

HAGEN'S SMALL MINNOW MAYFLY (EPHEMEROPTERA: BAETIDAE) IN NORTH AMERICA¹

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ABSTRACT: The study of newly acquired larvae and adults of *Dipheter devinctus* associated by rearing in California showed larvae to be indistinguishable from those of *D. hageni*. This, and the further observation from extensive materials that male genitalia differences previously accorded the two species do not hold up but are highly subject to individual and population variability, are the basis for placement of *D. devinctus* as a junior subjective synonym of *D. hageni*, n. syn. The complex nomenclatural history of the North American species and monobasic genus as well as characterization are reviewed, and distribution is documented.

The history of nomenclature and of discovery surrounding the now relatively well known North American baetid species *Dipheter hageni* (Eaton), or Hagen's Small Minnow Mayfly, is complex. The species was originally described as *Cloe unicolor* Hagen (Hagen 1861) based on a female adult taken in the District of Columbia, the type of which resides at the Museum of Comparative Zoology (MCZ) at Harvard University. Eaton (1871) recombined the species with the genus *Baetis* Leach. Somewhat later, when the original name was found to have been used previously by Curtis (1834) for another species, Eaton (1885) renamed Hagen's species *Baetis hageni* Eaton. American workers for much of the 20th Century, however, did not use the replacement name proposed by Eaton (e.g., McDunnough 1923, Traver 1935, Burks 1953), but continued to refer to the species as *B. unicolor*. McDunnough (1923) purportedly associated males with the females of the species in Canada, but later (McDunnough 1925a) indicated that his identification was actually applicable to *B. brunneicolor* McDunnough.

McDunnough (1921, 1925a) and Traver (1935) indicated that *Baetis unicolor* (Hagen) could not be identified with certainty based on re-examination of the type by both Nathan Banks (see McDunnough 1921) and James Needham (see Traver 1935). Burks (1953) also claimed that the species was unrecognizable and therefore could not confirm Walsh's questionable identifications of the species from Rock Island, Illinois collected in the 1860's.

Edmunds (1962) provided clarification that the use of Hagen's name *unicolor* was incorrect according to applicable nomenclatural rules. He therefore upheld Eaton's rejection of the secondary homonym in question and the use of the newer name *Baetis hageni*, and for some 25 years hence the species was known as *B. hageni* (e.g. Edmunds et al. 1976). Careful restoration of the

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type of *B. hageni* by Edmunds (1962) revealed that the species was equivalent to what had in the meantime been described as *Baetis herodes* Burks from Illinois and Indiana (Burks 1953), and as a result Edmunds synonymized the latter name with the former. Edmunds (1962) also indicated that several adult specimens from throughout much of eastern North America, identified by Herman Spieth as *Baetis parvus* Dodds and deposited at the American Museum of Natural History, were actually *B. hageni*. Finally, because Burks (1953) had also associated and described the larval stage of his *B. herodes*, Edmunds (1962) was able to show that larvae from Ontario previously described as *B. parvus* by Ide (1930) were also applicable to *B. hageni*, and had represented the first larval description of the species.

In their comprehensive study of larvae of *Baetis* in North America, Morihara and McCafferty (1979) showed that *B. hageni* was a highly unique species that was probably most closely related to *B. devinctus* Traver, based on similarities of the adults (the latter remained unknown in the larval stage). Morihara and McCafferty (1979) confirmed the Edmunds conclusions regarding synonymy and further showed that *B. parvus*, originally described from Colorado by Dodds (1923) was also a junior synonym of *B. hageni*. Morihara and McCafferty (1979) also restudied the larvae that Burks (1953) had associated with the species. As a result of reared associations of larvae and adults of *B. hageni* in Indiana by Morihara and McCafferty (1979), those authors showed that the male larva described by Burks was actually *B. macdunnoughi* Ide, but that he had correctly associated the female larva.

