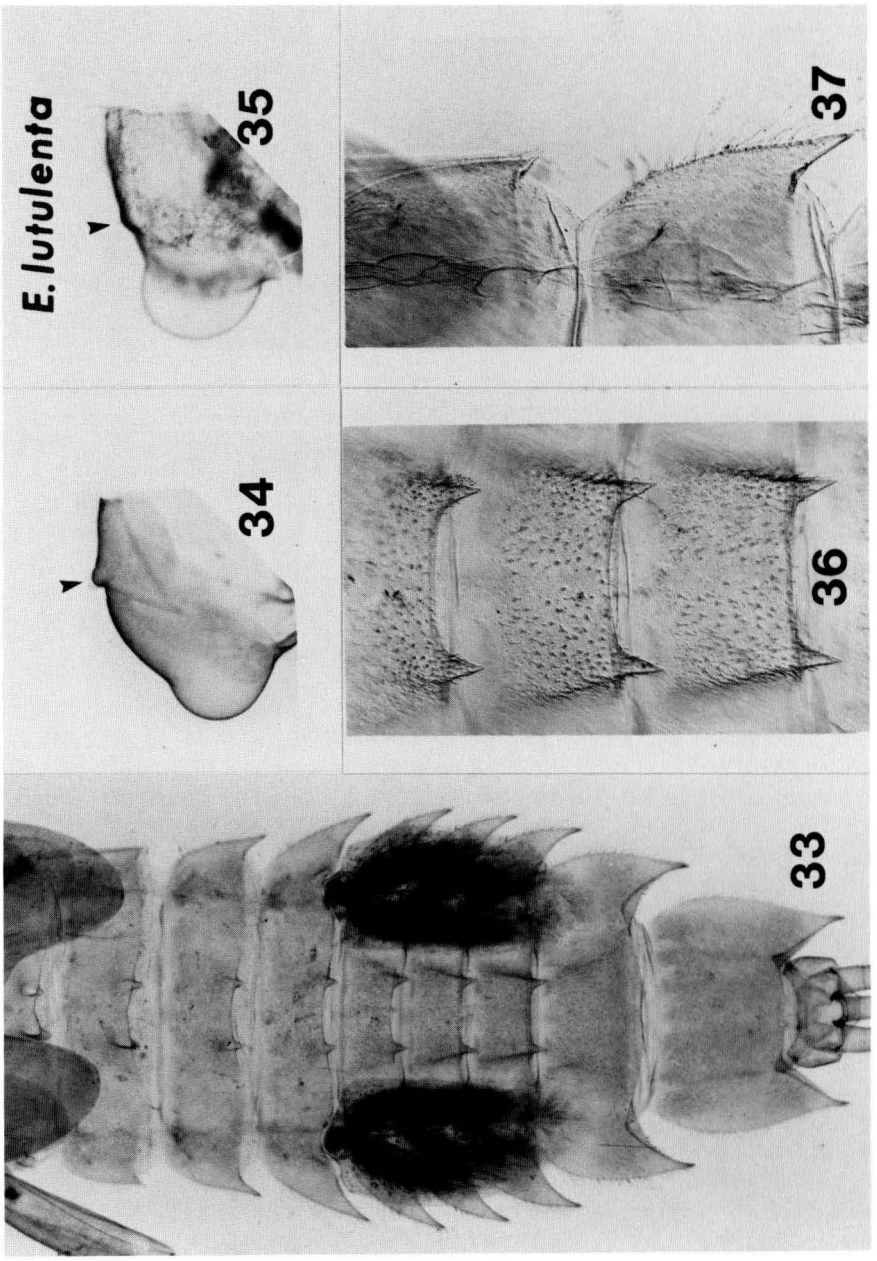
FIGURES 18-22. *Eurylophella doris*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **18**, dorsal view of abdomen; **19**, anterior view of right side of head, male; **20**, anterior view of right side of head, female; **21**, dorsal view of terga 5-7; **22**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



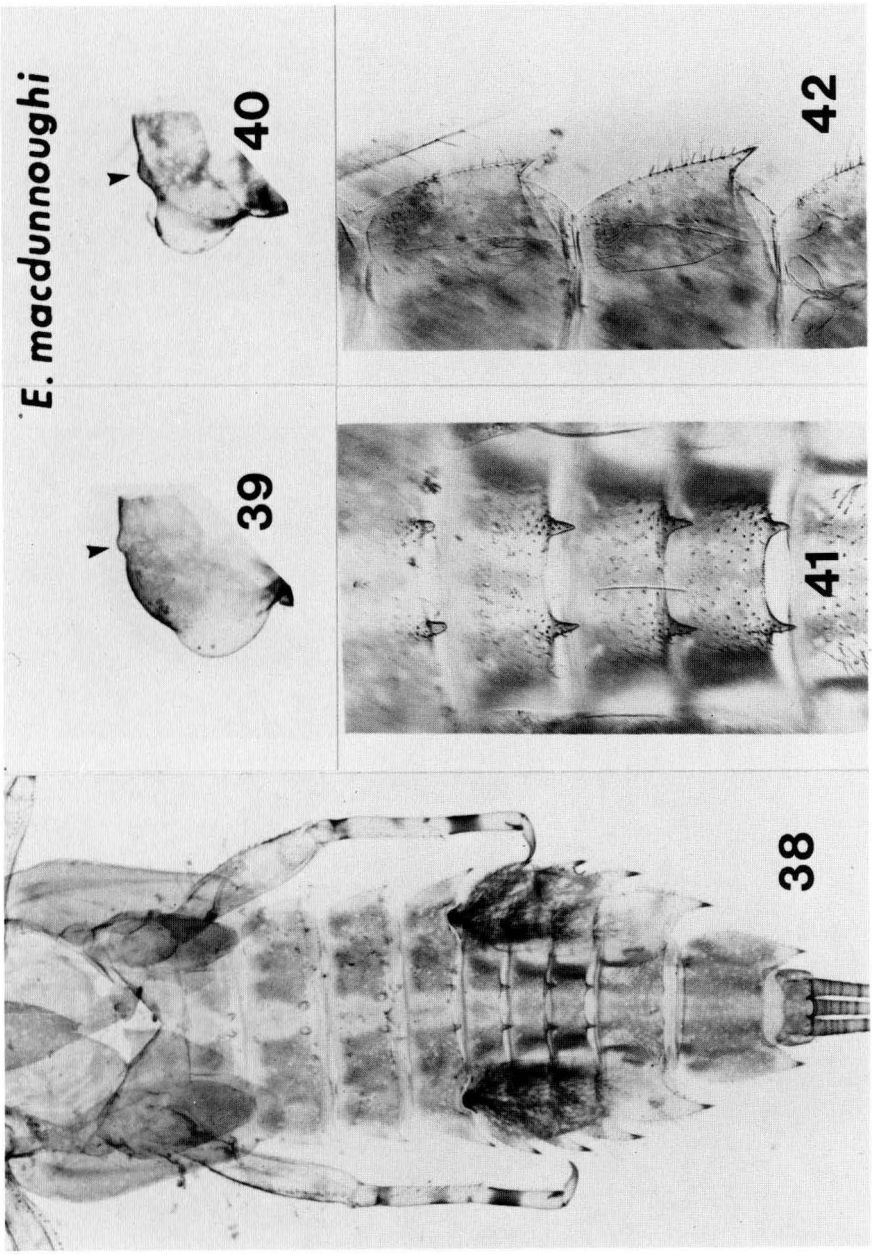
FIGURES 23-27. *Eurylophella enoensis*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **23**, dorsal view of abdomen; **24**, anterior view of right side of head, male; **25**, anterior view of right side of head, female; **26**, dorsal view of terga 5-7; **27**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



