

Research Article

Taxonomic Review of the *Caudatella heterocaudata* (McDunnough) and *C. hystrix* (Traver) Complexes (Insecta: Ephemeroptera: Ephemerellidae)

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Caudatella columbiella (McDunnough, 1935), new combination, (Insecta: Ephemeroptera: Ephemerellidae) is removed from synonymy with *Caudatella heterocaudata* (McDunnough, 1929), and a new junior synonym is recognized, based on comparative examination of type material and larval exuviae associated with adults from the type locale of *C. columbiella* (= *C. californica* (Allen and Edmunds, 1961), new status, new synonym). *Caudatella circia* (Allen and Edmunds, 1961), new status, is recognized as a strict specific synonym of *C. heterocaudata* (McDunnough, 1929) (= *C. circia* (Allen and Edmunds, 1961), new synonym). A neotype is designated for *Caudatella hystrix* (Traver, 1934), based on a specimen collected in Western Montana, USA, during June 2000. Morphological differences between the type specimen of *C. hystrix* and the type specimens of its two junior synonyms, *Ephemerella cascadia* Allen and Edmunds, 1961, and *E. spinosa* Mayo, 1952, are detailed. An identification key for larvae of the genus *Caudatella* is included.

1. Introduction

The genus *Caudatella* Edmunds (Insecta: Ephemeroptera: Ephemerellidae) is restricted to Western North America, where larvae live in mountain streams, often associated with aquatic moss [1]. Larval and winged stages of *Caudatella* are distinguished from other Ephemerellidae genera by the median caudal filament being wider at the base and longer than the cerci. *Caudatella* was described initially as a subgenus of *Ephemerella* Walsh [2], but it was subsequently elevated to genus [3]. All nominal *Caudatella* species and subspecies were described originally as *Ephemerella*.

Caudatella contains ten nominal species and subspecies, with six of them recognized as valid in the most recent revisionary synopsis of the genus [4]: *C. edmundsi* (Allen, 1959); *C. heterocaudata heterocaudata* (McDunnough, 1929) [5] (= *Ephemerella columbiella* McDunnough, 1935 [6]); *C. heterocaudata californica* (Allen and Edmunds, 1961) [7]; *C. heterocaudata circia* (Allen and Edmunds, 1961) [7]; *C. hystrix* (Traver, 1934) [8] (= *Ephemerella spinosa* Mayo, 1952; = *Ephemerella cascadia* Allen and Edmunds, 1961 [7]);

C. jacobii (McDunnough, 1939) (= *Ephemerella orestes* (Allen and Edmunds, 1961) [7]).

Aspects of *Caudatella* species taxonomy have remained questionable despite recent revisionary work [4], especially subspecies designations and species that are polytypic. The subspecies classifications, in particular, are questionable because they were established at a time when mayfly taxonomists tended to define any distinct morphological variant as a nominal subspecies; currently, subspecies designations usually are reserved for geographically isolated variants. This paper addresses issues associated with the *C. heterocaudata* and *C. hystrix* species complexes.

2. Materials and Methods

Specimens were examined with dissecting microscopes and are deposited at the following institutional collections: California Academy of Sciences, San Francisco California, United States of America (CAS); Canadian National Collection of Insects, Ottawa, Ontario, Canada (CNC); Cornell University Insect Collection, Ithaca, New York, United States of

America (CUIC); Purdue University Entomological Research Collection, West Lafayette, Indiana, United States of America (PERC).

2.1. Primary Type Material Examined

2.1.1. *Ephemerella californica*. HOLOTYPE: United States of America, California, Madera County, Sierra National Forest, Chilacoot Creek, 1 mile above Bass Lake, 19-VI-1959, R. K. Allen, larva (PERC).

2.1.2. *Ephemerella cascadia*. HOLOTYPE: United States of America, Oregon, Clackamas County, Branch of Still Creek on road to Timberline Lodge, Mt. Hood, 30-VIII-1958, G. F. Edmunds, Jr., & R. K. Allen, larva (PERC).

2.1.3. *Ephemerella circia*. HOLOTYPE: United States of America, Oregon, Douglas County, Umpqua River, Sawyer Rapids, 26.5 mi E of Reedsport, 17-VI-1958, Mike Johnson, larva (PERC).

2.1.4. *Ephemerella columbiella*. HOLOTYPE: Canada, British Columbia, Peachland, Trepanier Creek, 4-VII-1934, A. N. Gartrell, male adult (reared from larva) (CNC).

