J. New York Entomol. Soc. 111(4):174–193, 2003

REVISIONARY CONTRIBUTIONS TO NORTH AMERICAN *EPHEMERELLA* AND *SERRATELLA* (EPHEMEROPTERA: EPHEMERELLIDAE)

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Abstract.—The study of population variability and the reexamination of type material of certain Ephemerellidae species has revealed changes in status and new synonyms. *Ephemerella dorothea* Needham, 1908 [=*E. infrequens* McDunnough, 1924, *new synonym*, =*E. mollitia* Seemann, 1927, *new synonym*] is divided into two subspecies: *E. d. dorothea*, *new status*, and *E. d. infrequens, new status* [=*E. mollitia*, *new synonym*]. New synonyms were discovered for the following: *Ephemerella excrucians* Walsh, 1862 [=*E. inermis* Eaton, 1884, *new synonym*, =*E. argo* Burks, 1947, *new synonym*, =*E. crenula* Allen and Edmunds, 1965, *new synonym*, =*E. lacustris* Allen and Edmunds, 1965, *new synonym*, =*E. rossi* Allen and Edmunds, 1965, *new synonym*, =*E. rama* Allen, 1968, *new synonym*], *E. invaria* Walker, 1853 [=*E. rotunda* Morgan, 1911, *new synonym*, =*E. vernalis* Banks, 1914, *new synonym*, =*E. feminina* Needham, 1924, *new synonym*, =*E. fratercula* McDunnough, 1925, *new synonym*, =*E. inconstans* Traver, 1932, *new synonym*, =*E. choctawhatchee* Berner, 1946, *new synonym*, =*E. simila* Allen and Edmunds, 1965, *new synonym*, =*E. floripara* McCafferty, 1985, *new synonym*], *E. mucronata* (Bengtsson), 1909 [=*E. moffatae* Allen, 1977, *new synonym*], *Serratella micheneri* (Traver), 1934 [=*E. altana* Allen, 1968, *new synonym*], *S. serrata* (Morgan), 1911 [=*S. sordida* (McDunnough), 1925, *new synonym*, =*S. carolina* (Berner and Allen), 1961, *new synonym*, =*S. spiculosa* (Berner and Allen), 1961, *new synonym*], and *S. tibialis* (McDunnough), 1924 [=*S. sequoia* (Allen and Collins), 1968, *new synonym*]. The larval description of *E. altana* is based on *E. excrucians* larvae that were associated erroneously with an adult of *E. altana* (=*S. micheneri*, *new synonym*). Variability and new distribution data are documented for each species, and records based on misidentifications are corrected. New diagnostic characters are provided for certain species.

Our examination of many long series and the type material of certain *Ephemerella* Walsh and *Serratella* Edmunds species (Ephemeroptera: Ephemerellidae: Ephemerellinae) revealed newfound variability and geographic distribution data for several species that occur in North America. Allen and Edmunds (1965) and Berner and Pescador (1988) suggested possible new synonyms for certain ephemerellid species, but too few specimens were available for them to show sufficient variability. Our new data have enabled us to recognize new synonyms for seven species, provide new descriptive data, and emend historical distribution records. Furthermore, we discovered that certain larval exuviae were associated incorrectly with the male adult of *E. altana* Allen, which led to the inclusion of two species from different genera in the type series for that species. This study is a further contribution to our revision of the mayfly family Ephemerellidae (e.g., Jacobus and McCafferty, 2000, 2001a, 2002a, b, 2003a, b, 2004; Jacobus et al., 2002; McCafferty, 2001; McCafferty et al., 2003).

In the species accounts that follow, we list a synopsis of junior synonyms under each senior name. We provide diagnoses for mature larvae and male adults, and notes on variability in larvae and adults. In the Discussion section for each species, when appropriate, we emend distribution records and discuss problems associated with accurate identification. In the Material Examined section, we utilize the following abbreviations for specimens: L = larva, S = subimago, A = adult, E = exuviae, M = male, F = female. A total listing of materials

examined exceeds space constraints; therefore we list only representative materials. Some materials examined in this study were collected in conjunction with the All Taxa Biodiversity Inventory (ATBI) project underway in Great Smoky Mountains National Park (GSMNP) (Kaiser, 1999; Pedersen, 1999; Gibbs, 2002) or as part of the "Mayflies of the Great Plains" series (e.g., McCafferty et al., 2001). Material examined is deposited with the following individuals or institutions: BYU—Brigham Young University, Provo, Utah; CAS—California Academy of Sciences, San Francisco, California; CNC—Canadian National Collection of Insects, Ottawa, Ontario; CRP—Charles Parker, United States Geologic Survey, Gatlinburg, Tennessee; CUIC—Cornell University Insect Collection, Ithaca, New York; DRL—David Lenat, North Carolina Department of Environment, Health, and Natural Resources, Raleigh, North Carolina; FAMU—Florida A & M University, Tallahassee, Florida; FIEC—Freshwater Institute, Winnipeg, Manitoba; INHS—Illinois Natural History Survey, Champaign, Illinois; IRCW—Insect Research Collection, University of Wisconsin-Madison, Madison, Wisconsin; MCZ—Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts; PERC—Purdue University Entomological Research Collection, West Lafayette, Indiana; SEMC—Snow Entomological Museum, University of Kansas, Lawrence, Kansas; SWH—Stephen Hiner, Blacksburg, Virginia; UMMZ—University of Michigan Museum of Zoology, Ann Arbor, Michigan; VPIC—Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

SPECIES ACCOUNTS

Ephemerella dorothea Needham, 1908

Ephemerella infrequens McDunnough, 1924, **new synonym**
Ephemerella mollitia Seemann, 1927, **new synonym**

Diagnosis. *Mature larvae* may be distinguished from congeners by the following combination of characteristics. The posterior margins of larval abdominal terga usually are without any prominent tubercles; however, very slightly developed, rounded, protuberances may be present. The lateral margins of abdominal terga are not strongly serrate and have numerous small, stout setae present (contrast with notes on the valid species *E. catawba* Traver, under *E. excrucians* Walsh). The tarsal claws usually are more gradually incurved than those of other *Ephemerella* species, including *E. excrucians* (Johnson, 1978: fig. 2b).

Male adults may be distinguished from congeners based on the structure of the genitalia (McDunnough, 1924: fig. 6; Allen and Edmunds, 1965: fig. 15; Allen, 1968: figs. 6, 9; Johnson, 1978: fig. 1a). The apicolateral margins of the penes lobes are relatively straight and parallel, and there are stout, dorsal and ventral spines present on these lobes. Forceps segment two has a distinct apical expansion (see Johnson, 1978). Male adults of *E. dorothea* are distinguished from those of *E. excrucians* by the shape of the penes.

Larval variability. Some larvae may have very weakly developed, paired, rounded, protuberances on the hind margin of some abdominal terga; however, many individuals lack any such protuberances (Johnson, 1978). Body coloration is variable, and some larvae have a thin, pale, mediodorsal stripe. The length of subapical setae on the forefemur varies within populations of *E. dorothea* (see *E. excrucians* Larval variability section).

Adult variability. The number of dorsal and ventral stout spines on the penes varies. There may be 3–20 total ventral stout penes spines, occurring apically and in two irregular medial rows (Traver, 1935; Allen and Edmunds, 1965). Body color is variable, ranging from pale

to brown. Body size is variable and is not reliable in differentiating *E. dorothea* and *E. excrucians*, as has been suggested in the past (e.g., McDunnough, 1928).

Discussion. Our simultaneous examination of reared material from eastern and western North America revealed that *E. dorothea* was conspecific with the western species *E. infrequens* McDunnough and *E. mollitia* Seemann. However, adult specimens from eastern and western populations showed consistent coloration differences. Given the geographically consistent color difference, we propose two subspecies for *E. dorothea*: *E. d. dorothea* Needham, **new status**, and *E. d. infrequens* McDunnough, **new status**. We treat and diagnose each subspecies separately, below.

Larvae of *E. excrucians* and *E. dorothea* are difficult to distinguish from one another. *Ephemerella dorothea* larvae are very similar to *E. excrucians* larvae that have only slightly developed or no abdominal protuberances. The only putative difference separating the two species as larvae is the relative shape of the tarsal claws. The claws of *E. excrucians* usually are bent more at the apex than those of *E. dorothea*. This character should be used with caution, however, when identifying material. Although *E. dorothea* larvae have been reported from widespread locales (e.g., Randolph and McCafferty, 1998), adults have been reported only from states and provinces with Appalachian topography (Needham, 1908; Traver, 1935; Wright and Berner, 1949; Sweeney and Vannote, 1982; McDunnough 1931b; Burian and Gibbs, 1991; Randolph and McCafferty, 1998). Therefore, many reports of *E. dorothea* larvae may represent *E. excrucians* (see below). These observations underscore the need for rearing certain *Ephemerella* species for proper identification of larvae.

Based on the reared and adult material we have examined, we consider *E. dorothea* to be restricted in geographic distribution to hilly or mountainous regions of North America with streams of considerable gradient and relatively high water quality, with *E. d. dorothea* occurring in the East and *E. d. infrequens* in the West.

