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REVISIONARY CONTRIBUTIONS TO THE GENUS *DRUNELLA* (EPHEMEROPTERA: EPHEMERELLIDAE)

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Abstract.—We establish new subjective synonyms for five *Drunella* species from the Nearctic, east Palearctic, and Oriental regions: *Drunella cryptomeria* (Imanishi, 1937) [=*Ephemerella* nM Imanishi, 1940, new synonym; = *D. lepnevae* (Tshernova, 1949), new synonym; = *D. longipes* (Tshernova, 1952), new synonym; = *D. fusongensis* Su and Gui, 1995, new synonym], *D. ishiyamana* Matsumura, 1931 [= *E. latipes* Tshernova, 1952, new synonym], *D. lata* (Morgan, 1911) [= *D. cornuta* (Morgan, 1911), new synonym, = *E. depressa* Ide, 1930, new synonym, = *D. cornutella* (McDunnough, 1931), new synonym, = *D. longicornis* (Traver, 1932), new synonym], *D. submontana* (Brodsky, 1930) [= *E. svenhedini* Ulmer, 1936, new synonym], and *D. walkeri* (Eaton, 1884) [= *D. wayah* (Traver, 1932), new synonym]. Morphology, phenotypic plasticity, and biology are discussed for these species and for *D. allegheniensis* and *D. tuberculata*, and new diagnoses are provided. The specific epithet of *D. doddsii* is corrected to its original orthography.

Drunella Needham (Ephemeroptera: Ephemerellidae) is one of the largest and most diverse genera of the mayfly subfamily Ephemerellinae (sensu McCafferty and Wang, 2000). *Drunella* species occur in high quality streams throughout North America and Asia (Allen, 1980). Needham (1905) described the genus based on the western North American species *Ephemerella grandis* Eaton. Needham (1927b) later relegated *Drunella* to subgeneric status under *Ephemerella* Walsh, but Tshernova (1972) and Allen (1980) recognized it again at the genus level. Allen and Edmunds (1962) provided a detailed account of the nomenclatural history of *Drunella*.

Previous studies of *Drunella* have been limited by the "small number" of specimens used to delineate life stages of species (Allen and Edmunds, 1962), and the need for "more material" has been noted repeatedly (e.g., McDunnough, 1931b; Traver, 1935). We have been able to examine new and historical material, including long series of single life stages, adults and larvae from reared associations, repeated samplings from single collection sites, and samplings from throughout the geographic range of species. This extensive material and published data have enabled us to recognize new synonyms for the Asian species *D. cryptomeria* (Imanishi), *D. ishiyamana* Matsumura, and *D. submontana* (Brodsky), and for the North American species *D. lata* (Morgan) and *D. walkeri* (Eaton). Variability is documented for each of these species and also for the North American species *D. allegheniensis* (Traver) and *D. tuberculata* (Morgan). The latter two species are treated here because certain variants may be difficult to distinguish from one another and from *D. walkeri* variants. Species are treated in alphabetical order below. Diagnostic characters will distinguish sympatric congeners from one another, especially if series are available for study.

Our examination of nearly all nominal species revealed some shared characteristics that previously may have been construed as unique to individual species or species groups. For example, Traver (1932) described a "partial 'adhesive disc'" present on the abdominal sterna of *D. wayah* (Traver). All the *Drunella* species treated here, and nearly all other *Drunella*

species we have examined, have such a field of fine hairlike setae on the abdominal sterna. The length of these setae, and the density of their distribution, varies greatly between individuals. However, the setae are most consistently longest and most dense on the lateral regions of the most posterior sterna. Notable exceptions to this include *D. doddsii* (Needham) (see note on orthography, below) and *D. pelosa* (Mayo), which have very thick fields of setae ventrally. Longer setae may be found on anterior sterna of *D. doddsii*, and the distribution of these long setae is relatively even on *D. pelosa*.

Allen and Edmunds (1962) provided illustrations of the heads of several North American *Drunella* species. Based on these illustrations, the orientation and placement of the lateral branches of the epicranial suture may be construed as species specific in *Drunella*. This is not the case, however, because examination of larvae revealed that the lateral branches consistently are present anterior to the compound eyes, pass through the center of the lateral ocelli, and converge posterior of the lateral ocelli (e.g., see Dance, 1979: fig. 4). The use of the epicranial suture as a taxonomic character in Ephemeroptera was discussed by Wang and McCafferty (1996).

In the Material Examined section under each species heading, we utilize the following abbreviations for specimens: L = larva, S = subimago, A = adult, E = exuviae, M = male, F = female. Material examined is deposited with the following institutional or personal collections: Canadian National Collection of Insects, Agriculture and Agri-Food Canada, Ottawa, Ontario (CNC); Colorado State University Insect Collection, Ft. Collins, Colorado, USA (CSUC); David Lenat, North Carolina Department of Environment, Health, and Natural Resources, Raleigh, North Carolina, USA (DRL); Hokkaido University, Sapporo, Japan (EIHU); Illinois Natural History Survey Insect Collection, Champaign, Illinois, USA (INHS); Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm, Sweden (NHRS); Purdue University Entomological Research Collection, West Lafayette, Indiana, USA (PERC); The Royal Ontario Museum, Toronto, Ontario, Canada (ROME); Stephen Hiner, Blacksburg, Virginia, USA (SWH); Seoul Women's University, Seoul, Korea (SWU); University of Michigan Museum of Zoology, Insect Division, Ann Arbor, Michigan, USA (UMMZ); and Virginia Polytechnic Institute and State University, Blacksburg, Virginia, USA (VPIC). Some material examined was collected in conjunction with the All Taxa Biodiversity Inventory (ATBI) of Great Smoky Mountains National Park, Tennessee and North Carolina, USA (GRSM) (Sharkey, 2001; Jacobus and McCafferty, 2003b). This study of *Drunella* represents a further contribution to our revision of Ephemerellinae (Jacobus and McCafferty, 2002; 2003a, c, d). Preliminary cladistic evidence (Jacobus and McCafferty, unpubl.) indicates that the five subgenera recognized by Allen (1980) have been arbitrarily applied and may not be supportable, based on their present concepts. Therefore, we do not utilize Allen's (1980) subgeneric concepts in the present study. In forthcoming publications we will discuss the phylogenetic systematics of the Ephemerellinae and provide comprehensive identification keys (Jacobus and McCafferty, unpubl.).

Our study of the historical literature revealed that the species *D. doddsii* (Needham) has been recorded consistently as *D. doddsi*, **incorrect spelling**. Needham's (1927b) original naming and description of *D. doddsii* were published in March 1927. Needham and Christensen (1927) (April) and Needham (1927a) (June) misspelled the specific epithet in subsequent discussions of the species in the same year, which apparently led to perpetuation of the error thereafter. Even if the change of spelling had been deliberate, the use of the first spelling, which ends in "*-ii*," is mandated by Section 4 of Article 33 of the current International Code of Zoological Nomenclature (1999).

SPECIES ACCOUNTS

Drunella allegheniensis (Traver, 1934)

Ephemerella allegheniensis Traver, 1934 (orig. comb.).

Diagnosis. *Drunella allegheniensis* larvae have very short, marginal, hairlike setae on the head, legs, and abdominal terga compared to *D. tuberculata* and *D. walkeri*, with which morphological variants may be confused. *Drunella allegheniensis* usually has more claw denticles than sympatric congeners, and in *D. allegheniensis*, these denticles are situated along most of the length of the claw, rather than basally only (see, e.g., material examined from Fannin County, Georgia). *Drunella allegheniensis* does not have long setae that protrude dorsally from the hind margins of abdominal terga 8 and 9. The abdominal terga have paired, oblique, submedian ridges, and each ridge terminates in a blunt spine on the hind margin. The abdominal sterna are marked with dark-colored "lateral streaks and dots, and a curving row of four. . .dots between" (Traver, 1934). Maculae present on the abdominal sterna of *D. allegheniensis* larvae usually are smaller, darker, and more distinct than those found in *D. tuberculata*. The median row of dots on the abdominal sterna contains dots subequal to the size of the lateral dots.

Adults reared from larvae have a dorsally oriented, posteromedian, mesothoracic projection. Maculae present on the abdominal sterna of *D. allegheniensis* adults usually are smaller, darker, and more distinct than those found in *D. tuberculata*. Male adults have penes with lateral margins that are relatively parallel and a genital forceps segment 2 that is only slightly expanded distally and proximally. Kondratieff et al. (1981) considered *D. allegheniensis* male adults to have a dorsal "lanceolate submedian excavation" of the penes that is more shallow than that of *D. tuberculata*.

Larval variability. Larvae from Stokes County, North Carolina have the blunt, dorsal, head and thoracic spines less developed than in typical *D. allegheniensis*, such that their spines are similar in general appearance to those of *D. tuberculata*. The sharp, lateral spine on the middle of the lateral edge of the prothorax varies in development. The claws have 3–7 denticles. The development of abdominal segment 8 posterolateral projections in *D. allegheniensis* larvae (Traver, 1934) varies between individuals from a single population from Cherokee County, North Carolina. Ventral abdominal maculae coloration varies, from light brown to black.

