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DIURA WASHINGTONIANA (HANSON) RESURRECTED FROM SYNONYMY WITH *D. NANSENI* (KEMPNY) (PLECOPTERA: PERLODIDAE), SUPPLEMENTED WITH A DESCRIPTION OF THE LARVA AND EGG AND COMPARISON TO OTHER CONGENERS

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ABSTRACT

Diura washingtoniana (Hanson, 1940) is reinstated from synonymy with *D. nanseni* (Kempny, 1900). The adult male and female are more completely described and the larva and egg of this species are described for the first time. Diagnostic features for *D. washingtoniana* are presented and this species is compared to the following congeners: *D. nanseni*, *D. bicaudata* (Linnaeus, 1758) and *D. knowltoni* (Frison, 1937) using line illustrations, scanning electron photomicrographs, and color photographs.

Keywords: Plecoptera, Perlodidae, *Diura washingtoniana* (Hanson, 1940), species propria, adult redescription, larval and egg description

INTRODUCTION

Two Nearctic species were added to *Diura* Billburg, 1820 when Hanson (1940) described *Dictyopterygella washingtoniana* from the Lakes of the Clouds between Mount Washington and Mount Monroe in the eastern United States and *Dictyopterygella hudsonica* from Baker Lake in northern Canada. Later Brinck (1949), in a comprehensive study on Swedish stoneflies, synonymized *Dictyopterygella* Klapálek, 1904 with *Diura* and *D. washingtoniana* and *D. hudsonica* with the Palearctic species *Diura nanseni* (Kempny, 1900) and *Diura bicaudata* (Linnaeus, 1758) respectively. The species synonymy of *D. hudsonica* with *D. bicaudata* has not presented any difficulty and was suggested by Hanson in his study as a possible outcome. The synonymy of *Diura washingtoniana* with *D. nanseni*, however, is more problematic.

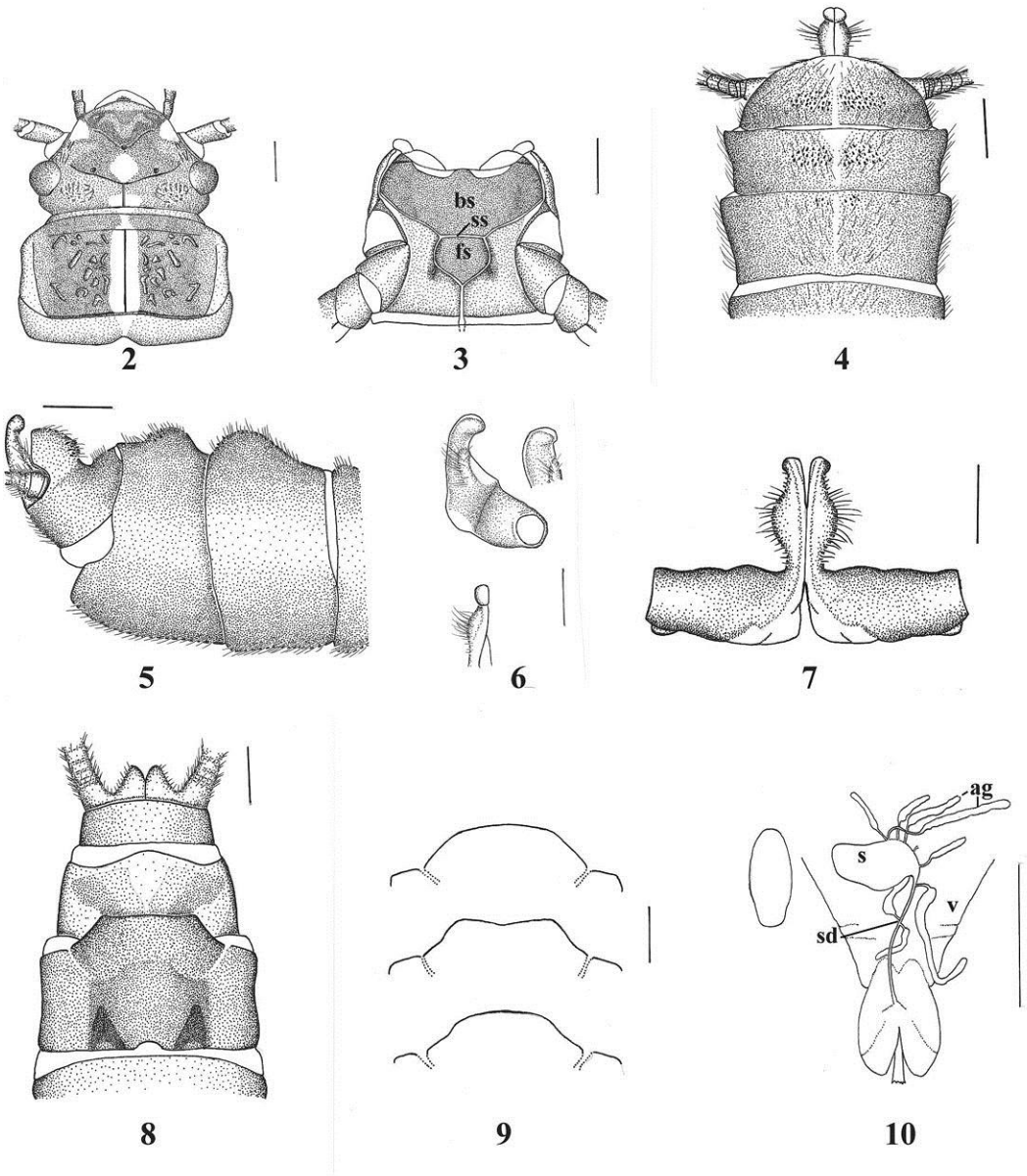
Brinck's conclusion regarding the synonymy of *D. washingtoniana* with *D. nanseni* was based on the apparent close similarity of these two allopatric forms. However, this assessment did not result

Fig. 1. *Diura washingtoniana*. Female and male habitus.

from Brinck's observation of representatives of *D. washingtoniana*, but on his interpretation of Hanson's original written description and illustrations of this species. Later, upon examining representatives of the Nearctic population, Brinck (1954) did note the existence of morphological differences between these two forms and concluded that they were separate geographic races or subspecies. The former he referred to as 'subsp. *washingtoniana* Hanson' and the latter as '*f. typica*'.

