

**EVALUATION OF MAYFLY SPECIES ORIGINALLY DESCRIBED AS
BAETIS LEACH (EPHEMEROPTERA: BAETIDAE) FROM CALIFORNIA**

W. P. MCCAFFERTY, M. D. MEYER, R. P. RANDOLPH, AND J. M. WEBB

(WPM) Department of Entomology, Purdue University, West Lafayette, IN 47907, U.S.A. (e-mail: mccafer@purdue.edu); (MDM) Department of Biology, Chemistry, and Environmental Science, Christopher Newport University, 1 University Place, Newport News, VA 23606, U.S.A.; (RPR) Section of Evolution and Ecology, University of California, Davis, CA 95616, U.S.A.; (JMW) Department of Environmental Management and Ecology, La Trobe University, Albury/Wodonga Campus, P.O. Box 821, Wodonga, Victoria, Australia 3689

Abstract.—Eight species of mayflies described in *Baetis* Leach from California are evaluated for validity, generic classification, and distribution. Taxonomic status quo is maintained for the southwestern *Baetis adonis* Traver [= *B.* sp. A Morihara and McCafferty, = *B. caelestis* Allen and Murvosh], *B. devinctus* Traver [synonym of *Dipheter hageni* (Eaton)], and *B. leechi* Day [synonym of *Fallceon quillieri* (Dodds)]. *Baetis alius* Day is shown to be common in the northwestern U.S.A. and somewhat variable but distinctive as larvae; *B. moqui* Wiersema, Nelson and Kuehnl is shown to be a junior synonym of *B. alius*, **new synonym**. *Baetis diablus* Day is correctly placed to genus but remains unknown as larvae and has been rarely taken only in California; it is possibly a variant of *B. tricaudatus* Dodds. *Baetis palisadi* Mayo is correctly placed to genus, and based on discovered larvae has diagnostic mandibles and labial palpi among *rhodani* group species; it is apparently endemic to California and of environmental concern. *Baetis piscatoris* Traver is correctly placed to genus, relatively common in California, and based on discovered larvae is the only known *rhodani* group species with elongate gills. *Baetis sulfurosus* Day belongs in *Fallceon* Waltz and McCafferty, as evidenced by discovered larvae; it is also a junior synonym of the western *F. thermophilus* (McDunnough), **new combination, new synonym**, and is distinct from western congeners by size and color pattern of larvae, and hindwings and subgenital plate of adults.

Key Words: mayflies, Ephemeroptera, Baetidae, California

Eight species of Ephemeroptera were originally described from California by Traver (1935), Mayo (1952), and Day (1954): *B. adonis* Traver, *B. alius* Day, *B. devinctus* Traver, *B. diablus* Day, *B. leechi* Day, *B. palisadi* Mayo, *B. piscatoris* Traver, and *B. sulfurosus* Day. *Baetis devinctus* and *B. leechi* have since proven to be junior synonyms of the relatively common and well-known species *Dipheter hageni* (Eaton) (see Meyer and McCafferty 2001) and *Fallceon quillieri* (Dodds) (see Morihara and McCafferty 1979), respectively. The concepts of *Baetis adonis* and *B. alius* as both adults and larvae have become more solidified, both species have been shown to occur in other parts of the

western U.S.A., and *B. adonis* has proven to be a senior synonym of other named species (e.g., Morihara and McCafferty 1979, McCafferty and Silldorff 1998, Lester et al. 2002; Meyer and McCafferty 2007a, 2007b). The other four species have been very poorly known and anomalous because of the dearth of reports associated with them and the fact that they have remained unknown as larvae. Even the generic placement of these latter species could be in question, particularly for the very large-sized species *B. diablus* and *B. palisadi*, both of which approach the size of species of *Moribaetis* Waltz and McCafferty, a genus recently reported from the southwestern U.S.A. (McCafferty 2007a).

The purpose of the present study has been to evaluate the taxonomic status of the eight species in terms of species validity, new synonymies with which they may be associated, and correct generic placement in light of the considerable revisionary work on the family Baetidae that has occurred since the 1950s. The evaluations are based on a detailed examination and review of type materials along with fresh collections, both reported and not reported previously, including reared, associated larvae that were not known previously for three of the species. From this we are able to determine validity and generic classification, to provide comparative information and diagnoses for identification of the valid species, and to draw conclusions regarding possible endemism in California, general distribution, and environmental status. It is not our purpose here to provide formal illustrated keys because these are best treated within a larger familial or ordinal framework in the future. Diagnostic characters are adequately represented by ample citations of applicable figures already available in the published literature. The present work is a necessary precursor to

the publication of a multi-year faunistic study of the mayflies of California (Meyer and McCafferty in prep.). To a large degree it contributes to resolving what has historically been a very tenuous taxonomy of Californian Baetidae (see also McCafferty and Silldorff 1998, Durfee and Kondratieff 1999; Meyer and McCafferty 2001, 2003; Wiersema and McCafferty 2004, Jacobus and McCafferty 2005, McCafferty 2007c) and to the recent on going inventory and evaluation of the western North American mayfly fauna (e.g., McCafferty et al. 1993, 1997; Lugo-Ortiz and McCafferty 1995; McCafferty and Randolph 1998, in press; Randolph and McCafferty 2000, 2005; Lester et al. 2002, McCafferty 2007d; Meyer and McCafferty 2007a, 2007b; McCafferty and Meyer 2007, McCafferty and Newell 2007).

In the following narratives, the species are treated alphabetically by the name under which they were originally described.