Waltz and McCafferty (1987a) designated *B. hageni* to be the type of their new North American genus *Dipheter* Waltz and McCafferty. The species has thus been known as *D. hageni* since that time (e.g., McCafferty 1996). *Dipheter* is not related to *Baetis* and other related genera of the *Baetis* complex as is shown, for example, by the absence of a villopore in the larval stage. Waltz and McCafferty (1987a) further distinguished the genus by the lack of gills on abdominal segment 1 in combination with a reduced prostheca of the right mandible. The only other species placed in *Dipheter* was *D. devinctus* Traver, a species that Morihara and McCafferty (1979) had deduced from adults was closely related to *D. hageni*. Traver (1935) in her description of *D. devinctus* (as *Baetis*) compared it with *B. parvus* and had indicated that it differed from the latter only in its possession of a tubercle on the medial margin of the forceps base of the male genitalia. Waltz and McCafferty (1987a) indicated that their generic placement of *D. devinctus* was based on the study of reared but undescribed larvae of the species, with no other details provided at the time.

Soldán and Thomas (1983) described the species *Baetis rhithralis* Soldán and Thomas from larvae and adults from Algeria. Waltz et al. (1994) placed that species in the genus *Dipheter*. At about the same time, Novikova and Kluge (1994) considered *Dipheter* as a subgenus of *Baetis*. Waltz and

McCafferty (1997) reiterated conclusively that *Dipheter* could not be a sub-genus of *Baetis* because it did not even belong to the same complex of genera, as shown, for example, by the fact it did not possess a villopore. Lugo-Ortiz and de Moor (2000) were able to study the type material of the Soldán and Thomas species from Algeria and showed that it is actually a member of the Old World genus *Nigrobaetis* Kazlauskas, rather than *Dipheter*. Thus *Dipheter* appears restricted to North America, and its listing among world genera (Lugo-Ortiz and McCafferty 1999) for the Palearctic region should therefore be emended.

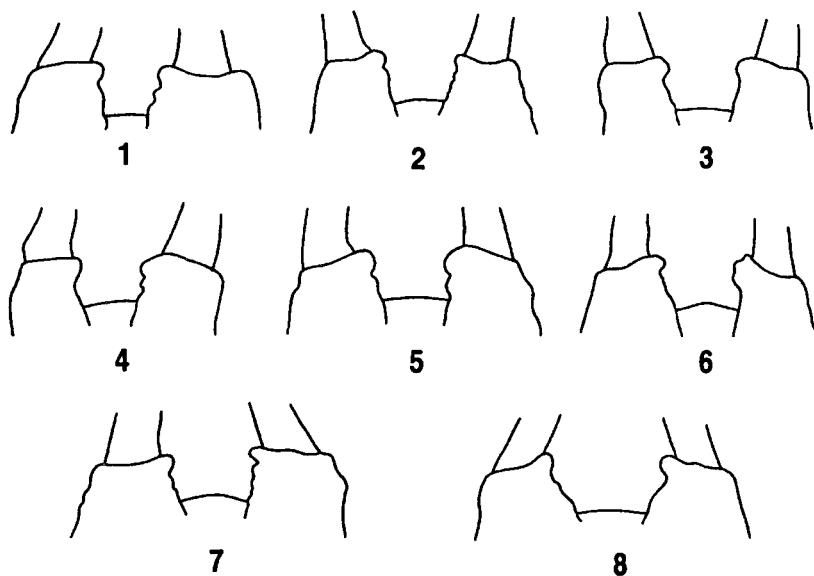
The North American range of *Dipheter hageni* is relatively widespread. In Canada, it is known from New Brunswick to British Columbia in the southern tier of provinces (McDunnough 1925b, Walley 1927, Eidt 1975, Scudder 1975, Morihara and McCafferty 1979, Flannagan and Flannagan 1982, McCafferty and Randolph, 1998), but has yet to be reported from Newfoundland and Prince Edward Island. In northern Canada, it is known only from Nunavut (Cobb and Flannagan 1980, Randolph and McCafferty 2001). The species is not known from Alaska, but its range in the conterminous United States is considerable. The only large geographic region in which it is not represented is the southwest region (see McCafferty and Waltz 1990), and it is not known from the southern tier of southeastern states and Georgia. Otherwise, the species has been reported as relatively widespread in the southeast, northeast, and northwest regions (Traver 1935, Edmunds 1954, Allen and Edmunds 1956, Newell 1970, Moss and Lichtwardt 1975, McCafferty and Provonsha 1978, Newell and Minshall 1978, Dellucchi and Peckarsky 1989, McCafferty 1990, Burian and Gibbs 1991, McCafferty et al. 1993, Long and Kondratieff 1996, Grant et al. 1997, McCafferty et al. 1997, Sarver and Kondratieff 1997, Randolph and McCafferty 1998, Pescador et al. 1999, McCafferty et al. 2001).

