

Best wishes,
LDC

Michael Hubbard

FUNCTION OF CAUDAL FILAMENTS AND CORRELATED STRUCTURES IN
MAYFLY NYMPHS, WITH SPECIAL REFERENCE TO *BAETIS* (EPHEMEROPTERA)

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ABSTRACT

Laboratory and field experiments demonstrate that caudal filaments of Baetis tricaudatus and Rhithrogena hageni nymphs do not effectively deter stonefly predators or aid in molting. A field study along a section of a Rocky Mountain stream shows that length of the terminal filament in Baetis nymphs is correlated with a combination of factors and not specifically to current velocity.

Subapical setae on the claws of Baetis bicaudatus and B. tricaudatus nymphs are probably mechanoreceptors which may be used to detect subtle changes in flow and thus assist in orienting nymphs into the current. All species of Baetis nymphs with subapical setae on claws also have a reduced terminal filament and inhabit fast water areas.

RÉSUMÉ

Des expériences en laboratoire et en nature démontrent que les filaments caudaux des nymphes de Baetis tricaudatus et de Rhithrogena hageni ne facilitent pas la mue de ces Plécoptères, ni ne découragent leurs prédateurs. Une étude en nature, réalisée le long d'une section d'un ruisseau des Montagnes Rocheuses, révèle que la longueur du filament terminal des nymphes de Baetis est corrélée à un ensemble de facteurs, et non spécifiquement à la vitesse du courant.

Les soies subapicales portées par les griffes des nymphes de Baetis Bicaudatus et de B. tricaudatus sont probablement des mécanorécepteurs qui peuvent être utilisés pour détecter de légers changements de débit du courant, et ainsi aider les nymphes à s'orienter dans le courant. Toutes les espèces de Baetis dont les nymphes possèdent des soies subapicales sur les griffes, présentent aussi un filament terminal réduit, et fréquentent les zones à courant rapide.

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INTRODUCTION

Our objective is to study numerous functions that have been attributed to mayfly caudal filaments by examining: (1) success of a stonefly predator feeding on two species of mayfly nymphs with and without (excised) caudal filaments; (2) molting rate of these two species with and without caudal filaments and time required to generate filaments; (3) longitudinal distribution of two- and three-tailed *Baetis* nymphs in a Rocky Mountain stream of Alberta, Canada; (4) whether there is any difference between two and three-tailed *Baetis* nymphs in avoiding a stonefly predator in this stream; and (5) relationships between reduction of the middle (terminal) caudal filament in *Baetis* nymphs and corresponding changes in claw structure.

Most mayfly nymphs possess three caudal filaments. However, of 60 North American mayfly genera, seven (Baetidae: *Baetodes* Needham and Murphy, *Heterocloeon* McDunnough, *Pseudocloeon* Klapalek; Oligoneuriidae: *Lachlania* Hagen; Heptageniidae: *Epeorus* Eaton, *Ironodes* Traver, *Spinadis* Edmunds and Jensen) possess two lateral filaments and lack the terminal filaments as nymphs (Edmunds *et al.*, 1976).

Within the genus *Baetis*, relative length of the terminal filament to that of the lateral filaments varies greatly in nymphs. There is only one representative, *B. hudsonicus*, in which the terminal filament is similar in length to the lateral filaments. In all other species, nymphs possess a terminal filament that is shorter than the lateral filaments. Of the 24 described North American species of *Baetis* nymphs, seven (*B. lapponicus* gp.-*B. amplus*, *B. insignificans*, *B. lapponicus*; *B. rhodani* gp.-*B. bicaudatus*, *B. foemina*) possess a terminal filament that has been reduced to five segments or less (Moriyama and McCafferty 1979).

Baetid nymphs possessing three well-developed caudal filaments with overlapping setae or hairs are well suited for swimming away from and settling onto the substrate (Percival and Whitehead 1929, Hughes 1966, Corkum and Clifford 1980). Although *Baetis* nymphs with a reduced terminal filament occur in fast flowing water, the adaptive significance of two lateral filaments and a reduced terminal filament is unclear.

Dodds and Hisaw (1924) and Hora (1930) related degree of reduction of the terminal filament in mayfly nymphs with increased current velocity in headwater regions of streams. We anticipated that if *Baetis* nymphs with two rather than three caudal filaments were better adapted to fast flowing water, then these nymphs might also have some morphological

modification of claws enabling them to maintain their position on substrates.

Hynes (1970) was not convinced that reduction of the terminal filament was necessarily a morphological adaptation to fast water. Nymphs of one African genus, *Dicercomyzon* (Tricorythidae) (flattened body with an adhesive pad and no terminal filament), are atypical as they inhabit slow water (Venter 1961). Hynes suggests that these features of *Dicercomyzon* nymphs enable them to adhere to vegetation and avoid predation.

We have collected many mayfly nymphs with caudal filaments broken off. These appendages may aid nymphs in avoiding predators, *i.e.* the predator seizes a caudal filament, the prey escapes and is able to regenerate the damaged filaments (e.g. Schmidt 1951).

MATERIALS AND METHODS

Laboratory Studies

Caudal filaments and vulnerability in predation.