Baetis adonis Traver, 1935

This species was originally described from adults taken from the San Gabriel Mountains of southern California (Traver 1935). McCafferty and Silldorff (1998) associated larvae with this species by rearing samples from Santa Barbara County. The larvae had been originally described as *Baetis* sp. A by Morihara and McCafferty (1979), and later formally named *B. caelestis* Allen and Murvosh by Allen and Murvosh (1983). The latter name was synonymized with *B. adonis* by McCafferty and Silldorff (1998). The species is a distinctive member of the *rhodani* species group (Morihara and McCafferty 1979) and is known from scattered localities ranging across the southwestern U.S.A. and northern Mexico (e.g., McCafferty et al. 1997).

Based on the presence of robust setae on the gill margins (Morihara and McCafferty 1979: fig. 19g) but the lack

thereof at the posterior margin of the terga among the *rhodani* group species of *Baetis*, the larvae will easily key to *B. sp. B* [sic], which was an inadvertent transposition with sp. A in the key of Morihara and McCafferty (1979). McCafferty and Silldorff (1998) elaborated characteristics and variability of the adults, and showed that the adults could range considerably in coloration (olive brown, red brown, and yellow brown) and in size (5.0–7.0 mm in length), and had *rhodani* type genitalia. As a result, adults of *B. adonis* will not key out reliably when using the key of Day (1956), which relies heavily on size and coloration. The moderate medial development of the male genital forceps segment 2 combined with the partially fused terminal segment (McCafferty and Silldorff 1998: fig. 1) may be of aid in diagnosing this species among *rhodani* group species.

Baetis alius Day, 1954

This species was originally described from adults and larvae taken in Sonoma County, northern California by Day (1954). Morihara and McCafferty (1979) gave a more detailed larval description after determining that the brief larval description given by Day (1954) was applicable to both *B. alius* and *B. tricaudatus* Dodds, which were collected together and undifferentiated by Day. *Baetis alius* is a distinctive species that has not been placed to any named species group of *Baetis* Leach. It has become better known in recent years, being found from throughout much of the northwestern U.S.A., apparently being more common in Oregon and Idaho than in California (Lester et al. 2002; Meyer and McCafferty 2007a, 2007b).

Baetis alius is very similar to *B. moqui* Wiersema, Nelson and Kuehn, which was described from a small population of larvae taken in the Colorado River drainage area of south-central Utah

(Wiersema et al. 2004). The range of larval morphological variability we have recently seen in larval *B. alius*, apparent from the collections from the Northwest (and including the intermountain West Colorado drainage area of Utah and Colorado), suggests that *B. moqui* is equivalent to *B. alius*. For example, *B. alius* larvae have variously reduced gills 1 among and within populations. Gills 1 are either reduced to about one-half to much less the length of abdominal segment 2, are somewhat truncated to somewhat rounded, and lack the tracheation typical of the other gills, or they are absent. We found extreme variability throughout the range of the species, including 15 topotypical larvae of *B. alius* we examined that were collected in the 1940s, 1950s, and 47 topotypical larvae collected in 2007. We also found that the relative size of gills 1 varies among individuals within a population depending on the age of the larvae, with gills 1 inversely becoming proportionately smaller as size of the larvae increases. Gills 1 were not mentioned in the description of *B. alius* larvae by Morihara and McCafferty (1979). This omission along with the fact that the presence or absence of gills 1 is critical to the first couplet of Morihara and McCafferty (1979) larval key [the absence thereof directing the user to only *B. hageni* (Eaton) (= *Diphetero hageni*)], suggests that Morihara and McCafferty (1979) had assumed that gills 1 of *B. alius* were like those of *B. tricaudatus* (which in some larvae can be considerably reduced) and had been knocked off and missing from most specimens of *B. alius* they examined. Thus, when comparing the larvae of *B. moqui* with the Morihara and McCafferty (1979) description of *B. alius*, Wiersema et al. (2004) would have come to the conclusion that the condition of gills 1 were different in the two species. This is clearly not the case, because across the entire geographic

range of *B. alius* (topotypical, other parts of California, Oregon, Washington, Idaho, Utah, and Colorado), gills 1 of many larvae show the small variation described for *B. moqui*, and in some specimens can be present on one side but not the other. All larvae of *B. alius* that we have studied lack a distinctive, dorsal, sclerotized point on tergum 1 that otherwise occurs at the dorsal base of gills 2–7, but a small gill socket is apparent, whether gills 1 are absent or not, suggesting that vestigial gills are naturally present but weakly joined to the abdomen and often broken off. Supposed mouthpart differences are accurately depicted by Wiersema et al. (2004: figs. 2–4, 11–13) but hold up only if one is comparing topotypical material. They do not take into account intermediates and ranges of variation that become apparent when populations from throughout much of the Northwest are examined. Within the range of *B. alius*, mouthpart variation encompasses the type described for *B. moqui*: The arrangement of dorsal setae on segment 2 of labial palpi is sometimes out of line as is common to many *Baetis* species; for example, larvae of *B. alius* from Gunnison County, Colorado, tend to have linear setae with one to three setae out of line and thereby appear to have labial palpi that have partially clustered and partially linear setae, depending on one's interpretation. The width of the first incisors of the mandibles range from being broad and somewhat bifid (Wiersema et al. 2004: fig. 2), as we have seen in two of the topotypical larvae of *B. alius* and recently collected larvae from Yosemite National Park and northwestern states, to more slender first incisors of most topotypical larvae (Mori-hara and McCafferty 1979: fig. 33b). In both the planate and angulate mandibles of *B. alius* from Oregon, Idaho, and Colorado, we have found that there can be apparently three or four incisors (but actually four in many individuals) in the outer