Dipheter devinctus has been reported from four counties in California (Traver 1935, Day 1956), a state where it evidently co-occurred with *D. hageni*.

VARIABILITY

As part of our current study of the California Ephemeroptera fauna, we realized that the unknown larval stage of *D. devinctus* needed to be discovered and described so that *D. hageni* and *D. devinctus* could be differentiated as larvae where their ranges overlap. In this respect, we were able to acquire larvae and adults from Marin County, California (see Material Examined) that were associated through rearing by Lawrence Serpa. Male adults had the typical form of genitalia that had historically been associated with *D. devinctus*. A thorough examination of the morphology of the larvae indicated that they were identical to those described for *D. hageni* by Morihara and McCafferty (1979), with the exception that one leg of one specimen was found to have one less claw denticle than the range reported for the latter species. That difference, however, is inconsequential.

The identicalness of the larvae that could now be associated with either name, strongly suggested to us that there was actually only one species involved. Baetid workers in general (e.g., Müller-Liebenau 1970, Morigara and McCafferty 1979, Waltz and McCafferty 1987b, Lugo-Ortiz and McCafferty 1996, 1998) have found that larval differences are foremost in species level discernment. Nonetheless, we undertook a comprehensive study of male genitalia in extensive materials of both *D. hageni* and *D. devinctus* to determine if perhaps adults but not larvae demonstrated species differences. We found that the medial shape of the forceps base—the character used to separate the species of *Dipheter*—varied considerably among *D. hageni* individuals from non-California populations. Variability (Figs. 1-5) included having very little or undetectable medioapical development to having a somewhat developed apical rim medially to having what has been referred to as a tubercle medioapically, as originally associated with *D. devinctus* (Traver 1935). This characteristic not only varied between populations, but also varied within populations, and in some cases was found to vary from the left to right forceps base on the same individual. We also found variability in California material (Figs. 6-8).



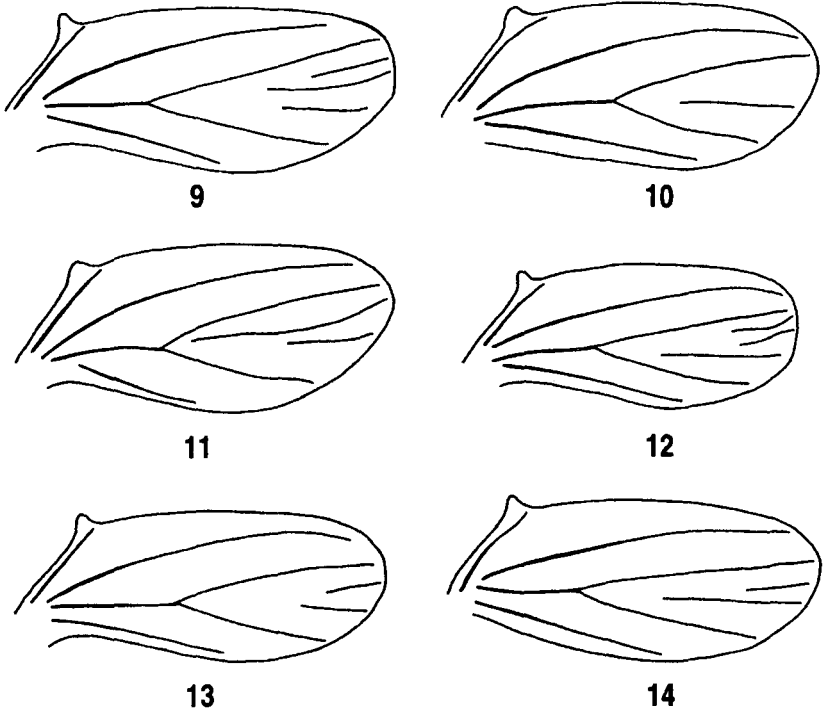
Figs. 1-8. *Dipheter hageni* adult male genitalia [Var. = variant, Pop. = population]. 1. Var. 1 (ID), 2. Var. 2 (IN Pop. 1), 3. Var. 3 (IN Pop. 2), 4. Var. 4 (IN Pop. 2), 5. Var. 5 (MT), 6. Var. 6 (CA Pop. 1), 7. Var. 7 (CA Pop. 2), 8. Var. 8 (CA Pop. 2).