Laboratory studies were conducted to determine feeding success of nymphs of a stonefly predator, *Isogenoides elongatus* (Hagen), on *Rhithrogena hageni* Eaton and *Baetis tricaudatus* Dodds nymphs with caudal filaments and with filaments excised. Nymphs were collected from the Pembina River, near Entwistle, Alberta (53°36'N, 115°00'W). River water temperature was 5°C; this temperature was maintained in an environmental chamber in the laboratory. The mayfly nymphs were of developmental stage II (Clifford 1970) and ~~were a~~ ~~(+/- caudal filaments) x 2 (+/- predator) x 2 (+/- light) factorial~~ therefore relatively small.

Each of 40 experimental cells consisted of 200 ml of aerated dechlorinated water in a glass bowl (10.5 cm diam. x 4 cm depth), containing a stone and 1 g of prepared instant oatmeal. Experiments were conducted using a 2 (+/- caudal filaments) x 2 (+/- predator) x 2 (+/- light) factorial design for each mayfly species with five trials for each condition and a 12 hr light-dark cycle. All three caudal filaments of experimental nymphs were cut to a length equaling the width of the 10th abdominal segment. Stonefly nymphs were starved for 24 hr before the experiment. There were five prey and one predator (when present) per bowl. Numbers of mayfly nymphs present were recorded each day at the beginning and end of the light phase and then, if necessary, prey were replenished. After five days, insects were preserved and foreguts of predators were analyzed.

A student's t-test was used to determine if there was a difference in the number of prey eaten by predators during light and dark phases. Two-way analysis of variance was used to determine influence of the predator and existence of caudal filaments on two mayfly species in light and dark.

Caudal filaments and molting rate

A second experiment compared molting rates between *R. hageni* and *B. tricaudatus* nymphs with and without caudal filaments (n=16-19 nymphs). Drenkelfort (1910) suggested that "pulling" movement of filaments was mainly responsible for the nymph escaping from its old exoskeleton at ecdysis. Each of the four experimental cells consisted of a glass bowl (20 cm diam. x 6 cm depth) containing 1 liter of aerated dechlorinated water, 10 stones, TetraMin food

Table 1. Distribution of *Baetis* nymphs collected at sites along the Highwood River, 24 June 1979.

Site	Location		Distance from river's source (km)	Altitude (m)	Current Velocity (cm/s) Mean At 3cm above bed	Nymphal number							
	Latitude	Longitude				<i>B. bicaudatus</i>				<i>B. tricaudatus</i>			
						I	II	III	IV	I	II	III	IV
1.	50°30' ²⁶ 44"	114°49'47"	7.69	1735	68.54	29.94	1	62	17				
2.	50°25'19"	114°44'28"	20.51	1615	31.08	13.48	1	15	15				
3.	50°23'35"	114°40'39"	33.33	1550	44.70	16.89	10	24	58	2	1		
4.	50°23'19"	114°35'23"	38.46	1460	51.22	28.24	2	10	5		19		
5.	50°24'20"	114°29'50"	44.46	1415	43.00	22.56	18	5	13	7	30	2	
6.	50°26'00"	114°26'30"	46.15	1370	70.86	32.78	6	1	2	22	18	2	

* Size categories (I, II, III, IV) are based on wing-pad development (after Clifford 1970).

and mayfly nymphs. Caudal filaments were cut as previously described. Temperature was constant at 5°C and a 12 hr light-dark cycle was used. Numbers of mayfly exuviae were recorded and preserved daily for 50 days. For nymphs with excised filaments, we predicted regeneration time of the filaments by plotting increase in length of caudal filaments against time.

Caudal filaments and longitudinal distribution in a stream.

A field study was conducted at six sites along a section of the Highwood River (Table 1) in the Rocky Mountain Forest of Alberta to determine distribution of baetid nymphs having two (*B. bicaudatus*) and three caudal filaments (*B. tricaudatus*). Insects were collected by taking a 1 min. kick sample (mesh opening: 180 microns) from a riffle area at each site.

The following parameters were recorded at the time each site was sampled: land-use, aquatic, overhanging and riparian vegetation, current velocity (Gurley Pigmy Meter) stream width and maximum depth, bottom type, air and water temperature, pH and dissolved oxygen. Altitude, distance from stream source and stream order were obtained from topographic maps. Water samples were immediately refrigerated and additional chemical characteristics analyzed 1 week later using standard methods (American Public Health Association 1971). Gower's similarity coefficient (Sneath and Sokal 1973) was used to determine similarity between stream sites based on 31 physical and chemical parameters.

Caudal filaments and vulnerability to predation.

An *in situ* experiment was conducted on the Highwood River using flow-through plastic containers (28.5 cm x 17 cm x 13 cm) with and without the stonefly predator *Hesperoperla pacifica* (Banks) and either two-tailed (*B. bicaudatus*) or three-tailed (*B. tricaudatus*) nymphs. *Baetis bicaudatus* Dodds and *B. tricaudatus* nymphs were collected from site 2 (upstream) and site 6 (downstream), respectively (Table 1). The experiment was conducted midway between the two collecting sites. Twelve 2 cm holes were drilled into both ends of each container. Netting (mesh opening: 180 microns) was secured over the holes to exclude extraneous organisms and prevent experimental organisms from escaping. Each container was half filled with clean stones from the stream bed. Predators had been starved for 4 hrs before the experiment. Fifteen mayflies (developmental stage III) representing two- or three-tailed forms and one predator were added to the containers (10 trials). There were two control replicates (no predators) for each mayfly species (total number of experimental cells = 24). After 24 hrs, the containers were retrieved and the remaining nymphs collected. Foreguts of the stonefly nymphs were analyzed for prey remains. A one-way analysis of variance was used to test for differences between species remaining in the experimental cells.