2.1.5. *Ephemerella heterocaudata*. HOLOTYPE: United States of America, Wyoming, Yellowstone National Park, Upper Geyser Basin, 29-VII-1928, J. McDunnough, male adult (CNC).

2.1.6. *Ephemerella hystrix*. NEOTYPE (new designation), United States of America, Montana, Sweet Grass County, small tributary of Big Timber Creek, at canyon road crossing, 1 mile south of Big Moon Campground, 46°1'30"N, 110°8'48"W, 10-VI-2000, W. P. McCafferty et al., larva (CUIC).

2.1.7. *Ephemerella spinosa*. HOLOTYPE, United States of America, California, Inyo County, 4-VII-1938, larva (specimen number 8645) (CAS).

2.2. Other Material Examined

2.2.1. *Ephemerella californica*. United States of America, California, Los Angeles County, San Gabriel River at Camp Bonita (62°), 16-VI-1959, R. K. Allen, one larva, paratype (PERC).

2.2.2. *Ephemerella cascadia*. United States of America, Oregon, Clackamas County, Branch of Still Creek on road to Timberline Lodge, Mt. Hood, 30-VIII-1958, G. F. Edmunds, Jr., & R. K. Allen, two larvae (same collection data as holotype) (CNC); United States of America, Washington, Pierce County, Mt. Rainier National Park, spring-fed stream, Westside Road, 1.2 miles north of Highway 706, 16-VI-2004, emerged 21-VI, Kondratieff, Schmidt, three male adults, one female adult, associated larval exuviae (PERC).

2.2.3. *Ephemerella columbiella*. Canada, British Columbia, Peachland, Trepanier Creek (same collection locale as holotype), A. N. Gartrell, sub 15-VII-1934, adult 17-VII-1934, one set larval exuviae (CNC); same locale and collector, sub 6-VII-1934, adult 10-VII-1934, one set larval exuviae (CNC); same locale and collector, sub 5-VII-1934, adult 6-VII-1934, one set larval exuviae (CNC).

2.2.4. *Ephemerella heterocaudata*. United States of America, Wyoming, Yellowstone National Park, Firehole River, above Chimney Bridge, 22-VII-1928, J. McDunnough, nine larvae (CNC).

2.2.5. *Ephemerella hystrix*. Canada, British Columbia, Keremos, Shingle Creek Road, sub 26-VII-1935, adult 28-VII-1935, A. N. Gartrell (699-1192) (CNC); United States of America, Montana, Sweet Grass County, small tributary of Big Timber Creek, at canyon road crossing, 1 mile south of Big Moon Campground, 46°1'30"N, 110°8'48"W, 10-VI-2000, W. P. McCafferty, et al., (same collection data as neotype), five larvae (PERC).

3. Systematic Accounts

3.1. *Caudatella heterocaudata* Species Complex. This species complex is defined herein to contain two nominal species. Adults and larvae of these two related species are distinguished from congeners by abdominal sterna that have three longitudinal stripes and by cerci that are much shorter than the median filament (usually less than half as long).

Caudatella heterocaudata has been divided into three nominal subspecies: *C. h. heterocaudata*, *C. h. californica*, and *C. h. circia* [7]. Allen and Edmunds [7] listed *Ephemerella columbiella* as a junior synonym of *C. heterocaudata* based on its falling within their concept of variability for the latter species. Remarkably, they listed *E. columbiella* with the *C. h. heterocaudata* subspecies [7]. The former is removed from synonymy with the latter, below.

3.1.1. *Caudatella columbiella*: New Combination

Larval Diagnosis. In contrast to *C. heterocaudata*, *C. columbiella* has paired medial spines on abdominal tergum 1, the other paired medial spines sharp at the tips, and cerci that are approximately one-sixth the length of the median filament, or about one-half the length of the abdomen.

Adult Diagnosis. Male adults of *C. columbiella* (forewing length ca. 6 mm) are smaller than those of *C. heterocaudata* (forewing length at least 7 mm), and *C. columbiella* male adults usually have abdominal maculation that is not as highly contrasted from the base coloration [5, 6].

Remarks. *Caudatella columbiella* (newly revised concept) is known from Southern British Columbia and Central California [6, 7], which is within the geographic distribution of the more widespread *C. heterocaudata* [7]. Based on the consistent differences detailed above, *C. columbiella*

should be a valid species and not a synonym of *C. heterocaudata*.