Ephemerella dorothea dorothea Needham, 1908, new status

Diagnosis. *Ephemerella d. dorothea* is distinguished from *E. d. infrequens* by adult caudal filaments that are pale with tan shading and which have no dark rings at the apex of each segment.

Material examined. CANADA, **Quebec**: Covey Hill, 15-VI-1927, GS Walley, 3MA, 1FA, 3MS, 2FS [CNC]. USA, **New York**: Herkimer Co, Old Forge, VII-1905, 1MA (*E. dorothea* holotype fragments, allotype and SE parts on slide) [CUIC]; **Massachusetts**: Hampshire Co, North Amherst, 13-VI-1939, JR Traver, 1MA [PERC]; South Hadley W of Notch, 27-V-1952, 1MA, 1FA, 2LE [PERC]; **Pennsylvania**: Chester Co, Doe Run Cr, 1 mi W Upland, 15-VI-1967, JW Richardson, 2MA, 2FA [PERC]; Main Br of E Br White Clay Cr at Rt 926, Stroud Estate, 8-VI-1967, JWR, 4MA; 5-VI-1968, 20MA, 15FA [PERC]; **Virginia**: Carroll Co, New R at Rt606, 20-IV-1980, emerged 12-V, Kondratieff, 3MA, 1E, 1L [VPIC]; Grayson Co, Lewis Fork, Rt 603, 5-IV-1982, emerged 29-IV-1982, Kondratieff, 5MA, 1FA, 1SE, 5LE [VPIC]; Nelson Co, Hargove Cr at Rt 651 off Rt 718, 3-V-1980, Kondratieff, 33MA, 32FA, 3MS, 4SE, 10LE, 8L [VPIC].

Ephemerella dorothea infrequens McDunnough, 1924, new status

Diagnosis. *Ephemerella d. infrequens* is distinguishable at the subspecies level by adult caudal filaments that are white with dark brown rings at the apex of each segment.

Discussion. We could not locate type material for *E. mollitia*. Therefore, our analyses of *E. mollitia* are based on the original description and illustrations (Seemann, 1927), Traver's (1935) redescription of the type material, and reared additional material from California that corresponds to the original concept of the species. Figures of *E. mollitia* penes by Allen and Edmunds (1965: fig. 12) and Allen (1968: fig. 11) appear somewhat distorted when compared to material we examined. Refer instead to figures cited in the *E. dorothea* Diagnoses section.

Traver's (1935) record of *E. mollitia* from San Juan County, New Mexico is referable to *E. excrucians* (see *E. excrucians* material examined).

Material examined. CANADA, **Alberta**: Waterton Lakes, 14-VII-1923, J McDunnough, 1MA (*E. infrequens* holotype, genitalia on slide) [CNC]. USA, **California**: Amador Co, Ione Rd, 9 mi W Jackson, 1-IV-1950, WC Day, 4MA, 2FA, 6LE [CAS]; Sutter Cr, 1-IV-1950, WC Day, 2FA, 1SE, 2LE [CAS]; Inyo Co, N Fk Oak Cr, 25-VI-1963, CP Alexander, 1MA (parts on slide) [PERC]; Lake Co, St Helena Cr, 12-IV-1952, WC Day, 5MA, 1MS, 1FS, 1SE, 3LE, 10L [CAS]; Napa Co, Sage Cr, 9-IV-1950, WC Day, 3MA, 1FA, 4LE [CAS]; Santa Clara Co, Smith Cr, Mt Hamilton, 7-IV-1951, WC Day, 7MA, 2FA, 2LE, 1L [CAS]; **Colorado**: Moffat Co, Yampa R at Steamboat Springs, 25-VI-1962, AW Knight, 3MA [PERC]; **Montana**: Lincoln Co, Bull Cr, nr Bull Lake, 5-VII-1964, 1MA [PERC]; Tobacco R, Hwy93 nr Eureka, 3-VII-1964, 2MA [PERC]; ?Ravalli Co, Mill Cr at Hwy93, 3,200′, 28-VI-1964, 1MA [PERC]; **Oregon**: Clatsop Co, Big Cr, 9-V-1947, SG Jewett Jr, 1MA [PERC]; Deschutes Co, Tumalo SP, 20-VI-1954, GF Edmunds Jr, 10MA [PERC]; Jefferson Co, Deschutes R nr Warm Springs, 29-V-1986, blacklight, SJ Peratt, 1MA, 2FA [PERC]; **Utah**: Utah Co, Provo R at US89-91, 29-VI-1947, G Edmunds, 1MA [PERC]; **Wyoming**: Fremont Co, Bull Lake Cr, nr Bull Lake at Hwy26, 20-VII-1967, RW Baumann, 2MA, 2FA, 3MS, 1FS [PERC]; Sublette Co, Green R, 15 mi N Pinedale, Hwy189, 18-VII-1967, RW Baumann, 1MA [PERC]; Teton Co, river running out of Jenny L, 19-VII-1967, RW Baumann, 1MA [PERC].

Ephemerella excrucians Walsh, 1862

Note: syn. with *E. invaria* (Walker) by Eaton, 1868, but later recognized as valid; e.g., by Eaton, 1884.

Ephemerella inermis Eaton, 1884, **new synonym**
Ephemerella semiflava McDunnough, 1926 (Burks, 1953)
Ephemerella argo Burks, 1947, **new synonym**
Ephemerella ora Burks, 1949 (McCafferty, 2001)
Ephemerella crenula Allen and Edmunds, 1965, **new synonym**
Ephemerella lacustris Allen and Edmunds, 1965, **new synonym**
Ephemerella rossi Allen and Edmunds, 1965, **new synonym**
Ephemerella rama Allen, 1968, **new synonym**

Diagnosis. *Mature larvae* may be distinguished from congeners by the following combination of characteristics. The posterior margins of larval abdominal terga usually are without any prominent tubercles; however, paired protuberances (e.g., Allen and Edmunds, 1965: figs. 37, 40; Allen, 1968: fig. 24) may be present on the hind margin of some abdominal terga. The lateral margins of abdominal terga are not strongly serrate and have numerous small, stout setae present. This is in contrast to *E. catawba* Traver, which has lateral margins that are serrate; there are fewer setae present; and those setae are stouter than such setae on *E. excrucians*. In contrast to *E. dorothea*, tarsal claws of *E. excrucians* larvae are relatively strongly incurved, and the incurved portion is often darker in color than the rest of the claw.

Male adults are distinguished from congeners by characters associated with the genitalia: a slight to indistinguishable apical expansion on genital forceps segment two, the shape of the penes (cf. e.g., McDunnough, 1925: fig. 1), and the presence of dorsal, and sometimes ventral, stout spines on the penes.

Larval variability. We found that *E. excrucians* larvae are variable in color and structure. The coloration of caudal filaments of individuals from single populations varied from striking, brown and white banding to solid in color. General body coloration varied from pale and speckled with brown to solid brown. Reared material from McCone County, Montana (see Material examined, below), included some larvae having the body color characterization of *E. lacustris* (Allen and Edmunds, 1965; Allen, 1968). Populations of *E. excrucians* larvae from Richmond County, North Carolina (see below) contained several body color morphs, including that characteristic of *E. argo* (Burks, 1953: fig. 173). Furthermore, the general color pattern that has been used to diagnose *E. argo* is associated with certain individuals of several other ephemerellid species, including *E. invaria* (see Traver 1935 and material examined from Elkhart County, Indiana and Ashe County, North Carolina), *E. mucronata* Bengtsson (see material examined from Germany), *Eurylophella temporalis* (McDunnough) (see material examined listed below), and *Serratella micheneri* (Traver) (see material examined from Lane County, Oregon).

Larvae we examined were variable with respect to the development of small tubercles or protuberances on the thorax and abdomen, and gradations were apparent within single populations. Abdominal protuberances were slight or completely absent, such as described for *E. argo*, *E. excrucians*, and *E. inermis* (Leonard, 1949; Burks, 1949, 1953; Allen and Edmunds, 1965; Jensen and Edmunds, 1966; Johnson, 1978) or small and produced on terga 3 or 4 to 8 or 9, such as described for the larvae of *E. altana* (Allen, 1968), *E. crenula*, and *E. rossi* (Allen and Edmunds, 1965). Allen and Edmunds (1965) noted variability in the development of abdominal tubercles in *E. crenula*, and they described a pair of variable tubercles on the prothorax of that species. We discovered that samples from single populations contained individuals with or without these small prothoracic tubercles. Also, the presence and relative development of posterolateral projections on abdominal segment 3 varied within samples from single populations, including the type series of *E. lacustris*.

Johnson (1978) used the density and length of subapical setae on the forefemur to differentiate *E. inermis* from *E. infrequens*. We found that the length and density of these setae vary within populations of *E. excrucians* (see e.g., material examined from Cheyenne County, Kansas; Brown County, Nebraska; and Transylvania County, North Carolina). The number of denticles on the tarsal claws varied within and among populations. Specimens collected from near the eastern Tennessee type locale of *E. rossi* usually have 3–5 such denticles. However, specimens sampled from populations in southern North Carolina had 7 denticles on each of the tarsal claws.