Morphological Studies

Claws of *B. bicaudatus* and *B. tricaudatus* nymphs were observed with a scanning electron microscope (SEM). To prepare the dissected claws for observation, they were first sonicated in 70% ethanol to remove debris. The claws were dehydrated in a graded ethanol series, transferred to absolute acetone and allowed to dry. After the claws were mounted on stubs with

Table 2. Number of *B. tricaudatus* and *R. hageni* nymphs (with and without caudal filaments) eaten by *Isogenoides elongatus* nymphs in the light and dark

	LIGHT		DARK	
	<i>B. tricaudatus</i>	<i>R. hageni</i>	<i>B. tricaudatus</i>	<i>R. hageni</i>
with	3	2	13	5
caudal	5	3	6	6
filaments	5	0	7	2
	3	2	10	6
	3	0	12	2
	<hr/>	<hr/>	<hr/>	<hr/>
	19	7	48	21
without	9	1	11	4
caudal	5	1	9	6
filaments	7	0	15	1
	7	1	11	6
	4	1	13	2
	<hr/>	<hr/>	<hr/>	<hr/>
	32	4	59	19

Table 3. Significance of effects from a 2-way ANOVA test of caudal filaments (C.F.) and predators on number of mayfly nymphs taken of each species in the *light*

<i>Species</i>	<i>Replicates</i>	<i>C.F.</i>	<i>Predators</i>	<i>C.F. x Predators</i>
<i>B. tricaudatus</i>	0.815	6.796**	79.889***	4.993*
<i>R. hageni</i>	2.432	1.018	9.163**	1.018

* $p < 0.05$, ** $p < 0.025$, *** $p < 0.001$

Table 4. Significance of effects from a 2-way ANOVA test of caudal filaments (C. F.) and predators on number of mayfly nymphs taken of each species in the *dark*

<i>Species</i>	<i>Replicates</i>	<i>C.F.</i>	<i>Predators</i>	<i>C.F. x Predators</i>
<i>B. tricaudatus</i>	1.058	1.524	128.476***	1.524
<i>R. hageni</i>	3.000	0.281	47.531***	0.031

*** $p < 0.001$

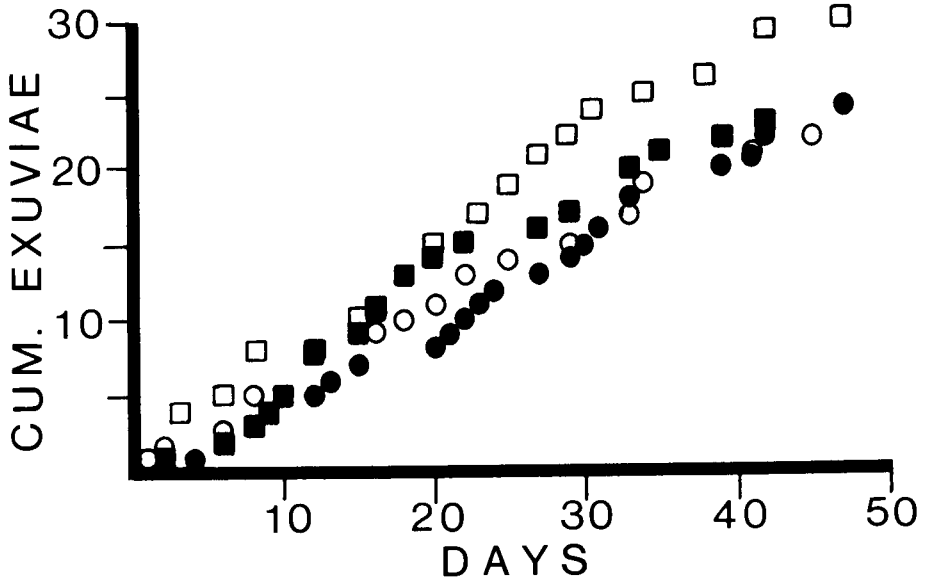


Figure 1. Cumulative number of nymphal exuviae of *Baetis tricaudatus* with (■) and without (□) caudal filaments and of *Rithrogena hageni* with (●) and without (○) caudal filaments over time.

