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Taxonomy of *Eurylophella coxalis* (McDunnough) with notes on larval habitat and behavior (Ephemeroptera:Ephemerellidae)

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Abstract. Larval stages have been associated for all of the known species of *Eurylophella* in eastern North America except for *E. coxalis*. The larva of *E. coxalis* is described herein from a reared series of specimens. Adults are redescribed and eggs are described for the 1st time, as are notes on larval habitat and behavior. Association of *E. coxalis* completes our knowledge of the life stages of a presumed different species, *Dentatella bartoni*, which was previously known only from the larval stage. This larva is now determined to be the larval stage of *E. coxalis*. Further, characters used to diagnose *Dentatella danutae* have shown that this taxon is not different from what has been called *D. bartoni*. Thus, *Dentatella bartoni* (Allen) and *D. danutae* McCafferty are now placed as subjective junior synonyms of *E. coxalis*. A conservative criterion requiring that apomorphic characters be discernable in both larval and adult life stages is proposed for recognizing mayfly genera when knowledge of life stages and/or the phylogenetic nature of diagnostic characters is incomplete. Field and laboratory observations of live *E. coxalis* larvae show this species to be associated with cold, swift, alkaline streams containing coarse inorganic substrates with well-developed periphyton.

Key words: Ephemeroptera, Ephemerellidae, *Eurylophella*, *E. coxalis*, *Dentatella*, *D. bartoni*, *D. danutae*, taxonomy, ecology.

The genus *Eurylophella* contains a diverse assemblage of 14 species that are broadly distributed within lotic and lentic habitats in eastern North America. Larval and adult stages are known for all but 1 of these taxa, *Eurylophella coxalis* (McDunnough). The adult stages of *E. coxalis* were described by McDunnough (1926) from a series of male and female imagos collected from several sites in southern Québec and Ontario. McDunnough (1926) placed *E. coxalis* in the *bicolor–lutulenta* species group based on studies of the male genitalia. In a later study of the *bicolor–lutulenta* species group, McDunnough (1931) attempted an association and description of an unknown larva (i.e., one he could not associate with any known species of *Eurylophella*) as the larva of *E. coxalis*. Allen and Edmunds (1963) revised the taxonomy of the *Eurylophella*, but were unable to resolve the questionable status of the larval stage of *E. coxalis*. Despite Allen and Edmunds's (1963) clear indication of the uncertain status of the larval description, inclusion of *E. coxalis* in their larval key subsequently led to some confusion and numerous misidentifications.

Funk and Sweeney (1994) provided the most detailed analysis of the larvae of the eastern North American *Eurylophella* to date. They showed that the larva tentatively assigned to *E. coxalis* by McDunnough (1931) was actually *E. enoensis* Funk. However, the larva of *E. coxalis* remained unknown, so the species could not be placed with the new species groups defined therein. The status of the larval stage of *E. coxalis* has remained uncertain until now. However, solving the mystery of the larval stage of *E. coxalis* has yielded an unexpected bonus because it also resolved a similar yet opposite problem of another species that was described only from the larval stage.

Allen (1977) described a new species of *Ephemerella* in the subgenus *Dannella* from larvae collected from Lake Huron, and named it *E.* (*Dannella*) *bartoni* in honor of the collector, David Barton. This unusual larva has been the center of considerable taxonomic debate because its characters seemed to overlap those of both *Eurylophella* and *Dannella* (see account of taxonomic discrepancies between these 2 genera by McCafferty and Wang 1994). Further, McCafferty and Wang (1994) placed *bartoni* (at that time in *Dannella*) in the genus *Eurylophella* based on their phylogenetic studies of the species of the *Timpanoga* complex. McCafferty and Wang (1994) believed the *bartoni* lineage represented a distinct subgeneric branch within the *Eurylophella* clade, and defined *Dentatella* as a new subgenus for this group. McCafferty (2000) elevated

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TABLE 1. Physicochemical variables at the North Branch of the Sugar River, New Hampshire, associated with collections of *Eurylophella coxalis* larva. Depth and velocity were measured where larvae were found. Dissolved oxygen (DO) was measured near the bottom (b) or close to the surface (s) at these same locations. – = measurement not taken.

Date	Air temperature (°C)	Water temperature (°C)	Depth (m)	Velocity (m/s)	pH	Specific conductance (μS/cm)	DO (mg/L)
27 June 1999	33.2	28.1	–	–	8.1	177	–
23 March 2000	19.0	4.9	0.80	0.48	8.1	70	–
			0.50	0.52	8.1	70	
1 April 2000	9.4	4.7	0.80	0.59	8.2	49	10.6(s)/10.4(b)
			0.60	1.09	8.2	49	10.6(s)/10.4(b)
			0.60	1.05	8.2	49	10.6(s)/10.4(b)
11 May 2000	14.4	12.8	1.00	0.51	8.0	94	9.8(s)/8.6(b)
			0.55	0.69	8.0	94	9.8(s)/8.6(b)
			0.35	0.82	8.0	94	9.8(s)/8.6(b)

Dentatella to genus and described a new species (*D. danutae*) in this group. The inability to associate adults with the larvae of *Dentatella bartoni*, and now with the new species *D. danutae*, have been obstacles to systematic studies of the Eurylophellini.

The purpose of my paper is to provide detailed descriptions of all life stages of *Eurylophella coxalis*, and present new data on the larval habitat and behavior of this species. In addition, I examined 1) the taxonomy of the genus *Eurylophella* in association with its presumed sister group *Dentatella*, and 2) the related problem of recognizing mayfly taxa above the species level when knowledge of the life stages and the phylogenetic nature of diagnostic characters is incomplete.

Methods

Study area

Larvae of *E. coxalis* reared for this study were obtained from the North Branch of the Sugar River, Croydon Flat, New Hampshire (lat 43°24′56.28″N, long 72°10′50.52″W). Instream habitat variables are summarized in Table 1. This site is a 3rd-order stream (255 m elevation) with a channel width of ~30 m, and a streamlink magnitude (Shreve 1967) of ~20. Several 1st-order tributaries upstream of the sampling site had small impoundments; the nearest impoundment was ~2 km upstream. The most abundant channel substrate particle groups were cobble (75–300 mm diam., ~70%); coarse gravel (75–19 mm, ~10%); and fine gravel (19–4.80 mm, ~5%). Rooted aquatic vascular plants were absent except near the stream banks. Land use within 1 km of the study site was predominately forest with sparse settlement. Abundance of riparian vegetation was tree shrubs, coniferous trees (hemlocks and pines), mixed deciduous trees, and grasses/low shrubs.

Physicochemical measurements

Average current velocity where larvae occurred was measured with a digital pygmy-type current meter. Measurements of current velocity were made at ~0.6 the depth at points where larvae were collected. Dissolved oxygen values were determined using a Hanna® dissolved oxygen meter calibrated in the lab using a zero oxygen standard. Water temperatures were taken in areas not in direct sun and with the sensor fully submerged for at least 3 min. Measurements of pH, specific conductance, and depth were made at points where larvae were collected.