Adult variability. Some *D. allegheniensis* adults have a few faint maculae on the hindfemora, and therefore, certain adult variants of *D. allegheniensis* may be difficult to distinguish from certain *D. tuberculata* or *D. walkeri* variants.

The mesothoracic projection probably varies in size, but the extent of such has not yet been determined. This projection corresponds to the posteromedian mesothoracic spine of the larva. Certain larval variants of *D. tuberculata* (see below) have a well-developed posteromedian mesothoracic spine that is larger than that found in certain variants of *D. allegheniensis*. Therefore, size variability of the spine in larvae, as demonstrated by our material examined, suggests parallel variability in the adult.

Discussion. Wang and McCafferty (1995) discussed the presence of vestigial larval characters in alate stages.

Kondratieff et al. (1981) suggested a seasonal separation of *D. allegheniensis* and *D. tuberculata* where they co-occur in Virginia, with the former maturing in late summer and the latter maturing in late spring. Specimens from the Little River, Oconee County, South Carolina reflected this apparent separation, in that mature *D. tuberculata* larvae were collected

in May, and mature *D. allegheniensis* larvae were collected in August. There appears to be less temporal separation, however, in the Middle Fork French Broad River, Transylvania County, North Carolina, where early instar *D. allegheniensis* and late instar *D. tuberculata* were collected together in July. There appears to be little, if any, temporal separation of the two species in Panther Creek, Graham County, North Carolina, where similarly developed larvae of *D. allegheniensis* and *D. tuberculata* were collected together in August. Apparently, the two species are not always separated seasonally at locations where they co-occur.

The distribution of *D. allegheniensis* appears restricted to the Blue Ridge Range of eastern North America, based on our material examined and historical records (Traver, 1934; Allen and Edmunds, 1962; Kondratieff et al., 1981).

Material examined. USA, **Georgia:** Fannin Co, Ocoee R, IX-1975, Kondratieff, 2L (CSUC); Rabun Co, Talullah R, 2 mi N of Talullah Falls, 488 m elev, 20-VIII-1969, JB Wallace et al., 5L (PERC); Stephens Co, Panther Cr, 1 mi N of Yonah Dam, 229 m elev, 20-VIII-1969, JB Wallace et al., 5L (PERC). **North Carolina:** Cherokee Co, Murphy, 29-VII-1930, HT Spieth, 80L (PERC); Graham Co, Panther Cr at SR1233, cc#7963, 10-VIII-1999, DL, NC, TM, CF, 2L (DRL); Stokes Co, Dan R, V-1982, 3L (PERC); Transylvania Co, M Fk French Broad R at SR1131, cc#8849, 8-VII-2002, 4L (DRL). **South Carolina:** Oconee Co, Chauga R at Chauga River Valley Development, 25 m elev, 14-VIII-1969, JB Wallace et al., 2L (PERC); Oconee Co, Little R at SC11, 253m elev, 7-VIII-1969, JB Wallace et al., 2L (PERC). **Virginia:** Montgomery Co, Little R at Rt787, 8-IX-1980, BC Kondratieff, 5MA, 2FA, 1SE, 6LE, 1L (emerged 11-IX-1980) (VPIC); same locale but 2-IX-1981, Kondratieff, 2MA, 1FA, 2LE (VPIC). **West Virginia:** Hampshire or Hardy Co, Cacapon R, 13-VIII-1930, JR Traver, 2L (*D. allegheniensis* paratypes) (CNC); same data, but JG Needham, 5L (PERC).

Drunella cryptomeria (Imanishi, 1937)

Ephemerella cryptomeria Imanishi, 1937 (orig. comb.).
Ephemerella nM Imanishi, 1940, **new synonym** (syn. with *E. longipes* by Tshernova, 1952).
Drunella lepnevae (Tshernova, 1949), **new synonym** (orig. as *Ephemerella*).
Drunella longipes (Tshernova, 1952), **new synonym** (orig. as *Ephemerella*, syn. with *D. lepnevae* by Tshernova et al., 1986).
Drunella bicornis (Gose, 1980) (orig. as *Ephemerella*, syn. by Ishiwata, 2001).
Drunella fusongensis Su and Gui 1995, **new synonym** (syn. with *D. lepnevae* by Kluge, 2004).
Drunella criptomeria (Imanishi): Bae and Soldán 1997, **incorrect spelling**.
Drunella criytomeria (Imanishi): Lee et al. 2001, **incorrect spelling**.

Diagnosis. *Drunella cryptomeria* larvae have a pair of suboccipital spines on the head, and they lack genal and frontoclypeal projections. The forefemora are relatively narrow, compared to most other *Drunella* species. Variable, paired spines are present on the hind margins of most abdominal terga.

Male adults (see Tshernova et al., 1986 for further diagnosis) have the genital forceps with segment 3 approximately three times as long as wide, and segment 2 has distinct, but not large, distal and proximal expansions (Imanishi, 1937: fig. 6, Tshernova et al., 1986: fig. 1). Penes have lateral margins that are relatively parallel.

Larval variability. Individuals from certain populations have paired, posterior spines on the abdominal terga that are more blunt than those of individuals from other populations. Also, the

Mongolian specimens we examined have a much denser field of setae on the abdominal sterna than do the Korean specimens we examined.

Discussion. Imanishi (1937) described *D. cryptomeria* based on adults only. Larvae recently were associated with reared adults by Ishiwata (2001). Ishiwata (2001) also showed that larvae identified previously as *D. cryptomeria*, e.g., by Yoon and Kim (1981), Gose (1985), Yoon and Bae (1988), Bae et al. (1994), Ishiwata and Inada (1996), Bae et al. (2000), and Quan et al. (2002) are referable to *D. ishiyamana*, due to an incorrect synonym proposed by Gose (1980).

Gose (1970) correctly associated *Ephemerella* nG Imanishi (only larva known) with *Ephemerella yoshinoensis* Gose (only adult known), but later Gose (1980) incorrectly synonymized these two names with *D. cryptomeria* (only adult known). It is probable that the mistake resulted from a comparison of only adults, given that adults of many *Drunella* species are similar with respect to body color and genitalia structure, even when their larvae are highly distinct.

Yoon and Kim (1981) reported *D. bicornis* (=*D. cryptomeria*) larvae from Korea, but Yoon and Bae (1988) treated these reports as misidentifications of *D. lepnevae*. We consider all these names and *D. longipes* (Tshernova) and *D. fusongensis* Su and Gui (previously synonymized with *D. lepnevae* by Tshernova et al. (1986) and Kluge (2004), respectively) synonymous, based on our comparison of series of larvae, reared material, and published descriptions (Imanishi, 1937, 1940; Tshernova, 1949, 1952; Gose, 1980; Su and Gui, 1995).

Material examined. MONGOLIA, **Egiyn-gol**, 40 km S of Khubsugul, 23/24-VIII-1997, N Kluge, 2MA, 1SE, 1 MS emerging from LE, 1L (PERC). KOREA (North), **Ryanggan Prov.**, Chonwon R, Li Myong Su, 24-VI-1986, 6L (PERC); Myohyang Mtns, Chou Liu (?) stream, 31-V-1986, 4L (PERC).

Drunella ishiyamana Matsumura, 1931

Ephemerella nG Imanishi, 1940 (syn. with *Ephemerella latipes* by Tshernova, 1952; syn. with *Ephemerella yoshinoensis* by Gose, 1970).

Ephemerella latipes Tshernova, 1952, **new synonym** (syn. with *D. cryptomeria* by Tiunova and Belov, 1984).

Ephemerella ishiyama Matsumura: Edmunds 1959, **incorrect spelling**

Ephemerella yoshinoensis Gose, 1963 (syn. with *D. cryptomeria* by Gose, 1980; syn. with *D. ishiyamana* by Ishiwata, 2001).

Diagnosis. Mature larvae have the frontal shelf with a distinctive medial notch. The head has three distinct transverse ridges between the occiput and the lateral ocelli (Kluge, 1997) that are covered with small excrescences. The ecdysial line passes through the middle of these ridges, and as a result, the ridges appear to be paired bumps. The distinctive forefemur, which is wider than that of *D. submontana*, has an upper surface with ridges that separate it into sections that appear sculpted. Two to four setae usually are present along the middle of the hind margin of the forefemur. The abdominal terga have paired, submedian ridges, and each ridge terminates in a short spine on the hind margin.

Male adults (Gose, 1963: fig. 6) have genital forceps segment 3 approximately twice as long as wide. Forceps segment 2 has only slight distal and proximal expansions. The penes have lateral margins that are relatively parallel. The genitalia are relatively pale in color.

Larval variability. Samples from single populations contained multiple morphological variants, in which the anterior margin of the frontal shelf is convex, truncate, or slightly concave. Suboccipital spines are absent in specimens collected from northern populations of

D. ishiyamana, but small subocciptal spines are present on specimens from the central part of its range. Larger spines are present on specimens collected from the southernmost part of its known range, demonstrating a clinal gradation of this character.