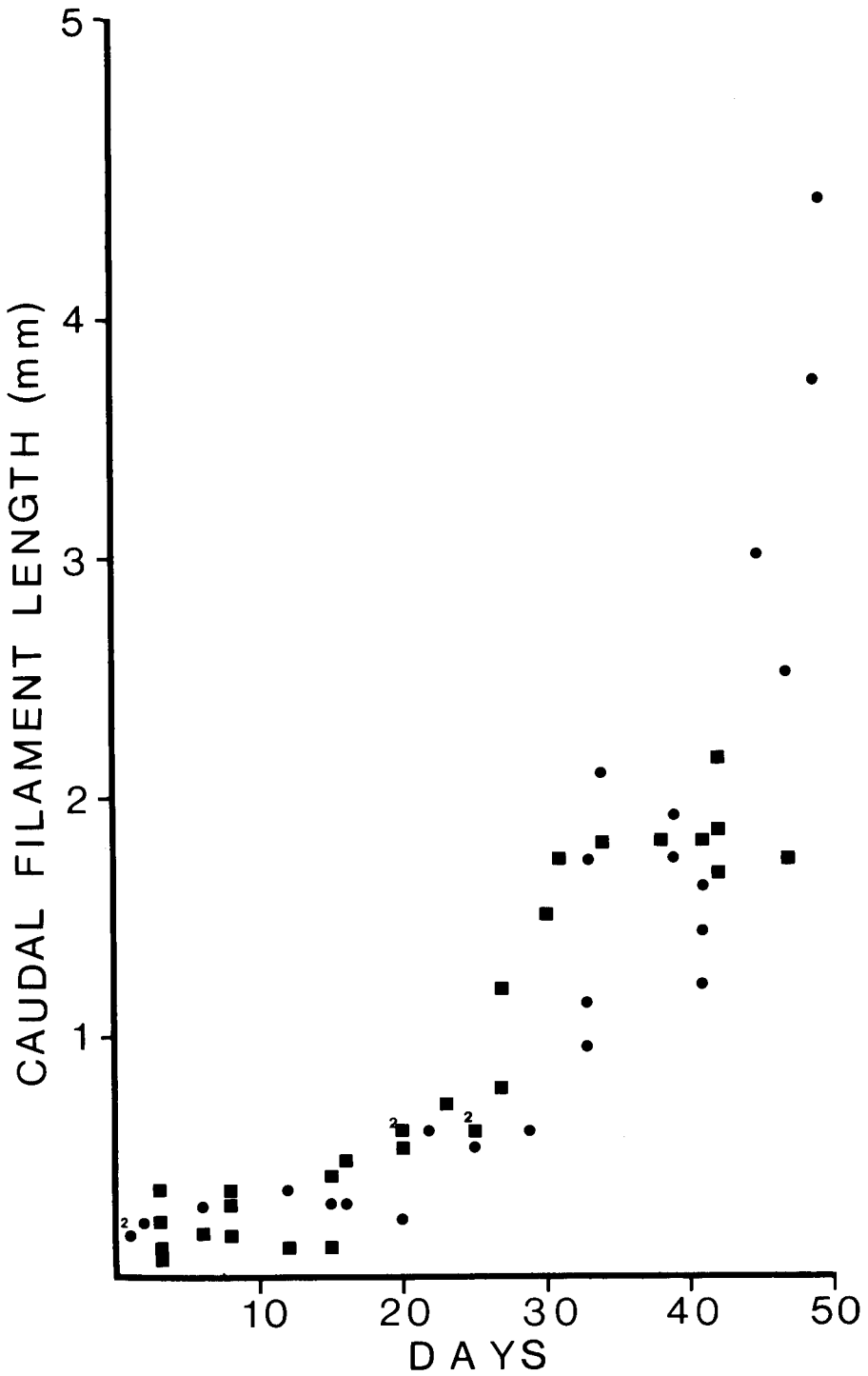


Figure 2. Total length of regenerated caudal filaments for *Baetis tricaudatus* (■) and *Rhithrogena hageni* (○) nymphs versus time.

conducting tape, and a gold-palladium layer applied to the stub, they were ready for observation.

RESULTS

Laboratory Studies

Caudal filaments and vulnerability to predation.

Isogenoides elongatus (Hagen) nymphs ate significantly more *B. bicaudatus* than *R. hageni* nymphs in light and dark (Table 2). There were, however, significantly more prey taken by predators in the dark (Student's *t*: $p < 0.01$). Based on the replicated two-way analysis of variance (ANOVA) tests, removal of caudal filaments had no effect on the number of *R. hageni* nymphs captured (Tables 3 and 4). During the light only, predators caught significantly more *B. tricaudatus* nymphs without caudal filaments than with filaments ($p < 0.025$).

Caudal filaments and molting rate

Removal of caudal filaments had no effect on the molting rate of either mayfly species (Fig. 1). Mortality (7.5 nymphs, S.D. = 3.5) was comparable in both species whether or not filaments were excised.

To predict regeneration time of the excised filaments, regression equations were calculated for the increasing caudal filament length (expressed as mm) versus time (days) for the two species. Logarithmic transformation of the dependent variable gave the best regression fit for both species (Fig. 2):

$$B. tricaudatus \quad \hat{Y} = 1.056e^{0.023X} \quad R^2 = 0.865 \quad (1)$$

$$R. hageni \quad \hat{Y} = 0.948e^{0.028X} \quad R^2 = 0.823 \quad (2)$$

The longest natural filament length for *B. tricaudatus* and *R. hageni* nymphs representing this sample population was 4.16 mm and 6.78 mm, respectively. Using these values, the above equations would predict that regeneration of caudal filaments of *B. tricaudatus* in 59.6 days and those of *R. hageni* in 70.3 days.

Caudal filaments and longitudinal distribution.