group of incisors, with the outermost two tending to overlap or coalesce, so that in a mandible with worn incisors, an interpretation of a wide outer incisor among three in an outer group could easily be made, as apparently in the original description of *B. moqui*, or an interpretation of narrow outer incisors among three in the outer group might also be made as in the description of Mori-hara and McCafferty (1979) of *B. alius*. The paraglossae can be interpreted to be narrow and distomedially projecting as described for *B. moqui*, depending on the angle of view or slide preparation. The dorsal abdominal color pattern in which segments 3–4 and 7–8 are darkened for the most part, is essentially the same in *B. alius* as that described for *B. moqui* (degree of color development in segment 2 and 6 tends to be variable, with the two ends of the spectrum apparently represented by topotypical larvae of *B. alius* from California and original material *B. moqui* from Utah). We have seen intermediate color forms of *B. alius* commonly from Idaho and the west slope of Colorado. Significantly, material from the originally taken *B. moqui* larvae in Utah that we examined had a pronotal pattern (suggestive of a pair of cat-eyes) that matches the species-specific pattern shown by fig. 33e of Mori-hara and McCafferty (1979) for *B. alius*. Unfortunately, this pronotal pattern is now faded in specimens collected in the 1940s and 1950s. From all of the discussion above, the obvious and predictable range of variability along with distinct similarities warrant placing *B. moqui* as a junior subjective synonym of the somewhat variable *B. alius*, **n. syn.**

Baetis alius larvae can be diagnosed as those *Baetis* with labial palpi uniquely having the inner margin of segment 2 slightly convex to nearly straight as opposed to variously concave. A first indication that larvae may be this spe-

cies, however, is usually suggested by what appear as pronounced white spots near the gills on the lateral edge of those abdominal terga that are otherwise dark. Additional characteristics that may aid in identifying this species include the absence of an inter-antennal keel; the presence of a developed middle tail without medial dark banding in well-marked individuals; the presence of rounded gills with gills 1 much smaller than other gills, or the absence of gills 1; and in fresh, well-marked individuals, a pair of eyelike markings on the pronotum and variable dorsal abdominal color patterning that includes a distinctly light segment 5, with segments 6–8 or 7–8 mostly (medially) darkened.

Baetis devinctus Traver, 1935

Traver (1935) described this species from adults taken from the central-coastal area of California (Santa Cruz County). This species was placed by Waltz and McCafferty (1987) in the genus *Dipheter* Waltz and McCafferty, a non-*Baetis* complex group fundamentally different than *Baetis*, based primarily on the similarity of its male genitalia with that of the *Dipheter* type species, *D. hageni* (Eaton). Based on larvae associated with adults by rearing, Meyer and McCafferty (2001) showed that *D. devinctus* was a junior synonym of the widespread, transcontinental *D. hageni*. In addition to the absence of a femoral villopore, *Dipheter hageni* larvae are more readily identifiable by the consistent absence of gills 1 in combination with a reduced prostheca on the planate mandible (Moriyama and McCafferty 1979: fig. 34b), relatively light terminal one or two abdominal terga (Moriyama and McCafferty 1979: figs. 35a, 35b), and presence of an inter-antennal keel on the head. Adult variability in terms of forceps bases and hindwing venation were treated and illustrated in detail by Meyer and McCafferty (2001).

This transcontinental species (McCafferty and Meyer 2007) will be shown to occur commonly throughout much of California (Meyer and McCafferty in prep.).

Baetis diablus Day, 1954

This species was described by Day (1954) based on relatively large-sized adults taken from Mt. Diablo in Contra Costa County in the central-coastal area of California. Day (1954) gave a brief description suggesting that the forked vein 2 of the hindwings was diagnostic and the male genitalia were of the *moffatti* type (typical of *rhodani* group of *Baetis* species). Because there have been no other published reports of the species since its description and larvae have not been associated with the adults, the species has remained somewhat anomalous. Based on a combination of hindwing venation (Day 1954: fig. 4) and the large body size (8.0–8.5 mm. as per our reexamination of original materials), it could be surmised that it was possibly equivalent to the large western species *Baetis magnus* McCafferty and Waltz or *B. tricaudatus*, both of which can reach the *B. diablus* size, or even the mainly Neotropical genus *Moribaetis* Waltz and McCafferty, whose Central and North American species are actually somewhat larger (see McCafferty 2007a). The forked vein 2 of the hindwings in the outer half of the wings has been found variably in the latter three taxa, although uncommonly reported in *Baetis* (Edmunds 1952, Waltz and McCafferty 1985, Durfee and Kondratieff 1993, McCafferty and Lugo-Ortiz 1998, McCafferty 2007a).

Study of the type material of Day's species indicated several differences with the detailed description of *B. magnus* adults given by Durfee and Kondratieff (1993), particularly in regard to the former lacking the diagnostic abdominal and femoral patterning associated with

B. magnus. It should be noted, however, that the type material of *B. diablus* appears somewhat faded due to age of preservation. Besides being somewhat smaller than the Central and North American species of *Moribaetis*, *B. diablus* does not have other characteristics typical of the adults of the latter, e.g., its hindwings are larger in proportion to the forewings (ca. 20%) (North and Central American *Moribaetis* hindwings are 11%–16% length of forewings, and *B. tricaudatus* and *B. magnus* hindwings are 20%–25% length of forewings) and do not have a basally marginated costal process that is somewhat distally oriented. Also, the forewings lack any pigment staining, and the stalk of the turbinate portion of the eyes is more extended than in *Moribaetis*. Male adults of *Moribaetis mimbresaurus* McCafferty, the recently discovered Nearctic species described from Arizona, additionally differ from *B. diablus* in having a distinctive subgenital plate associated with the male genitalia, an unforked vein 2 of the hindwings, and an abdomen devoid of distinct markings (McCafferty 2007a: figs. 2, 4–5).