Discussion. Ishiwata (2001) conducted rearing experiments and showed that larvae of *D. ishiyamana* had been misidentified as *D. cryptomeria* (see Discussion for the latter species, above). Tiunova and Belov (1984) synonymized *D. latipes* (only larva known) under *D. cryptomeria*, presumably based on the incorrect concept of *D. cryptomeria* larvae created by Gose's (1980) incorrect synonymy (see above, under *D. cryptomeria*). In light of the corrected species concepts (Ishiwata, 2001) and the material we examined, we place *E. latipes* as a synonym of *D. ishiyamana*.

Larvae reported below from China and Vietnam represent the first reports of *D. ishiyamana* from the Oriental Region. Other Ephemerellinae species with a Far East Palearctic/East Oriental distribution include *Ephacerella longicaudata* (Ueno) (Allen, 1986) and *Uracanthella punctisetae* (Matsumura), which was reported as *Serratella rufa* (Imanishi) by Zhou et al. (1997) and as *Uracanthella rufa* by Tong and Dudgeon (2000).

Material examined. CHINA, **He Nan Prov.**, Song Xian County, Bai Yun Shan, 19-VII-2002, Jianxin Cui et al., 8L (PERC); JAPAN, 7-VIII-1903, Ishiyama, 1MA (*D. ishiyamana* type) (EIHU). **Nara Pref.**, Nakai stream, Unokawa, Kawakami, 8-VI-2002, T Fujitani, 7L (PERC). KOREA, Chungcheongbuk-do Jecheon Bongyan, Nomogyegok, 22-VIII-1995, 101L (SWU). KOREA (South), Sagimac Stream, trib Sacheon R, Kangneung Area, 16-VIII-1978, GF&CH Edmunds, S Nam, J Choe, 27L (PERC); Sangcheon R, nr Sokcho, Mt Sorak, 15/16-VIII-1978, GF&CH Edmunds, S Nam, J Choe, 78L (PERC). VIETNAM, **Loa Cai**, Sapa, Muong Hoa Ho R, 5/12-V-1995, D Currie, B Hubley, 2L (ROME); same data, 2L (PERC); 1.5 m wide stream nr mtn pass on rd from Sapa to Lai Chau, 8-V-1995, D Currie, 1L (ROME).

Drunella lata (Morgan, 1911)

Ephemerella lata Morgan, 1911 (orig. comb.).

Drunella cornuta (Morgan, 1911), **new synonym** (orig. as *Ephemerella*, nec *Ephemerella cornuta* Gose, 1980).

Ephemerella inflata McDunnough, 1926 (syn. by McDunnough, 1931b).

Ephemerella depressa Ide, 1930 (syn. with *D. cornuta* by Allen and Edmunds, 1962), **new synonym**.

Drunella cornutella (McDunnough, 1931), **new synonym** (orig. as *Ephemerella*).

Drunella longicornis (Traver, 1932), **new synonym** (orig. as *Ephemerella*).

Ephemerella cornuta Morgan—variety A. Traver, 1932 (Allen and Edmunds, 1962 recognized this variant as equivalent to *D. longicornis*).

Diagnosis. Mature larvae have a pair of variable frontoclypeal projections and a relatively well-developed median ocellar spine. Genal projections are absent. The upper surface of the forefemur is apparently smooth. Abdominal terga have paired, oblique, submedian ridges, but these ridges do not terminate in a spine on the hind margin.

Male adults have genital forceps segment 3 three times or more as long as wide, and segment 2 is bowed and usually has large distal and proximal expansions. The lobes of the penes usually are somewhat broadly rounded apically, as illustrated by McDunnough (1931b: Plate XII, figs. 3–5), Steger (1931: fig. 6), Traver (1932: fig. 1; 1935: fig. 153), Burks (1953: figs. 120–122), and Allen and Edmunds (1962: figs. 6–8).

Larval variability. Larvae vary considerably in color (Traver, 1932). We found that mature larvae grade through the body size characterizations of *D. cornuta* and *D. cornutella* (e.g., McDunnough, 1931a, b; Traver, 1932, 1935; Allen and Edmunds, 1962). Allen and Edmunds (1962: fig. 22a–e) showed that the development of frontoclypeal projections varied considerably in what they considered *D. cornutella*. We found an even greater range of development, including very short projections, such as those historically associated with *D. lata*, and longer projections, such as historically associated with *D. longicornis*. Frontoclypeal projection development usually is consistent within samples taken from a single population, although the curvature of these projections may vary considerably between individuals. Samples from different populations, however, show different degrees of development. Based on specimens we examined, including topotypic *D. cornuta* larvae from Salisbury, Connecticut, the frontoclypeal projection characterizations attributed to *D. lata*, *D. cornutella*, *D. cornuta*, and *D. longicornis* appear arbitrary. The median ocellar spine varies in some populations, ranging from very blunt to sharply pointed, as characterized for *D. cornuta*.

The relative development of the foretibial projections varies, and in some individuals, the projection is more curved than in others. In some larvae, the forefemora may appear relatively wider, such as described for *E. depressa* Ide (1930). We observed the shorter mid- and hindtibiae that McDunnough (1931b) described for *D. cornutella* in all morphotypes. The number of denticles on the claw varies, but is usually less than five, as noted by Allen and Edmunds (1962).

Adult variability. Equivalent, highly variable adults (see below) have been reared from each larval morphotype. Traver (1935) described size and color variation in adults. Female adults are typically lighter in color than males, such as described by McDunnough (1926) for *E. inflata* McDunnough.

Series of male adults that we examined show remarkable variation in the development of subgenital projections (ranging from absent to wide and blunt, or produced and pointed) and the shape and expansion of the genital forceps. This variability is most apparent in samples from Oswego and Sullivan Counties, New York, and in series of adults reared from larvae collected in Giles and Grayson Counties, Virginia. The degree to which the penes lobes are spread apart (Traver, 1935) varies within series reared from a single larval morphotype. The tips of the penes lobes of a few specimens are slightly sharper than most. The degree of upwards bending of *D. lata* penes is less than that of certain other *Drunella* species (McDunnough, 1931b), such as *D. walkeri*; however, the angle of the bend, as seen from the lateral view, is slightly variable. The length of forceps segment 3 varies and includes the short length variety (or even shorter) attributed to *D. cornutella* (McDunnough, 1931b). Some adults reared from larvae of the *D. cornutella* morphotype had forceps segments 3 much longer. Steger (1931) reared alates corresponding to the concept of *D. cornutella* from larvae of the *D. cornuta* morphotype (Traver, 1935).

Discussion. Koss (1968) and Studemann and Landolt (1997) provided equivalent egg data for *D. cornuta*, *D. cornutella*, and *D. lata*.

McDunnough (1931a) compared and contrasted the morphology and biology of *D. cornuta* and *D. cornutella*, and suggested a slower development and later emergence in early August for *D. cornutella*. We noticed that certain Quebec *D. lata* variants (corresponding most closely to the original concept of *D. lata*) emerged also in late July and early August. Steger (1931) noted that mature larvae were collected from various New York sites from May through July, and possibly from a West Virginia location in late August. Ulfstrand (1968) showed that separate populations of the same ephemerellid species can have different life cycle patterns,

and Dobrin and Giberson (2003) showed that several mayfly species co-occurring in an eastern Canadian coldwater stream exhibited a reduction in the synchronization of life-cycle patterns. The putative species synonymized here have been collected together from the same streams (Morgan, 1911; Traver, 1932; Penrose et al., 1982).

McDunnough (1931b) discussed his misidentification of some Quebec specimens of *Ephemerella dorothea* Needham (McDunnough, 1925) under the name *D. cornuta* (McDunnough, 1928). Genitalia labeled by McCafferty and Wang (2000: fig. 49) as *D. grandis* actually are attributable to *D. lata*. Edmunds (1962) had mistakenly listed the type locale of *D. lata* as New York (Jacobus and McCafferty, 2001b).