Material examined, comparative study, and terminology

Male and female imagos from across the known range of *E. coxalis* were studied as were the holotype, allotype, and paratypes. Study of specimens of *Dentatella* was limited to the holotype and 1 paratype of *D. bartoni* from the type locality in Ontario. Specimens of *D. danutae* could not be obtained for study, but comparative studies were made using information pro-

vided in the species description. All specimens were observed for morphological characters and body and appendage coloration under stereoscopic and compound light microscopy (up to 1000× magnification). Wings, legs, and bodies were measured using an ocular micrometer (nearest 0.01 mm). Larval exuviae were measured with exuviae held flat without compressing the body. Means and SDs were calculated for all continuous data, and ranges and medians were determined for ratio data; medians were estimated by interpolation. Standard morphometric parameters of larvae given by Funk and Sweeney (1994) used in this study were: FWL_1, PLP_2, ITD_5, SMT_5, ITD_7, SMT_7, and PLP_9 (definitions in Table 2). Lengths of abdominal tergites and whole abdomens were measured along the midline, and abdominal widths were measured perpendicular to the midline. Data were analyzed separately by sex to examine variation among sexes, and then were pooled to study overall variation. Lengths of foreleg segments of male imagos were compared to the lengths of the fore tibiae and expressed as ratios. Ranges of ratios are given with each ranges median value. Eggs were dissected from reared females in 95% ethanol and slide mounted in CMC®-10. Care was taken to remove only eggs in the posterior portions of oviducts to minimize differences related to egg maturation. Egg chorion features were examined using phase-contrast microscopy (400 and 1000×). Length measurements were made on 10 eggs chosen haphazardly using an ocular grid.

Comparative studies were restricted to external morphological characters from specimens preserved in alcohol or from pinned specimens. Larvae in or near the final instar were used for description of color patterns, but differences in patterns were assessed among several instars to examine variation associated with growth. Changes in larval morphology also were examined among successive instars. Description of adult pterothoracic structures followed the terminology and abbreviations of Kluge (1994).

Live larvae were collected using a 1-m^2 kick screen, placed in plastic bottles with aerated water, and transported on ice to the laboratory. There, larvae were reared in glass culture dishes (~20 cm diameter) containing aerated water from the sample site. Periphyton-covered stones also were collected and placed with larvae to provide substrate and food. Water in rearing dishes was monitored each day to ensure that physicochemical conditions were similar to field conditions. Larvae were checked daily to monitor growth. Subimagos were removed upon emergence and placed into separate subimago boxes and larval exuviae were preserved. Imagos were preserved in 80% ethanol with the subimaginal and larval exuviae.

***Eurylophella coxalis* (McDunnough)**

Ephemerella coxalis McDunnough 1926:186; McDunnough 1931:37 (in part); Traver 1935: 589 (in part); Burks 1953:73, 2 figs (in part); Allen and Edmunds 1963:617, 4 figs (in part); Funk and Sweeney 1994:259; McCafferty and Wang 1994:574.

Ephemerella (*Dannella*) *bartoni* Allen 1977:217, 2 figs; **NEW SYNONYMY.**

Ephemerella (*Eurylophella*) *bartoni*: McCafferty 1978:137.

Dannella (*Dentatella*) *bartoni*: Allen 1980:85; Funk and Sweeney 1994:210.

Eurylophlla (*Dentatella*) *bartoni*: McCafferty and Wang 1994:569.

Dentatella bartoni: McCafferty 2000:158.

Dentatella danutae: McCafferty 2000:158; **NEW SYNONYMY.**

Male imago (in alcohol). Body length 6.66–7.75 mm; forewing length 7.58–7.66 mm; forewing width 2.58–2.91 mm.

Head.—Eyes with upper portion tan, lower portion black. Compound eyes contiguous dorsally. Vertex and ocelli light brown to beige. Frontal shelf short with diagonal thin black streaks. Area below compound eyes shaded black. Antenna slightly darker brown than vertex, scape blackish.

Thorax.—Mostly pale with thicker edge of sclerous areas darker brown. Pronotum with deep lateral grooves and distinctive black marks on surface, along medial ridge, and on outer edges. Mesonotum with paired gray streaks on either side of medial longitudinal suture (MLs) in area of anterior notal process (ANP) and anterior notal transverse impression (ANi). Distinctive black marks near bases of forewings and lateral to ANP and ANi. Submedioscutum with thin black line and symmetrical small black lines along MLs in area of scuto-scutellar impression (SSLi). Parascutellum darker than surrounding areas with grayish axillary cord extending to edge of scutellum and terminating in

short finger-like process. Metanotum much darker brown than mesonotum and extensively shaded black. Pleural areas mostly pale, but distinctive black shading on some areas of epimera and episterna above leg bases. Ventrally, pro-, meso-, and metasterna light brown with thickened edges slightly darker.

Wings.—Forewings as in Fig. 1. Wing membrane mostly unpigmented. Forewing base brown. Stigmatic area opaque white. Cross veins of stigmatic area merging to form small secondary row of cells near apex of wing. Major longitudinal veins pale except for subcosta, which is light brown. All cross veins and intercalary veins pale. Hind wings (Fig. 2) with membrane pale as in forewing. All veins of hind wing pale. Anterior margin of hind wing with shallow concave depression distal of low costal projection.

Legs.—Ranges of ratios and median values of segments of forelegs as follows: 0.46–0.64, Med. = 0.53: 1.0 (2.16–2.76 mm): 0.05–0.09, Med. = 0.06: 0.35–0.50, Med. = 0.46: 0.38–0.51, Med. = 0.42: 0.23–0.33, Med. = 0.27: 0.12–0.17, Med. = 0.14. All coxae and trochanters with distinctive black shading. Fore femora pale with black shading forming apical band. Mid- and hind femora with more extensive black shading, but mostly concentrated near apex. Tibia and tarsi of all legs mostly pale with black shading limited to apical areas around joints. Tarsal claws brownish gray.

Abdomen.—Terga (Fig. 3) background color pale yellow or yellowish brown suffused with distinctive black marks dorsally and laterally. On terga 1–8, paramedial pale spots flanking central black area present (Fig. 3). Sometimes paired pale spots appear as paired pale median lines over length of terga 1–8. Paramedial spots most distinctive on terga 1–3. Tergite 1 with anterior medial black spot and medial pale areas fused posteriorly producing a single large pale band. All pale spots flanked by black streaks laterally accentuating contrast between pale areas and dark areas. Laterally, all segments with distinctive black spiracular spots or oblong streaks. Edges of all terga margined with black, especially anterior lateral corners. Terga 6 and 7 with lateral areas more extensively shaded with black than other terga. All sterna pale. Vestiges of posterolateral projections present on terga 4–6. Genitalia (Fig. 4) with penes fused with broad v-shaped apical notch and deep parallel sided subapical groove. Base of penes broad without protuberances. Forceps 3-segmented. Small, somewhat triangular tubercle present between forcep bases on posterior edge of styliger plate.

Caudal filaments.—Pale, sometimes with faint yellowish tinge, but no bands. Terminal filament subequal to cerci.