Adult variability. The relative apical expansion of genital forceps segment 2 varies within single populations. In some individuals it is absent, such as described for *E. rossi* (Jacobus and McCafferty, 2001a: fig. 2), and in other individuals it is slightly developed. Allen and Edmunds (1965) noted this variability in populations of *E. inermis*. The number and placement of stout spines on the penes of some *E. inermis* individuals (Allen and Edmunds, 1965) is the same as the number of such spines on *E. excrucians* (McDunnough, 1925; Burks, 1949, 1953; Allen and Edmunds, 1965), *E. rossi* (Jacobus and McCafferty, 2001a), and *E. argo* (Burks, 1949; Allen and Edmunds, 1965). Body color varied from light tan to dark

brown. The coloration of the caudal filaments varies from brown, to white with brown rings at the apex of each segment.

The genitalia of *E. excrucians* individuals may differ slightly in appearance, due to artifacts of fixation, preservation, and slide-mounting. For example, close examination with a light microscope of one set of unmounted penes revealed that the ejaculatory ducts had opened, and internal apicomedial flaps, which usually lie superjacent to the penes lobes, were visible and distinctive (see material examined from Pierce County, Wisconsin). These penes demonstrated the "median chitinized ramus" on each penes lobe that was described for *E. rama* by Allen (1968).

Discussion. The greater length of the male adult foreleg had been the primary morphological character that distinguished the lake dwelling *E. lacustris* from other variants of *E. excrucians*. Our measurements of the male adult holotype of *E. lacustris* revealed that the total length of the foreleg is 1.3 mm less than indicated by Allen and Edmunds (1965) and Allen (1968). The respective lengths of the forefemur and foretibia were 1.9 mm and 2.2 mm. All other foreleg segment lengths were as given by Allen and Edmunds (1965). The occurrence of *E. excrucians* in Yellowstone Lake (the type locale of *E. lacustris*) is not that unusual, considering that certain other primarily rheophilic Ephemerellidae also have been collected from waveswept lakeshores (Ueno, 1928; Macan, 1979). For example, the common and widespread Palearctic species *Serratella ignita* (Poda) was seasonally abundant in the shoreline waters of Lochs Awe, Lomond, and Morar, in Scotland. *Serratella ignita* presumably has a late summer emergence from these locales (Smith et al., 1981), similar to that reported for *E. lacustris*.

Our examination of larvae reported from Kentucky (Randolph and McCafferty, 1998) and Virginia (Kondratieff and Voshell, 1983) as *E. catawba* revealed that they are actually *E. excrucians*. Furthermore, we believe material reported from Wisconsin as *E. catawba* by Shapas and Hilsenhoff (1976) is also *E. excrucians* because all Wisconsin *E. catawba* material that we examined from IRCW proved to be misidentified *E. excrucians*. *Ephemerella excrucians* was reported previously from Wisconsin as *E. inermis* (Hilsenhoff, 1987; Randolph and McCafferty, 1998). The feeding habits reported by Shapas and Hilsenhoff (1976) for *E. catawba* coincide with those reported for *E. inermis* (Hawkins, 1985). At the present, we consider *E. catawba* to be restricted in distribution to the Central Highlands of the United States (sensu Ceas and Page 1996) (see Traver, 1932, 1937; Brimley, 1938; Wright and Berner, 1949; Allen and Edmunds, 1965; Carlson, 1973; Berner, 1977; Faulkner and Tarter, 1977; McCafferty and Provonsha, 1978; Kondratieff and Voshell, 1983; Daniels and Morse, 1992; Feldman and Connor, 1992; Randolph and McCafferty, 1998).

Larvae of *E. excrucians* and *E. dorothea* sometimes inhabit the same streams in western North America (Johnson, 1978). We found that the two co-occur also in eastern North America (for example Lewis Fork, Grayson County, Virginia). Johnson (1978) suggested that *E. excrucians* and *E. dorothea* larvae (as *E. inermis* and *E. infrequens*, respectively) have different habitat requirements. For example, *E. excrucians* has been collected from sand and gravel substrate in Michigan (Leonard, 1949), and larvae that we reared to the adult stage from McCone County, Montana (see Material examined, below) were collected from a relatively low gradient, moderate current area of the Missouri River that had considerable algal growth. *Ephemerella d. infrequens* larvae, however, are restricted to cool, swift streams with rock and cobble substrates (Seemann, 1927; Johnson, 1978). The larval habitat of the eastern subspecies *E. d. dorothea* appears to be relatively similar. Kondratieff and Kirchner (1982) provided detailed description of the habitat of one such stream, Lewis Fork, a high gradient and high quality headwater tributary of the New River that drains part of Mt. Rogers, the highest peak in

Virginia. In light of these potential differences, material reported as *E. dorothea* from warm, low gradient streams in regions such as the USA deep South and midwest (e.g., Louton, 1975; Berner and Pescador, 1988; Randolph and McCafferty, 1998) should be re-examined with the possibility that they are instead the more tolerant *E. excrucians*. Notably, adults resembling *E. excrucians* were reared from larvae reported as *E. dorothea* from east Texas (Wiersema, 1998) and Michigan (Leonard and Leonard, 1962: fig. 76).

Needham (1901, 1905) incorrectly provided descriptions and illustrations of other species under the name *E. excrucians* (McDunnough, 1931a, b). Published reports of *E. excrucians* from New York listed by Jacobus and McCafferty (2001b) were based on these misidentifications.

Material examined. *Ephemerella catawba*: USA, **North Carolina**: Cascades, Danbury, 3-V-1930, JR Traver, 1L (paratype, parts on slide) [CUIC]; Catawba R, JR Traver, 21-VI-1929, 1LE (from *E. catawba* holotype, on slide), 1MA (*E. catawba* paratype, parts on slide) [CUIC]; Swain Co, GSMNP, ATBI sampling sites, 33L [PERC]. **Tennessee**: Blount/Cocke/Sevier Cos, GSMNP, ATBI sampling sites, 64L [PERC]; Sevier Co, GSMNP, Bunches Cr, 14-VII-1999, B Nichols, L Curry, emerged 17/25-VII, J Cooper, 3MA, 3SE, 3LE (one set genitalia on slide) [PERC].

Ephemerella excrucians: CANADA, **Ontario**: Horning's Mills, "B. Cr," 8PM, 19/21-VI-1928, FP Ide, 2MA [CUIC]; Horning's Mills, "F. & B. Cr," 27-VI-1928, FP Ide, 2MA (genitalia on slide) [CUIC]. USA, **Arizona**: Apache Co, E Fk Little Colorado R at East Fork Camp, Apache NF, 3-VII-1964, R K Allen (*E. altana* paratypes) [CAS]; Diamond Cr on Hwy73, Ft Apache Indian Res, 6-VII-1964, R K Allen, 3L (*E. altana* paratypes) [CAS]; Paradise Cr on Hwy73, Ft Apache Indian Res, 6-VII-1964, R K Allen, 2L (*E. altana* paratypes) [CAS]; E Fk White R at E Fk Campground, 5840 ft elev, 26-VI-1966, R K Allen, 7L [CAS]; E Fk White R at Rock Creek Ranger Sta, Ft Apache Indian Res, 5/6-VII-1964, R K Allen, 24L, 1LE (*E. altana* paratopotypes) [CAS]; E Fk White R, 3 mi N Rock Creek Ranger Sta, Ft Apache Indian Res, 6-VII-1964, R K Allen, 16L (*E. altana* paratypes) [CAS]; N Fk White R nr Hawley Lake Rd, 6150 ft elev, 27-VI-1966, 3L [CAS]; stream at Greer, 8500 ft elev, 27-IV-1966, R K Allen, 4L [CAS]; Navajo Co, N Fk White R at White River, Ft Apache Indian Res, 5-VII-1964, 1L (*E. altana* paratype) [CAS]; **Colorado**: Arkansas Canyon, PR Uhler, "99," (*E. inermis* lectotype), MCZ Type 33521, 1MA (genitalia in glycerin, secured on pin) [MCZ]; same data, "2," 1FA [MCZ]; same data, "103," 1FA [MCZ]; no locale data, P. R Uhler, "100," 1MS [MCZ]; Denver Co, Denver, 27-VI, "125," 1MS [MCZ]; El Paso Co, W Monument Cr in Air Force Acad, 14/16-VI-2000, 4L [PERC]; **Illinois**: Rock Island Co, Rock Island, "691," Walsh, (*E. excrucians* lectotype), MCZ type 11213, 1MA (genitalia on slide) [MCZ]; same data, "692," (*E. excrucians* paralectotype), 1FA [MCZ]; Wabash Co, Wabash R at Mt Carmel, 2-IV-1932, Frison & Ross, 2L (three legs on slide) [INHS]; **Indiana**: Pike Co, White R at Rogers, 16-IV-1936, emerged 7-V, Ross & Mohr, (*E. argo* holotype), 1MA (genitalia on slide) [INHS]; same collection data, 2L [INHS]; same locale, but 4-IV-1940, Mohr & Burks, 1L [INHS]; same data, but IV-1940, 2L (parts on slide); **Kansas**: Cheyenne Co, South Fork Republican R, 11 mi W, 7 mi S StFrancis, 5-VI-1979, D Huggins, PM Liechti, 157L [SEMC]; **Michigan**: Houghton Co, North Branch Otter R, T52N, R35W, S25, 22-VI-1949, JW & FA Leonard, 11A [UMMZ]; Otter R, T52N, R35W, S25, 22-VI-1949, JW & FA Leonard, 1FA, 1E [UMMZ]; Lake Co, Pere Marquette R, T17N, R13W, Sec 16, 1MA, 1E [UMMZ]; T17N, R13W, S16, 7MA (one set genitalia in vial), 13FA, 7SE [UMMZ]; **Montana**: Fergus Co, E Fk Big Spring Cr at Heath, 46°59′56″N, 109°16′27″W, 11-VI-2000, WP McCafferty et al., 5MA, 2FA, 6MS, 2FS, 6SE (parts on slide) [PERC]; Glacier