Because there evidently is no distinction between either the larvae or the adults of what have been called *D. hageni* and *D. devinctus*, we herein formally place *D. devinctus* as a subjective junior synonym of *D. hageni*, n. syn. It was of interest to us that among Day's collected California materials in our possession, there were adult specimens he collected together in 1950 that he identified variously as *D. devinctus*, *D. hageni*, and *D. parvus*. This is now certainly explicable based on the subsequent synonymy of *D. parvus* by Morihara and McCafferty (1979) and on our present synonymy of *D. devinctus*. Day may have been suspicious of the integrity of the species in California because he did not mention his *D. hageni* or *D. parvus* material in his later review of California mayflies (Day 1956).

In identifying adults of *Dipheter* among other similar baetid adults in North America, the presence of a forked second vein originating in the basal half of the hindwings has been utilitarian (e.g., see key couplet 34 in Edmunds and Waltz 1996). Waltz and McCafferty (1987a) and Durfee and Kondratieff (1993) had shown that a forked second vein was not entirely exclusive to *Dipheter*, however, because it can occur in some *Baetis* species, but originating in the distal half of the wing or barely so. When examining variability in the adults of *D. hageni*, we found the presence of the fork was stable, but there was variability with respect to the position of the fork (originating at approximately midlength or somewhat basad of midlength) and the number and relative development of the marginal intercalaries within the fork (one to three of various lengths) (Figs. 9-14). Variability in the intercalaries is to be expected in baetid hindwings, but we would caution that the position of the origin of the fork of a forked second vein must now be used with caution because occasionally variants of the very common species *B. tricaudatus* Dodds and some variants of *D. hageni* demonstrate a fork originating very near the midlength of the wing.

MATERIAL EXAMINED

The following materials are deposited in the Purdue Entomological Research Collection, West Lafayette, Indiana. ARKANSAS: Newton Co, Mill Cr, St Rd 7, 1 mi S Dogpatch, V-29-1974, McCafferty et al. (larvae). CALIFORNIA: Napa Co, Sage Cr, V-13-1950, Day (adults); Marin Co, Lagunitas Cr, .5 mi W Jewell, VIII-26-1982, Serpa (larvae, adults reared). COLORADO: Saguache Co, Los Pinos Cr, 6 mi SW St Work Ranch, VI-28-1976, Alstad, Taylor (larvae). IDAHO: Bingham Co, Blackfoot, VIII-8-1963, Edmunds (adults); Blaine Co, Trib Big Wood R, VII-24-1964, Jensen et al. (adults); Bonneville Co, Snake R, Palisades, US Hwy 26, VI-28-1964, Jensen, Richardson (larvae); Boundary Co, Deep Cr, US Hwy 95, 5 mi N Naples, III-26-1965, Nebeker (larvae); Custer Co, Warm Cr at Challis, VIII-15-1963 (larvae). INDIANA: Crawford Co, Stinking Frk Blue R, St Rd 66, 1.5 mi S Sulfur Springs, V-14-1976, Provonsha, Minno (larvae); Dubois Co, Trib Flat Cr, St Rd 64, 2 mi W Mentor, V-14-1975, Provonsha, Minno (adults); Fountain Co, Bear Cr nr Fountain, V-26-1978, Provonsha, Minno (larvae); Jennings Co, Green Br, Crosly St. Fish & Wildlife Area, V-7-1974, Provonsha, Dersch (larvae); Lawrence Co, small stream 6 mi SW Bedford, Hwy. 460 W, IV-7-1978, Minno, Bloodgood (adults); Sugar Cr, 1 mi S



Figs. 9-14. *Dipheter hageni* adult hindwing [Var. = variant, Pop. = population]. 9. Var. 1 (ID), 10. Var. 3 (IN Pop. 2), 11. Var. 5 (MT), 12. Var. 6 (CA pop. 1), 13. Var. 7 (CA Pop. 2), 14. Var. 8 (CA Pop. 2).