Baetis tricaudatus is a ubiquitous, polytypic species whose larvae have been taken from the type locality of *B. diablus*. It is certainly within the realm of possibility that *B. diablus* represents an adult color variant of *B. tricaudatus* (with dark submedial stripes on abdominal terga according to the original description of fresh material), and would therefore be synonymous with the latter. We are taking a conservative approach and retaining *B. diablus*, until such time that further evidence of any equivalency with *B. tricaudatus* may be revealed by associated larvae, where more definitive structural characteristics tend to reside. If *B. diablus* proves to be a separate species, it may likely be endemic to California, and its relative rarity may warrant that the species be given special

environmental consideration at the state and federal levels.

Baetis leechi Day, 1954

This species was described from adults taken from the coastal valley of Napa County in the north-central region of California (Day 1954), and was subsequently reported from Los Angeles, Merced, and Stanislaus Counties in other regions of the state (e.g., Leland and Fend 1998). While still known only as adults, it was synonymized with *Baetis quilleri* Dodds (now known as *Fallceon quilleri*) by Morihara and McCafferty (1979) based on similarities including the hooked costal process of the hindwings (e.g., Traver 1935: fig. 163), which remains diagnostic for this particular species of *Fallceon* in western North America.

Larvae of *F. quilleri*, which were originally described by Morihara and McCafferty (1979) have been seen from throughout the state of California (Meyer and McCafferty in prep.) and commonly throughout the West Coast (Meyer and McCafferty 2007a, 2007b) and Rocky Mountains (McCafferty, Randolph, and Jacobus in prep.). The description of the larvae of *F. quilleri* by Morihara and McCafferty (1979) applies well in terms of size and typical color pattern, but the species in the larval stage is structurally similar to its congeners in the western United States (see Morihara and McCafferty 1979, Allen and Murvosh 1987, and details under *B. sulfur-osus* Day, below).

Baetis palisadi Mayo, 1952

Baetis palisadi was described from adults taken in the Sierra Nevada Mountains, Inyo County, in eastern California (Mayo 1952). The species has not been reported since its description and has remained somewhat anomalous. We have examined adults and larvae associated by rearing, taken in Sonoma Coun-

ty in 1982. This discovery has allowed us to confirm the integrity of both the genus and species classification, and to provide a comparative diagnosis of adult and larval stages.

Based on both male adult genitalia and larval armature characteristics, *B. palisadi* falls within the *rhodani* group of the genus *Baetis*, as originally postulated by Morihara and McCafferty (1979). It differs from other *rhodani* group species in the adult stage by being the only very large-sized species (ca. 8.0 mm.) having males with highly contrasting hyaline abdominal segments 2–6. Although this type of abdomen is found in the smaller California *rhodani* group species *B. piscatoris* Traver (see below), it is more typical of *fuscatus* group species, such as *B. flavistriga* McDunnough and *B. intercalaris* McDunnough. This latter group, however, has smaller adults in addition to male genitalia distinct from that of the *rhodani* group. The relatively narrow hindwings with three unforked veins combined with the lack of intercalaries (Mayo 1952: fig. 3) is also diagnostically significant when comparing the hindwings of the also large *B. magnus* and *B. tricaudatus* (e.g., Durfee and Kondratieff 1993: figs. 8–19) and *B. diablus* (Day 1954: fig. 5), or the smaller *B. piscatoris* (see below).

Baetis palisadi larvae differ from other *rhodani* group species and all other North American *Baetis* species by having labial palpi that are relatively narrow with an elongate segment 2 barely (or not noticeably) wider apicomediaally than the small bulbous segment 3. Also, the outer group of fused incisors on the mandibles is oblique, distinctly going from medially shorter to laterally longer, thus making the mandibles appear somewhat blade-like. Relatively similar labial palpi and mandibles are associated with some Central and North American species of *Moribaetis*, a group also made up of large-sized individuals, but somewhat

larger than the largest *Baetis* species (*B. diablus*, *B. magnus*, *B. palisadi*, *B. tricaudatus*) (see above). Relatively similar labial palpi to those of *B. palisadi* can be seen in *M. maculipennis* (Flowers) and *M. salvini* (Eaton) (Waltz and McCafferty 1985: figs. 29, 36), and mandibles relatively similar to those of *B. palisadi* are found in *M. macaferti* Waltz (Waltz and McCafferty 1985: figs. 7, 8), although other *Moribaetis* palpi are more bladelike in the extreme (Waltz and McCafferty 1985: figs. 26, 27, 35, 36). These similarities are clearly due to convergence, because any suggestion that *B. palisadi* belongs in the genus *Moribaetis* is negated by the presence of a femoral villopore in *B. palisadi*. This characteristic is associated only with the *Baetis* complex of genera within the Baetidae, which does not include *Moribaetis*, a member of the *Baetodes* complex of genera (Lugo-Ortiz and McCafferty 1996, McCafferty and Baumgardner 2003). In addition to the presence of a femoral villopore, which can sometimes be difficult to see, many other characteristics associated with *Baetis* rather than *Moribaetis* are evident in *B. palisadi*. For example: somewhat smaller size of the adults and mature larvae; absence of pigment staining in the forewings; relatively long stalk to the male adult turbinate eye (Mayo 1952: fig. 5) rather than a relatively short stalk (McCafferty and Lugo-Ortiz 1998: fig. 2, McCafferty 2007a: fig. 2); narrowly pointed, somewhat round- or triangular-based tergal scales rather than rectangular-based, broadly pointed tergal scales as best viewed on the larval abdominal integument; parallel-sided labrum (Morihara and McCafferty 1979: fig. 16a) rather than one narrowing basally (Waltz and McCafferty 1985: figs. 15, 25, 34); and moderately curved tarsal claws that lack asymmetrical subtending setae in the larvae rather than terminally hooked claws with one to three subtending setae

restricted to one side of the claw (Waltz and McCafferty 1985: fig. 40).