Brinck did not reference his conclusions to a specific species concept, but use of the subspecies category has been associated with the polytypic species of the reproductive isolation species concept (e.g., Mayr 1941, 2000, Mayr & Ashlock 1991, Ross 1974). In Plecoptera the subspecies has been employed by a number of workers (e.g., Aubert 1956, 1964, Berthélemy 1971, Berthélemy & Baena-Ruiz 1984, Hynes 1982, Ikonomov 1978, Kovács et al. (2012), Sanchez-Ortega & Ropero-Montero 1993, Stark et al. 1988, Theischinger 1983, 1984, Vinçon & Zhiltzova 2004, Vinçon & Ravizza 2005, Vinçon & Murányi 2009, Zhiltzova 1972, 1973, 1978, Zwick 1972 (1971), 1972, 1975, 1978a, 1978b). The decision of whether closely related allopatric populations are to be ranked as subspecies or species is generally dependent on the amount of morphological differences that exist between them. Here it is assumed that the degree of morphological differentiation corresponds to the degree of reproductive isolation. This correlation, however, has been questioned (Cracraft 1992) and some cladists (e.g., Cracraft 1989, 1992, Eldredge & Cracraft 1980, Nixon & Wheeler, 1990, Wheeler & Platnick 2000) have proposed using a phylogenetic species concept. This concept views reproductive isolation as just one of a number of outcomes of genetic divergence associated with speciation and that the species is the smallest lineage diagnosable by a unique suite of character states. Approaches for discriminating phylogenetic species are provided by Davis & Nixon (1992). Since the phylogenetic species concept regards the species itself as the terminal taxon, a subspecies that is demarcated by diagnosable features should be regarded as a species.

In any case, aside from Hitchcock's (1974) use



Figs. 2–10. *Diura washingtoniana*, adult. 2. Head and pronotum, dorsal. 3. Mesothorax, ventral. bs = basisternum, fs = furcasternum, ss =sternacostal suture. 4. Male terminalia, dorsal. 5. Male terminalia, lateral. 6. Paraproct caudal projections, lateral and frontal. 7. Paraprocts, ventral. 8. Female terminalia, ventral. 9. Examples of female subgenital plate variation. 10. Spermatheca and vagina. ag = accessory glands, s = spermatheca, sd = spermathecal duct, v = vagina. Scale bars = 0.5 mm.

of the trinomen to refer to the *D. washingtoniana* form, Brinck's conclusion concerning the subspecies status of this eastern Nearctic population appears not to have been adopted in published studies by workers (e.g., Stark et al. 1986, Lillehammer 1988, Stark et al. 1998, Nelson 2001, Kondratieff 2004) and was not incorporated into any modern stonefly catalogs (Illies 1966,

Zwick 1973, DeWalt et al. 2018). Thus, both the eastern Nearctic and Palearctic forms (with available names *D. washingtoniana* and *D. nanseni*) are currently referred to by the single name *Diura nanseni*.

To clarify the status of the name *D. washingtoniana* the adult male and female of this Nearctic form were reexamined and the larva and egg are described for the first time. This form is also compared to the Palearctic *D. nanseni* as well as two additional species, *D. bicaudata* and *D. knowltoni* Frison, 1937. This examination confirms Brink's 1954 observation of morphological discontinuities between *D. washingtoniana* and *D. nanseni*. It does not support, however, the taxonomic conclusion of that study or the conclusion of Brink's earlier 1949 work that *D. washingtoniana* is a synonym of *D. nanseni*. The diagnostic differences between *D. washingtoniana* and other species in this genus indicate, from the phylogenetic species perspective, that this form is a valid species and, therefore, is resurrected from synonymy with *D. nanseni*.

METHODS

Adult and larval anatomical features were examined in 70% ethanol using a Wild M-5 and Olympus SZX 12 stereomicroscopes. Eggs, and certain larval and adult structures were also examined and photographed using scanning electron microscopy (SEM). Prior to SEM examination these structures were removed from preserved specimens and placed in acetone, cleaned for 1–2 minutes in an ultrasonic cleaner and then dehydrated in increasing ethanol concentrations to 99% and then placed in 1,1,1,3,3,3-hexamethyldisilazane. Subsequently they were attached to aluminum stubs and coated with gold using a Hummer IV (Anatech Ltd.) sputter coater. Mounted specimens were studied using a JEOL JCM-5000 Bench top SEM (Neoscope) at the University of Tennessee at Chattanooga. Color photographs of adult head, pronotum, and male and female terminalia of each species were captured using either an Olympus DP 70 attached to the Olympus MVX microscope or Nikon D3200 digital camera attached to the Wild M-5 microscope.

Acronyms used in this study and for sources of the material used in this study are as follows: BYU-Monte L. Bean Life Science Museum, Brigham Young University, Provo, Utah, USA; CHNC – Charles H. Nelson Collection, University of Tennessee, Chattanooga, Tennessee, USA; CRN – laboratory notes and photographs of C.R. Nelson; PZC= Peter Zwick Collection, Schlitz, Germany; RASC – Russian Academy of Sciences, Far Eastern Branch, Institute Biology & Soil Sciences, Vladivostok, Russia; USNM – United States National Museum, Washington, DC, USA.