On 24 June 1979, two-tailed *Baetis* (*B. bicaudatus*) nymphs were found at all six sites on the Highwood River (Table 1). Three-tailed forms (*B. tricaudatus*) occupied the downstream three sites, below 1500 m in altitude. Nymphs of both species occupied fast-water areas. There was no relationship between distance downstream from the headwaters with either mean current velocity ($r = -0.019$) or flow 3 cm from the stream bed ($r = 0.175$). Clearly, the two

populations are not separated by water flow.

The dendrogram resulting from the Gower similarity analysis depicts the three upstream sites as distinct from the downstream sites (Fig. 3). The distribution of *B. tricaudatus* nymphs is associated with the downstream grouping. Between sites 3 and 4 (the two groupings), Etherington Creek enters the Highwood River. Stream width, specific conductance, alkalinity

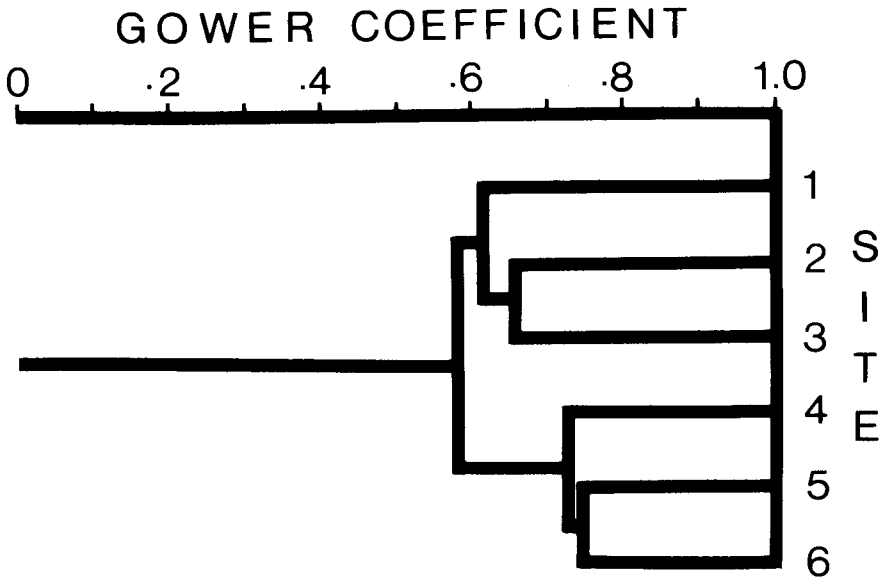


Figure 3. Dendrogram showing similarities between physical-chemical characteristics at sites along the Highwood River. Location of sites are indicated in Table 1.