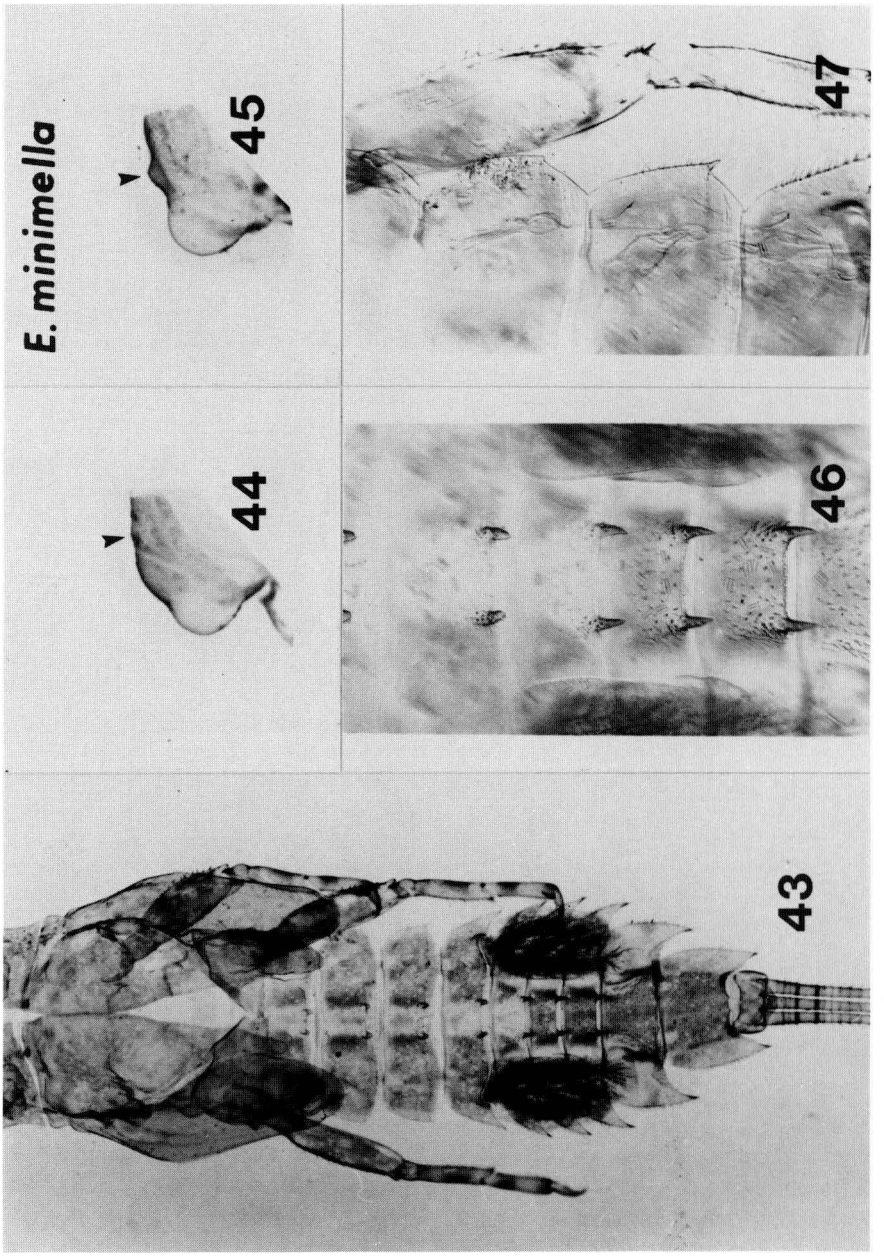
FIGURES 28-32. *Eurylophella funeralis*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **28**, dorsal view of abdomen; **29**, anterior view of right side of head, male; **30**, anterior view of right side of head, female; **31**, dorsal view of terga 5-7; **32**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