RESULTS

Taxonomy

***Diura washingtoniana* (Hanson, 1940), species propria**

Presidential Springfly

http://lsid.speciesfile.org/urn:lsid:Plecoptera.speciesfile.org:TaxonName:502549

Figs. 1 - 30

Dictyopterygella washingtoniana Hanson 1940:147. Holotype ♂, (USNM), Lakes of the Clouds, Mt. Washington, New Hampshire, USA
Diura nanseni Brinck 1949:65, in part
Diura nanseni "subsp. *washingtoniana*" Brinck 1954:199
Diura nanseni Illies 1966:383, in part
Diura nanseni Zwick 1973:228, in part
Diura nanseni washingtoniana Hitchcock 1974:230
Diura nanseni Stark et al. 1998: 56
Diura nanseni Nelson 2001:616, in part
Diura nanseni Kondratieff 2004:152, in part
Diura nanseni DeWalt et al. ~~2017~~ 2018: in part

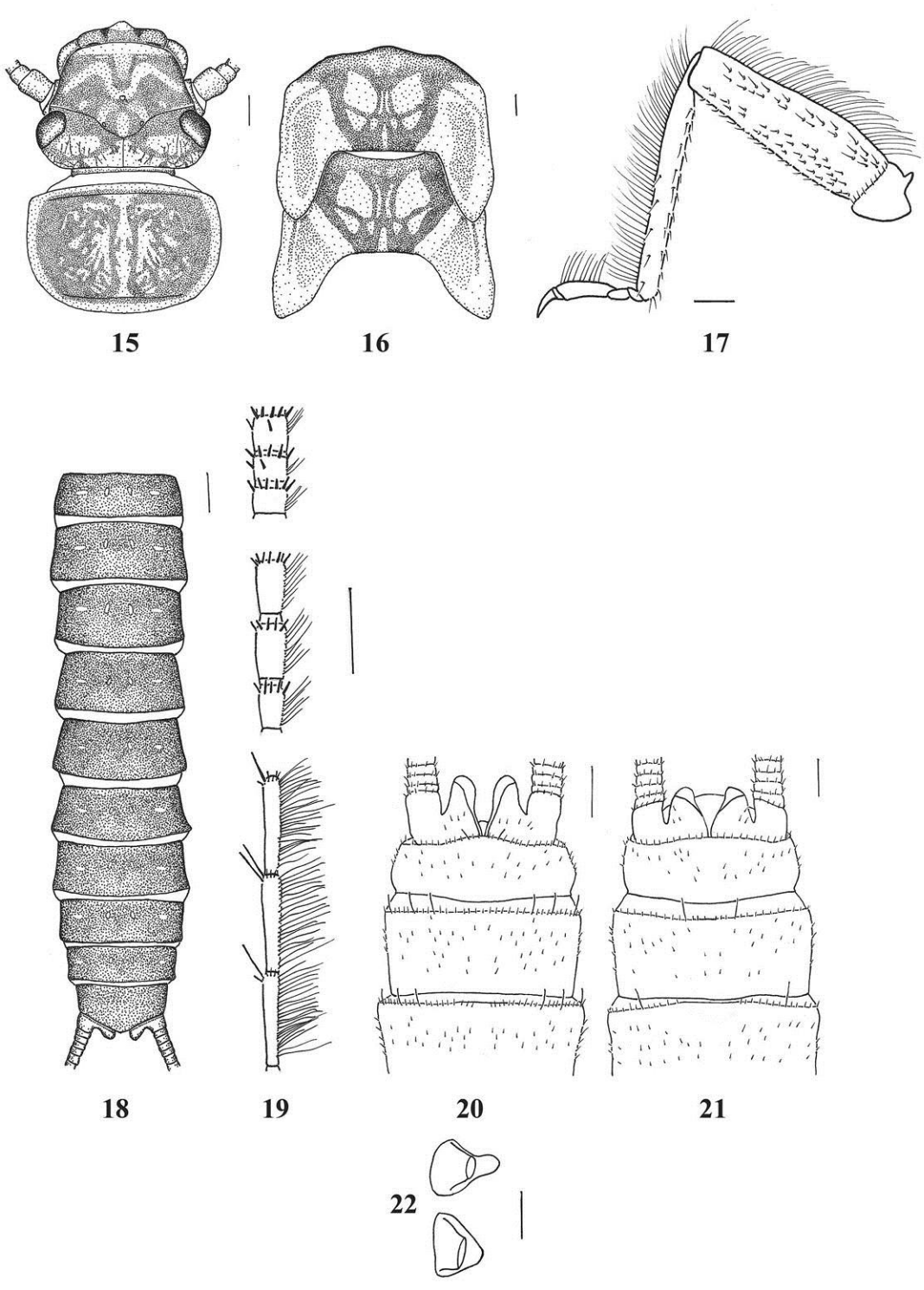
Material examined. Specimens of *D. washingtoniana* examined for this study are consistent with previous descriptions and illustrations (Hanson 1940, Brinck 1954, Hitchcock 1974, and Kondratieff 2004) of this species: **USA**; *New Hampshire*; Coos County, Lakes of the Clouds between Mt. Washington and Mt. Monroe, collector unknown, 4 July 1907, 1♂, 1♀ (paratopotypes) (CHNC). Same site, D. Arenburg,

Figs. 11–14. *Diura washingoniana* adult (Coos County, New Hampshire, USA). 11. Head and pronotum, dorsal. 12. Male terminalia, dorsal. 13. Male paraprocts, lateral, 14. Female terminalia, ventral.