Material examined. CANADA, **Nova Scotia:** Annapolis R, 25-VI-1940, EL Bousefield, 2L (PERC); Cape George, Antigonish, 19-VI-1936, J McDunnough, 10L (CNC); Antigonash Co, Malignant Brook at Old Margvale Rd, jct Hwy245, 22-VI-1993, Baumann, Kondratieff, 1MS (pharate adult genitalia dissected out) (CSUC); Cr I Route 5, Baddeck, Cape Breton Island, 20-VI-1936, J McDunnough, 10L (CNC); Cape Breton Island, nr Margaree Har, 6-VII-1950, EL Bousefield, 3L (PERC). **Prince Edward Island:** Prince Co, Miminegash R at Hwy151, W of Lauretta, 19-VI-1993, Kondratieff, Baumann, 1L (CSUC). **Quebec:** Knowlton, 2-VIII-1929, J McDunnough, "10," 1MA (INHS); Knowlton, 7-VIII-1929, GS Walley, 1MA, "10," (*D. cornutella* paratype)(PERC); Bolton Glen Cr at Knowlton, 9-VII-1929, LJ Milne, 22L (CNC); Bolton Pass Cr at Knowlton, 3-VIII-1929, LJ Milne, 2L (CNC); Penny's Pasture Cr, Knowlton, emerged 12-VII-1929, LJ Milne, 2LE (CNC); Island of Orleans, Dauph Brook, 24-vii, René Malouin, 3L (CNC); Island of Orleans, Brook, 24-VII, René Malouin, 1L (CNC); LaPeche R at Wakefield, 12-VI-1930, J McDunnough, 1L (CNC); same locale but 25-VII-1930, GS Walley, 12L (CNC); Wakefield, 24-VI-1931, 8-VIII-1931, LJ Milne, 9L (CNC); Wakefield, 28-VII-1926, GS Walley, 1MA, "61," (*E. inflata* paratype)(PERC); Wakefield, 28-VII-1926, GS Walley, 1MA, 1SE, "61," (CNC); Sutton Mt Cr at Sutton, 11-VII-1929, J McDunnough, 33L (CNC). USA, **Connecticut:** Litchfield Co, Salisbury, 1L (*D. cornuta* NEOTYPE) (CNC); Middlesex Co, Hammonasset R at Killingworth, 25-V-1960, CRH, 10L (PERC). **Georgia:** Rabun Co, Betty's Cr, 5 mi W of Dillard, 20-VI-1973, B Stark, 1L (PERC); Coleman R at confluence with Talullah R, Coleman River Scenic Area, 610 m elev, 15-VII-1969, JB Wallace et al., 2L (PERC). **Kentucky:** Breathitt Co, Quicksand, 8-V-1947, POR&MWS, 4L (INHS); Clay Co, Goose Cr at confluence with Mud Lick Cr at Lipps, 9-V-1978, 1L (PERC); county uncertain, Jackson, 8-V-1947, Ritcher&Sanderson, 1L (INHS); **Maine:** Aroostook Co, Mud Lake on Fish R, 27-VII-1939, 1L (INHS); Aroostook Co, Soldier Pond, 22-VII-1939, 1L (INHS); Washington Co, stream along Hwy6, between Topsfield and Lake Lambert, 1-VI-1998, B Zwellig, 6L (CSUC). **Massachusetts:** Hampshire Co., E Br Mill R at Williamsburg, 5-V-1964, RW Koss, 2L (PERC); Mill R at North Hatfield, 15-III-1964, RW Koss, 2L (PERC). **Michigan:** Crawford Co, AuSable R, T26N, R2W, Sec13, 16-VII-1948 through 26-VII-1948, JW&FAL, 5MA, 3FS, 2SE, 7LE, 1L (UMMZ); AuSable R at Reith Haven, 26-VII-1948, JW&FAL, 2MA (UMMZ); S Br AuSable R, 2-VIII-1948, JW&FAL, 1MA, 1SE, 1LE (UMMZ); Grand Traverse Co, Boardman R, T26N, R10W, Sec18, 5-VIII-1950, EB Hayden, Jr, 13L (UMMZ); Houghton Co, Otter R, 18-VI-1949 through 28-VI-1949, FA&JW Leonard, 39L (UMMZ); Lake Co, Pere Marquette R, T17N, R13W, Sec16, 28-VII-1947, 3MA, 1FA, 4SE, 4LE, 20L (UMMZ); Oceana Co, White R at Pines Point Rec Area, access at campground, Manistee NF, 6-VII-1996, P Randolph, C Ellis, 4L (PERC). **New Hampshire:** Carroll Co, Thompson Falls, Gorham, 20-VII-1929, McDunnough, Walley, 13L (CNC); Coos Co, Imp Cr, Pinkham Notch nr Mt Washington, 23-VI-1941, Frison&Ross, 2L (INHS); Grafton Co, Ammonoosic R at Zealand Campsite,

US302, 16-VI-1976, WP McCafferty, AV Provonsha, M Minno, 2L (PERC); Zealand R nr Sugarloaf Campsite, 16-VI-1976, WP McCafferty, M Minno, AV Provonsha, 10L (PERC); Warren, 21-VI-1941, Frison&Ross, 1L (INHS). **New Jersey:** Sussex Co., 23-VI-1973, RL Jacques, Jr., 5L (PERC). **New York:** Green Lake, 16-V-1931, JRT, 1L (PERC); Albany Co, Catskill Cr, 1.9 mi N of Preston Hollow, 15-VI-1964, DW Root, 2MA (PERC); Hamilton Co, Cedar R, nr Indian Lake, Adirondack SP, 20-VI-1941, Frison&Ross, 1L (INHS); Oswego Co, Salmon R at Hwy13, SE Pulaski, 17-VI-1997, Kondratieff, Baumann, 1L, 16MA, 1FA (CSUC, PERC); Sullivan Co, Beaver Kill at Old Rt 17, 4-VI-2000, SW Hiner, 8MA (two sets genitalia on slides), 3SE, 5S (SWH). **North Carolina:** Avery Co, nr Banners Elk, 3-VI-1936, JR Traver, 1L (PERC); Heaton, 3-VI-1936, JR Traver, 8L (PERC); Haywood Co, Hazelwood, 24-IV-1938, Ross, Burks, 4L (INHS); Haywood Co, Plott Cr at end of Rt 1173, 7-VII-1981, Kondratieff, 2FA, 1LE, 8L (VPIC); Rocky Br of Allen Cr at Rt 1219, 7-VII-1981, Kondratieff, 2MA, 2FA, 3LE, 1L (VPIC); Jackson Co, Balsam, 24-IV-1938, Ross, Burks, 15L (INHS); Jackson Co, Cedar Cr nr Glenville, 30-VI-1929, JR Traver, 3L (CNC); Madison Co, Hot Springs, Pisgah NF, 15-VI-1934, HH Ross, 8L (INHS); McDowell Co, Catawba R at Andrews Geyser, 15-VI-1929 through 17-VI-1929, 2MA, 2FA, 1FS, 4SE, 4LE (PERC). **Pennsylvania:** Fayette Co, Meadow Run at PA381, Ohiopyle, 39°51′48″N, 79°29′43″W (WGS84), 26-V-2002, LM Jacobus, 2L (PERC); Snyder Co, Middle Cr at Beavertown, vi-1939, CM Wetzel, 3L (INHS); Westmoreland Co, Furnace Run at Laughington, 15-VII-1976, JS Weaver, 1MA (CSUC). **South Carolina:** Pickens Co, Estatoe Cr, Laurel Valley Rd, 35°03′N, 82°49′W, 13-V-1997, S Spichiger, 9L (PERC). **Tennessee:** Blount and Sevier Cos, GRSM, 8 ATBI collecting sites, 14/19-V-2001, CD&RP Randolph, LM Jacobus, 60L (PERC); Sumner Co, Bledsoe Cr at jct 31E & Rt231, 9-IV-1994, B Kondratieff, RF Kirchner, 7L (CSUC). **Vermont:** Addison Co, Battell SP, 19-VI-1952, Coler, 4L (PERC); Windhams Co, Whetstone Brook at Brattlesboro, 20-VI-1976, WP McCafferty, AV Provonsha, M Minno, 82L (PERC). **Virginia:** Amherst Co, Cragshaw Cr, 14-IV-1976, G Knaver, 1L (VPIC); Bath Co, Jackson R, V-1973, B Strickler, 10L (VPIC); Giles Co, Big Walker Cr, 25-IV-1976, R Young, 6L (VPIC); Giles Co, Big Stoney Cr at Rt635, 14-VI-1977, Powell, 1MA, 1SE (VPIC); Giles Co, Sinking Cr at Newport, Rt 42, 26-V-1981, emerged 2-VI-1981, Kondratieff, 5MA, 3FA, 7LE (VPIC); Grayson Co, Fox Cr at Rt 603, 18-VII-1981, Kondratieff, 7MA, 8FA, 1FS, 1SE, 12LE, 10L (VPIC); Roanoke Co, 10-V-1976, J Harrison, 3L (VPIC); Rockingham Co, North Fk, jct Rt259/Rt280, 6-V-1979, RG Bellinger, 11L (VPIC); Smyth Co, Lewis Fork nr Lewis Fork Trail at Rt603, 14-VIII-1979, Kondratieff, 1L (VPIC). **West Virginia:** Mingo Co, Laurel Cr, 2 mi S of Dingess, 29-V-1993, Kondratieff, Kirchner, 7L (CSUC); Wayne Co, Millers Fork at Beech Fork, 15-V-1986, Kondratieff, 1L (CSUC); no other data, D Tarter, 1L (PERC).

Drunella submontana (Brodsky, 1930)

Ephemerella submontana Brodsky, 1930 (orig. comb.).

Ephemerella svenhedini Ulmer, 1936, **new synonym**.

Drunella traverae (Allen and Edmunds, 1963) (orig. as *Ephemerella*, syn. by Kluge, 2004).