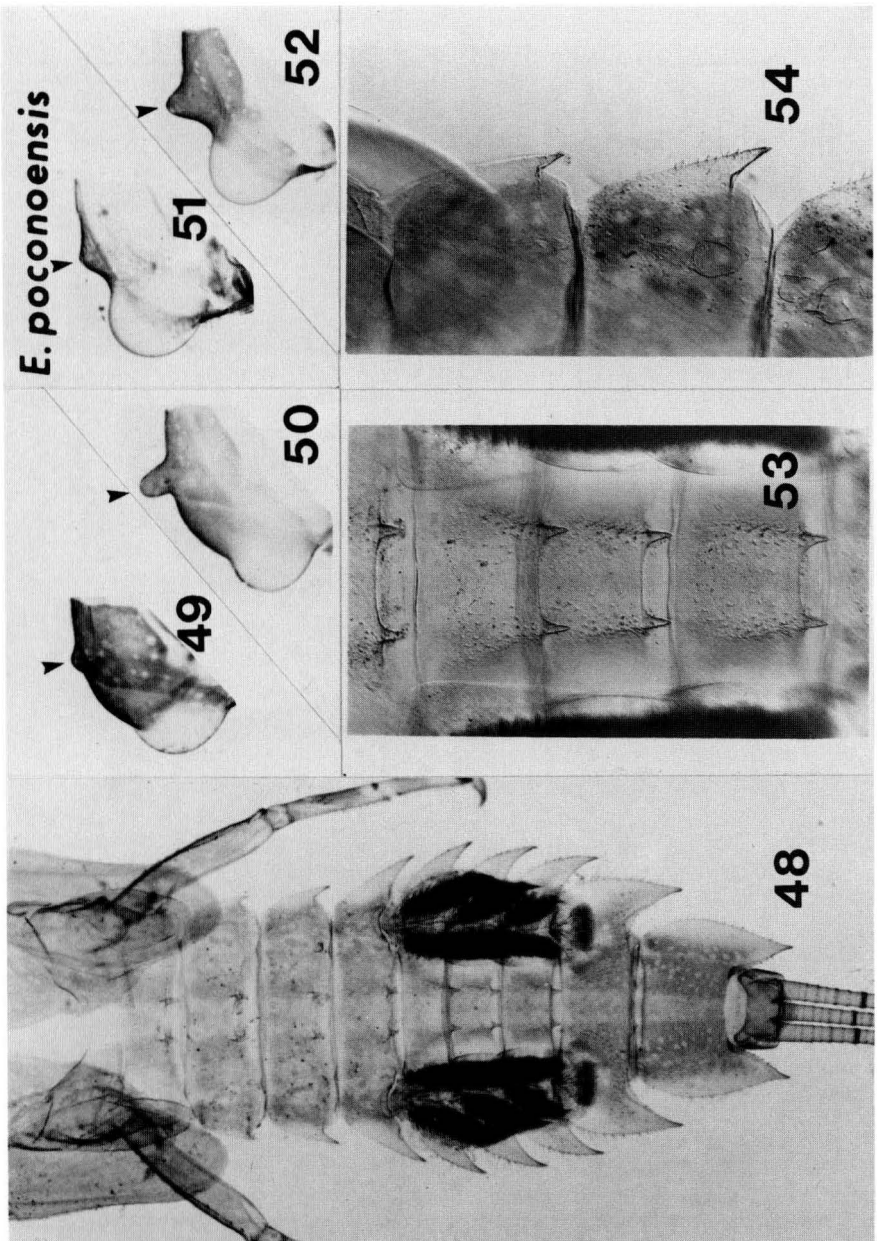
FIGURES 33-37. *Eurylophella lutulenta*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **33**, dorsal view of abdomen; **34**, anterior view of right side of head, male; **35**, anterior view of right side of head, female; **36**, dorsal view of terga 5-7; **37**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



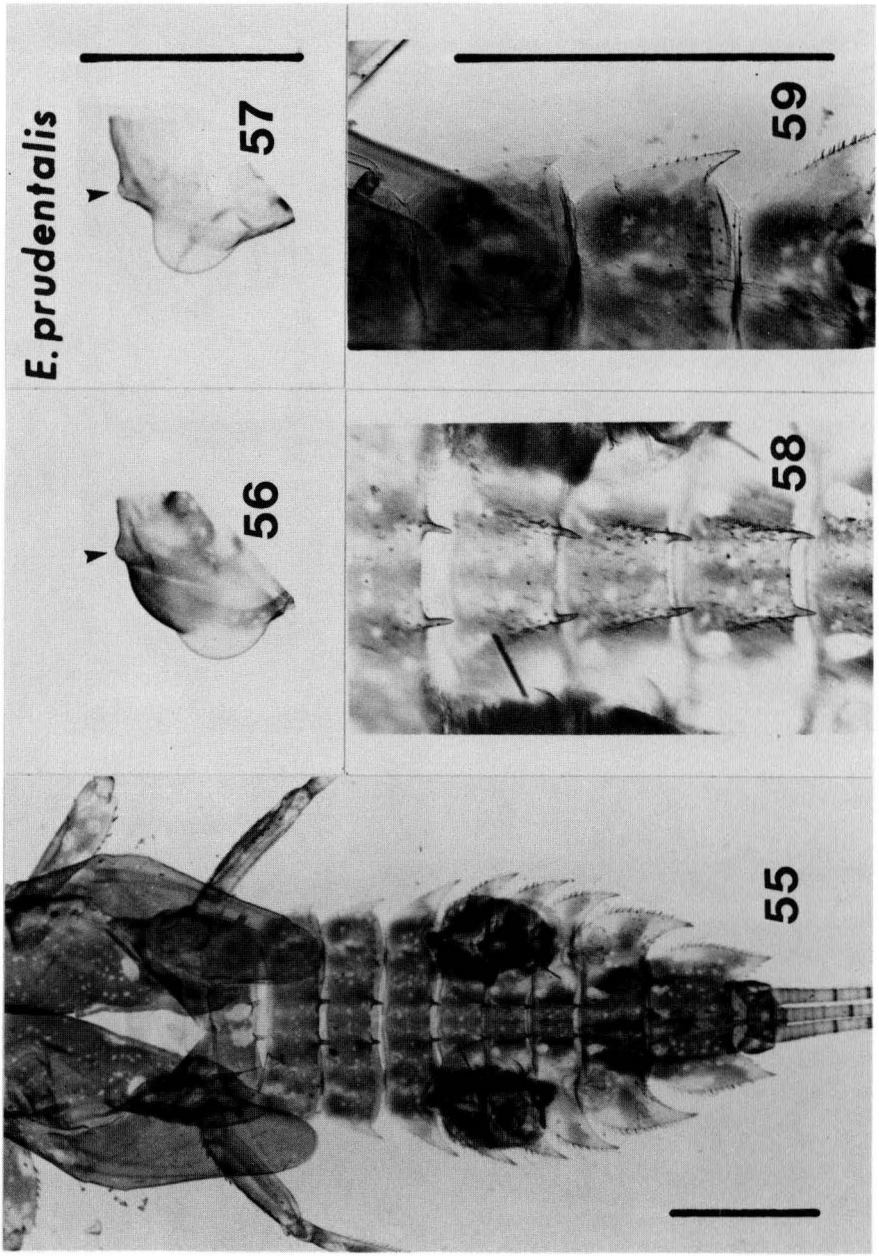
FIGURES 38-42. *Eurylophella macdunnoughi*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **38**, dorsal view of abdomen; **39**, anterior view of right side of head, male; **40**, anterior view of right side of head, female; **41**, dorsal view of terga 4-7; **42**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