Caudatella columbiella must have been considered synonymous with the *C. h. heterocaudata* subspecies [7] independent from the recognition of the other two nominal subspecies, because larval exuviae associated with adult specimens of *C. columbiella* from the type locale (listed as having been examined by Allen and Edmunds [7]) are indistinguishable from the holotype of *C. h. californica*. *Caudatella californica*, new status, therefore, should be recognized as a species separate from *C. heterocaudata* and as a subjective junior synonym of *C. columbiella* (= *C. californica*, new status, new synonym).

3.1.2. *Caudatella heterocaudata*

Larval Diagnosis. In contrast to *C. columbiella*, *C. heterocaudata* does not have paired medial spines on abdominal tergum 1, and the other paired medial spines are blunt at the tips. The cerci are longer than those of *C. columbiella*, being approximately one-third the length of the median filament, or about the same length as the abdomen.

Adult Diagnosis. Male adults of *C. heterocaudata* (forewing length at least 7 mm) are much larger than those of *C. columbiella* (forewing length ca. 6 mm), and *C. heterocaudata* male adults usually have more contrast between the dark maculation and base coloration of the abdomen [5, 6].

Remarks. Allen and Edmunds' [7, Figure 3] is actually a ventral view of the *C. heterocaudata* penes that was labeled incorrectly as a dorsal view; all of their other penes figures are correctly labeled as dorsal views.

Caudatella heterocaudata circia was described originally as a subspecies of *C. heterocaudata* that has prominent, characteristic setose, wartlike protuberances on the pro- and mesonota of the thorax; the adults are not known [7]. Its status as more than merely a morphological variant must be regarded as questionable, however, due to observed variation in the development of the characteristic dorsal protuberances on the thorax (the defining character of the subspecies) within the type locale population (Willamette River, Lane County, Oregon, United States of America) [7]. Furthermore, this nominal variant and typical *C. heterocaudata* "probably meet and intergrade" elsewhere near the type locale [7]. Based on current views of subspecies in Ephemeroptera and of morphological variation among species of Ephemerellidae, *C. h. circia* should be considered a strict species synonym of *C. heterocaudata* (= *C. circia*, new status, new synonym).

3.2. *Caudatella hystrix* Complex. This species complex consists of one polytypic species. Larvae are distinguished from congeners by having long, almost hook-like, paired medial spines on the middle abdominal terga. Adults are distinguished from congeners by having abdominal sterna with broad medial maculation that occupies most of the segment, usually taking the form of a chevron shape

[7], and male penes with the gonopores in a subparallel or convergent orientation and with dorsally or medially directed projections on the dorsal aspects of the penes.

The name *Ephemerella hystrix* was established based on a single larva collected from western Montana, United States of America [8] that had been described prior to its formal naming [9]. The concept of the species later was expanded to be polytypic, encompassing the nominal species *Ephemerella spinosa* [10] and *Ephemerella cascadia* [11], based on variation of the defining characteristics of the nominal species from throughout their geographic ranges.

In order to emphasize the polytypic nature of *C. hystrix* and to provide a base for future study of *Caudatella* diversity, the type specimens and some additional material of the three nominal species included in the polytypic concept of *C. hystrix* are discussed under the heading of their original generic combinations. In each case, the type specimen is a larva.

3.2.1. *Ephemerella hystrix*. The *E. hystrix* holotype was collected 29 June 1906 from Big Blackfoot River, Potomoc, Montana, United States of America [8]. The last direct report of the *E. hystrix* holotype was made in 1954 [10]. The specimen's deposition location was listed in 1961 [7], but no evidence indicates that it was examined directly by those authors at that time.

Unfortunately, the type specimen (no. 1287.1) of *E. hystrix* is missing from the Cornell University Insect Collection (E. R. Hoebeke, pers. comm.). Correspondence with personnel from insect collections at the California Academy of Science, Florida A & M University (Tallahassee, Florida, USA) and Purdue University also failed to locate the specimen. Almost all existing mayfly specimens examined by R. K. Allen, W. C. Day, and G. F. Edmunds, Jr., are housed in these three collections, and thus these were selected as the locations most likely to house the specimen in question, if it were still in existence.