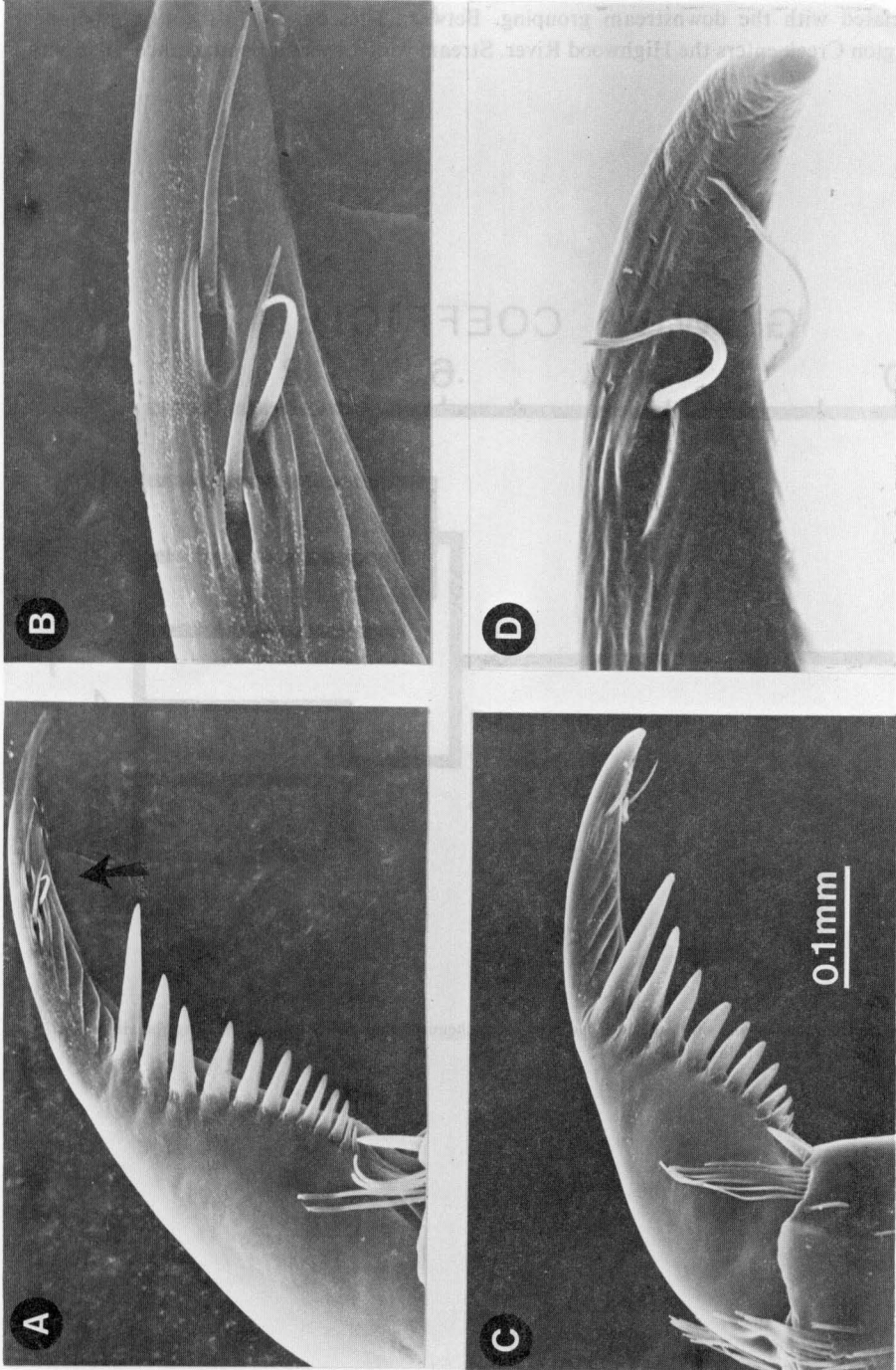


Plate 1. Scanning electron photomicrographs of claws and subapical setae of *Baetis bicaudatus* (A & B) and *B. tricandatus* (C & D). Photographs of C & D are of different specimens.

The distribution of *B. tricandatus* nymphs sites as defined from the downstream sites (Fig. 3). The distribution of *B. tricandatus* nymphs populations are not separated by water flow.

is associated with the downstream group. How-
Elkington Creek in the Highwood River, Susque-

Table 5. A summary of *Baetis* nymphs with a reduced terminal filament and the existence of subapical setae on the claws. Data obtained from Morihara & McCafferty (1979), Müller-Jenau (1969, 1971, 1974a) and Keffermüller (1980).

Species	Terminal Filament (t. f.) and Lateral Filaments (L)	Subapical Setae on Claws
North America:		
<i>B. lapponicus</i> gp:		
<i>B. amplus</i>	t.f. = stub ¹	-2
<i>B. insignificans</i>	t.f. = stub	-
<i>B. lapponicus</i>	t.f. = stub	+
<i>B. rhodani</i> gp:		
<i>B. bicaudatus</i>	t.f. = stub	+
<i>B. foemina</i>	t.f. = stub	+
<i>B. tricaudatus</i>	t.f. < L (.1-.8) ³	+
<i>Baetis</i> sp. A	t.f. < L (.4-.8)	+
<i>Baetis</i> sp. B	t.f. < L (.4-.8)	-
Western Palearctic:		
<i>B. alpinus</i> gp:		
<i>B. alpinus</i>	t.f. < L	+
<i>B. melanonyx</i>	t.f. < L (.5)	+
<i>B. lapponicus</i> gp:		
<i>B. lapponicus</i>	t.f. = stub	+
<i>B. sinaicus</i>	t.f. = stub	-
<i>B. lutheri</i> gp:		

(continued on next page)

Table 5 (continued)

Species	Terminal Filament (t. f.) and Lateral Filaments (L)	Subapical Setae on Claws
<i>B. lutheri</i>	t.f. < L (.5)	+
<i>B. meridionalis</i>	t.f. < L (.5)	?
<i>B. nigrescens</i>	t.f. = stub	+
<i>B. vardarensis</i>	t.f. < L (.5)	+
<i>B. rhodani</i> gp:		
<i>B. canarensis</i>	t.f. < L (.5)	+
<i>B. pseudorhodani</i>	t.f. = stub	+
<i>B. gemellus</i>	t.f. < L (.6)	?
<i>B. rhodani</i>	t.f. < L (.75)	-

¹ stub = a terminal filament of 5 segments or less (Moriyama and McCafferty 1979)

² + = present, - = absent, ? = unknown.

³ (.n) = ratio of length of terminal filament to that of the lateral filaments.

and salinity all increase after the confluence of the two streams.

Caudal filaments and vulnerability to predation.

There was no mortality or loss of nymphs in control cells of the *in situ* predator-prey experiment conducted on the Highwood River. Fewer *B. bicaudatus* and *B. tricaudatus* nymphs were found in cells containing *H. pacifica* nymphs. Contents of predator foreguts indicated that nymphs of both mayfly species were eaten without preference. We tentatively conclude from this short-term study that neither two-tailed nor three-tailed *Baetis* nymphs had an advantage in avoiding predators.

Morphological Studies

Morphological studies showed one pair of subapical setae on each *B. tricaudatus* claw and as many as three pairs on the claws of *B. bicaudatus* (Plate 1).