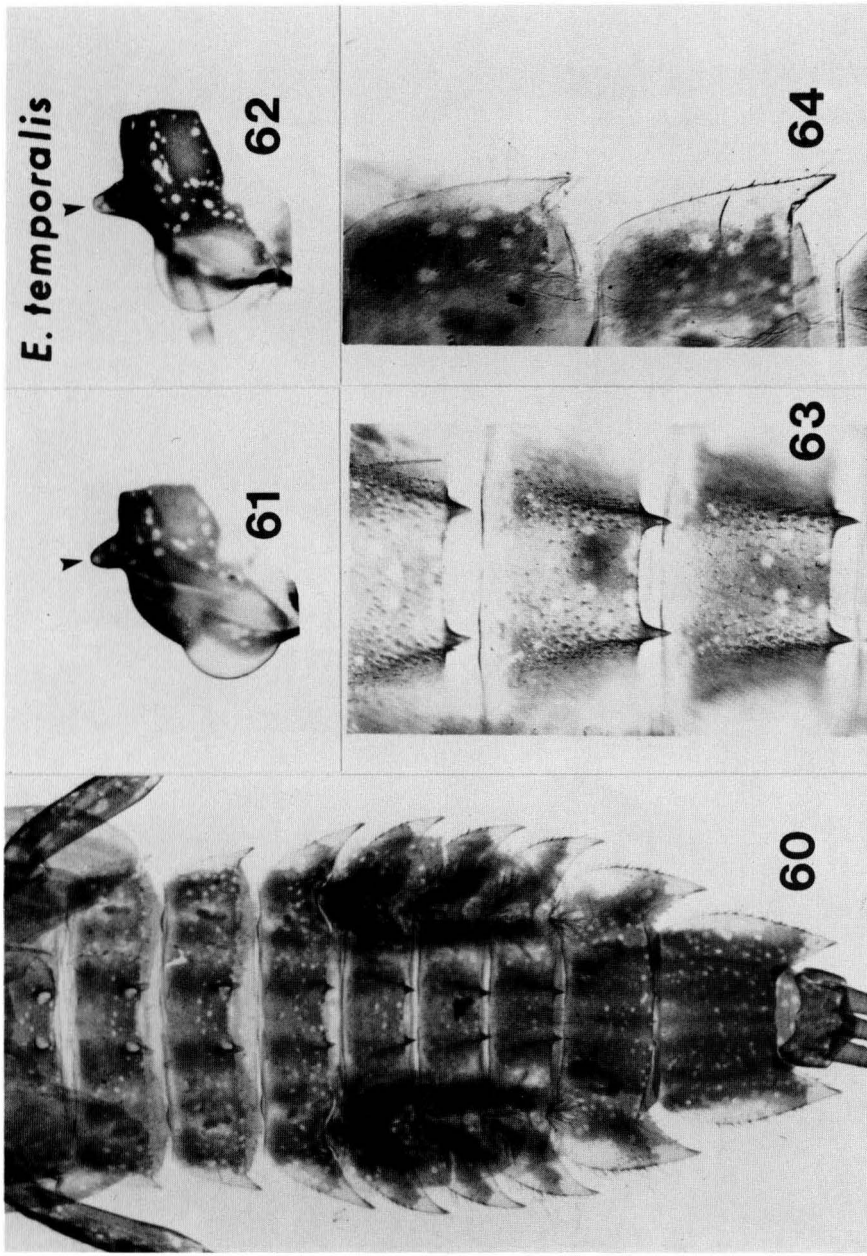
FIGURES 43-47. *Eurylophella minimella*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **43**, dorsal view of abdomen; **44**, anterior view of right side of head, male; **45**, anterior view of right side of head, female; **46**, dorsal view of terga 4-7; **47**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



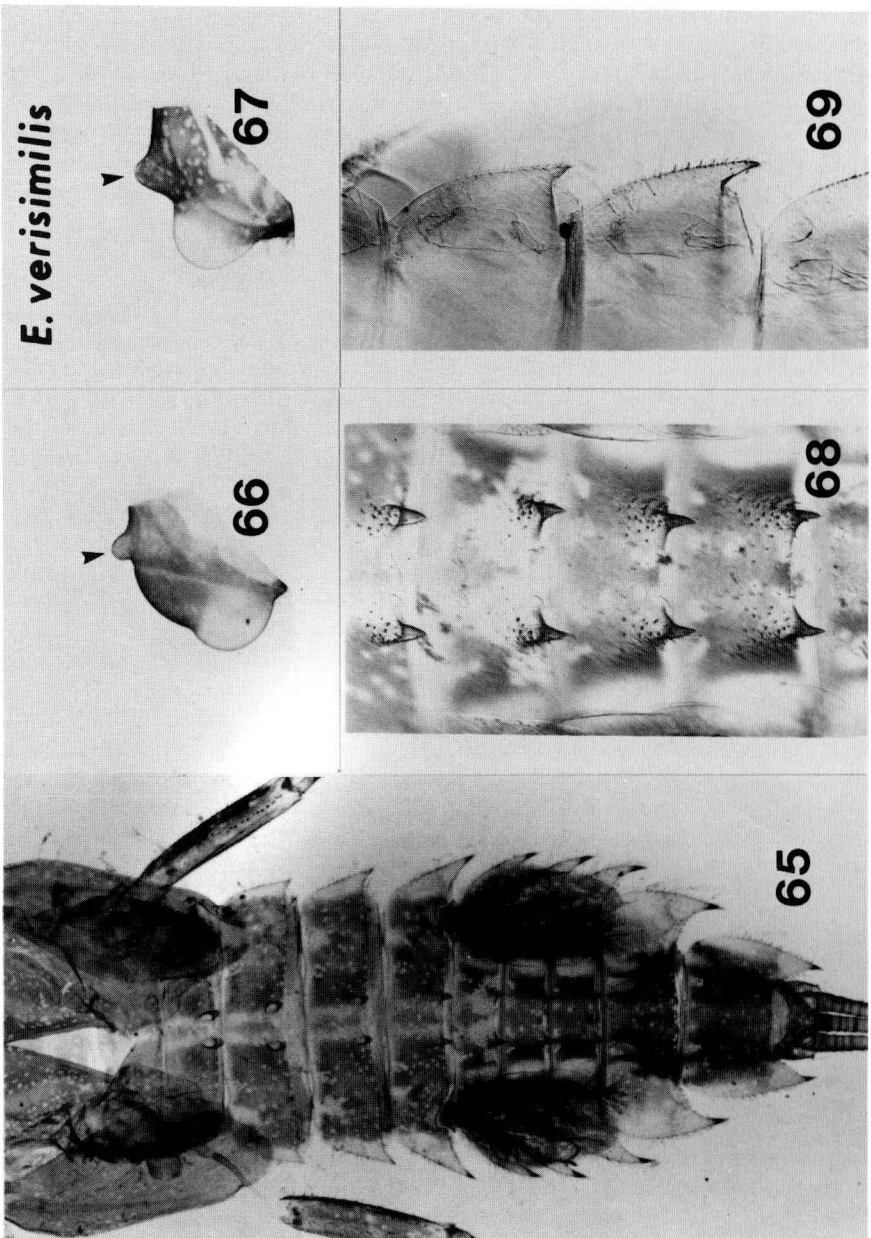
FIGURES 48-54. *Eurylophella poconoensis*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **48**, dorsal view of abdomen; **49**, anterior view of right side of head, male (individual with small occipital tubercles); **50**, anterior view of right side of head, male (individual with long occipital tubercles); **51**, anterior view of right side of head, female (individual with small occipital tubercles); **52**, anterior view of right side of head, female (individual with long occipital tubercles); **53**, dorsal view of terga 4-7; **54**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