In order to maintain the identity of *E. hystrix*, *sensu stricto*, and to provide a basis for future study of *Caudatella* species diversity, a neotype is designated for *E. hystrix* (see Primary Type Material Examined), which was selected from a series of specimens collected from western Montana in June 2000. The lost holotype of *E. hystrix* also was collected from western Montana in June [8]. The new specimens match the lost *E. hystrix* holotype descriptions [8, 9, 12] and Traver's [12, Figure 53.b]. The neotype designation herein satisfies the conditions and recommendations of Article 75 of the *International Code of Zoological Nomenclature* [13].

The neotype larva of *E. hystrix* does not have spicules on the dorsal surfaces of the large, paired medial spines of abdominal terga 5–7, and these medial spines have tips that curve slightly outwards. The abdominal terga have dark medial coloration, and the legs have numerous long, hairlike setae along the outer margins. Most of the abdominal sterna have distinct chevron-shaped maculae [7].

3.2.2. Junior Synonym: *Ephemerella cascadia*. The somewhat discolored *E. cascadia* holotype has the medial spines of the

abdominal terga with long spicules dorsally, as shown in Allen and Edmunds' [7, Figure 25], and these paired spines have a subparallel orientation of the apical portions. The legs have relatively few long, hairlike setae on the outer margins. The abdominal sterna have a solid dark brown color pattern [7].

Previous study indicated that the maculation of larval sterna can be variable [11], but sometimes the extent of maculation is dependent upon which instar is examined. The medial sternal maculation of recently reared adults appears to be consistent with the type concept of *E. cascadia* (solid color). Reexamination of this material from Washington (previously listed as *C. hystrix* [4]) revealed that the gonopores of the penes are not strongly oriented medially, as historically indicated for *C. hystrix* [7]. More specimens of both nominal variants should be studied to determine whether this is a consistent difference because the orientation of the penes lobes of preserved specimens can vary dramatically.

3.2.3. *Junior Synonym: Ephemerella spinosa.* *Ephemerella spinosa* has abdominal terga that lack medial coloration, and the paired medial spines on the abdominal terga have dorsal spicules. The medial spines on abdominal terga 5–7 are distinctly more divergent than the others and have tips that curve inwards. The legs have numerous long, hairlike setae on the outer margins. Most of the abdominal sterna have distinct chevron-shaped maculae. No adults have been associated with this name.

Ephemerella spinosa Mayo, 1952, should not be confused with *Ephemerella spinosa* Morgan, 1911, a nomen nudum [4], nor should it be confused with *Ephemerella spinosa* Ikononov, 1961, a preoccupied name, which correctly was renamed *E. ikononovi* Puthz, 1971 [14]. *Ephemerella ikononovi* is the type species of the genus *Quatica* Jacobus and McCafferty [4].

4. Updated Taxonomic Synopsis of the Genus *Caudatella*

Caudatella edmundsi (Allen, 1959) [15]

Caudatella columbiella (McDunnough, 1935) [6],
comb. n.

=*Ephemerella californica* Allen and Edmunds, 1961
[7], stat. n., syn. n.

Caudatella heterocaudata (McDunnough, 1929) [5]

=*Ephemerella circia* Allen and Edmunds, 1961 [7],
stat. n., syn. n.

Caudatella hystrix (Traver, 1934) [8]

=*Ephemerella spinosa* Mayo, 1952 [10]

=*Ephemerella cascadia* Allen and Edmunds, 1961
[7, 11]

Caudatella jacobi (McDunnough, 1939)

=*Ephemerella orestes* Allen and Edmunds, 1961
[7, 16].

5. Key to Larvae of the Genus *Caudatella* Edmunds

- (1) Maxillary palp vestigial; tarsal claw with two prominent rows of denticles—(*edmundsi*).
- (1') Maxillary palp with three distinct segments; tarsal claw with only one distinct row of denticles—(2).
- (2) Paired medial spines on abdominal terga long and curved (at least on middle segments), some almost hook like—(*hystrix*).
- (2') Paired medial spines on abdominal terga relatively straight, none longer than respective segment—(3).
- (3) Cerci approximately two thirds length of median filament; abdominal sterna with solid color, never with longitudinal stripes or other such markings—(*jacobi*).
- (3') Cerci less than one-half length of median filament; abdominal sterna almost always with three dark, longitudinal markings—(4).
- (4) Cerci approximately one-third length of median filament (about the length of the abdomen); distinct pair of medial spines present only on abdominal terga 2–9, with the spine tips blunt—(*heterocaudata*).
- (4') Cerci approximately one-sixth length of median filament (about half the length of the abdomen); distinct pair of medial spines present on abdominal terga 1–9, with the spine tips sharp—(*columbiella*).

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