Female imago (in alcohol). Body length 5.33–7.08 mm; forewing length 6.91–9.16 mm; forewing width 2.12–2.91 mm. Female similar to male in morphology and most color patterns except where noted below. Head pale yellow with extensive black shading between compound eyes. Eyes small and widely separated. Vertex between compound eyes with transverse row of 4 black marks. Bases of ocelli with black shading. Frons with more extensive black shading. Abdominal sterna 1–9 mostly pale except for black spots near pleural fold and thin lateral black line on sternum 9. Occasionally vestiges of posterolateral projections present on mid-abdominal segments. Subgenital plate (Fig. 5) with v-shaped apical notch. Posterolateral projections on tergite 9 reach midpoint of posterior extension of posterior margin of subgenital plate.

Eggs (in CMC®-10): Mean length 0.22 mm. Eggs (Fig. 6) oval to capsule shaped with chorionic features. Polar caps and attachment structures absent. Ridges of chorion join, forming reticulate network of large polygons. Micropylar opening usually midway between ends of capsule at intersection of major surface ridges.

Larva (Fig. 7) (in alcohol). Well-developed or dark wing pads. Body length 6.33–7.67 mm (6.95 ± 0.40, mean ± SD, n = 10).

Head.—Vertex of head brown with many small light speckles. Black diagonal streaks present along posterolateral edge of compound eyes of male larva; head of female larva with only isolated black spots. Male larva with inner edges of compound eyes margined with row of long hairlike setae that extend anteriorly from vertex only about as far as division in epicranial suture. Female larva without distinctive row of setae, but with more or less well-defined tufts of long hairlike setae close to division of epicranial suture. Male larva with 2 groups of distinctive black spots just posterior to division of epicranial suture; female larva lacking spots. Male larva with 2 black marks separated by a lighter brown area between division of epicranial suture and median ocellus. Female larva lacking these marks, but have black shading around lat-

TABLE 2. Morphometric parameters of abdominal tergites of *Eurylophella coxalis* larvae. Values for mature larvae were determined from larval exuviae of reared specimens and larvae at or near the black-wing-pad stage of development. ML = midline length (mm), LWT = length of tergite plus tubercles (mm), PLP = length of posterolateral projection as ratio, ITD = inter-tubercle distance (mm), SMT = submedian tubercle ratio of M1:ITD, M = mature male larvae, F = mature female larvae, B = both mature male and female larvae, All = all mature larvae, larval exuviae, and early instars starting at a body length 3.16 mm, Med. = median estimated by interpolation.

	Tergite 2		Tergite 5			
Sex (*n*)	M1 mean ± SD	PLP range	M1 mean ± SD	ITD_5 mean ± SD	LWT mean ± SD	SMT_5 range
M (5)	0.27 ± 0.02	0.36–0.61	0.26 ± 0.02	0.46 ± 0.05	0.29 ± 0.02	0.52–0.60
F (5)	0.30 ± 0.05	0.22–0.61	0.27 ± 0.02	0.44 ± 0.04	0.31 ± 0.03	0.58–0.65
B (10)	0.29 ± 0.04	0.22–0.61 Med. = 0.47	0.26 ± 0.02	0.45 ± 0.04	0.30 ± 0.03	0.52–0.65 Med. = 0.58
All (15)	0.26 ± 0.06	0.00–0.61 Med. = 0.36	0.23 ± 0.05	0.40 ± 0.08	0.27 ± 0.05	0.42–0.65 Med. = 0.58

eral ocelli, which is absent in males. Dorsal occipital tubercles absent in both sexes. Male larva with irregular black marks on gena anterior and ventral to compound eyes. Female larva lacking extensive shading on gena, but may have scattered black spots. Fringes of long hairlike setae on outer lateral edge of head in both sexes extending from posterior corner of compound eye to clypeus. Scattered long hairlike setae over frons and clypeus of both sexes. Paired black spots often present on frons of male larva just above clypeus. Dorsal area of compound eye of male with brown shading punctuated with light freckles as on vertex. Lateral portion of compound eye of male without additional pigments. Female larva without differential pigmentation of compound eye. Antennae mostly pale. Male larva may have a black mark on the scape and pedicel in addition to brown shading. Flagellum of both sexes with small hairlike setae at annuli.

Mouthparts (Figs 8–13).—Dorsal and ventral aspects of labrum as in Fig. 8. Labrum with a shallow anterior emargination. Anterior and lateral with many long hairlike setae. Dorsal surface with transverse median row of long distinctive hairlike setae extending almost perpendicular to plane of surface of labrum; other setae oriented more or less parallel to surface of labrum. Ventrally 2 large patches of medially directed setae present. Left and right mandibles (Figs 9, 10): outer incisors of right mandible with bifid tip and small tuft of setae near tip of dorsal point, outer incisors of left mandible with teeth apparently fused forming single cutting unit with apical serrations and small tuft of setae on dorsal edge near tip. Inner incisors of both mandibles with 2 large teeth. Protheca arise close to base of inner incisor on both mandibles. Right mandible with row of long hairlike setae below molar surface. Left mandible with only small cluster of setae below molar surface. Dorsal surface of both mandibles shaded light brown with patches of long hairlike setae along exposed outer lateral edges. Maxillae (Fig. 11): maxillary palp absent. Galea-lacinia more or less rectangular with outer apical corner formed into heavy blunt spine with basal patch of setae on dorsal surface. Apical edge with 2 large sharp spines and secondary row of slightly smaller heavy spinelike setae. Small patches of setae midway along inner edge on dorsal and ventral surfaces. Labium (Fig. 12): glossa and paraglossa subequal in length. Labial palpi 3-segmented, with segment 3 slightly darker than proceeding segments and cluster of several short spinelike setae at tip. Dorsal and lateral areas of segments 1 and 2 with long hairlike setae. Dorsal inner edges of segments 1 and 2 with several campaniform setae. Dorsal, lateral, and apical areas of glossa and paraglossa with many long hairlike setae. Ventral medial surfaces of most of labium lacking extensive setae, only scattered small hairlike setae and small groups of campaniform-like setae present. Hypopharynx as in Fig. 13.