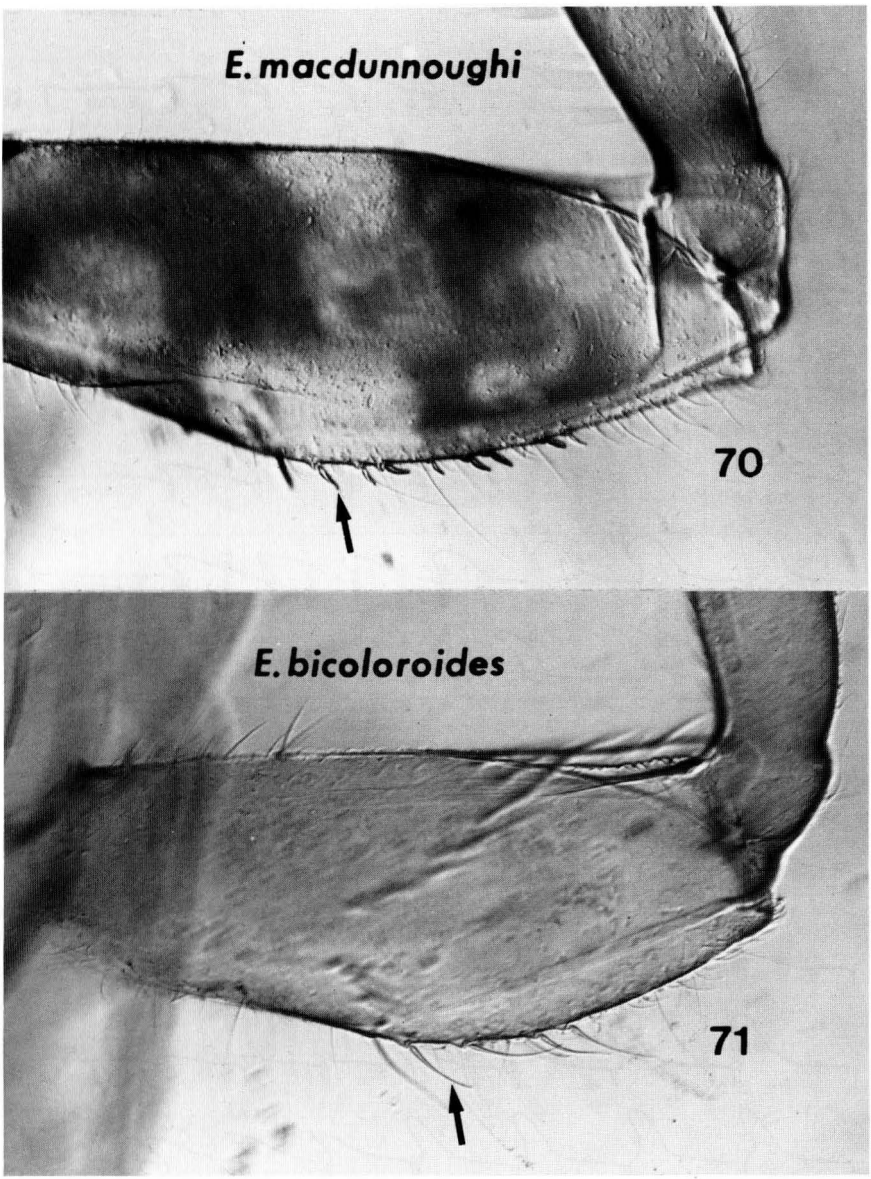
FIGURES 55-59. *Eurylophella prudentalis*, larval exuviae; **55**, dorsal view of abdomen (line = 1 mm); **56**, anterior view of right side of head, male (scale same as in 57); **57**, anterior view of right side of head, female (line = 1 mm); **58**, dorsal view of terga 4-7 (scale same as in 59); **59**, dorsal view of posterolateral projections on abdominal segments 2 and 3 (line = 1 mm).



FIGURES 60-64. *Eurylophella temporalis*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **60**, dorsal view of abdomen; **61**, anterior view of right side of head, male; **62**, anterior view of right side of head, female; **63**, dorsal view of terga 5-7; **64**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



FIGURES 65-69. *Eurylophella verisimilis*, larval exuviae (magnifications same as in Figs. 55-59 for respective body parts); **65**, dorsal view of abdomen; **66**, anterior view of right side of head, male; **67**, anterior view of right side of head, female; **68**, dorsal view of terga 4-7; **69**, dorsal view of posterolateral projections on abdominal segments 2 and 3.



FIGURES 70-71. Right fore leg of larval exuviae, dorsal view, showing spines (arrows) on hind margin of femur; **70**, *Eurylophella macdunnoughi*; **71**, *Eurylophella bicoloroides*.