Drunella borakensis (Allen, 1971) (orig. as *Ephemerella*, syn. by Allen, 1974).

Drunella nasiri (Ali, 1971) (orig. as *Ephemerella*, transferred to *Crinitella* by Hubbard and Peters, 1978, transferred to *Drunella* by Jacobus and McCafferty, 2003d, syn. by Kluge, 2004).

Drunella kabulensis (Allen, 1973) (orig. as *Ephemerella*, syn. by Kluge, 1997).

Ephemerella sevenhedini Ulmer: Gui 1985, **incorrect spelling**.
Ephemerella svenhenidi Ulmer: You and Gui 1995, **incorrect spelling**.

Diagnosis. Larvae have the frontal shelf with a shallow medial notch. Distinct suboccipital spines are present, and the head is relatively smooth between the occiput and the lateral ocelli (Kluge, 1997). Distinctive ridges are present on the upper surface of the forefemur, but the forefemur is not as wide as that of *D. ishiyamana*. Abdominal terga have paired, submedian ridges, and each ridge terminates in a spine on the posterior margin of the abdominal tergum.

Male adults (Kustareva, 1976: fig. 2c; Landa and Soldán, 1983: figs. 67, 68) have genital forceps segment 3 approximately twice as long as wide. Forceps segment 2 is little expanded distally and proximally. The penes have lateral margins that are relatively parallel. The genitalia are relatively dark in color.

Larval variability. In addition to larval size and color variability discussed by Kustareva (1976), we found that the relative development of suboccipital spines is variable within single populations. The shape of these spines varied from sharp to blunt. On most individuals, the suboccipital spines projected parallel to one another, but some individuals had the spines with a slightly divergent orientation.

Adult variability. The preservation of adult specimens affects their appearance and color. The *E. svenhedini* Ulmer holotype is a pinned specimen. The penes on this type are folded together, and the forceps are shriveled and twisted as illustrated by Ulmer (1936: figs. 1, 2) and You and Gui (1995: fig. 143a, b). The shape of forceps segment 3 is difficult to ascertain for *E. svenhedini* because of the contorted state of the forceps. Careful examination, however, revealed that segment 3 was elongate and typical of *Drunella*. The pinned type is slightly darker than other *D. submontana* adults and subimagos preserved in alcohol, but it does fall within an expected range of color variability.

Discussion. *Drunella submontana* is a primarily central Asian species (e.g., Braasch, 1981; Landa et al., 1982; Landa and Soldán, 1983; Tshernova, 1972; Kluge, 1997). The presence of *D. submontana* (as *E. svenhedini*) in central China represents part of the easternmost extent of its geographic range.

Brodsky (1930) provided an incomplete description of *D. submontana* larvae in the original description of the species. Based on these larval characteristics, Ueno (1953) reported the species from central Asia, and Allen and Edmunds (1963) assigned it to *Drunella*. The larva later was described more completely by Tshernova (1972). Allen and Edmunds (1963) and Allen (1971, 1973) had not seen this latter larval description (Allen, 1974) when they described *D. traverae* (Allen and Edmunds), *D. borakensis* (Allen), and *D. kabulensis* (Allen), respectively, based on larvae only. Our examination of *D. kabulensis* and *D. traverae* type material revealed no consistent differences from other *D. submontana* material, including reared, associated material from Tajikistan.

Material examined. AFGHANISTAN: **Kabul Prov.**, Kabul R nr Dara Paghman, 29-VI/7-VII-1967, M Nazim, 17L (*D. kabulensis* paratypes) (PERC); Kabul R nr Paghman, 10 mi SW of Kabul, 1-VIII-1967, G Sharafi, M Zaher, RE Pfadt, 8L (PERC); Kabul R nr Paghman, 26-VII-1967, M Nazim, 26L (*D. kabulensis* paratopotypes) (PERC); Kabul R nr Paghman, 9-VIII-1967, G. Sharafi, M. Zaher, R. E. Pfadt, 6L (*D. kabulensis* paratypes) (PERC). **Paktia Prov.**, Ghaljaii, Gardez, 28-VII-1967, G Sharafi, M Zaher, RE Pfadt, 8L (*D. kabulensis* paratypes) (PERC); Shewat, 10 mi NE Gardez, 9-VI-1967, G Sharafi, M Zaher, RE Pfadt, 1L (*D. kabulensis* paratype) (PERC); CHINA: "Kina, S. Kansu; Sven Hedins Exp Ctr. Asien, Dr *Hummel*; 30/6" 1MA (*E. svenhedini* holotype) (NHRS). INDIA: **Kashmir**, Sind Valley, ca.

30 mi NE Srinagar on road to Tangmang, elev. ca. 6,500', 5-IX-1968, C. Weins, 3L (PERC); 22 mi W Srinagar on road to Tangmang, elev ca. 6,500', 5-IX-1968, C Weins, 7L (PERC); "L.11" stream E of Nuvla, 31-V-1933, Yale N India Expedition, GE Hutchinson, 1L (*D. traverae* holotype, parts on slides). TAJIKISTAN: **Kolai-Humb. Distr.**, Pamirs, nr nulvand, 20-IX-1987, N. Kluge, 1MA, 1SE, 1MS, 2LE (PERC).

Drunella tuberculata (Morgan, 1911)

Ephemerella tuberculata Morgan, 1911 (orig. comb.).
Drunella conestee (Traver, 1932) (orig. as *Ephemerella*, syn. by McCafferty, 1993).
Ephemerella cherokee Traver, 1937 (syn. by Allen and Edmunds, 1962).

Diagnosis. Larvae almost always have prominent, paired, stout, suboccipital spines. In contrast to *D. walkeri*, a row of long, hairlike setae is present along the margin of the clypeus. Paired, oblique ridges are present on the abdominal terga. Each ridge terminates in a thick, blunt, stout spine on the posterior margin of the tergum. Hairlike setae are present on the hind margins of abdominal terga. Long, hairlike setae protrude dorsally on abdominal terga 8 and 9. Setae protrude posteriorly, recumbent against the body, on the more anterior segments.

Male adults have genital forceps segment 3 approximately three times as long as wide. Genital forceps segment 2 is little expanded distally and proximally. The penes lobes may be slightly convergent, as best illustrated by McDunnough (1931b: Plate XII, fig. 1), Traver (1932: fig. 27), Traver (1935: fig. 153), Burks (1953: fig. 118), and Allen and Edmunds (1962: fig. 9).

Larval variability. Traver (1932) noted that *D. conestee* (Traver) was "quite variable in size and color." McCafferty (1993) showed that *D. tuberculata* have variation in the relative development of the frontal shelf, genae, and body spines. A sharp, lateral spine is variably present or absent in the middle of the lateral edge of the prothorax. McCafferty (1993) also noted variation in the number of excrescences on the broad, upper, surface of the forefemur, and Allen and Edmunds (1962) noted variation in the number of "tubercles on the ventral (leading) edge" of the forefemur. We observed variation in the relative length of the tibial projection on the foreleg. The claws usually have five or fewer denticles (Allen and Edmunds, 1962).

Certain variants of *D. tuberculata* (see material examined from Blount County, Tennessee and Graham County, North Carolina) closely resemble *D. allegheniensis* in coloration and dorsal spine development, but these variants may be distinguished from *D. allegheniensis* by the presence of longer setae on the margin of the frontal shelf and long, dorsally projecting setae present on abdominal terga 8 and 9.

Certain *D. tuberculata* larval variants may be difficult to distinguish from *D. walkeri*, especially if silty debris has accumulated in the rows of long, marginal setae on the body. Such accumulation sometimes makes the specimen appear larger and more flattened, much like *D. walkeri* (see below). Specimens fixed in alcohol with their legs outspread appear much more flattened than specimens with legs held against the body. Debris also may obscure examination of the genal projections of the head, giving the impression that the genal projections are well developed, when, in fact, they are not. Some *D. tuberculata* specimens, however, do have remarkably long genal projections (see material examined, below, from Smyth County, Virginia).

Immature *Drunella* larvae often have character states substantially different from more mature larvae. For example, at least four different instars of *D. tuberculata* were collected together from Overflow Creek, Macon County, North Carolina on July 10, 1991. These included early instars matching McCafferty's (1985) description of "*Drunella* sp." from

a branch of the Chattooga River in Rabun County, Georgia. These immature larvae have distinctive paired, stout, bristlelike setae present on the posterior margins of abdominal terga 8 and 9. We found that these bristlelike setae are present also in later instars, but they are much more elongate and become obscured by the rows of marginal, long, hairlike setae that become more conspicuous in successive instars. Bristlelike setae or tufts of hairlike setae often appear at the sites of developing spines in early instars, and such setae may appear in lieu of spines in later instars. We have observed this phenomenon not only in various Ephemerellidae, but also in some African Baetidae (Jacobus and McCafferty, 2001a, 2003c).