Published records (Table 5) show that all species of *Baetis* nymphs with subapical setae on claws possessed a terminal filament which was greatly reduced (in some species to a stub) and also inhabited fast-flowing waters. In North America, subapical setae on claws has been reported in two species groups, *B. lapponicus* and *B. rhodani* (Moriyama and McCafferty 1979). In the western Palearctic, these setae are present in four groups: *Baetis* ^{alpinus} *B. lapponicus*, *Baetis* ^{littoralis} *B. rhodani* Müller-Liebenau 1969, 1971, 1974a). Species within these groups live in running waters at high altitudes and latitudes or on islands (McDunnough 1936, Müller-Liebenau 1971, Edmunds *et al.*, 1976, Cobb and Flannagan 1980). Nymphs of the one northern species, *Baetis macani bundyae*, that lack subapical setae on claws inhabit ponds (Lehmkuhl 1973). Müller-Liebenau (1974b) found subapical setae on nymphal claws of all three species of *Heterocloeon* McDunnough (= *Rheobaetis*); these nymphs also possess a reduced (one segment) terminal filament and inhabit swift-flowing rivers. We know of no other mayfly species in which nymphs possess subapical setae on claws.

DISCUSSION

Our laboratory study showed that stonefly predators ate more *B. tricaudatus* than *R. hageni* nymphs. Evidently, the flattened, clinging, *R. hageni* nymphs were more difficult for the stonefly nymphs to capture than the rounded, swimming, *B. tricaudatus* nymphs. This tends to support the hypothesis of Hynes (1970) that flattened nymphs adhering to substrate surfaces may offer protection against predation. Fewer *Baetis* nymphs with caudal filaments were eaten by predators during light periods. This was a minor advantage since predators fed significantly more at night.

In the field, there was no significant difference between two- and three-tailed nymphs. (*B. bicaudatus* and *B. tricaudatus*) in avoiding the stonefly nymph, *H. pacifica*. Based on these studies, we discard the idea that the major function of the caudal filaments of mayfly nymphs is to deter predators.

We also concur with Schmidt's (1951) view that caudal filaments do not assist in the molting process. Apparently, movement of caudal filaments does not significantly aid nymphs during molt as suggested by Drenkelfort (1910).

Species replacement along a stream channel is a common phenomenon (Ide 1935, Allan 1975, Hawkes 1975, Ward and Berner 1980). In headwater areas of mountain streams, Dodds

and Hisaw (1924) and Hora (1930) suggested that species of *Baetis* with progressively shorter terminal filaments live in habitats with increasing current velocities. Although both *B. bicaudatus* and *B. tricaudatus* nymphs occupied fast-water areas, we found no relationship between current velocity and stream site inhabited by these two- and three-tailed species of *Baetis*. The difference between no current and some current may be of major significance to an organism, whereas large differences among current velocities may be of minor importance (Philipson 1954).

Edmunds *et al.*, (1976) and Ward and Berner (1980) have indicated that *B. bicaudatus* nymphs live at high altitudes. Ward and Berner (1980) report the upstream limit of *B. tricaudatus* nymphs on St. Vrain Creek Colorado ca. 2400 m, several degrees of latitude south of our site. On the Highwood River, the upstream limit of *B. tricaudatus* at 1500 m (50°23' N) corresponds to the entrance of Etherton Creek. In our study, no single environmental factor influenced the distribution of the two mayfly species along a stream section. Rather, a combination of factors were correlated with the upstream limit of the three-tailed, *B. tricaudatus* nymphs.

Typically, fast-flowing water is well aerated and carries food to aquatic organisms. The organisms, however, must either avoid the force of the current or be able to maintain their position. *Baetis* nymphs frequently occupy the upper substrate surfaces and face into the current (Dodds and Hisaw 1924). Hora (1930) suggests that nymphs facing into torrential water must hold the caudal filaments together to aid water flow over their body. He conceives that the terminal filament may have been "pressed out of existence, metaphorically speaking, by the pressure of the lateral [filaments]." Perhaps caudal filaments act to reduce drag on nymphs exposed to current flow.

From morphological studies of *B. bicaudatus* and *B. tricaudatus* nymphs, we observed subapical setae on claws of both of these fast-water species. All species of *Baetis* with subapical setae on claws also have a reduced terminal filament. We suggest that these structures are mechanoreceptors. If so, they should be able to detect water-borne vibrations (McIver 1975). Although elliptical shape of the socket may restrict the directional movement of setae, it may be possible that these structures are used by nymphs to detect subtle changes in flow within the boundary layer (*sensu* Ambühl 1959). The setae may also assist in orienting nymphs into the current. These structures would be of particular importance to nymphs inhabiting upper substrate surfaces exposed to flowing water.

Popovici-Bazosanu (1906) suggested that caudal filaments may function as a respiratory organ. Since *Baetis* nymphs with a reduced terminal filament appear to be found in specific habitats (high altitude and latitude), gradual reduction in an appendage may be a response to lower respiratory demands in these cooler, fast-flowing waters.