Co, Glacier NP, Many Glacier Campground, 12-VII-1940, HH & JA Ross, 1MA (genitalia on slide) [INHS]; Judith Basin Co, Running Wolf Cr, 12 mi SE Stanford, 47°08′39″N, 110°15′45″W, 12-VI-2000, WP McCafferty et al., 16L [PERC]; McCone Co, Missouri R at Lewis & Clark RA, 8 mi SE Wolf Point at SR13, 48°4′2″N, 105°32′18″W (WGS84), 27-VII-2002, WP McCafferty, LM Jacobus, 1MA, 2FA, 1MS, 1FS, 3SE, 4LE, 4L [PERC]; Sweet Grass Co, Sweet Grass Cr, SW Porcupine Butte, 46°09′53″N, 110°06′46″W, 10-VI-2000, W P. McCafferty et al., 5L [PERC]; **Nebraska**: Brown Co, Long Pine Cr at Long Pine SRA, 42°23′27″N, 99°42′35″W, 6-VI-2000, W P. McCafferty et al., 174L [PERC]; **Nevada**: Washoe Co, Reno, 4-VI-1959, FD Parker, Type 10033, 1MA (*E. rama* holotype; genitalia missing) [CAS]; **New Mexico**: Colfax Co, Cimarron R at Cimarron, 6800 ft elev, 23-VIII-1970, R K. Allen, 3L [CAS]; Moreno Cr, 5 mi N Eagle Nest, 1-VII-1964, R K Allen, 5L (*E. altana* paratypes) [CAS]; Grant Co, W Fk Gila R at Rd 15, Gila NF, 6-V-1981, WP McCafferty, AV Provonsha, DW Bloodgood, 1MA [PERC]; Mora Co, Mora R at Mora, 1-VII-1964, R K Allen, 22L (*E. altana* paratypes) [CAS]; Rio Arriba Co, Rio Chama at Chama, 7950 ft elev, 29-VI-1964, RK Allen [CAS]; San Juan Co, Farmington, L [CUIC]; San Miguel Co, Pecos R at Pecos, 2-VII-1964, RK Allen, 60L (*E. altana* paratypes) [CAS]; Pecos R 1 mi N of Pecos, just below Lisboa Springs Fish Hatchery, 13-VII-1969, RW Koss, WP McCafferty, AV Provonsha, 6L [PERC]; Taos Co, Rio Chiquito, 3 mi S of Taos on Hwy3, 1-VII-1964, RK Allen, 61L [CAS]; Rio Grande at jct Rio Hondo on Hwy111, 30-VI-1964, RK Allen, 3L (*E. altana* paratypes) [CAS]; Rio Hondo on Hwy3, 30-VI-1964, RK Allen, 6L (*E. altana* paratypes) [CAS]; Rio Hondo at jct with Rio Grande on Hwy111, 30-VI-1964, RK Allen, 3L (*E. altana* paratypes) [CAS]; Rio Pueblo, 1 mi S of Penasco, Carson NF, 1-VII-1964, RK Allen, 10L (*E. altana* paratypes) [CAS]; **North Carolina**: Clay/Macon Cos, Black Gap, 24-IV-1938, HH Ross & BD Burks, (*E. crenula* paratypes), 4L [INHS]; Haywood Co, Hazelwood, 24-IV-1938, HH Ross & BD Burks, (*E. crenula* paratypes), 19L (legs on slides) [INHS]; Richmond Co, Naked Cr, SR1003, IV-1990, Lenat & Eaton, 24L [DRL]; Swain Co, Smokemont, 11-V-1944, TH Frison & HH Ross, (*E. crenula* paratypes), 6L (legs on slides) [INHS]; Transylvania Co, trib Toxaway R at Rt 1301, 35°9′26″N 82°59′28″W (WGS84), 15-V-2001, CD & RP Randolph, LM Jacobus, 76L [PERC]; **Oklahoma**: McCurtain Co, Hochatown, Mountain Fork R, 6-V-1939, Mrs R Weddle, "06702," 4MA (one set genitalia on slide), 1FA [INHS]; **Tennessee**: "Smoky Mountain," 11-VI-1931, JG Needham, (*E. rossi* paratypes), 13L [PERC]; Blount/Cocke/Sevier Cos., 18 ATBI sampling sites in GSMNP, 16/19-V-2001, CD & RP Randolph, LM Jacobus, 230L [PERC]; Sevier Co, Fighting Creek Gap, Gatlinburg, 15-V-1939, TH Frison, HH Ross, (*E. rossi* holotype), 1L [INHS]; Gatlinburg, 19-VI-1940, TH Frison et al., (*E. crenula* paratypes), 3L [INHS]; Mt LeConte, 14-VIII-1929, JR Traver, (*E. rossi* paratypes), 2L [PERC]; LeConte Cr at Gatlinburg, 14-V-1939, TH Frison & HH Ross, (*E. crenula* paratypes), 7L [INHS]; LeConte Cr at Twin Creeks, ca. 35°41′N 83°30′W (NAD27), LCLC01, 9/11-VI-1999, 2MA, 1FA, E, 1L [CRP]; Little R at Elkmont, 14-V-1939, TH Frison & HH Ross, (*E. crenula* holotype), 1L [INHS]; same collection data, (*E. crenula* paratypes), 2L [INHS]; **Utah**: Garfield Co, Sevier R at Hatch, 4-V-1947, DR Merkley, 12L [PERC]; **Virginia**: Grayson Co, headwaters of Lewis Fork, Rt 603, Lewis Fork Trail, 31-V-1982, Kondratieff, 6MA, 2FA, 1SE, 4LE, 3L [VPIC]; Page Co, Pass Run, 9-V-1976, GA Rubis, 2L [VPIC]; **Washington**: Spokane Co, Little Spokane R at Chattaroy, 23-VI-1940, HH & JA Ross, 1MA (genitalia on slide) [INHS]; **Wisconsin**: Dunn Co, Vance Cr, 27-IV-1983, 2L [IRCW]; Marquette Co, Chaffee Cr, 28-VI-1968, 40L [IRCW]; Pierce Co, Kinnickinnic R,WDNR water body #2601800, Lower Kinnickinnic Subwatershed (LK), T.27N, R19W, Sec. 18, NW, WDNR Fish Habitat 2, 21-VI-2000, Clarke Garry, 6MA

[PERC]; **Wyoming**: Sublette Co, Pine Cr at Pinedale, 17-VII-1967, RW Baumann, 3MA, 1FA [PERC]; Teton Co, Yellowstone Lake, West Thumb, Yellowstone NP, 17-VIII-1959, GF Edmunds and WL Peters, 1MA, 5L (*E. lacustris* holotype and paratypes) [PERC].

Eurylophella temporalis: USA, **North Carolina**: Richmond Co, Naked Cr, SR1003, IV-1990, Lenat & Eaton, 4L [DRL].

Ephemerella invaria (Walker) 1853

Ephemerella rotunda Morgan, 1911, **new synonym**
Ephemerella vernalis Banks, 1914, **new synonym** (syn. with *E. rotunda* by McDunnough 1931b; syn. refuted by Traver, 1935; syn. reinstated by Edmunds, 1959)
Ephemerella feminina Needham, 1924, **new synonym** (syn. with *E. rotunda* by McDunnough, 1926)
Ephemerella fratercula McDunnough, 1925, **new synonym**
Ephemerella inconstans Traver, 1932, **new synonym** (syn. with *E. vernalis* by Traver 1935; syn. refuted by McDunnough, 1938)
Ephemerella choctawhatchee Berner, 1946, **new synonym**
Ephemerella simila Allen and Edmunds, 1965, **new synonym**
Ephemerella floripara McCafferty, 1985, **new synonym**

Diagnosis. *Mature larvae* of *Ephemerella invaria* have paired, median projections on the posterior margins of abdominal terga 2 or 3 through 8 or 9 that are relatively small, flat, and somewhat spiculate. These projections are less developed than those found on *E. subvaria* McDunnough and *E. hispida* Allen and Edmunds, and they are most prominent on segments 4–7. They occasionally are difficult to ascertain.