Baetis palisadi may very possibly prove to be endemic to California, and because it has been only rarely taken, it may warrant special environmental consideration.

Baetis piscatoris Traver, 1935

This species was described from adults from the central-coastal Santa Cruz County, California (Traver 1935). There have been no published records of the species since that time, except for an incomplete record from Napa County given by Day (1956). We have seen additional material from several other central and northern California counties (Meyer and McCafferty in prep.), including reared material from Sonoma County. Based on the male adult description of the size, hindwing venation, abdominal color pattern, and genitalia, this species is correctly placed in the genus *Baetis* and in the *rhodani* group of species as indicated by Morihara and McCafferty (1979). Also based solely on adults, *Baetis piscatoris* would appear to fall within the range of variation common to the ubiquitous species *B. tricaudatus*. Traver (1935) admittedly was unfamiliar with *B. tricaudatus*, and the hindwing venational characteristics that Day (1956) used to key *B. piscatoris* will not work due to known variation in *B. tricaudatus* (Durfee and Kondratieff 1999, McCafferty 2007c). The larvae, however, show that *B. piscatoris* is a separate and valid species.

Larvae of *B. piscatoris* will key out to *Baetis bundyae* Lehmkuhl (as *B. macani bundyae*) in the key provided by Morihara and McCafferty (1979) when geographic location (tundra vs. non-tundra) in the key is discounted. However, other than the couplets that will place the species in *Baetis* rather than *Diphetero*, *Acentrella* Bengtsson, *Acerpenna* Waltz and McCafferty, or *Pseudocloeon* Kla-

pálek, this is based on morphological similarities such as length and shape of the gills and length of developed medial caudal filament. *Baetis piscatoris*, *B. hudsonicus* Ide, and *B. bundyae* are the only three species of *Baetis* in North America that have exceedingly long gills (Morihara and McCafferty 1979: figs. 22e, 23f), and of these, *B. piscatoris* and *B. bundyae* have a medial caudal filament about three-fourths the length of the cerci. *Baetis piscatoris* is fundamentally different than *B. bundyae* and *B. hudsonicus* because it is a member of the *rhodani* group of species whereas the latter two are members of the *vernus* group of species. As such, *B. piscatoris* larvae have distinctly robust setae on the base of the antennae and scattered on the paraprocts and sternum (see Morihara and McCafferty 1979: figs. 3, 11) (although sometimes relatively sparse as is the case with *B. piscatoris*). Such setae are not found in the *vernus* group species, although smaller setae may rarely occur scattered on the base of the antennae. A more convenient characteristic to use may be the development of the medioapical corner (thumb area) of segment 2 of the labial palpi. In *B. piscatoris*, it is very poorly developed (similar to Morihara and McCafferty 1979: fig. 24c, disregarding proportionality of segment sizes). In *B. bundyae*, we have recently found that the thumb area development ranges [as depicted in Morihara and McCafferty (1979)] from moderate development (fig. 22a) to considerable development (as in figs. 21b, 23b).

The male adult of *B. piscatoris* may be difficult to distinguish from *B. tricaudatus*, and is not possible with any consistency using the Day (1956) key. The typical size of *B. piscatoris* of ca. 6 mm. would be on the low end of the range for *B. tricaudatus*, and abdominal segments 2–6 of *B. piscatoris* appear to be more hyaline than what is typically a more pigmented area in *B. tricaudatus*.

Baetis sulfurosus Day, 1954

This species was described from adults taken in Sonoma and Napa Counties, California (Day 1954), and we have seen additional samples of adults of the species from several other counties in northern California (Meyer and McCafferty in prep.). Following the recombination of the poorly known western species *Baetis thermophilos* McDunnough to the genus *Acerpenna* by McCafferty (1999), the essentially similar species *B. sulfurosus* was transferred to that genus by Wiersema (2003). Both new combinations were based on the presence of a modified costal margin of the hindwings (see below). Historically, *A. sulfurosus* has not been well known because of limited collections of adults and the larvae remaining undiscovered. Recently, one of us (RPR) was able to rear material of the species from the type locality, yielding adult-larval associations. The results were surprising, based on previous assumptions about adult generic characterization.

The larvae of *A. sulfurosus* are morphologically similar to all North American *Fallceon* larvae, including the western and midwestern *F. quilleri* and the southwestern *F. sonora* (Allen and Murvosh), and are apparently separable from these latter species only by mature size and color pattern (see McCafferty 2007b, and see below). Such larvae are highly distinctive from other Baetidae genera, including *Baetis* and *Acerpenna*. Diagnostically, for example, North American *Fallceon* larvae have such features as the presence of an inter-antennal keel, labial palpi that lack development of the thumb area on segment 2, symmetrical gills 7, and tufts of setae on the mandibles between the prostheca and mola. Additional *Fallceon* characteristics can be found in Morihara and McCafferty (1979), Waltz and McCafferty (1987), and Lugo-Ortiz et al. (1994).