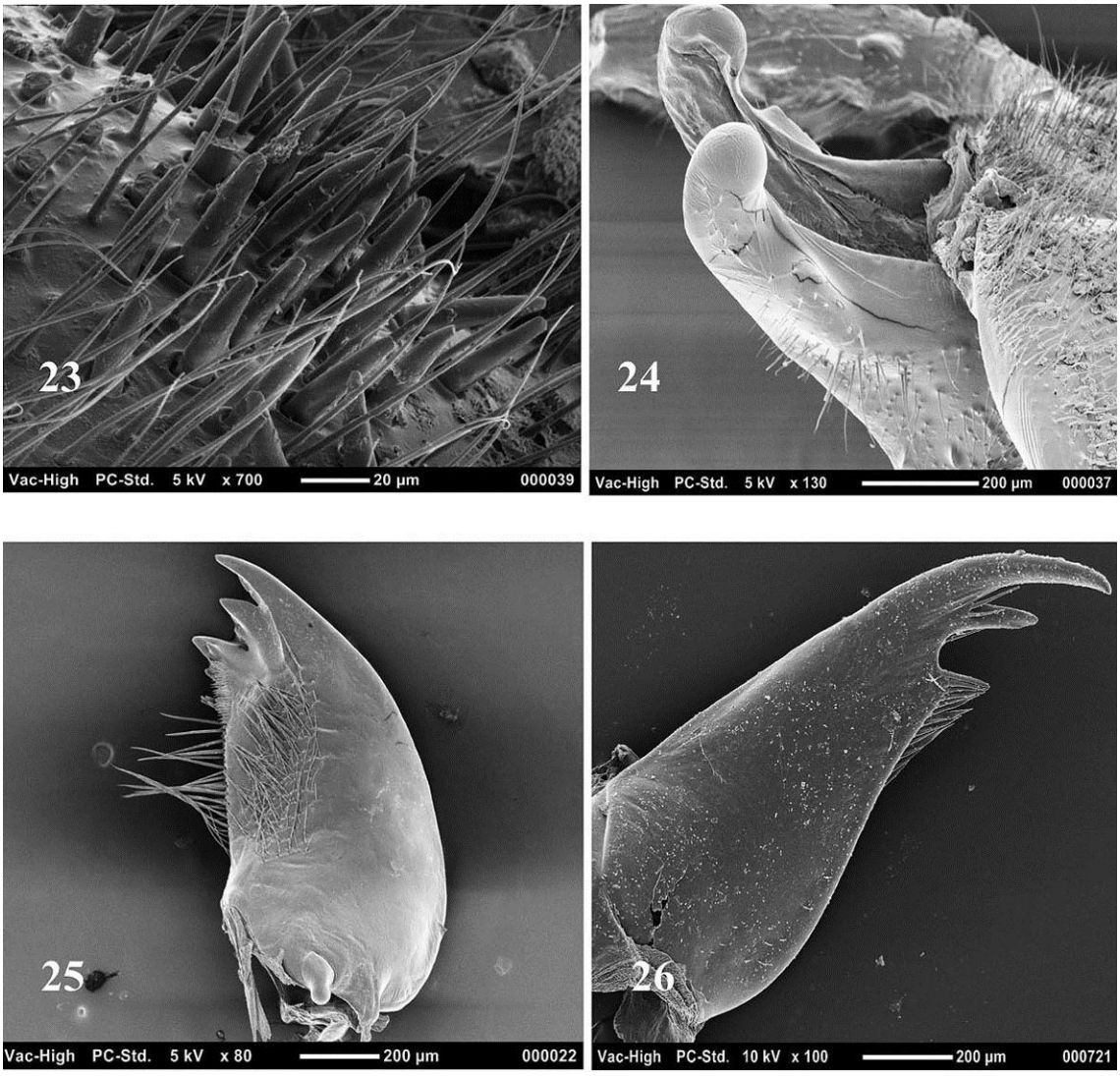
17 June 1939, 5♂, 4♀ (paratopotypes) (CHNC). Same site, C.H. Nelson and E.S. Nelson, 27 June 1996, 4 ♂, 11♀, 1 mature larva, 16 exuviae (CHNC), 1♂, 1♀ (BYU), [CRN laboratory photo voucher 4].

Adult habitus General color dark chestnut brown in life and in alcohol (Fig. 1, 11-14). The head dorsum exhibits an almost black X-band with an anterior margin that forms a distinct M-line (Figs. 2, 11). Anterior to the M-line is a lighter area that extends onto the clypeus; in some individuals it is shaped as a vague light M-band. Frontoclypeus with small orange-yellow oval-shaped spot near the base of each antenna and mandible. The interocellular area exhibits an orange-yellow subtriangular spot. The vertex and occiput is dark brown with a broad, longitudinal, orange-yellow, median band adjacent to, but clearly separated from, the interocellular area. Pronotum (Figs. 2, 11) dark brown and exhibiting a uniformly wide longitudinal, orange-yellow, median band. Meso- and metathoracic eusterna (Fig. 3) dark brown with lateral areas slightly more darkly pigmented. The mesothoracic sternum (Fig. 3) with a complete sternacostal suture (ss) separating the basisternum (bs) from the furcasternum (fs). Only the first two abdominal segments divided on each side by a pleural membrane into a separate tergum and sternum.

Male. Body Length 10.1 – 15.7 ($\overline{x}$ = 11.6) mm (n = 10). Macropterous, forewing length 7.0-8.3 ($\overline{x}$ = 7.7) mm (n=9). Tergum 8 (Fig. 4) partially divided by a narrow, longitudinal, pale median strip that extends from near the posterior margin to near the anterior margin; setose and bearing a few blunt, stout sensilla basiconica near the hind margin on each side of the median strip. Tergum 9 (Fig. 4)



Figs. 15–22. *Diura washingtoniana*, larva. 15. Head and pronotum, dorsal. 16. Meso- and metanota, dorsal. 17. Right mesothoracic leg, frontal. 18. Abdomen, dorsal. 19. Right cercus, ventral (basal, mid, and apical segments). 20. Male terminalia, ventral. 21. Female terminalia, ventral. 22. Male and female terminalia, lateral. Scale bars = 0.5 mm.