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LITERATURE CITED

- ALLAN, J. D. 1975. The distributional ecology and diversity of benthic insects in Cement Creek, Colorado. *Ecology* 56: 1040–1053.
- AMBÜHL, H. 1959. Die Bedeutung der Strömung als ökologischer Faktor. *Schweizerische Zeitschrift für Hydrologie* 21: 133–264.
- AMERICAN PUBLIC HEALTH ASSOCIATION. 1971. Standard methods for the examination of water and wastewater. 13th ed. A.P.H.A., New York.
- CLIFFORD, H. F. 1970. Variability of linear measurements throughout the life cycle of the mayfly *Leptophlebia cupida* (Say) (Ephemeroptera: Leptophlebiidae). *The Pan-Pacific Entomologist* 46: 98–106.
- COBB, D. G., and J. F. FLANNAGAN. 1980. The distribution of Ephemeroptera Biology in Northern Canada. p155–166. *In* Advances in Ephemeroptera. Eds. Flannagan, J. F., and K. E. Marshall. Plenum Publ. New York.
- CORKUM, L. D., and H. F. CLIFFORD. 1980. The importance of species associations and substrate types to behavioural drift. p. 331–341. *In* Advances in Ephemeroptera Biology. Eds. Flannagan, J. F., and K. E. Marshall. Plenum Publ. New York.
- DRENKELFORT, H. 1910. Neue Beiträge zur Kenntnis der Biologie und Anatomie von *Siphonurus lacustris* Eaton. *Zoologische Jahrbücher (Anatomie)* 29: 527–617.
- DODDS, G. S., and F. L. HISAW. 1924. Ecological studies of aquatic insects. 1. Adaptations of mayfly nymphs to swift streams. *Ecology* 5: 137–148.
- EDMUNDS, G. E., Jr., S. L. JENSEN, and L. BERNER. 1976. *The mayflies of North and Central America*. University of Minnesota Press, Minneapolis.
- HAWKES, H. A. 1975. River zonation and classification. p. 312–374. *In* River Ecology. Ed. B. A. Whitton. Blackwell Sci. Publ., Oxford.
- HORA, S. L. 1930. Ecology, bionomics and evolution of the torrential fauna, with special reference to the organs of attachment. *Philosophical Transactions of the Royal Society. B* 218: 171–282.
- HUGHES, D. A. 1966. On the dorsal light response in a mayfly nymph. *Animal Behaviour*. 14: 13–16.
- HYNES, H. B. N. 1970. *The Ecology of Running Waters*. University of Toronto Press, Toronto.
- IDE, F. P. 1935. The effect of temperature on the distribution of the mayfly fauna of a stream. *Publications of Ontario Fisheries Research Laboratory* 50: 1–76.
- KEFFERMÜLLER, M. 1980. Un Changement dans la Taxonomie de la Famille Baetide. p. 115–121. *In* Advances in Ephemeroptera Biology. eds. Flannagan, J. F., and K. E. Marshall. Plenum Publ. New York.
- LEHMKUHL, D. M. 1973. A new species of *Baetis* (Ephemeroptera) from ponds in the Canadian arctic, with biological notes. *The Canadian Entomologist* 105: 343–346.
- MCDUNNOUGH, J. 1936. A new arctic baetid (Ephemeroptera). *The Canadian Entomologist* 68:33–35.
- McIVER, S. B. 1975. Structure of cuticular mechanoreceptors of arthropods. *Annual Review of Entomology* 20: 381–397.
- MORIHARA, D. K., and W. P. McCAFFERTY. 1979. The *Baetis* larvae of North America (Ephemeroptera: Baetidae). *Transactions of the American Entomological Society* 105:

- 139-221.
- MÜLLER-LIEBENAU, I. 1969. Revision der Europäischen Arten der Gattung *Baetis* Leach, 1815 (Insecta, Ephemeroptera). Gewässer und Abwässer, 48/49. 214 S., Max-Planck-Gesellschaft. Dokumentationsstelle, Göttingen.
- MÜLLER-LIEBENAU, I. 1971. Ephemeroptera (Insecta) von den Kanarischen Inseln. Gewässer und Abwässer, 50/51: 7-40.
- MÜLLER-LIEBENAU, I. 1974a. Baetidae aus Südfrankreich, Spanien und Portugal (Insecta, Ephemeroptera). Gewässer und Abwässer, 53/54: 7-42.
- MÜLLER-LIEBENAU, I. 1974b. *Rheobaetis*: a new genus from Georgia (Ephemeroptera: Baetidae). Annals of the Entomological Society of America 67: 555-567.
- PERCIVAL, E. and H. WHITEHEAD. 1929. A quantitative study of the fauna of some types of stream-bed. Journal of Ecology. 17: 282-314.
- PHILIPSON, G. N. 1954. The effect of water flow and oxygen concentration on six species of caddis fly (Trichoptera) larvae. Proceedings of the Zoological Society of London. A. 124: 547-564.
- POPOVICI-BAZNOSANU, A. 1906. Contributions à l'étude de l'organisation des larves des Ephemerines. Archives de zoologie expérimentale et générale 5: 66-78.
- SCHMIDT, H. 1951. Amputation und Regeneration von Schwanzfäden und Abdominalsegmenten bei Larven der Ephemeridenart *Cloeon dipterum* L. und ihr Einfluss auf die Häutungsintervalle. Zool. (Phys) 62: 395-428.
- SNEATH, P. H. A. and R. R. SOKAL. 1973. *Numerical Taxonomy*. W. H. Freeman and Co., San Francisco.
- VENTER, G. E. 1961. A new ephemeropteran record from Africa. Hydrobiologia 18: 327-331.
- WARD, J. V. and L. Berner. 1980. Abundance and altitudinal distribution of Ephemeroptera in a Rocky Mountain stream. p. 169-177. In *Advances in Ephemeroptera Biology*. Eds. Flannagan, J. F., and K. E. Marshall. Plenum Publ. New York.