Adult variability. Adults vary in size, with many individuals appearing relatively robust, and a few appearing smaller and more slender. Wing vein color varies from the yellow historically associated with *D. conestee* to the dark brown historically associated with *D. cherokee* (Traver) (Traver, 1932, 1937; Allen and Edmunds, 1962). South Carolina alates reared from larvae of the *D. conestee* variety generally have pale femora. Variability in hindfemoral maculation has important ramifications for the proper identification of eastern Nearctic *Drunella* species, because Kondratieff et al. (1981) utilized this character to distinguish *D. tuberculata* and *D. allegheniensis* adults. Certain variants of *D. walkeri* (see below) also have little or no maculation on the hindfemora. *Drunella allegheniensis*, *D. tuberculata*, and *D. walkeri* are very similar as adults, but possibly may be separated by careful examination of the mesothorax, abdominal sterna, and the penes of the male (see Diagnosis, above). The ventral maculation of the abdominal sterna, however, is variable in *D. tuberculata*, and any differences in the length and thickness of genital forceps segment 3 between *D. tuberculata* and *D. walkeri* (McDunnough, 1931b) are only slight. Too few *D. tuberculata* adults reliably associated with larvae were available for us to determine the exact degree of variation of the forceps.

Discussion. *Drunella tuberculata* and *D. walkeri* co-occur as instars of similar maturity in the Second Broad River, Rutherford County, North Carolina and the Middle Prong, GRSM, Blount County, Tennessee. *Drunella tuberculata* also may co-occur with *D. allegheniensis* (see Discussion under *D. allegheniensis*).

Penultimate or final instars of *D. tuberculata* (confirmed by rearing) were collected during May, August, and October from Oconee County, South Carolina. These collection dates indicate either the presence of at least three synchronous generations per year or multiple cohorts with overlapping life cycles. This latter situation apparently pertains to certain other polytypic Ephemeroptera species (Dobrin and Giberson, 2003), and it may be the case for *D. lata* (see above). A classic example from *Stenacron* Jensen (Ephemeroptera: Heptageniidae) is explained by McCafferty and Huff (1978) and McCafferty and Pereira (1984).

Certain larval material listed below for which no locale is available likely corresponds to material reported from western North Carolina by Howell (1941).

Material examined. CANADA, **Ontario:** Ottawa Golf Club, 11-VIII-1925, 5MA (CNC). **Quebec:** Diable R at Biological Station, Mont Tremblant, 17-VII-1959, BV Peterson, 1L (PERC); Power Cr at Foster, 15-VII-1930, LJ Milne, 14L (CNC); Yamaska R at Foster, Foster Power Plant, 10-VII-1929, GS Walley, 1MA (reared from larva) (CNC). USA, **Georgia:** Fannin Co, Toccoa R, 12-VII-1975, 1L (CSUC); Rabun Co, Branch to Chattooga R on GA28, 2.8 mi N of SC state line, 640 m elev, 11-VI-1969, JB Wallace et al., 1L (PERC); Rabun Co, Chattooga R at Forest Service Rd 646, 579 m elev, 11-V-1969, JB Wallace et al., 1L (PERC); Rabun Co, Dick's Cr at Rt197, 576 m elev, 15-VII-1969, JB Wallace et al., 1L (PERC). **Maine:** Franklin Co, Oquossoc, 24-vii, 1MA (PERC); Washington Co, Kellyland, 20-vii, 1MA (PERC). **Maryland:** Prince George's Co, Paint Branch Creek nr Beltsville, 20-V-1930, A Rutledge, 1L, 1LE (INHS); same locale, but near powder mill bags, 4-VI-1930, A Rutledge, 1L

(PERC). **New York:** Rte11d, M.Champlain, 17-VI-1952, Coles, 3L (PERC). **North Carolina:** Buncombe Co, Mineral Cr, cc#6381, 30-VIII-1993, 10L (PERC); Burke Co, Henry R, cc#4529, 20-IV-1988, 6L (PERC); Graham Co, UT Little Buffalo Cr, cc#5325, 19-VI-1990, 5L (PERC); Graham Co, Panther Cr at SR1233, cc#7963, 10-VIII-1999, DL, NC, TM, CF, 2L (DRL); Graham Co, Snowbird Cr at NC1120, 20-VI-1990, cc#5320, 6L (PERC); Haywood Co, Cataloochee Cr at rd ca. 0.2 mi N of Palmer House, GRSM, 35°38′36″N, 83°4′38″W, 25-IX-2002, LM&PD Jacobus, 1L (PERC); Haywood Co, Jonathan's Cr, cc#5996, 18-VIII-1992, 11L (PERC); Henderson Co, Mills R at SR1337, cc#5881, 8-VII-1992, 6L (PERC); Jackson Co, stream on NC107, 3.5 mi N of state line, 1,067 m elev, 7-VIII-1969, JB Wallace et al., 2L (PERC); Jackson/Transylvania Cos, Whitewater R at Co Rt 171, 823 m elev, 1-VIII-1969, JB Wallace et al., 5L (mouthparts on slide)(PERC); Macon Co, Big Cr, cc#4194, 5-VIII-1987, 7L (PERC); Macon Co, branch to Chattooga R by Highlands, 746 m elev, 31-VII-1969, JB Wallace et al., 4L (PERC); Macon Co, Chattooga R by Highlands, 736 m elev, 31-VII-1969, JB Wallace et al., 3L (PERC); Macon Co, Edwards Cr, 5.6 mi on Walking Stick Rd from Highlands Biol Sta, 3-VII-1957, S&D Mulaik, 2L (PERC); Macon Co, Nantahala R, cc#5655, 10-VII-1991, 6L (PERC); Macon Co, Overflow Cr, 25-VIII-1938, T Howell, 3L (PERC); same locale, but cc#5026, 25-VII-1989, 6L (PERC); same locale, but cc#5654, 10-VII-1991, 14L (PERC); Macon Co, creek off NC106, nr Glen Falls by Highlands, 960 m elev, 23-VII-1969, JB Wallace et al., 2L (PERC); Macon Co, 0.9 mi from Hdqtrs, Coweeta Exp Forest, 30-VII-1957, S&D Mulaik, 4L (PERC); Macon Co, cat. no. 8-1055-1, no. 3861.4, L Berner, 5L (PERC); Macon/Swain Cos, 1.1 mi SW of Nantahala on Rt19 at county line, 20-VII-1957, S&D Mulaik, 5L (PERC); Rutherford Co, Second Broad R above Union Mills chip mill, 19-V-1999, KH, TM, DL, 1L (DRL); Swain Co, Collins Cr at Collins Cr Picnic Area, GRSM, 35°34′2″N, 83°20′11″W, 26-IX-2002, LM&PD Jacobus, 1L (PERC); Swain Co, Deep Cr, GRSM, 25-VIII-1931, 9L (PERC); Swain Co, GRSM, Flat Cr at Flat Creek Trail, downhill from 35°33′14″N, 83°9′50″W, 26-IX-2002, LM&PD Jacobus, 1L (PERC); Swain Co, Forney Cr, GRSM, 26-VIII-1931, JGN, 4L (PERC); Swain Co, Kanati Fk, 0.3 km upstream from Newfound Gap Rd (US441) (Kanati Fork Trailhead at 35°35′14″N, 83°21′48″W), 26-IX-2002, LM&PD Jacobus, 1L (PERC); Swain Co, Ocanaluftee R, 6-VII-1930, JR Traver, 1MS, 1FA, 1SE, 4LE (PERC); Swain Co, Ocanaluftee R, 28-VII-1930, 7L (CNC); Transylvania Co, Thompson R, cc#5072, 12-IX-1989, 11L (PERC); Transylvania Co, Mason Cr at SR1392, cc#8529, 24-VII-2001, JG, CT, NF, 1L (DRL); Transylvania Co, M Fk French Broad R at SR1131, cc#8849, 8-VII-2002, 2L (DRL); Transylvania Co, W Fk French Broad R, cc#5871, 6-VII-1992, 5L (PERC). **South Carolina:** Oconee Co, E Fk Chattooga R at Rt107, 1 km S of NC state line, "2U," 35°N, 83°4′W, 3-X-1997, S Spichiger, 1MA (genitalia on slide), 1MS, 2FA, 3FS, 2SE, 10LE, 8L (PERC); Oconee Co, E Fk Chattooga R at SC28, 2.2 mi N of Walhalla Fed Fish Hatchery, 847 m elev, 7-VIII-1969, JB Wallace et al., 3L (PERC); Oconee Co, E Fk Chattooga R at Walhalla FFH, 762 m elev, 1-VIII-1969, JB Wallace et al., 11L (PERC); Oconee Co, Little R at SC11, 3 mi S of Salem, 253 m elev, 11-V-1969, JB Wallace et al., 3L (PERC); Oconee Co, small stream at Co Rt 171, 1 mi S of jct Co Rt 413, 567 m elev, 1-VIII-1969, JB Wallace et al., 7L (PERC). **Tennessee:** Blount Co, Middle Prong at Gr Smoky Mtn Inst at Tremont, GRSM, 35°38′30″N, 83°41′25″W, 18-V-2001, CD&RP Randolph, LM Jacobus, 4L (PERC); Blount Co, Middle Prong at Tremont Rd, 50 m upstream from gate, Tremont, GRSM, 35°38′25″N, 83°41′23″W, 11-VI-2003, JM Webb, LM Jacobus, 1L (PERC); Cocke Co, Long Branch at Long Branch Rd, Cherokee NF, 22-V-1993, Kondratieff, Kirchner, 4L (CSUC); Sevier Co, Little R at Elkmont, 12/17-VI-1938, TH Frison, THF, Jr., 4L (INHS); same locale, but 14-V-1939, Frison, Ross, 1L (INHS). **Virginia:** Alleghany Co, Cowpasture R, 10 mi E of Clifton Forge, #73-53,