Male adults have a distinct subapical expansion of genital forceps segment 2 and penes with dorsal, and sometimes ventral, stout spines (cf. e.g., Spieth, 1940: fig. 1). The subapical expansion of genital forceps segment 2 is more distinct than that of *E. excrucians*, but weaker than that of *E. subvaria*. Wings of adults have veins, crossveins, and intercalaries that are lighter in color than those of *E. subvaria*.

Larval variability. The dorsal abdominal tubercles of most specimens are relatively sharp, but some are less so, such as described for *E. simila* (Allen and Edmunds, 1965). The relative development of these tubercles varied among and within populations, especially on the most posterior or anterior segments, including the characterization of tubercles typical for *E. rotunda*. In a few populations, however, abdominal tubercles were very difficult to discern on mature individuals, and abdominal tubercles often were not apparent on immature larvae. The relative development of posterolateral projections on abdominal segment 3, such as described for *E. inconstans* (e.g., Allen and Edmunds, 1965), varied among individuals from single populations, being absent in many. McCafferty et al. (1997a), for example, noted difficulty in differentiating *E. inconstans* from *E. rotunda*. Occipital bumps were present on the head of most individuals examined; however, the relative development of these bumps varied. Paired bumps on the prothorax, such as described for *E. simila* (Allen and Edmunds, 1965), varied in development also. Although the apical band of setae on the forefemur varied slightly among individuals from different populations and within single populations, a broad band of numerous setae was present on all mature individuals examined. Some setae were relatively short, and other setae were longer. Mature *E. invaria* larvae ranged in size from 6.0–13.3 mm, including

the size characterization of *E. choctawhatchee*. Samples from southern populations contained some mature individuals that were smaller than mature individuals from northern populations.

The color pattern of individuals also varied within single populations. Some individuals had many pale speckles, and others were solid brown. Paired white spots were present or absent on the hind margin of abdominal terga. Some individuals had a wide, pale, medial, dorsal stripe on the abdomen; some had a thin stripe; and some lacked a medial stripe. Individuals had color patterns similar to those described for *E. argo* (see above) and *E. floripara* (McCafferty, 1985). A single population of *E. invaria* from Ashe County, North Carolina, contained color variants resembling *E. argo*, *E. floripara*, and more typical *E. invaria*.

The holotype of *E. floripara* is a middle instar larva; however, the coloration of the specimen makes the wingpads appear dark, and thus the specimen appears mature. Fully mature larvae of *E. floripara* that we subsequently examined had fully developed maxillary palpi and numerous long setae on the caudal filaments, in contrast to the holotype. Populations from Watauga County, North Carolina, and ''Scottsville,'' North Carolina contained *E. floripara* color variants and more typical *E. invaria*. The *E. floripara* color variant was collected most commonly from the New River drainage basin.

Adult variability. Allen and Edmunds (1965) differentiated the male adults of *E. inconstans*, *E. invaria*, and *E. rotunda*, based upon the shape of a ventral, subgenital plate projection, and on the number and relative development of dorsal, stout spines on the penes. The shape of the subgenital plate projection varied somewhat, but most often, the angle at which the specimen was viewed affected the interpretation of this character. The number and relative development of ventral and dorsal stout spines on the penes varied within and among populations. Apicoventral spines on the penes were present medially in most specimens we examined, and the number of these spines, when present, varied from 1–4. A few individuals entirely lacked apicoventral spines. The latter is notable because Jacobus and McCafferty (2001a) differentiated the adult of *E. choctawhatchee* from other, similar, *Ephemerella* species, based on the absence of such spines.

McDunnough (1931b) and Burks (1953) distinguished *E. rotunda* from *E. invaria* by the presence of medioventral spines on the penes of *E. rotunda*. In *E. invaria* specimens we examined, the number of medioventral, stout spines varied from 0–10, with 0, 1 and 6–8 most commonly encountered. These medioventral spines, when present, are found in two oblique, longitudinal rows, almost directly beneath the medial dorsal spines. There were always dorsal, stout spines present on the penes of *E. invaria*. Although the length, robustness, and number of stout penes spines varied greatly among individuals and populations, the spines always were arranged similar to those figured by Spieth (1940: fig. 1) in his illustration of the lectotype genitalia. Notably, male adults reared from the type locale of *E. rotunda* (Steger, 1931) were typical of the *E. invaria* lectotype (Spieth, 1940).

Discussion. *Ephemerella fratercula* has been differentiated from congeners by the relatively high number of ventral spines (ca. 20) on its penes (Allen and Edmunds, 1965; Jacobus and McCafferty, 2002a). We rehydrated, cleared, and slide-mounted dissected male genitalia from one dried *E. fratercula* paratype to investigate these spines more thoroughly. Examination with a light microscope revealed that there actually were very few stout spines on the penes of *E. fratercula*. The number and placement of these spines fell within the range of variability of *E. invaria*. The apparent presence of additional ventral spines on the dried specimen may be due in part to considerable debris that was cleared away.

The male adult of *E. hispida* (Jacobus et al., 2002) has numerous ventral penes spines and very closely resembles a specimen from North Carolina that had been referred to *E. fratercula*

(see Jacobus and McCafferty, 2002a). Reared material of *E. hispida* from South Carolina compared favorably to the North Carolina specimen. The North Carolina record of *E. fratercula* thus should be considered a misidentification of *E. hispida*.

Larvae reported from Elkhart County, Indiana (Randolph and McCafferty, 1998) as *E. argo* and *E. dorothea* were misidentified *E. invaria*.

Material examined. *Ephemerella hispida*: USA, **North Carolina**: Watauga Co, Valle Crucis, 5-VI-1936, JR Traver, 1MA (genitalia and wings on slide) [CUIC]; **South Carolina**: Greenville Co, Watson Heritage Preserve, Matthews Cr, 7-V-1997 and 4-VI-1997, S Spichiger, 2MA, 2SE, 2LE [PERC].

Ephemerella invaria: CANADA, **Nova Scotia**: Baddeck R, 6-VII-1950, EL Bousefield, 1L [PERC]; **Quebec**: Cascades Point, 3-VI-1930, GS Walley, LJ Milne, 26L [CNC]; Covey Hill, 25-VI-1924, GS Walley, 1MA (*E. fratercula* paratype, genitalia in vial) [PERC]; Guerard Br, Island of Orleans, 20-III-1958, Rev. Rene Malouin, 7L [CNC]; Lachine, 8-VI-1926, FP Ide, 1MA, 1MS [CNC]; Old Chelsea, 8-V-1988, R Hutchinson, 1L [CNC]; Penny's Brook, 14-VI-1930, GS Walley, 1MA, 1MS, 2LE [CNC]. USA, **Florida**: Gadsden Co, Flat Cr at Co Rd 270A, 8 km S of Chattahoochee, 5-IV-1996, J Jones, 1MA, 1E [FAMU]; **Georgia**: Rabun Co, Chattooga R at US76, JB Wallace et al., 1L (*E. floripara* holotype) [PERC]; Rabun/Oconee Cos, Chattooga R at GA28, JB Wallace et al., 7L (*E. floripara* paratypes) [PERC]; **Indiana**: Elkhart Co, Elkhart R, 1 mi SE Millersburg at bridge on gravel road, 21-V-1972, WP McCafferty & AV Provonsha, 9L [PERC]; same locale, 25-V-1973, AV Provonsha, K Black, 3MA, 2L [PERC]; **Maryland**: Baltimore Co, Jones Falls at Green Spring Ave, N of Baltimore, 17-II-1970, RW Koss, 8L [PERC]; **Massachusetts**: Hampshire Co, Amherst, 2-VI-1939, JR Traver, 3MA [PERC]; Amherst, no other data, 2MA, 22FA [PERC]; E Br Mill R at Williamsburg, 5-V-1964, RW Koss, 55L [PERC]; North Amherst, Meadow St, 9-V-1956, MA Parsons, 14L [PERC]; South Hadley, 29-IV-1939, JRT, LMB, 5L [PERC]; **Michigan**: Crawford Co, AuSable R, T26N, R2W, S12, 5-VII-1951, JW & FA Leonard, 1MA [UMMZ]; Manistee R, T27N, R4W, S31, 27-V-1948, JW & FA Leonard, 1MA, 1LE [PERC]; **New Jersey**: Morris Co, Trout Br at Hacklebarney SP, 13-V-1978, DE Minnick, 3L [VPIC]; **New York**: Delaware Co, E Br Delaware R, downstream of Downsville, 3-VI-1999, 4MA, 2SE [SWH]; Tompkins Co, Beebe L, Ithaca, 31-V-1932, CNH, 4MA, 2FA [PERC]; Fall Cr at Beebe L, Ithaca, 31-V-1932, JR Traver, 10MA, 10FA, 2SE [PERC]; Ellis Cr, Ellis Hollow, 11-VI-1932, JRT, 1FA, 1LE [CUIC]; Fish Hatchery on pond, Ithaca, 12-VI-1932, "vial C.R.", 1MA (genitalia dissected) [CUIC]; **North Carolina**: "Willets," 23-III-1940, Frison, Mohr, Hawkins, 1L (legs on slide) [INHS]; "Woodlawn," 23-III-1940, Frison, Mohr, Hawkins, 1L (caudal filaments on slide) [INHS]; Ashe Co, N Fk New R, III-1989, DL & DP, 12L [DRL]; S Fk New R, "Scottsville," III-1994, Lenat & Penrose, 6L [DRL]; Buncombe Co, Black Mt, N Fk Swannanoa, May, Collection N Banks, (*E. vernalis* lectotype), Type 11421, 1MA (genitalia dissected, in vial on pin) [MCZ]; same data, (*E. vernalis* paralectotypes), 3FA [MCZ]; Guilford Co, nr Greensboro, 27-III/15-IV-1930, Traver, 7L [CNC]; Watauga Co, Morgan Br Clark's Cr at Townsend's Gap, Hanging Rock Mt, nr Valle Crucis, 20-V-1983, EL Morgan, 1MA, 1FA (parts of forceps in different proportions) [VPIC]; S Fk New R, SR1352, III-1990, Lenat & Penrose, 11L [DRL]; **Pennsylvania**: "Milltown," 11-V-1948, 1MA (genitalia on slide) [INHS]; Chester Co, E Br White Clay Cr at Stroud Estate, Rt926 (main branch), 20-IV-1966, JW Richardson, 1L [PERC]; **South Carolina**: Barnwell Co, Steel Cr nr confl Meyers Br, 12-III-1984, Kondratieff, 13MA (one set genitalia on slide), 7FA, 4SE, 10LE [PERC]; **Tennessee**: Anderson Co, Clinch R, 25-III/20-VI-2001, J Thurman et al., 15MA, 9MS, 4FA, 10FS,