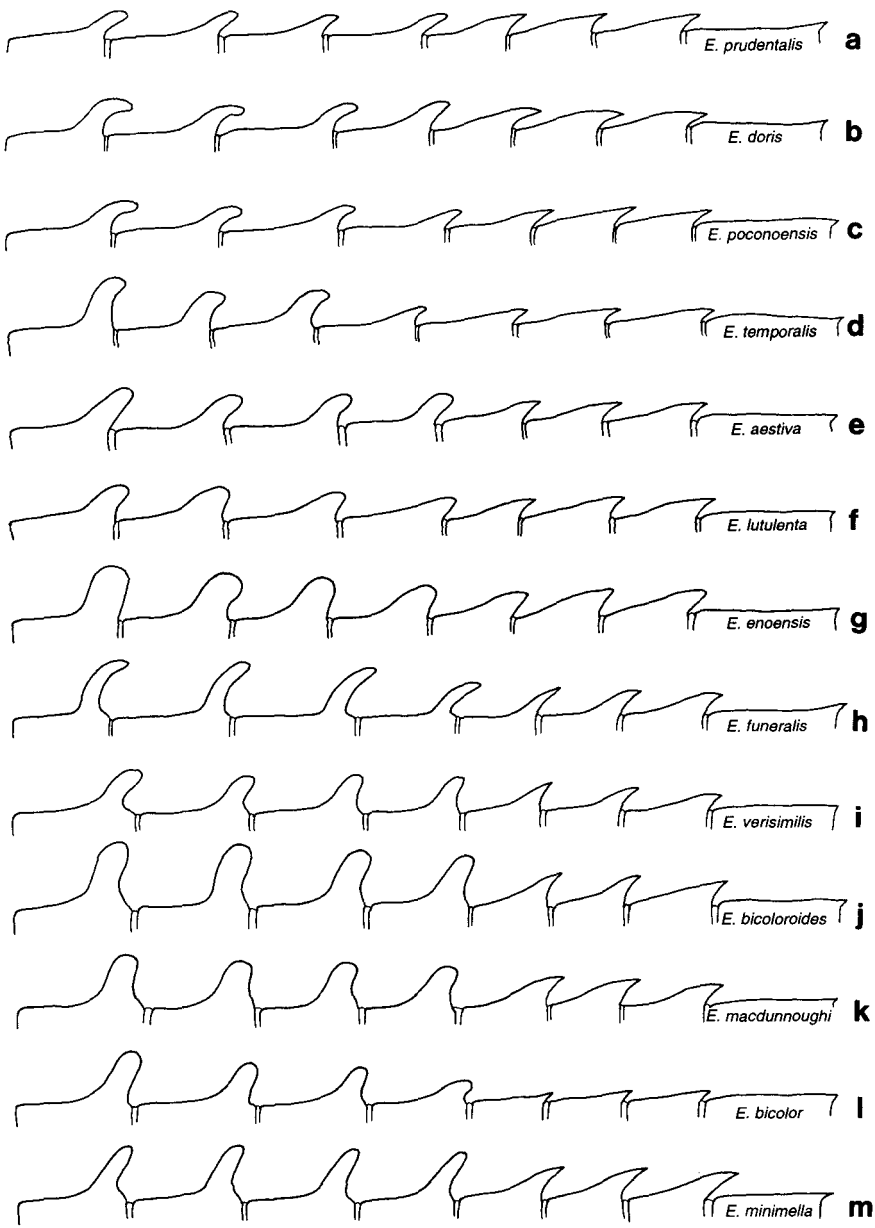


FIGURE 72. Abdominal segments 1-8 of larvae, lateral view of tergites showing shape of submedian tubercles typical of various *Eurylophella* species. Considerable variation exists in some species; see descriptions for explanation.

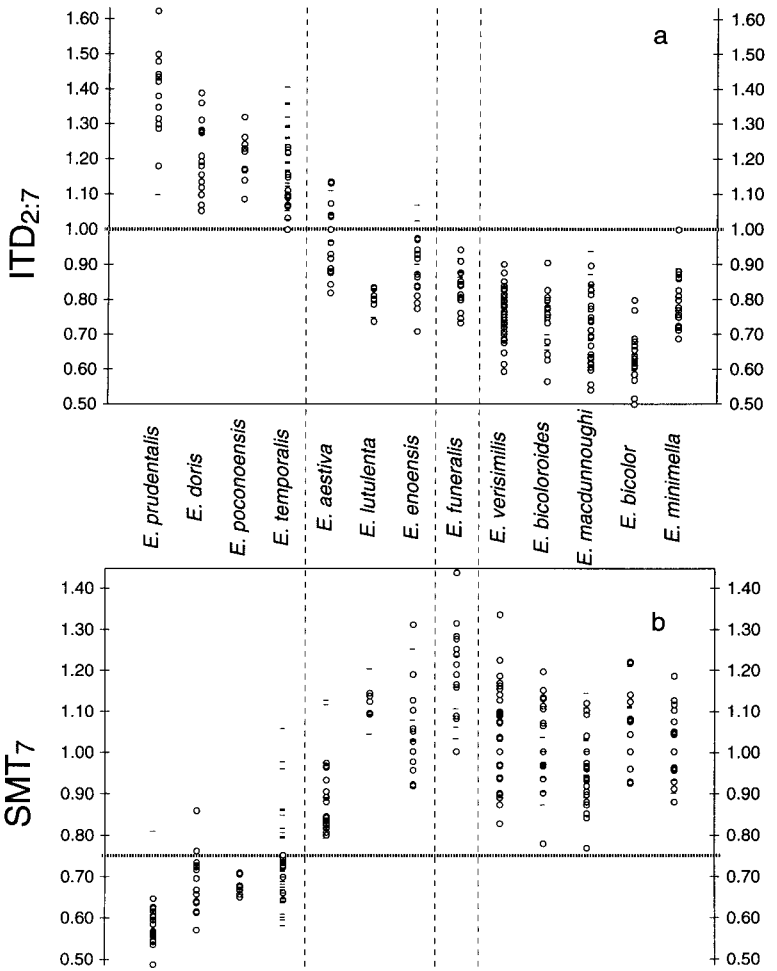


FIGURE 73. Graphs showing the distribution of $ITD_{2:7}$ and SMT_7 for *Eurylophella*, by species with vertical dashed lines dividing species groups. Dotted lines intersecting *y*-axes are cutoffs used in couplet 2 of the morphological key. **73a**, $ITD_{2:7}$ (ratio of distance between submedian tubercles on abdominal segment 2 to that between tubercles on segment 7; a/e in Fig. 1); **73b**, SMT_7 (ratio of ratio of distance between submedian tubercles on abdominal segment 7 to the length of that tergite at midline; e/f in Fig. 1). Symbols: circles represent specimens that have been electrophoresed; horizontal lines represent specimens of unknown genetic composition, mostly from geographically marginal areas (see text).