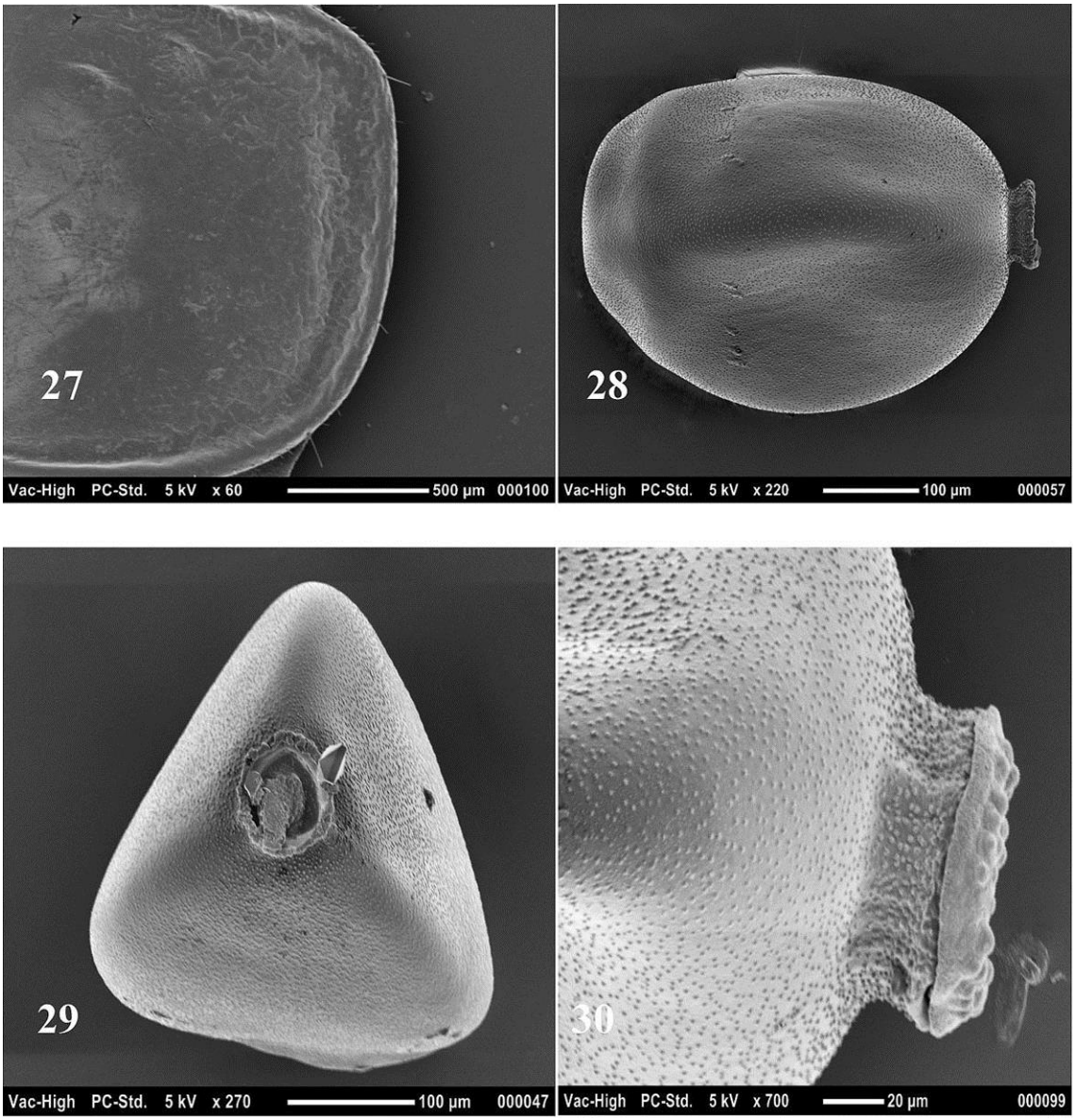
Figs. 23-26. *Diura washingtoniana* (Coos County, New Hampshire, USA). 23. Adult male tergum 10 with sensilla basiconica, dorsal. 24. Adult male paraprocts, biased lateral. 25. Larval left mandible, ventral. 26. Larval right lacinia, ventral.

nearly divided by a pale, narrow, longitudinal, lightly sclerotized area that is a U- or V- shaped at the hind margin and extends anteriorly as a narrow strip to near the front margin; setose with a posterior mesal patch of blunt, stout sensilla basiconica on each side of the median strip (Fig. 4). Tergum 10 in dorsal view (Fig. 4, 12) produced posteriorly; anterior half darker; divided by a paler, narrow, longitudinal, lightly sclerotized median strip that from the central broad triangular-shaped area at the posterior margin extends to the anterior margin; setose with a mesal patch of blunt, stout sensilla basiconica on each side of the median strip (Figs. 4, 23). Tergum 10 in lateral view posteromesally somewhat convex (Fig. 5). Epiproct absent. Paraprocts extend from cerci on each side to meet at the median where they abruptly project caudally and are appressed or lie close to each other (Figs. 4,

7). Inner surfaces of paraproct caudal projections membranous with outer surfaces largely sclerotized (Figs. 6, 7) and setose bearing both short as well as long, slender setae. Caudal projections in dorsal and ventral views (Figs. 4, 7, 12) digitate with outer surfaces broadly convex, apices somewhat bulbous; in lateral view (Figs. 5, 6, 13, 24) digitate, appearing boot-like as a result of upturned apices with broadly rounded margins.

Female. Body length 11.1 – 16.6 ($\overline{x}$ = 14.7) mm (n = 16). Macropterous, forewing length 8.9 – 11.7 ($\overline{x}$ =10.6) mm (n=16). Sternum 8 with mesal area darker than immediate lateral areas. Subgenital plate extends for a short distance over sternum 9 (Figs. 8, 14); shape variable (Fig. 9), lateral margins either broadly rounded or become abruptly narrowed posteriorly, posterior margin either evenly rounded or slightly excavated mesally or truncate; ca 3.1 – 4.4 times as wide as long. Sternum 9 bearing two oblique brown bands (Fig. 8). Spermatheca and vagina (Fig. 10) membranous; ~~elongate~~ spermatheca (s) elongate, somewhat sausage-link-shaped, approximately 2.3X longer than wide; spermathecal duct (sd) approximately 0.8X length of vagina (v); spermatheca and duct bearing accessory glands (ag).