Bono, VI-20-1974, Provonsha, Dersch (larvae, adults reared); Gulleets Cr, 1 mi N Needmore, IV-25-1975, Provonsha, Minno (adults); small stream 4.5 mi S Williams, VI-7-1978, Minno, Bloodgood (larvae); Spring Mill Cr at Spring Mill St Prk, IV-25-1975, V-14-1976, Provonsha, Minno (larvae); Martin Co, Lost R at Windom, VII- 3-1974, Provonsha et al. (larvae); Owen Co, Limestone Cr at St Rd 67, 1.5 mi W Gosport, IV-11-1975, Provonsha, Dersch; Perry Co, Poison Cr, 5 mi NW Derby, V-15-1975, Provonsha et al. (larvae); Oil Cr, 2.5 mi N Leopold, V-15-1975, Provonsha et al. (larvae); Tippecanoe Co, Flint Cr, West Point, IV-8, V-2,5-1975, Provonsha et al. (larvae, adults); Warren Co, W Brch Kikapoo Cr, 2 m. SE Winthrop, V-21-1976, Minno, Morihara (larvae); Little Pine Cr at Highbridge, IV-30-1972, Huff et. al. (larvae); Trib Little Pine Cr, 1 mi W Greenhill, III-25-1972 (larvae). MISSOURI: Barry Co, Roaring R, X-26-1971, Baumann (larvae); Jackson Co, Blue R, IX-28-1971, Lorenz (larvae). MONTANA: Glacier Co, Swiftcurrent Cr, Glacier Nat Prk, VII-24-1955 (adults). NORTH CAROLINA: Forsyth Co, Parkers Cr, III-1987 (larvae). OREGON: Jefferson Co, Metolius R, Riverside For Camp, VII-30-1966, Lehmkuhl (adults); Metolius R, Camp Sherman, VI-20-1954, Edmunds (adults); Metolius R headwaters, VI-15-1966, Lehmkuhl (adults); Wallowa Co, Wallowa R at Wallowa L, VIII-1952, Edmunds (adults). SOUTH DAKOTA: Beadle Co, Hitchcock, V-6-1959 (adults); Lawrence Co, Jim Cr, 3 mi S Nemo, VI-13-1975, McCafferty et al. (larvae); Pennington

Co, Rapid Cr , mouth Dark Cany, Rapid City, VI-13-1975 McCafferty et al. (larvae, adults). UTAH: Box Elder Co., George Cr, 7.5 mi. SE Yost, VII-12-1947, Preece (adults); Cache Co, Blacksmith Frk Cany, VI-14-1046, Harmston (adults); Iron Co, Red Rock Cany nr Parowan, VI-7-1951, Edmunds (adults); Salt Lake Co, Mill Cr, VII-10-1945, Edmunds (larvae); Emmigration Cany, VIII-8-1945, Edmunds (adults); Butterfield Cany, Salt Lake City, VII-4-1945, Mulaik (adults); Sanpete Co, San Pitch R, Fairview, VII-7-1945, Edmunds (adults); Huntington Cany, VII-9-1945, Edmunds (adults); Summit Co., Weber R below Peoa, X-18-1968 (larvae); Summit Co, Wanship, VIII-18-1945, Edmunds (adults); Tooele Co., S Willow Cany, VII-15-1945, Mulaik (adults); Utah Co., Aspen Grove Cr nr Jct, W lower Provo R, Wildwood, X-7-1968 (larvae); Provo R, Hwy 189/91, VII-2-1947 (adults); Orem, IX-16-1944, Edmunds (adults); Wasatch Co, Daniels Cany, VII-22-1947, Edmunds (adults). WYOMING: Laramie Co, Snowy Range Mnt, VII-10-1949, Denning (adults).

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