Based on larval characters, we can place Day's species in the genus *Fallceon*, as *F. sulfurosus* (Day), **n. comb.** A formal description of the newly discovered larvae will be provided by RPR elsewhere.

Examination of both recently sampled adults and original adult material used by Day showed that Day's depiction of the species was mostly but not entirely apropos. Characteristics can be viewed from the aspect of their generic applicability as follows: Day's drawing of the male genitalia is basically correct (Day 1954: fig. 7, Day 1956: fig. 27d), and it shows that the subgenital plate is not bilobed and therefore atypical of other North American *Fallceon* species (e.g., Kimmins 1934: fig. 15, Lugo-Ortiz et al. 1994: fig. 4). It is now clear that a bilobed process of the subgenital plate cannot be used as a characteristic of the genus *Fallceon*. With respect to genital forceps, Day (1954) stated that forceps segment 4 was one-half the length of the segment 3, but his drawing shows it to be a little over one-third the length. Our study of numerous genitalia of *sulfurosus* including fresh topotypical material and paratype material showed forceps segment 4 to vary between one-half and three-fourths the length of segment 3. Although a relatively long terminal forceps segment is typical of North American *Fallceon*, it has been established by its presence elsewhere (e.g., in *Acerpenna*) that such a segment is not a unique generic characteristic among Baetidae.

Day's figure of a hindwing of *F. sulfurosus* (Day 1954: fig. 8, Day 1956: fig. 27i) is correct regarding the development of the costal area and extension of the third vein from the base to beyond the midpoint of the wing. Day's species differs from some *Fallceon* adults (e.g., the common *F. quilleri*), in that the costal process of the hindwings is not hooked. McCafferty and Lugo-Ortiz (1994) con-

firmed that the hindwings of the western *F. eatoni* (Kimmins) also do not have a hooked costal process, and that this characteristic also varied among Cuban species of *Fallceon*. It is clear that a hooked costal process cannot be used as a distinguishing characteristic of the genus. The modified costal margin just distad of the costal process in the hindwings of *F. sulfurosus* can be described as including a short distal slope of the costal process and from there a costal margin that plateaus or expands out slightly but noticeably for a short distance from the distal base of the costal process, thus appearing to be unusually produced just beyond the costal process (Day 1954: fig. 8). See also Edmunds et al. (1976: figs. 248, 249) for the subtle differences in the post-costal process costal margin as seen in some baetid hindwings. The costal margin is not modified in other *Fallceon* alates, including the other western species also known as adults (e.g., Lugo-Ortiz et al. 1994: figs. 2, 3), nor is it in most other baetid adults with double marginal intercalaries in the forewings, excluding those *Acerpenna* and *Camelobaetidius* Demoulin that also have modified costal margins (see McCafferty 1999). Just as for the subgenital plate and costal process, the condition of the costal margin as found in the hindwings of *F. sulfurosus* is variable within *Fallceon*. Another slighter generic variability involves the third vein, which, for example, is extended well beyond the midpoint of the hindwings in both *F. sulfurosus* and *F. eatoni* (Day 1954: fig. 8, Lugo-Ortiz and McCafferty 1994: fig. 3) but varies somewhat in other *Fallceon*, such as sometimes being shorter in *F. quilleri* (Lugo-Ortiz et al. 1994: fig. 2).

Acerpenna thermophilos (as *Baetis*) was described from a male adult taken near Old Faithful in Yellowstone National Park (McDunnough 1926). The species has not been reported since then, except

for a record from the Eel River in California given by Traver (1935) and repeated by Day (1956). We have, however, seen a number of collections from northern California that were identified by various workers as this species, presumably by attempting to use the Day (1956) male adult California *Baetis* key (couplet 3 that tenuously separates *thermophilos* and *sulfurosus*). A comparison of *A. thermophilos* and *F. sulfurosus* shows that they are essentially the same in all respects. McCafferty (1999) and Wiersema (2003) placed these species in *Acerpenna* based on the modified costal margin of the hindwings, as discussed above. Because we find the exact same non-variable and variable generic characteristics in *B. thermophilos* that are found in *F. sulfurosus*, as discussed above, we also place McDunnough's species in the genus *Fallceon* as *F. thermophilos*, **n. comb.**

The supposed differences between *F. sulfurosus* and *F. thermophilos* given by Day (1954, 1956), i.e., 0.5 mm. body length difference, slight difference in the proximity of the third vein of the hindwings to the anal margin, and the differences in the proportional length of the terminal forceps segment, are nonexistent or inconsistent. For example, supposed wing shape and position of the third vein in the hindwings of the two are depicted by Day (1956) in his fig. 26i (*F. thermophilos*) and 27i (*F. sulfurosus*). Within a recently collected series of male adults taken swarming at the type locality of *F. sulfurosus* in California in 2007, there were individuals with hindwings that are similar to fig. 26i (*F. thermophilos*) and some that grade to similar to fig. 27i (*F. sulfurosus*). We have seen numerous slide mounts of hindwings and found that in materials taken together from the same locality the proximity of vein 3 to the hind margin appears variable based on the degree to which the hind margin of the wings tends