Larva. Body length estimated from 1 mature larvae and 16 exuviae 14.5 - 16.5 ($\overline{x}$ = 15.5) mm. General body color dark brown patterned with light markings; antennae, legs and cerci light brown. Frontoclypeal region (Fig. 15) dark brown, exhibiting a light anterior margin and a light mesolongitudinal spot just anterior to a transverse, light M-band connecting to the median ocellus. Interocellular region bears a mesal light oval-shaped spot and is bordered on each side by a light longitudinal band that extends toward the median ocellus from the lateral ocellus. Between the light longitudinal band and the antennal base of each side there is a small light round spot just anterior to the frontal suture. Vertex and occiput (Fig. 15) dark brown with two oval light bands adjacent to the eyes and between them a transverse triangular-shaped light median band; the three light bands are all patterned with dark brown lines. Labrum (Fig. 15) dark with a mid-anterior light spot bordered on each side by a dark brown band. Left mandible (Fig. 25) bearing three major and three minor teeth arranged as follows from dorsal aspect, a group consisting of one major tooth flanked on each side by a minor tooth, followed by a linear arrangement of a minor tooth and two major teeth; the ventral-most major tooth is the largest; teeth lack serrations; a row of acanthae arises from the bases of the three dorsal teeth. Maxillary lacinia triangular; bidentate (Fig. 26), subapical tooth shorter, approximately one-half length of apical tooth; 2 axillary setae at base of subapical tooth; single marginal seta found just below the subapical tooth; inner margin below teeth forms a pronounced shoulder; shoulder and apical third of inner margin below the shoulder bearing setae; scattered sub-marginal setae present. Gills absent. Pronotum (Fig. 15) with margins light; disc dark brown with light reticulate markings on each side of a light median band; anterior and posterior margins bearing row of short setae interspersed with a few long setae; lateral margins with few or no setae (Fig. 27). Mesothoracic and metathoracic nota (Fig. 16) dark brown and from anterior to posterior bearing four rows of light spots; first row bears two somewhat indistinct spots, the second and third each exhibit four spots and the fourth a single longitudinal band. Wingpads light with elongate dark brown markings. Legs (Fig. 17) with dorsal margins of the femur, tibia, and tarsi fringed with long, silky setae. Femur (Fig. 17) outer surface, except for narrow medial band, bearing numerous short thick setae. Tibia (Fig. 17) outer surface with setae on dorsal and ventral areas. Only abdominal segments 1 & 2 divided by a pleural membrane of each side into separate terga and sterna. Abdominal tergal areas (Fig 18) dark brown, each with anterior transverse row of light spots and a lighter posteromesal region. In lateral view paraprocts of mature male larva (Fig. 22) with apical sections narrow, elongate and turned dorsally; those of mature female larva somewhat pyramid-shaped with apices directed posteriorly, not narrowed or elongate. Stout setae lining eighth sternal margin of mature male larva interrupted mesally for a very short distance (Fig. 20); interrupted in the mature female larva for longer



Figs. 27-30. *Diura washingtoniana* (Coos County, New Hampshire, USA). 27. Larval pronotal margins, dorsal. 28. Egg, lateral. 29. Egg, dorsal. 30. Egg collar and anchor, lateral.

distance, approximately 0.3 width of segment (Fig. 21). Cercal segments (Fig. 19) with dorsal margins bearing a fringe of long silky setae; posterior margins bearing a whorl of short setae, beginning with segment 16 posterior margin bearing one or two long setae.

Egg. Length ca. 450 µm; width ca. 298 µm (n=1). General shape oval (Fig. 28); cross-section triangular (Fig. 29). Collar ring-shaped and stalked (Fig. 30). Anchor plate is mushroom-type of Isobe (1997), in Fig. 30 somewhat dorsally-ventrally compressed covering the collar margins and bearing globular processes. Chorionic surface dotted with numerous, slightly raised, similar-sized rounded protuberances (Figs. 28-30).

Diagnosis. *D. washingtoniana* is distinguished by the following combination of features: (1) male tergum 8 partially divided by a narrow, membranous, pale

median strip extending from near the posterior margin to near the anterior margin; (2) male tergum 9 nearly divided by a pale, narrow, longitudinal, lightly sclerotized area that is a U- or V- shaped at the hind margin and extends anteriorly as a narrow strip to near the front margin; (3) male tergum 10 divided by a narrow, membranous, pale median strip that from the central, broad membranous triangular-shaped area at the hind margin extends uninterrupted to the front margin; (4) male terga 8 – 10 bearing patches of blunt, stout sensilla basiconica; (5) male paraproct caudal projections in dorsal view with convex outer surfaces; (6) apices of male paraproct caudal projections broadly rounded and upturned to appear boot-like in lateral view.