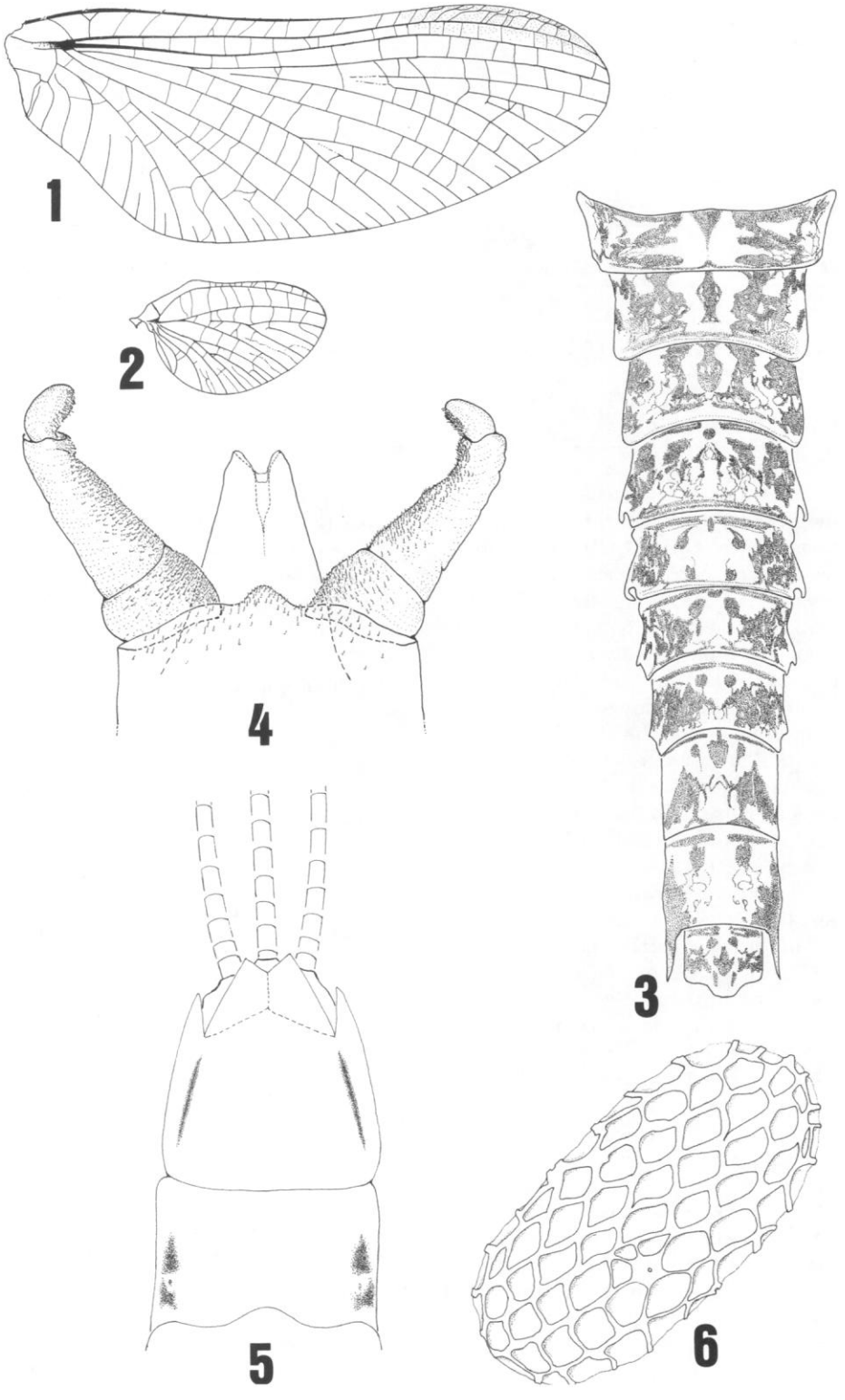
Thorax.—Pronotum brown with somewhat variable black spots. Single medial black spot present on anterior margin at beginning of me-

TABLE 2. Extended.

Tergite 7				Tergite 9	
M1 mean ± SD	IDT_7 mean ± SD	LWT_7 mean ± SD	SMT_7 range	M1 mean ± SD	PLP_9 range
0.24 ± 0.02	0.30 ± 0.02	0.26 ± 0.02	0.59–0.90	0.45 ± 0.04	0.52–0.76
0.25 ± 0.02	0.30 ± 0.03	0.28 ± 0.02	0.76–0.89	0.45 ± 0.03	0.67–0.77
0.25 ± 0.02	0.30 ± 0.03	0.27 ± 0.02	0.59–0.90 Med. = 0.85	0.47 ± 0.03	0.52–0.77 Med. = 0.70
0.23 ± 0.04	0.27 ± 0.06	0.26 ± 0.03	0.59–1.00 Med. = 0.85	0.43 ± 0.07	0.52 ± 0.86 Med. = 0.70

dian longitudinal suture (MLs), sometimes darkening MLs over half its length. Relatively consistent patterns of black marks lateral to MLs in both sexes (Fig. 7), but spots often darker on male larva compared with female larva. Lateral margins of pronotum slightly concave, moreso on female larva than on male larva. Anterior edge of pronotum with fringe of long hairlike setae, some of which may be extremely long and project vertically. Posterior margin of pronotum of male larva darkened with black shading; female usually lighter. Both sexes with tuft of hairlike setae at posterior end of MLs. Setae may be extremely long and project vertically on early instars. Mesonotum brown with lighter areas and many light freckles as well as scattered distinctive dark brown to black marks. Both sexes with paired distinctive medial dark brown to black marks on anterior edge of mesonotum (Fig. 7), sometimes joined to form a u-shaped spot. Symmetrical marks present on outer edges of submedioscutum (SMS), posterior scutal protuberance (Psp), between Psp on either side of MLs, and around bases of wing pads. MLs in area of scutellum (SL) darkened with black. Mesoscutum (MS), Psp, and SL low and rounded in profile. Scattered long hairlike setae present on dorsal surface of mesonotum. Lateral edges of mesonotum with many long hairlike setae. Metanotum brown with extensive black shading. Pleural areas pale compared to brown color of tergites, but with extensive black shading above coxa on epimeron and episternum of each segment.

Legs (Figs 7, 14, 15a–c).—Background color variable from light to dark brown with scattered small pale freckles. Coxae and trochanters with dorsal and lateral black marks. Femora and tibiae with variable brown to black bands or marks. Femora usually not banded, but have black marks near apex that can give the appearance of a band. Mean (± SD) maximum length of fore femora 0.90 ± 0.05 mm (n = 10). Mean (± SD) maximum width of fore femora 0.50 ± 0.03 mm (n = 10). Range of ratio of fore femora width to length 0.50–0.59 mm with a median value of 0.54 (n = 10). Tibiae sometimes with medial dark brown band or black shading producing an apparent band, but on some female larvae shading is more uniform and no band is apparent. Tarsi usually with medial brown shading producing a band. Outer lateral edges of tarsi with long hairlike setae, inner apical edges with row of 4 short spinelike setae. Color on femora and tibiae usually restricted to dorsal surface, ventral surface usually pale. Forefemora with elevated flat surface fringed with many long hairlike setae. Elevated surface extends from apex of femora proximally, covering 50–75% of dorsal surface (Fig. 14). Tarsal claws of all legs with single row of denticles. Row of denticles composed of both large and small forms (Fig. 15a–c). Small denticles always basal to large denticles and may only be visible at 400× magnification. Ranges of tarsal claw dentition given with range of large denticles followed by range of both large and small denti-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cles: foreclaw 4–6/4–7; mid claw 3–6/4–7; hind claw 2–6/4–6.