24-VI-1973, B Stark, 2L (PERC); Alleghany Co, Cowpasture R, 9-V-1976, AD Taylor, 2L (VPIC); Alleghany Co, Jackson R at I-64, 19-V-1980, J Queisser, 2L (VPIC); Bath Co, Big Back Cr at Jackson R, vi-1973, B Strickler, 1L (VPIC); Botetourt Co, Craig Cr, 9/14-V-1976, G Knaver, AD Taylor, 3L (VPIC); Clarke Co, Shenandoah R at Berryville, 12-V-1938, Eugene Surber, 9L (parts on slide) (PERC); Giles Co, Big Walker Cr at Rt622, 13-IV-1974, R Kroontje, 1L (VPIC); Hanover Co, New R at 460 bridge, 12-V-1976, L Hornick, 1L (VPIC); Hanover Co, New R, 20-VI-1976, 1FA (VPIC); Hanover Co, Pamunkey R at confl N&S Anna R's, 1-VII-1971, Simmons, Blood, 1L (VPIC); Hanover Co, South Anna R at Rt657, 7/27-V-1978, Kondratieff, Voshell, 9L (VPIC); same locale, but 12-VI-1978, JR Voshell, Jr., 7L (VPIC); Hanover Co, South Anna R at Rt657, 12-VI-1978, Kondratieff, 6FA (VPIC); Highland Co, Bull Pasture R, 4-V-1974, M Dunn, 1L (VPIC); Montgomery Co, Little R at Rt787, 15-VI-1981, Kondratieff, 2FS, 2LE, 1L (VPIC); Montgomery Co, New R, 21-IV-1974, D Simonet, L Townsend, 2L (VPIC); Montgomery Co, New R at Rt625, 18-VI-1977, Kondratieff & Powell, 4FA (VPIC); Montgomery Co, Tom's Cr at Rt655, 23-VI-1976, FC Carle, 1FA (VPIC); Orange Co, Rapidan R, 8-V-1976, T Lawall, 1L (VPIC); Page Co, S Fk Shenandoah R at Grove Hill, 17-V-1972, EW Surber, 2L (VPIC); Rappahannock Co, Thornton R at Hwy211, #73-50, 22-VI-1973, Stark, Baumann, Pine, 1L (PERC); Roanoke Co, Back Cr, 12-V-1976, G Knaver, 2L (VPIC); Roanoke Co, Roanoke R, 9-V-1976, J Harrison, 2L (VPIC); Rockingham Co, S Fk Shenandoah R at Goods Mill, 28-IV-1972, EW Surber, 1L (VPIC); Shenandoah Co, N Fk Shenandoah R at Mt Jackson, 16-VI-1971, EW Surber, 1L (VPIC); Smyth Co, N Fk Holston R at Rt620, 11-V-1986, Kondratieff, 1L (CSUC); same locale, 27-V-1992, B Kondratieff, RF Kirchner, 7L (CSUC). **No locale given:** J-84-no.676, 20-VII-1939, T Howell, 2L (PERC); 5-94-No.844, 13-VIII-1939, T Howell, 1L (PERC); stat.59(a), 20-VI-1930, 1L (PERC); stat.69, died 18-VII-1930, 1L (PERC); stat.78, 11-VII-1930, 1LE (PERC); "Stat.78(b)/6/22/30," 5L (PERC); stat.101, 10-VII-1930, 2L (PERC).

Drunella walkeri (Eaton, 1884)

Ephemerella walkeri Eaton, 1884 (orig. comb., renaming of *Baetis fuscata* Walker).
Ephemerella fuscata (Walker, 1853), (orig. as *Baetis*, nec *B. fuscata* Stephens, 1835).
Ephemerella bispina Needham, 1905, adult nec larva (syn. by McDunnough, 1931b; lectotype designated by Allen and Edmunds, 1962).
Drunella wayah (Traver, 1932), **new synonym** (orig. as *Ephemerella*, syn. with *D. tuberculata* by McCafferty, 1997).

Diagnosis. Larvae appear very dorsoventrally flattened. The mid- and hindlegs have somewhat expanded femora. Paired, posteromedial projections on the abdominal terga are flattened and triangulate. Long setae are present on the hind margins of abdominal terga, and these setae protrude dorsally on abdominal terga 8 and 9. The setae protrude posteriorly, recumbent against the body, on the more anterior segments. The most reliable character for separating *D. walkeri* larvae from sympatric congeners, however, is the absence of a row of long, hairlike setae on the clypeus.

Male forceps segment 3 may be shorter than that of *D. tuberculata*; otherwise, *D. tuberculata* and *D. walkeri* are very similar (McDunnough, 1931b) (see above). The penes may be slightly divergent, giving the penes a wider appearance. This is illustrated best by McDunnough (1931b: Plate XII, fig. 2), Traver (1935: fig. 153), Burks (1953: fig. 119), and Allen and Edmunds (1962: fig. 10). Many alates have the transverse shelf of the head produced on either side of the nasal carina.

Larval variability. McDunnough (1931b) noted color variants of pale gray and dark olive-brown, and dorsal abdominal maculation was usually present in specimens he examined. The shape and degree of development of the genae varies within samples from single populations, such as those from Big Otter River, Bedford County, Virginia, which contained both *D. walkeri* and *D. wayah* morphotypes. The anteromedian notch of the frontal shelf varies slightly in depth. The development of suboccipital spines ranges from small bumps (McDunnough, 1931b; Traver, 1935) to more prominent spines. For example, Jay Traver had noted the development of suboccipital spines in some larvae of her species, *D. wayah* (Howell, 1941). A sharp, lateral, spine (McDunnough, 1931b) is variably present or absent in the middle of the lateral edge of the prothorax. The relative expansion of the foretarsus and the length and curvature of the tibial projection varies slightly. This variation, however, encompasses the typical forms of *D. walkeri* and *D. wayah*. The number and relative prominence of tubercles along the edge of the forefemora varies sometimes between the right and left legs of a single specimen. The mid- and hindfemora are flattened and expanded, but the degree of expansion is variable to the extent that differences could not be distinguished between "typical" *D. walkeri* and *D. wayah*. The paired, posteromedian projections on the abdominal terga vary in shape. Some are barely visible, and others are long and sharp. Some posteromedian projections were reminiscent of those found in *Ephemerella invaria* (Walker) (Jacobus and McCafferty, 2003c).

Individual larvae sometimes differ in the degree of apparent dorsoventral flattening of the thorax. Traver (1932) noted that some *Drunella* larvae cling to rocks with the thorax "humped up." Some individuals appear arched, but others appear highly depressed when viewed laterally. The flattened appearance of the body diminishes somewhat as larvae grow, and many final instar *D. walkeri* are not much more flattened than some final instar *D. tuberculata*.

Adult variability. Some adults and subimagos may have the transverse shelf of the head produced on either side of the nasal carina. Forceps segment 3 varies slightly in length and width, occasionally appearing shorter and more slender in some specimens.

Adults also vary with respect to the degree of abdominal maculation. Those from Lake County, Michigan have faint median spots and oblique dashes, but others from the AuSable River, Crawford County, Michigan, have prominent maculation. The abdominal sternal maculation, when present, varies in color from light purple to black. McDunnough (1931b) and Allen and Edmunds (1962) had distinguished *D. walkeri* (as *Ephemerella fuscata*) from *D. tuberculata* based on the maculation of the abdominal sterna. We found this character to be variable, as indicated above, and thus included only adults positively associated with larvae in our analyses of *D. allegheniensis*, *D. tuberculata*, and *D. walkeri*. Lake County, Michigan, specimens demonstrated variability in the maculation of the adult femora. The femora ranged from being marked prominently with dark spots to being almost entirely pale with few, if any, faint dark spots. The latter characterization is similar to that described for *D. allegheniensis* by Kondratieff et al. (1981).

Discussion. Spieth (1940) and Allen and Edmunds (1962) discussed the identification and nomenclatural histories of *D. walkeri*. It remains a valid replacement name (Eaton, 1884) for *Ephemerella fuscata* (Walker, 1853), based on Article 59 of the current International Code of Zoological Nomenclature (1999).

Our analysis of *D. wayah* is based on material prepared and identified by Jay Traver that was collected at the same time and place as the *D. wayah* holotype and paratypes (Macon and Rowan Counties, North Carolina). Based on the discovery of new diagnostic characters of significance in *Drunella*, this material was found to be conspecific with *D. walkeri*, rather than *D. tuberculata*, as had been proposed by McCafferty (1997).