Comparison to Congeners

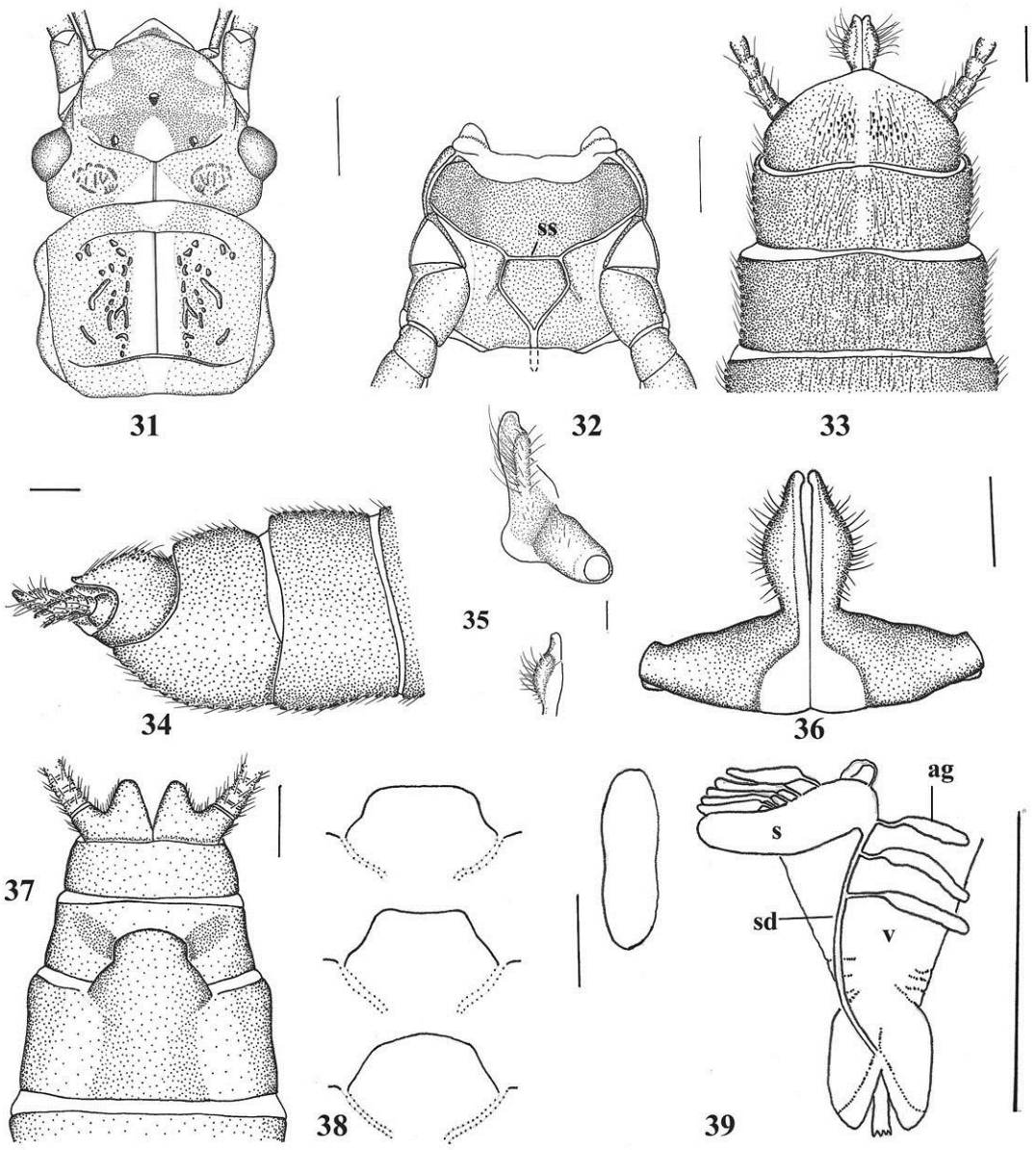
***Diura nanseni* (Kempny, 1900)**
Arctic Springfly
http://lsid.speciesfile.org/urn:lsid:Plecoptera.speciesfile.org:TaxonName:927
Figs. 31-45, 74-77

Isogenus nanseni Kempny 1900:90, type(s) not designated, Northland County (Susundalen, 1♂; Skarmodalen 1♂; Vefsen 1♂; Braendmo, 1♀), Norway
Diura nanseni Brinck 1949:65
Diura nanseni (f. typica) Brinck 1954:199
Diura nanseni Illies 1966: 383, in part
Diura nanseni Zwick 1973:228, in part
Diura nanseni DeWalt et al. 2018, in part

Material examined. Specimens of *D. nanseni* examined for this study are consistent with previous descriptions and illustrations of this species (Kempny 1900, Klapálek 1912, Bengtsson 1933 (as *Dictyopterygella subfissa – vide* Brinck 1949), Brinck 1949, 1952, Lillehammer 1974, 1988), **Russia**; *Russian Far East:* Amur River Basin, Zeya River Basin, Selemdzh River, near Fevral'sk, V. Teslenko, 14 June 2004. 1♂, 1♀ (RASC); **Sweden;** Fulufjället National Park, Njupeskär waterfall, P. Brinck, 11 July 1927, 2♂, 4♀ (CHNC). Lu. Lpm. Kvikkjokk (CRN: interpreted as Lule River of Lappmarken region), P. Brinck, 25 June 1944, 1♂, 1♀ (BYU), [CRN laboratory photo voucher D36].

Adult habitus. In life general color dark brown to black (Kempny 1900), when preserved in alcohol coffee or tan brown (Figs 40-45). Head dorsum with a dark brown X-band on frons (Figs. 31, 40); M-line less distinct than that of *D. washingtoniana*; small oval-shaped light spot near base of the antennae of each side; interocellular area with sub-triangular light spot; vertex and occiput with a transverse, light, median band adjacent to, but separated from, the interocellular spot. Markings on head, pronotum, and meso- and metaeusterna (Figs. 31, 32) similar to those of *D. washingtoniana*. A complete sternacostal suture (Fig. 32 ss) is present as well. As in *D. washingtoniana*, only abdominal segments 1 & 2 divided by the pleural membrane of each side into separate terga and sterna.