Abdomen (Figs 7, 16a–c).—Brown with variable amounts of black shading. Male larva may have extensive black overshading obscuring most of brown background color; female larva often with only scattered black marks. Both sexes with consistent patterns of paired paramedial and lateral black marks. Tergites 1 and 2 with paired paramedial pale spots margined with black, sometimes pale spots trail off into streaks on tergite 3. Medial black spot or streak present on tergites 1–4. Area of tergites beneath operculate gills with dark shading in both sexes. Tergites 6–8 with crescent-shaped paramedial marks. Tergites 2–9 with large distinct posterolateral projections. Morphometric parameters of abdominal terga length and width relationships, terga tubercle lengths, lengths of posterolateral projections, inter-tubercle distances and ratios are summarized in Table 2. Posterolateral projections on tergites 5–7 with tips slightly curved dorsally and thinner than projections on other tergites. Paired sharp paramedial tubercles present on posterior margins of tergites 5–7. Mean (± SD) midline length of abdomen 3.59 ± 0.35 mm (n = 10). Mean (± SD) width of abdomen 2.49 ± 0.18 mm (n = 10). Range of ratio of maximum midline length of abdomen to width of abdomen 1.00–1.45, with a median value of 1.45 (n = 10). Midline length of tergite 9 subequal to midline length of tergite 8 or slightly longer. Maximum midline length of tergite 9 only ~16% greater than midline length of tergite 8. Posterior median margins of tergites 1–7 with tuft of hairlike setae. Numerous hairlike setae present along lateral and posterior margins of all tergites. Dense tufts of long hairlike setae arranged as continuous band across middle portion of tergite 8. Dense medial clusters of setae on tergite 8 do not extend laterally beyond tips of operculate gills. Ventral surface of abdomen mostly pale with widely separated paired dark spots on sternites 1–8. Spots become thin dark lateral lines on sternite 9. Sternites 1 and 2 may have occasional extensive black shading.

Gills.—Abdominal gills present on segments 1 and 4–7. Gills on segment 1 small and filamentous with many hairlike setae. Gills on segment 1 usually extend dorsally and slightly medially from gill insertion with much of filament positioned next to posterior margin of forewing pad. Gills on segment 1 of early instars may be tapered to a point; on later instars gill 1 becomes more rounded apically. Gills on segment 4 operculate with large dorsal lamellae (Fig. 7) with posterior portion articulated transversely. Ventral lamellae of gill 4 forked with dorsal and ventral lobes on each division (Fig. 17). Ventral lamellae usually with 3–4 dorsal lobes and 5–7 ventral lobes. Operculate dorsal lamellae usually brown to dark brown with median pale area just proximal to articulation, often distal area below articulation pale brown.

Caudal filaments.—Banded with hairlike setae at articulations. Pale alternate bands extend over most of length of caudal filaments or are limited to basal half of filaments. Paired dark narrow rings separated by a pale band occur near base of each filament (Fig. 7).

Abbreviations and specimen label data

The following abbreviations were used to denote life stage and sex of specimens studied: ♂—male imago; ♀—female imago; S♂—subimago male; S♀—subimago female; L—larva; and LEX—larval exuviae. Numbers of specimens studied preceed abbreviations. Specimen label data are reported verbatim, except for year information, which is listed in 4-digit format.

Materials from the following collections were studied and are referred to by their abbreviations. Deposition of all materials is with the institutions indicated with each record. Materials without institution codes are retained in my research collection. CNC—Canadian National Collection, Ottawa, Ontario. CDB—Research Collection of David Barton, Department of Biology, University of Waterloo, Waterloo, Ontario. NHDES—Aquatic Insect Reference Collection, New Hampshire Department of Environmental Services, Concord, New Hampshire. SWRC—

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FIGS. 1–6. Imago of *Eurylophella coxalis*. 1.—Forewing. 2.—Hind wing. 3.—Abdominal terga of male imago. 4.—Male genitalia (ventral view). 5.—Female subgenital plate (ventral view). 6.—Egg showing micropylar opening.

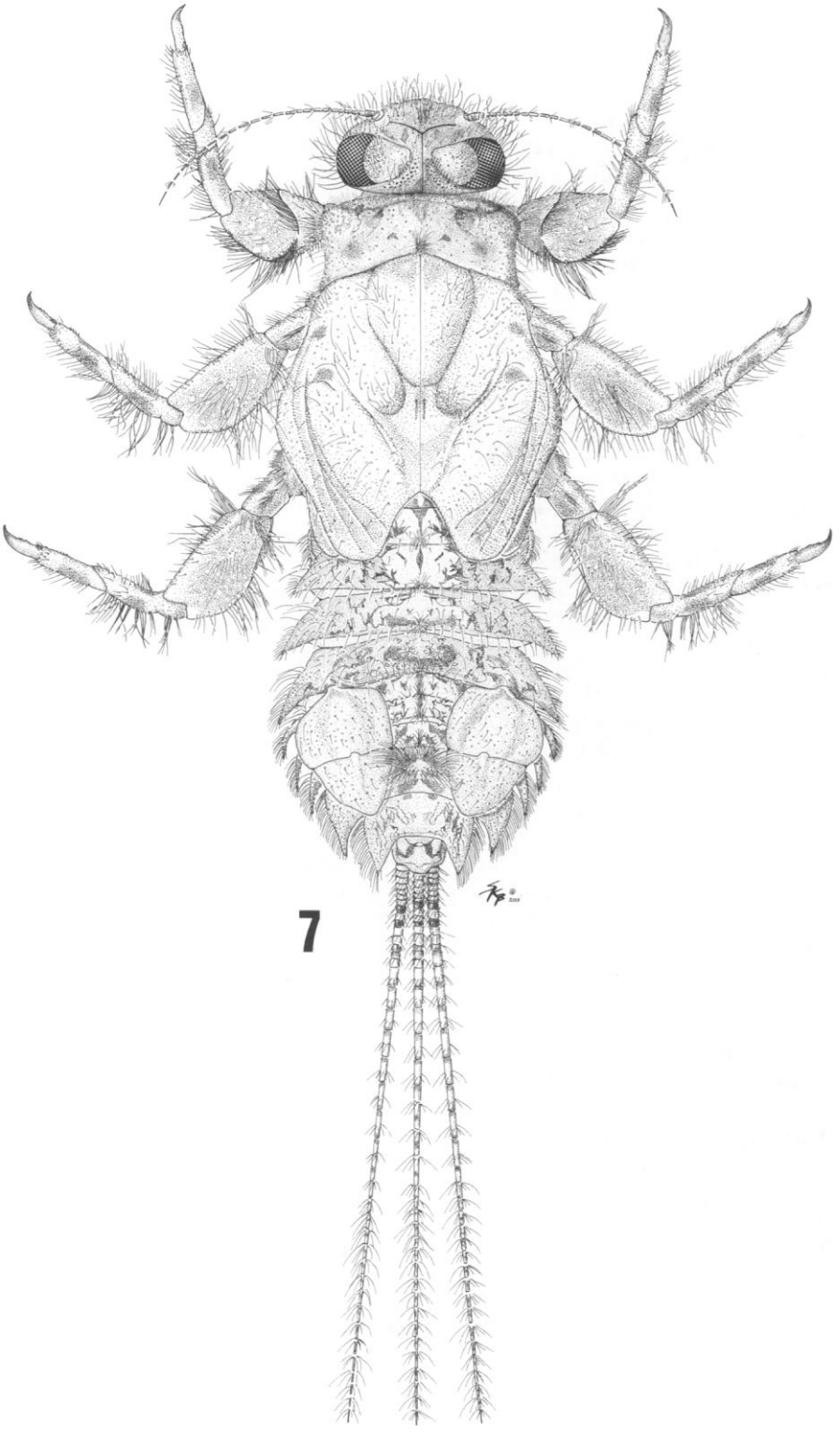


FIG. 7. Dorsal view of final instar male of *Eurylophella coxalis*.