15SE, 2L; 5-III/6-VI-2002, 4MA, 4SE, 1FS, 5MS, 1LE, 28L [PERC]; Sevier Co, 24-III-1940, Frison, Mohr, Hawkins, 2L [INHS]; Sullivan Co, S Holston R below dam, S Hiner, 7-IX-1997, 3MA, 2MS, 1SE; 18-III-2000, 1MA [SWH]; S Holston R tailwater, S Hiner, 22-III-1997, 1MA, 1FA, SE; 22-XI-1998, 1MA, 2FA; 7-XI-1999, 17MA, 3FA; 4-II-2001, 1MA, 1MS [SWH]; S Holston R, 3 mi upstream Bluff City, 16-III-1980, G Griffin, 4L [VPIC]; **Virginia**: Bath Co, Spring Br nr jct with Mill Cr nr Rt629, ca. 1,400 ft, 12-V-1979, CR Parker, 2MA, 4FA [VPIC]; Bedford Co, Big Otter R, 24-IV-1982, 12-III-1983, emerged 20/30-III, Kondratieff, 4MA, 6FA, 1MS, 1FS, 2SE, 9LE, 1L [VPIC]; N Otter Cr at Rt82, jct Rt639, 16-IV-1981, Kondratieff, 2MA [VPIC]; Botetourt Co, Bear Wallow Cr, 5 mi S Rt60, Buchanan, 11-IV-1979, emerged 29-IV, Kondratieff, 1MA, 1LE [VPIC]; New R, 20-IV-1980, 22/24-IV-1981, emerged 2/28-V, 4MA, 3FA, 3L, 3LE [VPIC]; Johns Cr nr Hunting Lodge, 30-IV-1977, T Grimes, 2MA, SE [VPIC]; Culpeper Co, Hazel R off Rt707, 22-III-1983, emerged 15-IV, 1MA, 1FA, 2LE [VPIC]; Floyd Co, Dodd Cr, 12-IV-1974, 23-III-1980, emerged 4/7-IV, 9MA, 3FA, 12LE, 24L [VPIC]; Little R, 12-IV-1974, 21-IV-1977, emerged 27-IV, 1MA, 1SE, 1L [VPIC]; Giles Co, 19-V-1964, RR Gerhardt, 9MA, 13FA [VPIC]; 6-IV-1968, F Benfield, 16L [VPIC]; Little Stony Cr, 2-III/13-V-1977, 29-IV-1978, 12-V-1978, 3/19-IV-1980, emerged 11/29-IV, 16/23-III-1983, emerged 12-IV, 9MA, 1FA, 1SE, 6L, 2LE [VPIC]; Sinking Cr, 19/21-V-1964, 26-V-1977, 17MA, 29-IV-1977, emerged 12-V, 1MA, 1SE, 26-III/13-IV-1974, 58L [VPIC]; Spruce Run, 20/26-III-1977, 13/19-IV-1978, emerged 28/30-IV, 3MA, E, 10L, 26-III, 19L [VPIC]; Halifax Co, Alton, 22-III-1940, Frison, Mohr, Hawkins, 5L [INHS]; Hanover Co, S Anna R at Rt657, 22-IV-1978, emerged 1–V, Kondratieff, JR Voshell, Jr., 1MA, 1FA, 2E, 3L [VPIC]; Henry Co, Smith R, 15-V/16-VIII-1977, 1MS, 1LE, 7L, 14-IV-1979, emerged 22-IV, 1FA, E, 26-IV-1980, emerged 24-IV, 2MA, 1FA, 1LE [VPIC]; Madison Co, Robinson R at Madison, 21-III-1940, Frison, Mohr, Hawkins, 11L [INHS]; Montgomery Co, 20-V-1962, Bolton, 1MA [VPIC]; Cedar Run nr confl spring at Rt643, STP, 31-III-1979, emerged 21-IV, Kondratieff, 1MA, 1LE [VPIC]; Flatewood's Branch at Rt603, 30-IV-1978, Kondratieff, 1MA, 1LE [VPIC]; Mill Cr, 4/29-V-1977, 11MA, 30FA, 23L, 29-III-1977, emerged 6/16-IV, 4MA, 2FA, E, 11L, 11-IV-1978, emerged 18/29-IV, 3MA, E, 18L, 5-VI-1978, 15MA, 18FA [VPIC]; N Fk Roanoke R, 16/27-IV-1974, 24L, 6/30-IV-1978, 2MA, SE, 1LE, 1L [VPIC]; Tom's Cr at Rt655, 27-V-1980, Kondratieff, 1MA, 1LE [VPIC]; Yellow Sulfur Springs at Rt642, 10/12-V-1980, Kondratieff, 3MA, 2FA, 1LE [VPIC]; Nottoway Co, Little Nottoway R, Rt49 nr Rt607, 27/28-II-1982, Kondratieff, 5L, 2MA, 1MS, 3FA, 5LE [VPIC]; Patrick Co, spring fed seep feeding into Rockcastle Cr at Rt605 off Rt8, 21-V-1978, Kondratieff, 9MA, 1FA [VPIC]; Tazewell Co, Station Spring Cr, 8-V-1982, emerged 21-V, Kondratieff, 10MA, 7FA, 1MS, 1SE, 4L, 3LE [VPIC]; 6/7-IX-1981, 1MA, 2FA, 2SE, 17LE, 3L, 6MA, 9FA, one gravid gynandromorphic adult [VPIC]; 18-V-1979, emerged 18-V/2-VI, 18MA, 11FA, 3SE, 3L, 17LE [VPIC]. **West Virginia**: Mercer Co, East R, 15-IV-1974, JP Newman, 1L [VPIC]; 15-V-1974, JD Miller, 1L [VPIC]; Monongalia Co, lights at Suncrest Bank, 16-VIII-1978, D. Rowe, 1MA [VPIC]; Monroe Co, Rich Cr, 18-V-1974, R Hanson, 2L [VPIC]; Rich Cr, V-1978, Scott Berglund, 1MA, 10FA [VPIC]; Nicholas Co, Jim's Br Panther Cr, 6 mi W Richwood on Rt39, 29-IV-1983, emerged 15-V, Kondratieff, 1MA, 5FA, 3LE, 2SE [VPIC]; Pendleton Co, Seneca Cr, 4-IV-1976, L Sherman, 3L [VPIC]; Preston Co, Fellowsville, 30-IV-1944, Frison & Ross, (*E. simila* paratypes), 14L (parts on slides) [INHS].

Ephemerella mucronata (Bengtsson) 1909

Ephemerella krieghoffi (Ulmer) 1920 (Belfiore et al., 1989)
Ephemerella sp. *nympha unicolorata* (Ikonomov) 1961 (Studemann et al., 1992)
Ephemerella mucronata unicolorata (Ikonomov) 1961 (Soldán, 1982)
Ephemerella moffatae Allen, 1977, **new synonym**
Ephemerella kreighoffi intermedia Keffermüller, 1979 (Studemann et al., 1992)

Diagnosis. *Mature larvae* of *Ephemerella mucronata* are distinguished from other *Ephemerella* species by distinctive, paired, longitudinal ridges on at least abdominal terga 4–9 (cf. e.g., Tshernova, 1952: fig. 102, Allen, 1977: fig. 1, Engblom, 1996: fig. 131, Studemann et al., 1992: Pl. XVIII). No sharp projections or tubercles are present along the median posterior margins of abdominal terga.

Male adults may be distinguished from congeners by their genitalia. Forceps segment 2 has an apical expansion; the penes have long, divergent, apical lobes; and the penes lobes lack spines (cf. e.g., Keffermüller, 1979: fig. 1; Harper and Harper, 1981: fig. 2; Studemann et al., 1992: figs. 332, 336).