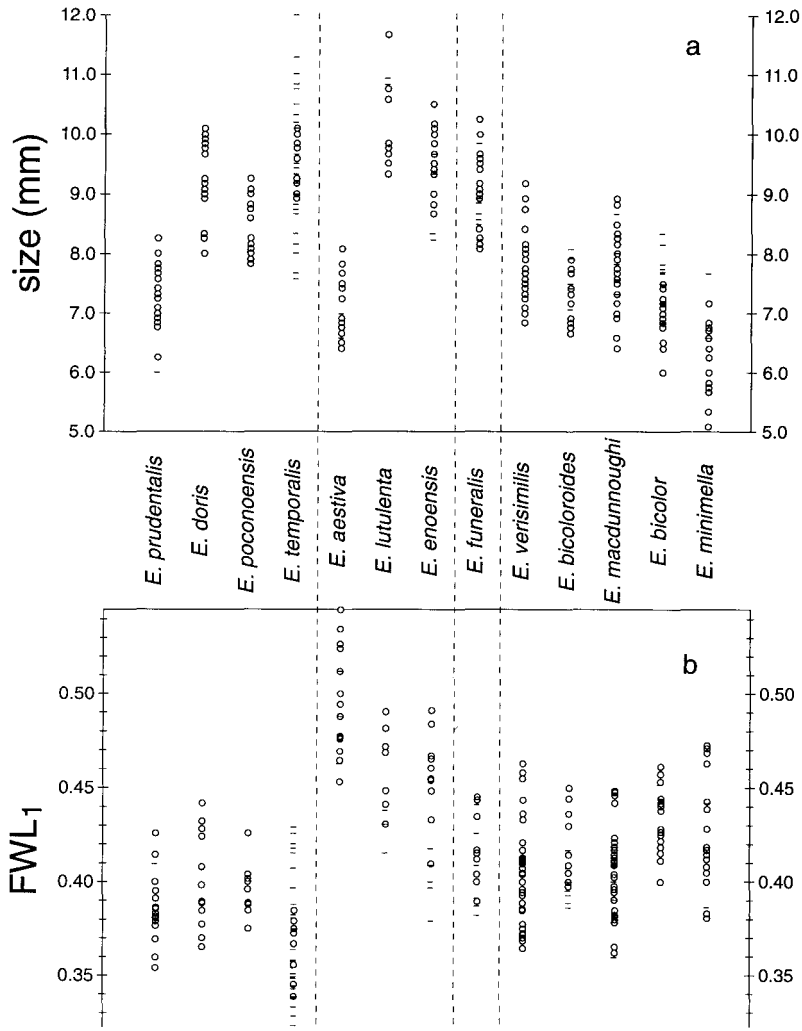


FIGURE 74. Graphs showing the size distribution of full-grown larvae and FWL_1 for *Eurylophella*, by species with vertical dashed lines dividing species groups. **74a**, size (length of body exclusive of tails); **74b**, FWL_1 (ratio of width to length of fore femur; j/k in Fig. 1). Symbols: circles represent specimens that have been electrophoresed; horizontal lines represent specimens of unknown genetic composition, mostly from geographically marginal areas (see text).

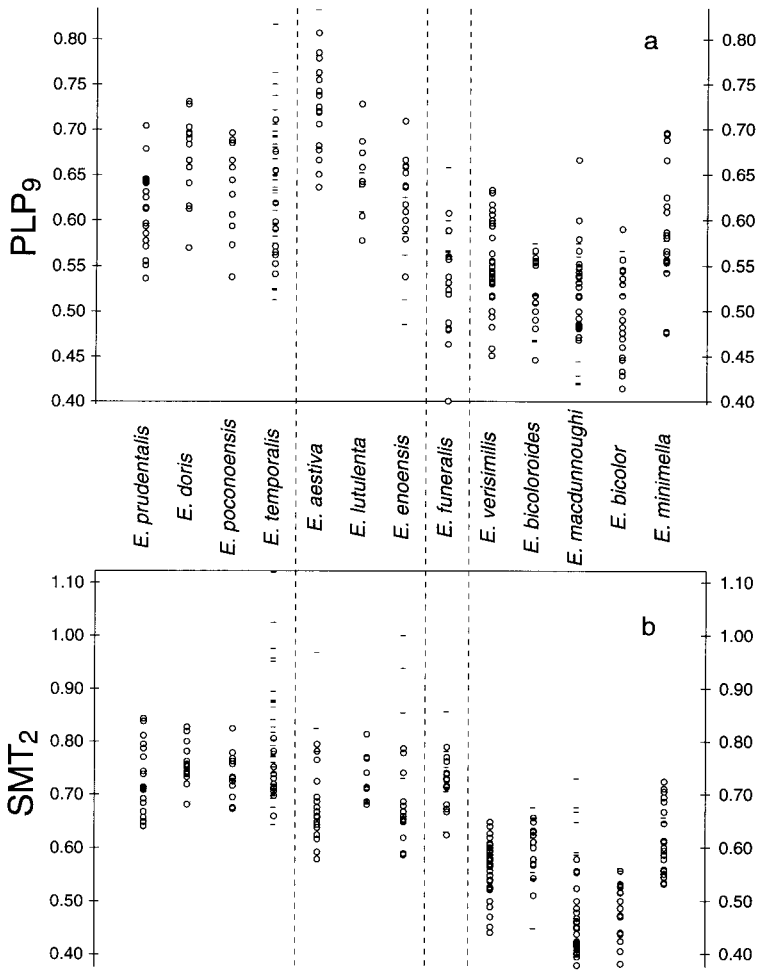


FIGURE 75. Graphs showing the distribution of larval PLP_9 and SMT_2 for *Eurylophella*, by species with vertical dashed lines dividing species groups. **75a,** PLP_9 [ratio of length of posterolateral projection on abdominal segment 9 to the length of 9th tergite exclusive of posterolateral projection; (h-i)/i in Fig. 1]; **75b,** SMT_2 (ratio of ratio of distance between submedian tubercles on abdominal segment 2 to the length of that tergite at midline;a/b in Fig. 1). Symbols: circles represent specimens that have been electrophoresed; horizontal lines represent specimens of unknown genetic composition, mostly from geographically marginal areas (see text).