Stroud Water Research Center, Avondale, Pennsylvania.

Material examined

Holotype of *Dentatella bartoni*: **CANADA, Ontario**: Nowdenvale, Lake Huron, 29.v.1974, D. Barton, 1L (CNC), Type Cat. #15640; **Paratype** of *Dentatella bartoni*: same, 1L (CDB).

Holotype of *Eurylophella coxalis*: **CANADA, Quebec**: Dorval, 20.vi.1925, F. P. Ide, 1♂ (CNC), Type Cat. #2070; **Allotype** of *Eurylophella coxalis*: same, 24.vi.1925, F. P. Ide, 1♀ (CNC), Type Cat. #2070; **Paratypes** of *Eurylophella coxalis*: **CANADA, Quebec**: Lachine, 23.vi.1925, F. P. Ide, 1♂, 1♀ (CNC) Type Cat. #2070; Dorval, 20.vi.1925, F. P. Ide, 1♂ (CNC) Type Cat. #2070; Dorval, 20.vi.1925, F. P. Ide, 1♂ (CNC) Type Cat. #2070; St. Annes, 24.vi.1925, F. P. Ide, 2♀ (CNC) Type Cat. #2070; same, 24.vi.1925, 1♀ (CNC) Type Cat. #2070; Coteau-du-Lac, 25.vi.1925, F. P. Ide, 1♀ (CNC) Type Cat. #2070; Beauharnois, 19.vi.1925, F. P. Ide, 2♀ (CNC) Type Cat. #2070.

Other material studied [CANADA], Nova Scotia: S. Milford, 28.vi.1934, J. McDunnough, 1♂ (CNC); **Ontario,** Fishers Glen, 1.vii.1925, G. S. Walley, 1♂ (CNC); Go Home Bay, Isle 144, Georgian Bay, 25.vi.1932, G. S. Walley, 1♀ (CNC); Nowdenvale, Lake Huron, 0.25 m depth, 1.v.1975, D. Barton, 1L (SWRC); Lake Joseph, site #0003-B04, 1.xi.1993, B. Bilyj, 3L (SWRC); **Quebec,** Knowlton, Brome Lake, 25.vi.1928, G. H. Fisk, 1♀ (CNC). **[USA], New Hampshire,** Cheshire Co.: Ashuelot River, Gilsum, above old dam, USEPA Reg. 1 Pilot Study kick sample #25623, 14.x.1993, 3L; Sullivan Co., North Branch of Sugar River, Croydon Flat (Log #154), ? .x.1997, 6L (NHDES); Skinner Brook, Grantham (Log #153), ? .x. 1997, 1L (NHDES); North Branch of Sugar River, Croydon Flat, 24.iv.1998, S. K. Burian, 1L; same, 11.v.2000, S. K. Burian, 3♂, 1S♂, 3♀, 1S♀, 8LEX, 15L.

Diagnosis

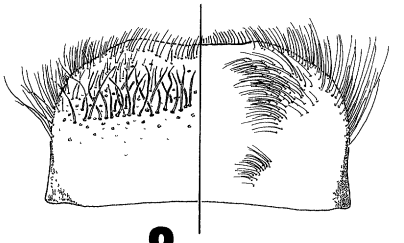
Larvae of *E. coxalis* can be easily separated from all other known North American species of *Eurylophella* by the presence of paired sharp tubercles on the posterior margins of tergites 5–7 only, the distinctive elevated flat areas on forefemora, paired dark bands at the base of caudal filaments, and extensive marginal setae on head, thorax, and abdomen. Imagos can be separated from those of all other North American species of *Eurylophella* by the distinctive color pattern on abdominal terga, black marks on coxa and trochanters, and pale unbanded caudal filaments.

Biology and Distribution

Larvae of *E. coxalis* were only found at depths >0.40 m, associated with unembedded particles ranging from small cobble (~75 mm diam. to small boulders ~300 mm). Substrates usually contained heavy biofilm. Although some larvae were collected from areas where current velocities approached 1.0 m/s, most individuals were collected from turbulent eddies downstream of groups of small to large boulders. Larvae clung tightly to the substrate, but once disturbed would pull their legs in close to the thorax and would drift, making no attempt to swim. Once drifting larvae touched an object they would immediately extend their legs and grasp its surface. Larvae moved very slowly in high current in a manner appearing to lessen the chance of being dislodged from the substrate. Larvae always were found clinging to the net rather than entrained in debris. Only 2 or 3 larvae usually were obtained in a single sample, suggesting a relatively even distribution within the habitat. Larvae often had a thick bacterial biofilm growing over the dorsal surfaces of the body and legs, suggesting a sedentary life style.

Larvae seemed to prefer the edges and undersides of stones within rearing dishes. Larvae were observed scraping the biofilm on stones with their foreclaws, appearing to ingest some of the loosened material; larvae also appeared to feed in small pockets of benthic detritus.

Eurylophella coxalis is apparently restricted to southern and eastern Ontario, Quebec, the Atlantic Provinces, and northern/central New England. All previous records based solely on larvae that were not identified as either *Dannella bartoni* or *Eurylophella bartoni* (= *E. coxalis*) must be disregarded because all previous taxonomic treatments of larvae were in error. However, historic records based on adults determined as *E. coxalis* should be considered valid. Records of *E. coxalis* adults and larvae from Canada indicate that the species inhabits rivers and the nearshore areas of large lakes. In Lake Huron, larvae were collected from limestone ledges, and McCafferty (1978) suggested an association



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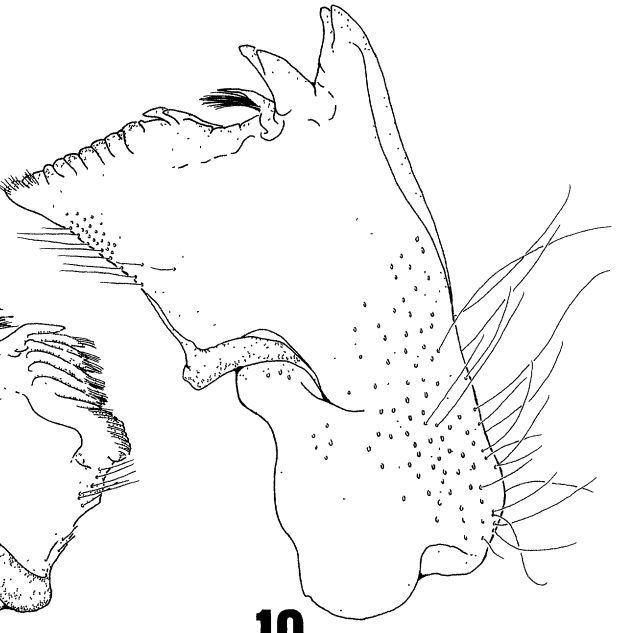