Larval variability. The longitudinal ridges on the abdomen vary from flat and inconspicuous to elevated and prominent. Some larvae have a body color pattern of prominent brown and white banding (see larval variability section for *E. excrucians*, above), and other larvae are solid brown and lack any such pattern. Some larvae appear to have more hairlike setae than others, and larvae vary in body size and the relative development of abdominal segment 9 posterolateral projections (Keffermüller, 1979; Belfiore et al., 1989).

Adult variability. Adults differ slightly in size and coloration. Male adult penes lobes may be slightly longer and more divergent in some individuals (Keffermüller, 1979; Belfiore et al., 1989).

Discussion. *Ephemerella moffatae* type material from Alberta and a larva from Montana were identical to some larvae of *E. mucronata* from Germany. At the time Allen (1977) described *E. moffatae*, *E. mucronata* was known only from the northern Palearctic, and there is no evidence that suggests he had seen specimens of the latter species. Harper and Harper (1981) reported *E. mucronata* from the Yukon and Northwest Territories, being first to recognize it as a Holarctic species.

Material examined. CANADA, **Alberta**: Athabasca R jct Calling R, 3-VI-1975, B Moffat, 1L (*E. moffatae* paratopotype) [FIEC]; **Yukon Territory**: Rampart House, 8-VIII-1951, JEH Martin, 2MA [CNC]. GERMANY: stream Breitenbach nr D-361 Schlitz/Pfordt, 16-IV-2002, Reimo Lieske, 12L [PERC]. USA, **Montana**: Gallatin Co, river into Hyalite Res nr Bozeman, 4-VII-2000, TD Waite, 1L [BYU].

Serratella micheneri (Traver) 1934

Ephemerella altana Allen, 1968, **new synonym**

Diagnosis. *Mature larvae* have well-developed, blunt protuberances, usually present on abdominal terga 2–8. The maxillary palpi are relatively long, and the tarsal claws are relatively blunt, as compared to certain other *Serratella* species (Allen and Edmunds, 1963).

Male adults have a lateral, sharp, dorsally oriented projection on each of the penes lobes, and each lobe bears short, blunt, apical processes. Penes lobes are divergent, giving the appearance of a relatively wide and deep, V-shaped, apical cleft (Traver, 1934: fig. 6; 1935: fig. 153). The foretibia is longer than the foretarsus (Traver, 1934; Allen and Edmunds, 1963).

Larval variability. Larvae vary in color (see comments in *E. excrucians* larval variability section). Dorsal abdominal protuberances vary in their development, such as described for *S. serrata* by Jacobus and McCafferty (2000).

Adult variability. Male adults may have two or three short, blunt, apical processes on the penes lobes, and the penes lobes of some individuals are more divergent than others.

Discussion. The holotype male adult of *E. altana* was identical to reared comparative material of *S. micheneri* from Arizona. Furthermore, the genitalia were identical to those illustrated by Traver (1934: fig. 6) when she described *S. micheneri* as new. *Ephemerella altana* was described with "each penis lobe with a round apical protuberance enclosed in a sheath" (Allen, 1968). This protuberance was not obvious in any material we examined, and it may have been an artifact of preservation of the specimen in alcohol or an artifact of slide mounting.

Some confusion of specimens must have occurred in the type series of *E. altana*, because the larval exuviae associated with the paratype male adult of *E. altana* (Allen, 1968) belongs to *E. excrucians* (see Material Examined for *E. excrucians*). Therefore, reports of *E. altana* larvae may be referable to *E. excrucians*. The report of *E. altana* larvae from Baja California Norte, Mexico (Lugo-Ortiz and McCafferty, 1994) and some reports from Catron and Grant Counties, New Mexico (McCafferty et al., 1997b), however, were based on *S. micheneri* larvae, rather than *E. excrucians*. Further confounding the issue, we have found alate *S. micheneri* and *E. excrucians* taken in the same sample, a situation that may have contributed to the mistaken identity of larvae by Allen (1968).

Material examined. MEXICO, **Baja California Norte**: Arroyo Potrero, Sierra San Pedro Mártir, 22-VI-1988, Baumann & Kondratieff, 11L [PERC]; Río San Rafael, Sierra San Pedro Mártir, Mike's Sky Rancho, 22-VI-1988, Kondratieff, 11L [PERC]. USA, **Arizona**: Apache Co, E Fk White R at Rock Creek Ranger Sta, Ft Apache Indian Res, 5/6-VII-1964, RK Allen, 3MA (*E. altana* holotype and paratypes) [CAS]; Yavapai Co, Verde R above Clarksdale, off Hwy89, 12-V-1969, RW Koss, AV Provonsha, 2L, 7LE, 1MS, 2FS, 1SE, 1MA [PERC]; **New Mexico**: Catron Co, Gila R at jct Little Cr, Gila Cliff Dwelling NM, 15-VII-1967, R & D Koss, 10MA [PERC]; Gila R, 42 mi N Silver City, jct Little Cr, 15-VII-1967, R & D Koss, 1MA (genitalia on slide) [PERC]; Gila R at jct Little Cr, N Silver City, 9-VII-1969, RW Koss, WP McCafferty, AV Provonsha, 34L [PERC]; San Francisco R at Glenwood, 21-VII-1970, RK Allen, 7L [CAS]; W Fk Gila R, 1.5 mi above jct Middle Fk, N of Silver City, Gila NM, 8-VII-1969, RW Koss, WP McCafferty, AV Provonsha, 10L (parts in vial) [PERC]; Grant Co, Gila R, 31 mi N Pinos Altos, 11-VII-1973, B Stark, 6L [PERC]; W Fk Gila R on Hwy527, 21-VII-1970, RK Allen, 6L [CAS]; W Fk Gila R at Rd 15, Gila NF, 6-V-1981, WP McCafferty, AV Provonsha, DW Bloodgood, 81MA, 20MS [PERC]; **Oregon**: Lane Co, Willamette R at Eugene nr Wastewater Trt Plant, 30-VIII-2000, 27L [PERC]; **Washington**: Lewis Co, Centralia, 26-VII-1936, HH Ross, 1MA (genitalia on slide) [INHS].

Serratella serrata (Morgan) 1911

Serratella sordida (McDunnough) 1925, **new synonym**
Serratella carolina (Berner and Allen) 1961, **new synonym**
Serratella spiculosa (Berner and Allen) 1961, **new synonym**

Diagnosis. *Mature larvae* have well-developed, blunt protuberances, usually present on abdominal terga 2 or 3 through 8 or 9. Protuberances on terga 4 to 7 are most prominent. The maxillary palpi are relatively reduced, but with three segments. Variously developed paired

tubercles may be present on the head and pronotum. Larvae have long, fine, hairlike setae on the legs and body.

Male adults have a lateral, sharp, dorsally oriented projection on each of the penes lobes, and the penes have small, lateral spinules. Penes lobes are situated closely parallel to one another. A pair of large, dark, patches is found on most of the abdominal terga. These pairs of patches cover most of the dorsal surface of the respective segment.

Larval variability. Jacobus and McCafferty (2000) documented variability in the larvae of *S. serrata* and provided a modified key for proper identification of that species, *S. carolina*, and *S. spiculosa*. The number and size of dorsal abdominal tubercles varied considerably in *S. serrata*, and the characters separating the above three species were restricted to the relative development of occipital tubercles, the number of maxillary palp segments, and the number of denticles on the tarsal claws. More recent examination of additional series of specimens, including reared material, has revealed that *S. serrata* larvae are more variable than previously assumed. We found a gradation in the relative development of occipital tubercles in mature larvae, ranging from that of *S. serrata* to that of *S. carolina*. *Serratella spiculosa* paratype larvae were not fully mature, and the spicules on the head occurred where tubercles were in *S. carolina* and *S. serrata*. Female larvae often had two distinct pairs of occipital tubercles, while male larvae from the same population had only one distinct pair. The prothoracic tubercles varied in their relative development. The number of denticles on the tarsal claws varied. Larvae are covered with various quantities and densities of long, fine, hairlike setae. Careful examination of type and other material revealed that, in contrast to the descriptions given by Berner and Allen (1961) and Allen and Edmunds (1963), *S. carolina*, *S. sordida*, and *S. spiculosa* had maxillary palpi with three segments, like those of *S. serrata*.

Adult variability. The base color of the abdomen varies from cream white to light brown. The dorsal color patches vary in color and intensity but always are present. Male adults associated with *S. carolina* larvae were typical of *S. serrata*.

Discussion. An Arkansas record of *S. sordida* (Peters and Warren, 1966) is applicable to *S. molita* McDunnough (see material examined listed below). Indiana records of *S. sordida* (Randolph and McCafferty, 1998) are applicable to *S. deficiens* Morgan (see material examined listed below).

Material examined. *Serratella deficiens*: USA, **Indiana**: Montgomery Co, Sugar Cr at Hwy 234, Pine Hills, 14-VI-1979, SAN, SGN, CMB, 2MA, 7FA [PERC].