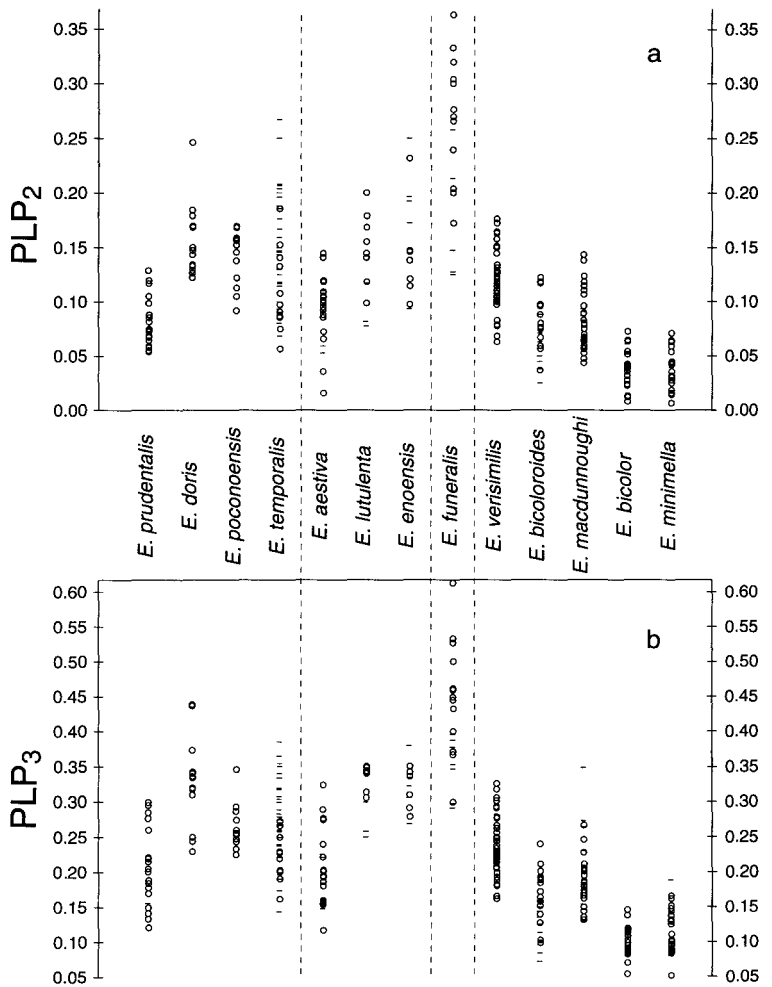


FIGURE 76. Graphs showing the distribution of larval PLP_2 and PLP_3 for *Eurylophella*, by species with vertical dashed lines dividing species groups. **76a,** PLP_2 [ratio of lengths of the posterolateral projections on abdominal segment 2 to the length of its tergite; PLP_2 = (c-d)/d in Fig. 1]; **76b,** PLP_3 (measured in the same manner as PLP_2, but for segment 3). Symbols: circles represent specimens that have been electrophoresed; horizontal lines represent specimens of unknown genetic composition, mostly from geographically marginal areas (see text).

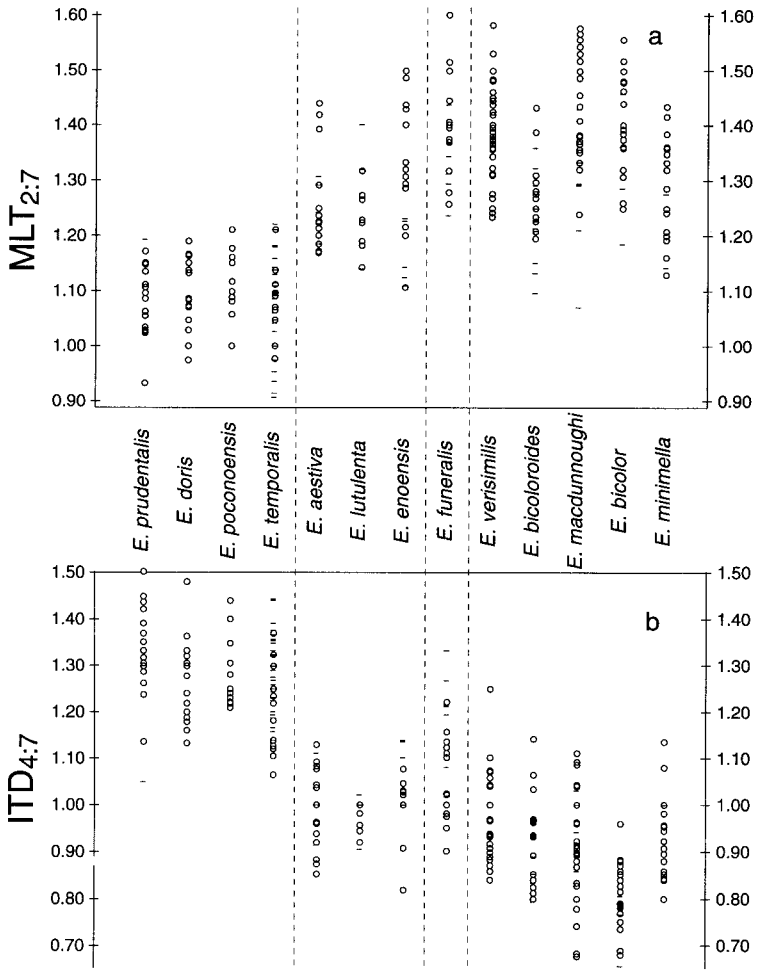


FIGURE 77. Graphs showing the distribution of larval $MLT_{2:7}$ and $ITD_{4:7}$ for *Eurylophella*, by species with vertical dashed lines dividing species groups. **77a**, $MLT_{2:7}$ (ratio of length of tergite 2 to that of 7, measured at midline; b/f in Fig. 1); **77b**, $ITD_{4:7}$ (ratio of distance between bases, measured center to center, of submedian tubercles on segment 4 to those of segment 7). Symbols: circles represent specimens that have been electrophoresed; horizontal lines represent specimens of unknown genetic composition, mostly from geographically marginal areas (see text).

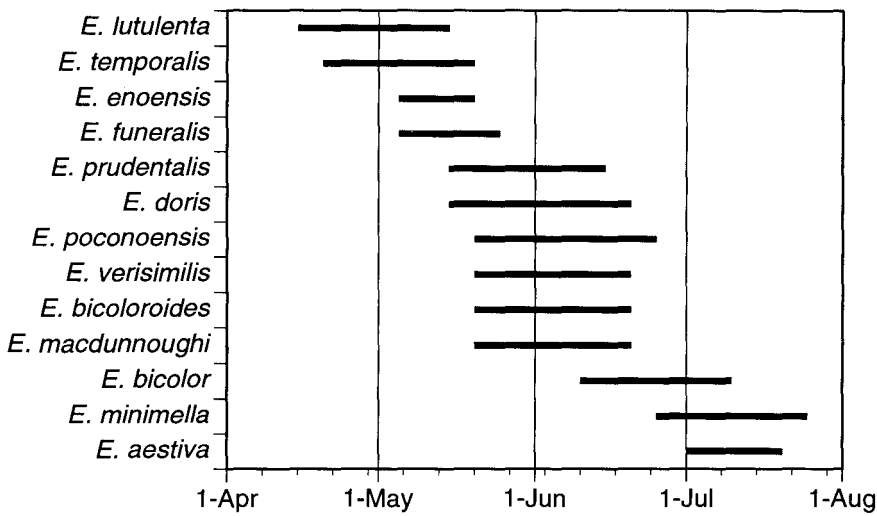


FIGURE 78. Temporal sequence of adult emergence periods for eastern North American species of *Eurylophella*, normalized for southeastern Pennsylvania (about 40° north latitude, elevation 100 meters).