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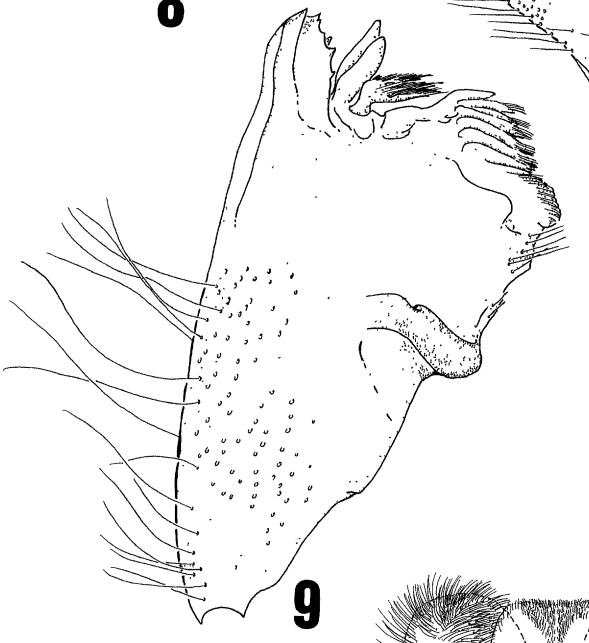

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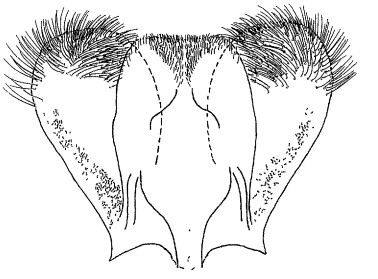

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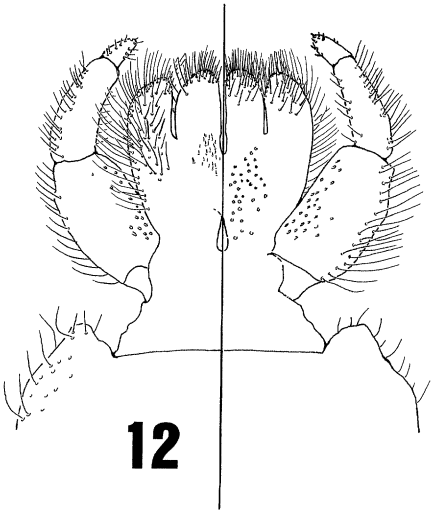

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with alkaline microhabitats. More recently, McCafferty (2000) indicated that *E. coxalis* also occurs in moderate-sized lotic habitats. Data from my study further associate this species with lotic, alkaline habitats. However, alkaline conditions at the North Branch of the Sugar River collection site (Table 1) are rare in other streams of the region, suggesting that *E. coxalis* may be rare in this area of New England. Alkaline aquatic microhabitats are more common in streams further north and west of New England (e.g., in the eastern Laurentian and lower Saint Lawrence systems where most species records occur); *E. coxalis* is also likely to be more common in these areas. It may be possible to predict the locations of unrecorded populations of *E. coxalis* in New England by mapping potentially suitable aquatic habitats by streamwater pH.

Discussion

Observation of live *E. coxalis* larvae in the field and laboratory has resulted in the 1st information on larval biology. Study of reared male and female imagos that were initially determined to be *Dentatella bartoni* showed that they closely matched the description of adults of *Eurylophella coxalis*; comparison of these specimens with the types of both *D. bartoni* and *E. coxalis* confirmed my determinations. This result clearly showed that the larval form known as *Dentatella bartoni* is actually the immature stage of *Eurylophella coxalis*. Further, comparative study of early instars from the series reared to adults of *E. coxalis* showed that diagnostic characters used to define the species *Dentatella danutae* were within the range of morphological variation of those for *E.coxalis*. Therefore, I herein designate *Dentatella bartoni* and *D. danutae* junior subjective synonyms of *Eurylophella coxalis*.

The discovery that adult and larval stages of *E. coxalis* were described as 3 different species solves 2 taxonomic problems at the species level, but complicates matters at the genus level. Comparison of presumed homologous diagnostic characters presented by Funk and Sweeney (1994) for the genus Eurylophella to those known for *Dentatella* (Allen 1977, McCafferty 1978, 2000, McCafferty and Wang 1994) showed that there are clear differences at the larval stage. Characters diagnostic of larvae previously placed in *Dentatella* include: 1) expanded forefemora with distinctive marginal and medial setae; 2) extensive marginal setae on head, thorax, and abdomen; 3) tufts of setae on dorsum of pronotum and abdominal segments, especially on tergite 8; 4) paired sharp submedian tubercles only on abdominal terga 5–7; 5) operculate gills on abdominal segment 4 somewhat pointed apically; and 6) abdominal tergite 9 subequal to or slightly longer than tergite 8. However, the phylogenetic importance of these characters has not been determined, and similar characters among other taxa of the Timpanogini show much variability. In addition, adults of these species are indistinguishable from those of the *Eurylophella*, except for color. The lack of adult structural characters and the high level of similarity among all other diagnostic characters of the *Eurylophella* suggest that a conservative approach be used in making higher taxon assignments. Further support of this conclusion is 1) that the phylogeny of the species of *Eurylophella* has not been constructed, and 2) related to the tenuous assertion based on knowledge of only 1 life stage that *Dentatella* is a monotypic group. Under these circumstances it is probable that maintaining *Dentatella* as a separate genus would result in a paraphyletic *Eurylophella*.

Convention in mayfly systematics once was to designate subgenera as a possible solution for such taxonomic problems (Edmunds 1962), but did so under an arbitrary phenetic *gap* criterion (i.e., a difference among characters/states observed among individuals of 2 presumed different yet related groups with no immediate phylogenetic evidence). This older convention required distinct gaps (i.e., differences) be observed among both larval and adult life stages for designation of a new genus or just among one or the other life stage for a subgeneric