Serratella molita: USA, **Arkansas**: Washington Co, Cove Cr, light trap, 19-V-1962, O&M Hite, 1FA [PERC].

Serratella serrata: CANADA, **Quebec**: Power Cr, 21-VII-1930, Foster, 1MS, 3LE [CNC]; Wakefield, 8-VII-1931, LJ Milne, 5L [PERC]; Yamaska R, 5/6-VIII-1930, LJ Milne, 2MA, 2MS, 1FS, 5LE (emerged in cage) [CNC]. USA, **Indiana**: LaGrange Co, Pigeon R at Co Rd 1100 E, 8-IX-1973, B. Schenck, 1L [PERC]; **Michigan**: Oceana Co, White R at Pines Pt RA, access at campground, Manistee NF, 6-VII-1996, P Randolph, C Ellis, 2L [PERC]; **New York**: Sullivan Co, Neversink R, below Monticello, 1.5 mi S of SR17, 18-VII-1997, K. Riva-Murray, 5L [PERC]; **North Carolina**: GSMNP, L Berner, (*S. carolina* paratypes), 3L [PERC]; Jackson Co/Transylvania Co, Whitewater R at Co Rt171, elev 823 m, 25-I-1969, JB Wallace et al., 1L [PERC]; Macon Co, L Berner, (*S. spiculosa* paratypes), 2L (fore- and midlegs on slide) [FAMU]; Cullasaja R at Rt 1672, 7-VII-1989, Kondratieff, 21MA, 6FA, 3MS, SE [VPIC]; Wayah Cr, 21-VIII-1955, L Berner, (*S. carolina* paratype), 1L [PERC]; Swain Co, GSMNP, ca. 0.5 km upstream from Deep Creek Campground, 35°34′00″N, 83°20′08″W, bucket light trap, J Cooper, 3-VIII-1999, 1MA (genitalia on slide) [PERC]; GSMNP, side rivulet of Deep Cr at Deep Creek

Campground, 35°27′39″N, 83°26′13″W, 03-VIII-2000, LM Jacobus, 1L (dissected in vial) [PERC]; Oconaluftee R at Tow String, 35°32.5′N, 83°17.9′W, 9-IX-2001, Lu Sun et al., 1L [PERC]; Transylvania Co, Davidson R, (*S. carolina* paratype), 1L [PERC]; Watauga Co, Beech Cr, VII-1997, CC No. 7903, D Lenat, 4L [PERC]; **Pennsylvania**: Allegheny R, 9-VII-1980, J Kennedy, 8L [VPIC]; Chester Co, E Br White Clay Cr at Stroud Estate, Rt926 (main branch), 23/27-VI-1966, JW Richardson, Jr., 1MA (dissected genitalia in vial), 1MS, 3FA [PERC]; **South Carolina**: Greenville Co, Matthews Cr at Asbury Youth Camp, 35°05′N, 82°38′W, 18-VII-1997, S Spichiger, 7L [PERC]; Oconee Co, E Fk Chattooga R at Walhalla Fed Fish Hatchery, elev 762 m, 1-VIII-1969, JB Wallace et al., 1L [PERC]; **Tennessee**: Blount Co, Abrams Cr, 100 m upstr Arbrams Falls Trailhead, 35.5921N, 83.8520W, 18-VI-2001, BD Heinold, 1MA, 16FA [INHS]; Polk Co, Sheeds Cr, 325 m N jct Forest Service Rd 221 and Big Frog Loop Rd, 16-VI-2000, DA & EL Etnier, JT Baxter, CA Walker, 5L [PERC]; **Virginia**: Amherst Co, Huff Cr BLT off Rt 690, 28-VI-1983, Kondratieff, 1MA [VPIC]; Carroll Co, New R at Rt606, 11-VI-1980, Kondratieff, 1MA [VPIC]; Craig Co, John's Cr, Rt 311, nr jct Rt611, 30-VI-1978, Kondratieff, BLT, 2MA [VPIC]; Culpeper Co, Hazel R at Rt 707, 14-VII-1979, Kondratieff, 1MA, 1SE [VPIC]; Hazel R, off Rt 707, Firth Farm, 9-VII-1982, Kondratieff, 2MA, 1SE [VPIC]; Montgomery Co, Radford Arsenal, VIII-1951, R Hoffman, 3MA, 8FA [VPIC]; Russell Co, Big Cedar Cr at Rt 19, V-1979, M Bass, 1MA, 4FA [VPIC]; **West Virginia**: Hardy Co, Lost R, 12-VIII-1930, JG Needham, 1L [PERC].

Serratella tibialis (McDunnough) 1924

Ephemerella angusta Traver, 1934 (Edmunds, 1954)
Serratella sequoia (Allen and Collins) 1968, **new synonym**

Diagnosis. *Mature larvae* of *S. tibialis* have relatively sharp, dorsally projecting, tubercles on abdominal terga 2 or 3 to 8 or 9. Very small, dark, excrescences are present in various quantities on the mesonotum, especially on and between the forewingpads. The maxillary palpi are longer than in similar species.

Male adults have twisted genital forceps. The penes have two, somewhat rounded, apicoventral lobes and no lateral, sharp, dorsally oriented, projections.

Larval variability. Immature larvae have dorsal abdominal tubercles that are less developed and caudal filaments that are proportionately longer than those of mature larvae.

Adult variability. *Serratella tibialis* male genitalia do not vary as much as possibly inferred from published illustrations. It is important to note that the illustration of *S. tibialis* male genitalia provided by Allen and Edmunds (1963: fig. 4) is incorrect. Consult McDunnough (1929: fig. 1) for a more accurate depiction.

Discussion. The holotype of *S. sequoia* is an immature larva. Comparison of this specimen with series of associated immature and mature *S. tibialis* specimens revealed that abdominal tubercle development, the length of the caudal filaments, and the setation of the forefemur were identical.

Material examined. USA, **California**: Tulare Co, Sequoia NF, Salmon Cr at Horse Meadow Campground, I-VIII-1965, WP Vann, (*S. sequoia* holotype), 1L [CAS]; **Idaho**: Custer Co, Salmon R at US93, 5 mi E Stanley, 5,900′ elev, 25-VII-1964, SL Jensen, PS Lombardi, FD Isenberg, 38L [PERC]; Idaho Co, Selway R, 7 mi NE Lowell, 28-V-1995, GF Edmunds, 13L [PERC]; Kootenai Co, Mica Cr, 4 mi S Coeur d'Alene, "2/8/1964," Edmunds, 5L [PERC]; **Montana**: Madison Co, Madison R at Burnt Tree, 27-VII-1981, 5MA, 3FA [PERC]; **Oregon**: Benton Co, Griffith Cr, trib Rock Cr, S of Philomath, 14-V-1967, E Evans, 1L [PERC];

Wyoming: Carbon Co, N Platte R, Sixmile Gap Campground, 20-VIII-1977, 4L [PERC]; Teton Co, Lava Cr at Hwy26, 24-VIII-1962, Douglas Q Anderson, 4L [PERC].

ACKNOWLEDGMENTS

We thank Boris Kondratieff (Ft. Collins, Colorado) for telling us about the collection of Ephemeroptera deposited with the Virginia Polytechnic Institute and State University. Donald G. Cobb (Winnipeg, Manitoba), R. Ed DeWalt (Champaign, Illinois), George F. Edmunds, Jr. (Salt Lake City, Utah), David Etnier (Knoxville, Tennessee), Colin Favret (Champaign, Illinois), Clarke Garry (River Falls, Wisconsin), Stephen Hiner (Blacksburg, Virginia), E. Richard Hoebeke (Ithaca, New York), Steven Krauth (Madison, Wisconsin), Dave Lenat (Raleigh, North Carolina), Reimo Lieske (Schlitz, Germany), John Morse (Clemson, South Carolina), Mark O'Brien (Ann Arbor, Michigan), T. Heath Ogden (Provo, Utah); Chuck Parker (Gatlinburg, Tennessee), Philip Perkins (Cambridge, Massachusetts), Jan Peters (Tallahassee, Florida), Wojciech Pulawski (San Francisco, California), Sven-Erik Spichiger (Annville, Pennsylvania), Lu Sun (West Lafayette, Indiana), John Thurman (Norris, Tennessee), J. Reese Voshell (Blacksburg, Virginia), Bob Wissemann (Corvallis, Oregon), and Robert Zuparko (San Fransisco, California) loaned or donated material for study. Ed Becker, Raymond Hutchinson, and Ian Smith (Ottawa, Ontario) assisted with a visit to CNC, and Steve Ashe, Brian Beatty, Andy Bentley, and Michael Engel (Lawrence, Kansas) assisted with a visit to SEMC. R. Patrick Randolph (Davis, California) assisted with some geographic distribution data. Michael Meyer (Lafayette, Indiana) reviewed an early draft of the manuscript. Discover Life In America, Inc. and the U. S. National Park Service provided funding and facilities, respectively, for fieldwork in GSMNP. This study was funded in part by USEPA fellowship 91601701-0 to LMJ, CanaColl Grant 178 to LMJ, and NSF grant DEB-9901577 to WPM.

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Received 22 July 2003; accepted 15 December 2003.