to fold over when the slide cover is placed on the wing. The hind margin rolling up can also be a problem in non slide-mounted hindwings. Also, Day (1954) claimed that segment 4 of the forceps of *F. sulfurosus* was proportionately half that of *F. thermophilos*. Traver (1935) had indicated that segment 4 of *F. thermophilos* was almost as long as segment 3 (but gave no exact dimensions), so Day could have known only that the *F. thermophilos* segment 4 was proportionately longer. Although we have been unable to access the single type specimen of *F. thermophilos* from the Canadian National Collection, or information about it, our finding of a range of segment 4 being one-half to three-fourths the length of segment 3 in type and topotypical material of *F. sulfurosus* suggests that the Wyoming type of *F. thermophilos* falls within that proportional range, thereby nullifying the supposed difference. Also because the line of demarcation between forceps segment 2 and 3 can be very difficult to determine and often not apparent even in slide-mounted genitalia of *Fallceon*, any measured proportions between segments 4 and 3 would in such cases essentially be only estimates. Notably, we have seen male adults identified as *B. thermophilos* by Day, that were collected by him together with paratype material of *B. sulfurosus* from Capell Creek, Napa County. The hindwings are slightly different in shape due to slide-mounting, but the genitalia are similar, with segment 4 of the forceps about one-half that of segment 3. Based on all of the above, we must consider *F. sulfurosus* a subjective junior synonym of *F. thermophilos*,
n. syn.

Fallceon thermophilos is relatively common in northern California, and it is possible that larvae have previously been identified as *F. quilleri* because of morphological similarities, with no regard to the mature larval size or color

pattern. We also predict that reexamination of *F. quilleri* larvae from Oregon, Idaho, Montana and Wyoming will show that some of those collections are also of *F. thermophilos*. *Fallceon quilleri* is the only species of *Fallceon* that keys out in the North American key of Morihara and McCafferty (1979) and the key to larvae provided by Lugo-Ortiz et al. (1994), and characteristics that would distinguish the various North American species of *Fallceon* in the larval stage could not have been taken into account at the time the keys were written, and thus historically all North American *Fallceon* larvae would by default key to *F. quilleri*. *Fallceon quilleri* larvae are typically ca. 5.0 to 6.0 mm. in length at maturity, and the dorsal abdominal color pattern includes light terga 8–10, and darker anterior terga with a broken light medial and submedial anterior margin and light anterolateral corners (Morihara and McCafferty 1979: fig. 37e). *Fallceon thermophilos* larvae are typically 4.0 to 4.5 mm. in length at maturity. In addition, the dorsal abdominal color pattern includes light terga 9–10; dark terga 3–8 with a trilobular, light trans-anterior border that becomes progressively more developed in anterior segments; light lateral pleural folds on all segments; a distinctive, prominent, light, medial spot in the posterior half of tergum 4 that appears to extend over into tergum 5; a light tergum 2; and tergum 1 with a prominent, light, medial spot. *Fallceon sonora* is the only other species known in the larval stage in the U.S.A., where it was reported from southern New Mexico by McCafferty (2007) and is reported herein from southern California, (see Material Examined below). Larvae of *F. sonora* are typically 3.0–3.5 mm. in length at maturity, and the dorsal abdominal color pattern typically includes alternating light and dark terga as follows: light terga 8–10, dark terga 6–7, light terga 4–

5, and dark terga 2–3, and light tergum 1 (Allen and Murvosh 1987: fig. 5).

Adults of *F. thermophilos*, *F. quilleri*, and *F. eatoni* (only known in the adult stage) are readily identifiable by differences in the hindwings as discussed in detail above (*F. thermophilos* with a small non-hooked costal process and modified costal margin, *F. quilleri* with a hooked costal process and unmodified costal margin, *F. eatoni* with a prominent non-hooked costal process and unmodified costal margin). In addition, *F. thermophilos* does not have the bilobed subgenital plate process as does *F. quilleri* and *F. eatoni*. We maintain that there is a strong possibility that the southwestern *F. sonora* and *F. eatoni* will prove to be the same species when their respective unknown stages become known. Between the two, they range from northern Mexico (*F. eatoni* and *F. sonora*), southern California (*F. sonora*) (see below), Arizona (*F. eatoni*) (McCafferty 2006), and New Mexico (*F. sonora*) (McCafferty 2007b).

MATERIAL EXAMINED

The material is arranged by species names as material had been originally identified in collections, but with current name indicated also. Abbreviations in parentheses are A = male adult, and L = larvae. Abbreviations in brackets are BM = The Natural History Museum, London; CAS = California Academy of Sciences; CNC = Canadian National Collection, Ottawa; CSU = Gillette Museum, Colorado State University, Fort Collins; EAI = EcoAnalysts, Inc., Moscow, Idaho; EPA = U.S. Environmental Protection Agency, Corvallis, Oregon; JMW = private collection of J. M. Webb; PERC = Purdue Entomological Research Collection; RPR = private collection of R. P. Randolph; USK = University of Saskatchewan, Saskatoon.