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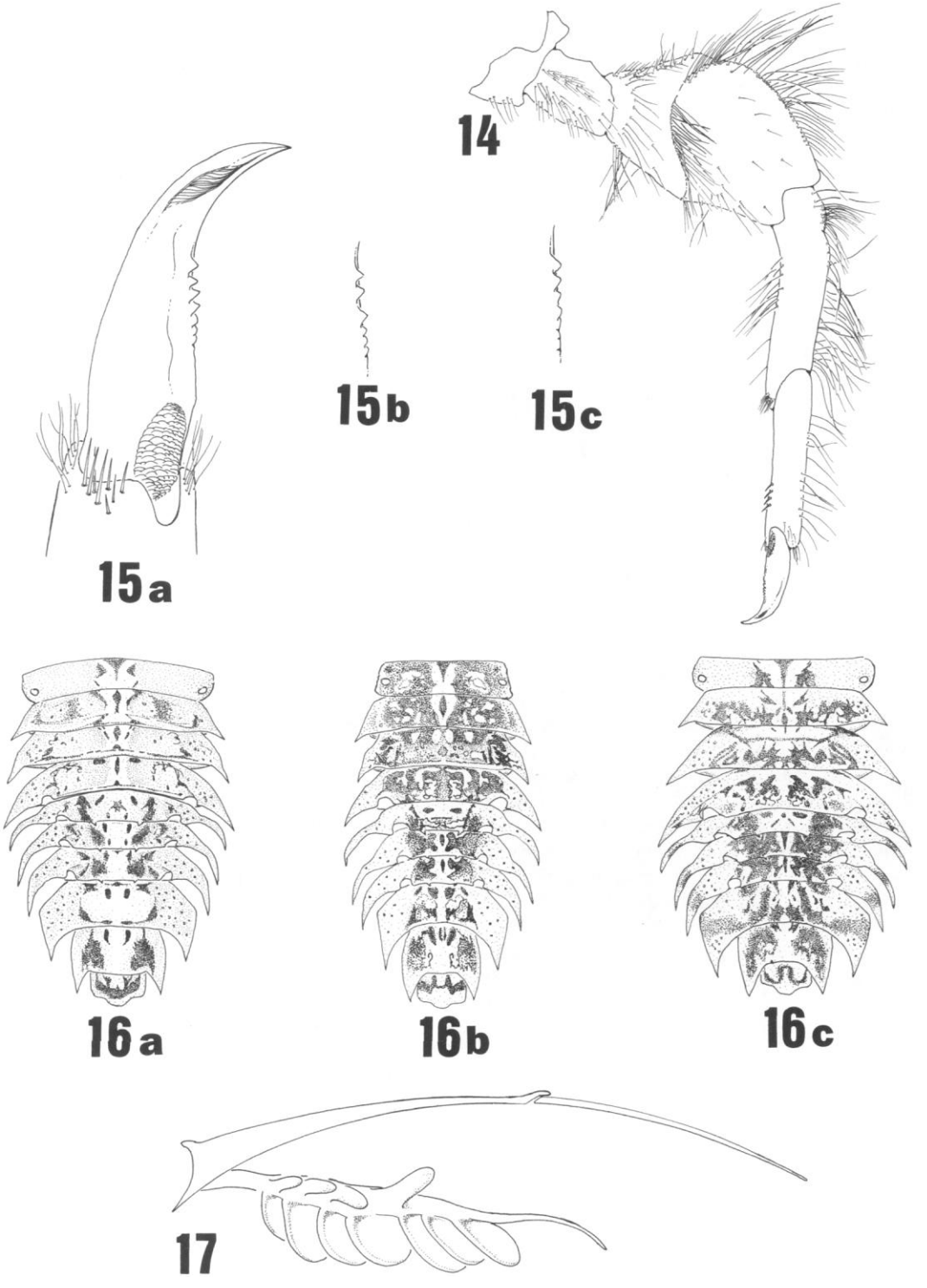
FIGS. 8–13. Mouthparts of final instar of *Eurylophella coxalis*. 8.—Labrum with dorsal surface on left and ventral surface on right. 9.—Left mandible (dorsal view). 10.—Right mandible (dorsal view). 11.—Right maxilla (dorsal view). 12.—Labium with dorsal surface on left and ventral surface on right. 13.—Hypopharynx (dorsal view).



FIGS. 14–17. Leg and abdomen variation of *Eurylophella coxalis* larva. 14.—Foreleg of final instar of *Eurylophella coxalis*. 15a.—Foreclaw. 15b.—Dentition of mid claw. 15c.—Dentition of hind claw. 16a.—Tergal color pattern of final-instar female. 16b.—Tergal color pattern of middle instar male. 16c.—Tergal color pattern of final instar male. 17.—Lateral view of gill 4 showing dorsal and ventral lamella.

group. I recommend that the intent of the previous convention be reconsidered because of its conservative approach, but replace the gap criterion with the requirement of apomorphic characters. Thus, for a monotypic group, genus-level status would require evidence of clear autapomorphic characters in both larval and adult life stages. The discovery of additional species with these same characters would subsequently convert these autapomorphies to synapomorphies at that level. Thus, I am recommending new subgeneric groups not be established, but rather that an extremely conservative approach be used when the phylogenetic nature of diagnostic characters has not been fully investigated and/or larval or adult life stages are unknown.

The conservative approach described here also will have the least effect on the current higher classification proposed by McCafferty (2000). The structure of the current classification of the Timpanoginae largely excludes the possibility of reducing *Dentatella* to a subgeneric group of the *Eurylophella* because this change would likely mean simultaneously reducing *Dannella* to the subgeneric level and eliminating the tribe categories. It seems prudent at this time to eliminate *Dentatella* and preserve the remaining structure. Generic status could be established if future phylogenetic studies of the species of *Eurylophella* produce evidence supporting genus-level status for *Dentatella*, or some new assemblage of taxa is identified.

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Literature Cited

ALLEN, R. K. 1977. A review of *Ephemerella* (*Dannella*) and the description of a new species. Pan-Pacific Entomologist 53:215–217.

ALLEN, R. K. 1980. Geographic distribution and reclassification of the subfamily Ephemerellinae (Ephemeroptera: Ephemerellidae). Pages 71–91 *in* J. F. Flannagan and K. E. Marshall (editors). Advances in Ephemeroptera biology. Plenum Publishing, New York.

ALLEN, R. K., AND G. F. EDMUNDS,JR. 1963. A review of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae) VII. The subgenus *Eurylophella*. Canadian Entomologist. 95:597–623.

BURKS, B. D. 1953. The mayflies, or Ephemeroptera, of Illinois. Bulletin of the Illinois Natural History Survey 26:1–216.

EDMUNDS, G. F., JR. 1962. The principles applied in determining the hierarchic level of highercategories of Ephemeroptera. Systematic Zoologist 11: 22–31.

FUNK, D. H., AND B. W. SWEENEY. 1994. The larvae of eastern North American *Eurylophella* Tiensuu (Ephemeroptera: Ephemerellidae). Transactions of the American Entomological Society 120:209–286.

KLUGE, N. JU. 1994. Pterothorax structure of mayflies (Ephemeroptera) and its use in systematics. Bulletin de la Société entomologique de France 99: 41–61.

MCCAFFERTY, W. P. 1978. A natural subgeneric classification of *Ephemerella bartoni* and related species (Ephemeroptera: Ephemerellidae). Great Lakes Entomologist 11:137–138.

MCCAFFERTY, W. P. 2000. A hierarchical classification of the Timpanoginae (Ephemeroptera: Ephemerellidae) and description of a new species from Quebec. Annals of Limnology 36:157–161.

MCCAFFERTY, W. P., AND T-Q. WANG. 1994. Phylogenetics and classification of the *Timpanoga* complex (Ephemeroptera:Ephemerellidae). Journal of the North American Benthological Society 13:569–579.

MCDUNNOUGH, J. 1926. Notes on North American Ephemeroptera with descriptions of new species. Canadian Entomologist 58:184–196.

MCDUNNOUGH, J. 1931. The *bicolor* group of the genus *Ephemerella* with particular reference to the nymphal stages (Ephemeroptera). Canadian Entomologist 63:30–42,61–68.

SHREVE, R. L. 1967. Infinite topologically random channel networks. Journal of Geology 75:178–186.

TRAVER, J. R. 1935. Part II. North American mayflies. Pages 239–751 *in* J. G. Needham, J. R Traver, and Y. C. Hsu (editors). The biology of mayflies. Comstock Publishing, Ithaca, New York.

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