Sampling from different stream sites in GRSM in June 2003 produced different instars of *D. walkeri*. Larvae collected together from any one location, however, were of similar instars. *Drunella walkeri* was collected together with *D. tuberculata* at some sampling sites (see Discussion for *D. tuberculata*).

One larva from Middlesex County, Connecticut had lost a leg as a younger instar. Two smaller legs were regenerated where one had been.

Certain larval material listed below for which no locale is available likely corresponds to material reported from western North Carolina by Howell (1941).

Material examined. CANADA, **New Brunswick:** NW Miramichi R, 13-VII-1951, EL Bousefield, 1L (PERC). **Nova Scotia:** Queens Co, Medway R at Hwy210, Bangs Falls, 24-VI-1993, B Kondratieff, Baumann, 1L (CSUC). **Ontario:** Ogoki, 24-VII-1952, JB Wallis, 1MA (CNC). **Quebec:** Cascades Point, 24-VI-1930, GS Walley, 32L (CNC); Mid Yamaska R at Fulford, 22-VI-1929, LJ Milne, 7L (CNC); St. Lambert, 4-VII-1927, GS Walley, 7MA, 2MS, 3FA (CNC). USA, **Connecticut:** Middlesex Co, Hammonasset R at Killingworth, 25-V-1960, CRH, 8L (PERC). **Georgia:** Fannin Co, Toccoa R, 24-III-1976, Kondratieff, 2L (CSUC); Rabun Co, Betty's Cr, 5 mi W of Dillard, #73-48, 20-VI-1973, B Stark, 4L (PERC); Rabun Co, Coleman R at confluence Talullah R, Coleman River Scenic Area, 610 m elev, 15-VII-1969, JB Wallace et al., 1L (PERC); White Co, Hwy129, 7 mi NW of Cleveland, #73-44, 19-VI-1973, B Stark, 1L (PERC). **Maine:** Penobscot Co, 4 mi W of East Corinth, 5-VI-1987, DE Ruiter, 4L (CSUC). **Massachusetts:** Hampshire Co, Batchelor Brook, South Hadley, 14-V-1949, T Dolan, JRT, 2L (parts on slide) (PERC). **Michigan:** Benzie Co, Platte R at Honor, 27-V-1939, Frison, Ross, 16L (INHS); Crawford Co, AuSable R, T26N, R2W, Sec13 (some labels read "at Rieth Haven"), 26-vi/18-VII-1948, JW&FA Leonard, 2MA, 5FA, 1FS, 4SE, 5LE (UMMZ); Crawford Co, AuSable R, T26N, R2W, Sec12, 5-VII-1951, LW&FA Leonard, 6MA (UMMZ); Grand Traverse Co, S Br Boardman R, T26N, R9W, Sec2, 27-VI-1947, JW&FA Leonard, 4L (UMMZ); Lake Co, Pine R at Walker Bridge, 5-VI-1936, JW Leonard, 2L (UMMZ); Lake Co, Pere Marquetter, 7-VII-1947, JW&FA Leonard, 2MA, 1FA (UMMZ); Lake Co, Pere Marquette R, T17N, R13W, Sec16, 29-vi/9-VII-1947, JW&FA Leonard, 18MA(3 dissected in vials), 61FA, 2MS, 2FS, 6SE, 4LE (UMMZ). **New Jersey:** Hunterdon Co, Musconetcong R at Rt31, 11-V-1980, Durniak, 6L (VPIC). **New York:** Hamilton Co, Cedar R nr Indian Lake, Adirondack Pk, 20-VI-1941, Frison, Ross, 3L (INHS); Oswego Co, Salmon R at Hwy13, SE of Pulaski, 17-VI-1997, Kondratieff, Baumann, 6L (CSUC, PERC). **North Carolina:** Haywood Co, Big Cr at Big Creek Picnic Area, GRSM, 35°45′5″N, 83°6′31″W, 12-VI-2003, JM Webb, LM Jacobus, 5L (PERC); Nash Co, Sandy Cr at SR1405, cc#9109, 21-IV-2003, 1L (DRL); Macon Co, Wayah Cr, 1-VII-1929, 2L (slide mounted)(-PERC); Nash Co, Swift Cr at SR1310 (downstream of Sandy Cr), cc#9113, 24-IV-2003, EB, TFM, BC, 3L (DRL); Rowan Co, nr Franklin, 1-VII-1929, JR Traver, 2L (CNC); Rutherford Co, Second Broad R above Union Mills chip mill, 19-V-1999, KH, TM, DL, 2L (DRL); Swain Co, Ocanaluftee R at turnoff on US441, ca. 5 mi N of Cherokee, GRSM, 35°31′59″N, 83°18′8″W, 15-V-2001, CD&RP Randolph, LM Jacobus, 2L (PERC); Swain Co, Twentymile Cr at Twentymile Trailhead nr Ranger Station, 35°28′7″N, 83°52′34″W, 18-V-2001, CD&RP Randolph, LM Jacobus, 1L (PERC). **Tennessee:** Blount Co, Abrams Cr, upstream from Cades Cove Picnic Area, GRSM, 35°36′14″N, 83°46′9″W, 16-V-2001, CD&RP Randolph, LM Jacobus, 9L (PERC); Blount Co, Abrams Cr at Cades Cove Picnic Area, GRSM, 35°36′19″N, 83°46′30″W, 16-V-2001, CD&RP Randolph, LM Jacobus, 16L (PERC); Blount Co, Anthony Cr at Anthony Creek Trail, ca. ¼ mi above horse camp, GRSM, 35°35′42″N, 83°45′48″W, 19-V-2001, CD&RP Randolph, LM Jacobus, 6L (PERC); Blount Co, Forge Cr at Parsons Branch

Rd/Forge Creek Rd, GRSM, 35°34′14″N, 83°50′53″W, 18-V-2001, CD&RP Randolph, LM Jacobus, 5L (PERC); Blount Co, Lynn Camp Prong Little R, Townsend, 15-V-1939, Frison, Ross, 1L (INHS); Blount Co, Mill Cr at Forge Creek Rd, GRSM, 35°35′3″N, 83°50′17″W, 18-V-2001, CD&RP Randolph, LM Jacobus, 4L (PERC); Blount Co, Middle Prong at Tremont Rd, 50 m upstream from gate, Tremont, GRSM, 35°38′25″N, 83°41′23″W, 11-VI-2003, JM Webb, LM Jacobus, 10L (PERC); Blount Co, Mill Cr in Cades Cove, 9-VI-1970, JB Wallace, FF Sherberger, 3L (PERC); Blount Co, Mill Cr nr Rabbit Creek Trailhead, Cades Cove, GRSM, 35°35′26″N, 83°51′10″W, 11-VI-2003, JM Webb, LM Jacobus, 8L (PERC); same locale, but 14-V-2001, CD&RP Randolph, LM Jacobus, 4L (PERC); Blount Co, Parsons Branch at jct Parsons Branch Rd&Hwy 72/129, GRSM, 35°29′59″N, 83°56′2″W, 18-V-2001, CD&RP Randolph, LM Jacobus, 3L (PERC); Cocke Co, Cosby Cr at Cosby entrance to GRSM, 35°46′59″N, 83°13′6″W, 17-V-2001, CD&RP Randolph, LM Jacobus, 1L (PERC); Sevier Co, Indian Cr at Maddron Bald Trail, N of Albright Grove, GRSM, 35°44′15″N, 83°16′41″W, 17-V-2001, CD&RP Randolph, LM Jacobus, 2L (PERC); Sevier Co, trib Little R at Jakes Cr trailhead above Elkmont Camp, GRSM, 35°38′45″N, 83°35′3″W, 16-V-2001, CD&RP Randolph, LM Jacobus, 1L (PERC). **Virginia:** Bedford Co, Big Otter R at Rt460, 23-IV-1982, Kondratieff, 3L (VPIC); Caroll Co, New R at Rt721 bridge, 20-IV-1980, S Golladay, 6L (VPIC); Floyd Co, Dodd Cr, 14-V-1974, JD Miller, 1L (VPIC); Floyd Co, Little R, 19-IV-1974, M Dunn, J Tertt, 1L (VPIC); Orange Co, Rapidan R, 29-IV-1974, T Baily, 1L (VPIC); same locale, but 29-IV-1976, 1L (VPIC); Pittsylvania Co, Sycamore Cr, 15-V-1976, P Murphy, 4L (VPIC); Prince Edward Co, Duckers Cr, 9-IV-1976, W Ruska, 2L (VPIC); Washington Co, S Fk Holston R nr Damascus, 24-IV-1977, GR Jenkins, 5L (VPIC). **No locale given:** "M68—No.429," 27-VI-1939, T Howell, 5L (parts on slides)(PERC); "M71—No.490," 27-VI-1939, T Howell, 1L (PERC); "Ephem. #05902," 24 MA (INHS).

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