Baetis adonis: (A, L reared), CA, Santa Barbara Co, Mission Cr, VI, VII-

1997, E. Silldorff [PERC]. *Baetis alius*: (Paratype A), CA, Sonoma Co, Russian R, Geyserville, 15-X-1949, W. Day [PERC]; (A,L), CA, Sonoma Co, Russian R, Geyserville, 12-XI-1949, W. Day [CAS, PERC]; (L), CA, Sonoma Co, Russian R, at bridge on Hwy 128, Geyserville, 26,29-IV-2007, R. P. Randolph [RPR]; (L), CA, Mariposa Co, Merced R at 3 Brothers, Yosemite National Park, 2004, M. Meyer; (L), CO, Gunnison Co, Texas Cr, above Taylor Reservoir, 27-VIII-1973, G. & C. Edmunds [PERC]; (L), ID, Idaho Co, Papoose Cr, 6-VIII-1996, R. Weldert [EAI]; (L), ID, Owyhee Co, Jordan Cr, 28-VIII-1998, S. Lindstrom [EAI]; (L) ID, Bannock Co, Caribou Co, Clark Co, Clearwater Co, Custer Co, Lemhi Co: see Lester et al. (2002); (L), OR, Coos Co, Upper Rock Cr, 2-VIII-2000 [EPA]; (L), OR, Grant Co, Clear Cr, 20-VII-2000, and Sponge Cr, 1-VIII-2000 [EPA]; OR, Jackson Co, Rogue R, Hwy 230, 24-VIII-1954, G. Edmunds [PERC]; OR, Klamath Co, Little Deschutes R, Crescent, 23-VIII-1954, G. Edmunds [PERC]; (L), UT, Garfield Co, Pine Cr, N Blue Spruce Camp, Dixie Natl For, 11-X-2001, P. & N. McCafferty [PERC]; (L), WA, Chelan Co, Peshastin Cr, 18-VII-2002, and Scotty Cr, 22-VII-2003 [EPA]. *Baetis bundyae*: (L), WY, Carbon Co, near Sand Lake, Medicine Bow National Forest, elevation 3017 m, 11-VII-1996, R. Rader [CSU]; (Paratype L) (L), NWT, Keewatin, Rankin Inlet, 28-VII-1972, D. Lehmkuhl (USK); (L reared), SK, stream at km 75 on Hwy 955, 30-VI-2000, J. Webb [JMW]. *Baetis devinctus* (= *Dipheter hageni*): (A, L reared), CA, Marin Co, Lagunitas Cr, 0.5 mi W Jewell, 26-VIII-1982, L. Serpa (PERC). *Baetis diablus*: Paratypes (A), CA, Contra Costa Co, Mt. Diablo, 12-IV-1952, E. Schlinger (CNC, PERC); (A), CA, Mono Co, Convict Cr, 27-II-1963, H. Kennedy [PERC]. *Baetis eatoni* (= *Fallceon eatoni*): (A paratype), Mex-

ico, N. Sonora, Morrison [BM]; *Baetis hudsonicus*: (L), MB, Churchill, 22-VII-1936, H. McLure [PERC]. *Baetis leechi* (= *Fallceon quilleri*): (Paratype A), CA, Napa Co, Conn Cr, 24-IX-1949, W. Day [CAS, CNC, PERC]. *Baetis moqui* (= *B. alius*): (L), UT, Garfield Co, Pine Cr, Box Death Hollow tributary, Pine Creek Rd, 28-VI-2001, K Kuehnl (PERC). *Baetis palisadi*: (A, L reared), CA, Sonoma Co, Little Sulphur Cr, as Pine Flat Rd, 20-III-1982, L. Serpa [PERC]. *Baetis piscatoris*: (A, L reared), CA, Sonoma Co, Copeland Cr, Fairfield Osborn Preserve, 24-VI-1980, L. Serpa (PERC). *Baetis sulfurosus* (= *Fallceon thermophilos*): (Paratype A) (A), CA, Sonoma Co, Sulphur Cr, 25-VIII-1951, W. Day [CAS, PERC]; (A), CA, Lake Co, Eel R, 10-IX-1946, H. Chandler (CAS); (A), CA, Siskiyou Co, Scott R, 3 mi N Kelsey Cr, VIII-1949, W. Day [PERC]; (A), CA, Napa Co, Capell Cr, 20-V-1950, W. Day [CAS, PERC]. *Baetis thermophilos* (= *Fallceon thermophilos*): (A), CA, Napa Co, Capell Cr, 20-V-1950, W. Day [CAS, PERC]; (A), CA, Siskiyou Co, Scott R, X-1949, W. Day [PERC]; (A), CA, Humboldt Co, Grizzly Cr, Redwoods State Prk, 11-VIII-1953, Arnaud [CAS]; (A), CA, Mendocino Co, South Fork Eel R, Leggett, 21-VII-1958, Alexander [PERC]. *Baetis tricaudatus* (originally misidentified as *B. alius*): (L, A reared), CA, Marin Co, Lagunitas Cr, 0.5 mi W Jewell, 15-VII-1982, L. Serpa [PERC]; (L), CA, Sonoma Co, Russian R, Geyserville, 12-XI-1949, W. Day [CAS]. *Fallceon eatoni*: (A), AZ, Gila Co, Salt River Canyon, IV-18-2005, W. Reeves [PERC]. *Fallceon sonora*: (L), CA, San Bernardino Co, Mojave R, at bridge on National Trails Hwy, Victorville, 10-VIII-2005, P. Randolph [RPR]. *Fallceon quilleri*: (A, L reared), TX, Brazos Co, Narasota R, Hwy 6, 30-VII-1969, Bjork [PERC]. *Fallceon sulfurosus* (= *F. thermophilos*): (A, L reared), CA, Sonoma Co, Russian R, at bridge on

Hwy 128, Geyserville, 26-IV-2007, (L) 26-IV-2007, P. Randolph [RPR].

ACKNOWLEDGMENTS

We thank the following individuals for their contributions to this study: Marlys Cappaert, Corvallis, OR; Boris Kondratieff, Fort Collins, CO; Wojciech Pulawski and Bob Zuparko, San Francisco, CA; Larry Serpa, San Francisco, CA; Nick Wiersema, Austin, TX; and Bob Waltz, West Lafayette, IN.

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