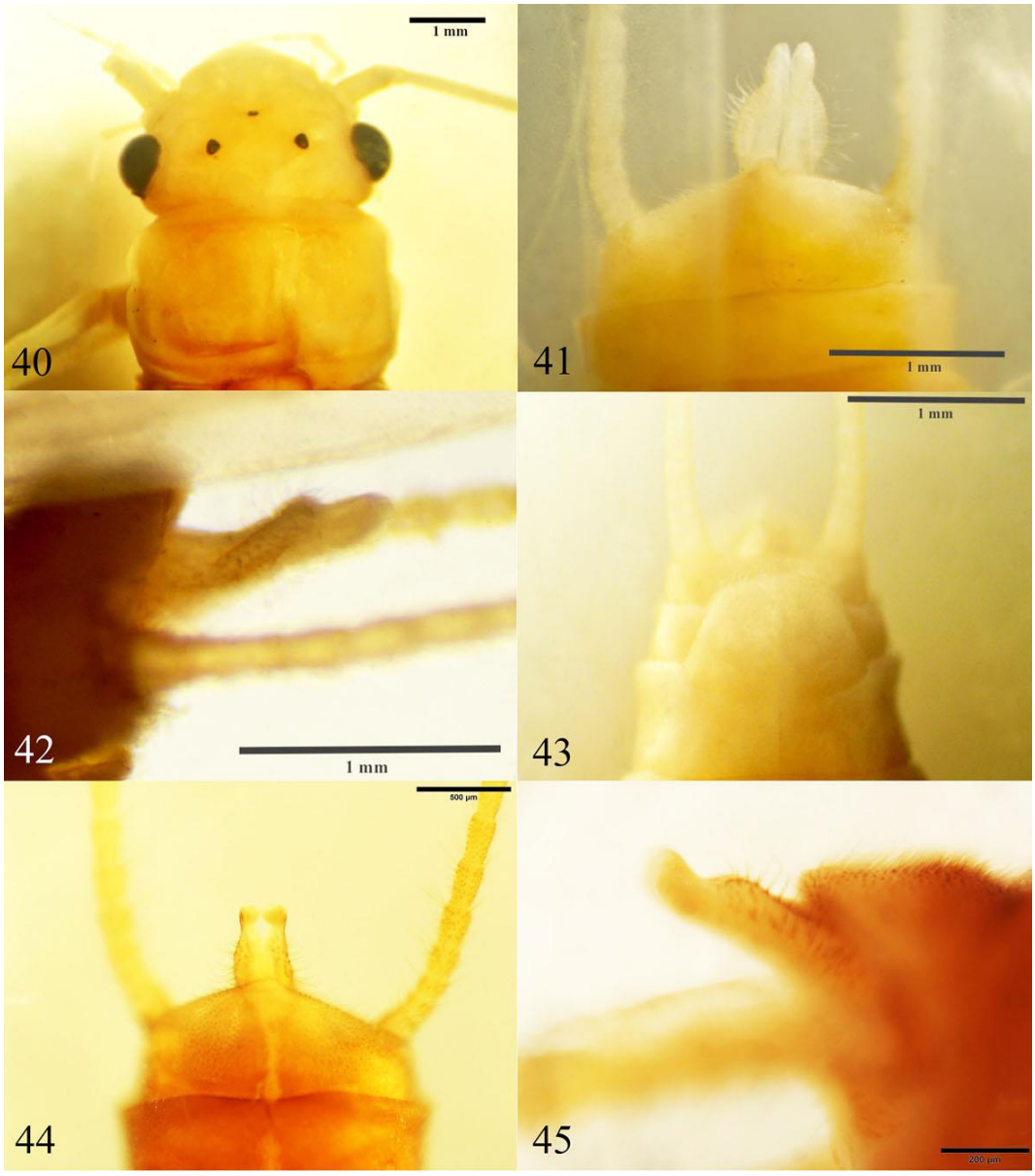
Male. Body length of *D. nanseni* (Lillehammer 1974) generally smaller than *D. washingtoniana*, approximately 0.5 to 0.9X the length of the latter. Macropterous, forewing length (Lillehammer 1974) similar to *D. washingtoniana*. However, micropterous populations are reported from Norway (Lillehammmer 1974, Saltveit and Brittain 1986) and Mongolia's Bayanhkongor province (Raušer 1968). In the latter case specimens are likely *D. bicaudata* as this species has been found in this province (see Material Examined section for *D. bicaudata* below). Tergum 8 (Fig. 33) with a median line of lightly sclerotized spots; setose but lacking blunt, stout sensilla basiconica. Tergum 9 pattern of sclerotization differs from *D. washingtoniana* in that the small mesal, shallow, U-shaped area at the hind margin (Fig. 33) is separated by a short distance from the anteriorly located narrow, longitudinal, lightly sclerotized median strip; setose but lacking blunt, stout sensilla basiconica (Figs. 34, 74). Tergum 10 pattern of sclerotization as well as the distribution of setae and blunt, stout sensilla basiconica similar to those exhibited by *D. washingtoniana* (Fig. 33). Epiproct also absent. Paraproct caudal projections in dorsal and ventral views (Figs. 33, 36, 41, 44) with outer surfaces more convex than those of *D. washingoniana*; setose with both short as well as long, slender setae; in lateral view (Figs. 34, 35, 42, 45, 75) they resemble a Bowie knife blade in that the apical frontodorsal margins are noticeably 'clipped out', terminating in broadly



Figs. 31-39 *Diura nanseni*, adult. 31. Head and pronotum, dorsal. 32. Mesothorax, ventral. ss = sternacostal suture. 33. Male terminalia, dorsal. 34. Male terminalia, lateral. 35. Paraproct caudal projections, lateral and frontal. 36. Paraprocts, ventral. 37. Female terminalia, ventral. 38. Examples of female subgenital plate variation. 39. Spermatheca and vagina. ag = accessory glands, s = spermatheca, sd = spermathecal duct, v = vagina. Scale bars = 0.5 mm.

rounded short tips that, unlike those of *D. washingtoniana*, are not bulbous or so sharply upturned as to appear boot-like.

Female. Body length (Lillehammer 1974) approximately 0.75 to 0.95X the length of *D. washingtoniana*. Macropterous, forewing length (Lillehammer 1974) similar to *D. washingoniana.* Subgenital plate shape variable (Figs. 37, 38, 43) (Brinck 1949, Lillehammer 1974); somewhat narrower than that of *D. washingtoniana*, ca 2.0 – 2.5X



Figs. 40–45. *Diura nanseni*, adult. 40–43 (Russian Far East, Russia). 40. Head and pronotum, dorsal, 41. Male terminalia, dorsal. 42. Male paraprocts, lateral. 43. Female terminalia, ventral. 44-45 (Lule, Lappmark, Sweden). 44. Male terminalia, dorsal. 45. Male paraprocts, lateral.

wider than long. Spermatheca and vagina similar to those of *D. washingtoniana* (Fig. 39), spermatheca (s) appears somewhat more elongate, approximately 3.5X longer than wide; spermathecal duct (sd) 0.9X length of vagina (v); spermatheca and duct bearing accessory glands (ag).

Larva. Originally described by Brinck (1949), other descriptive information provided by Brinck (1952), Saltveit (1978), and Lillehammer (1988). Similar to that of D. *washingtoniana*, including pronotum lateral margins with few or no spinulae.

Egg. Initially described by Lillehammer (1988,

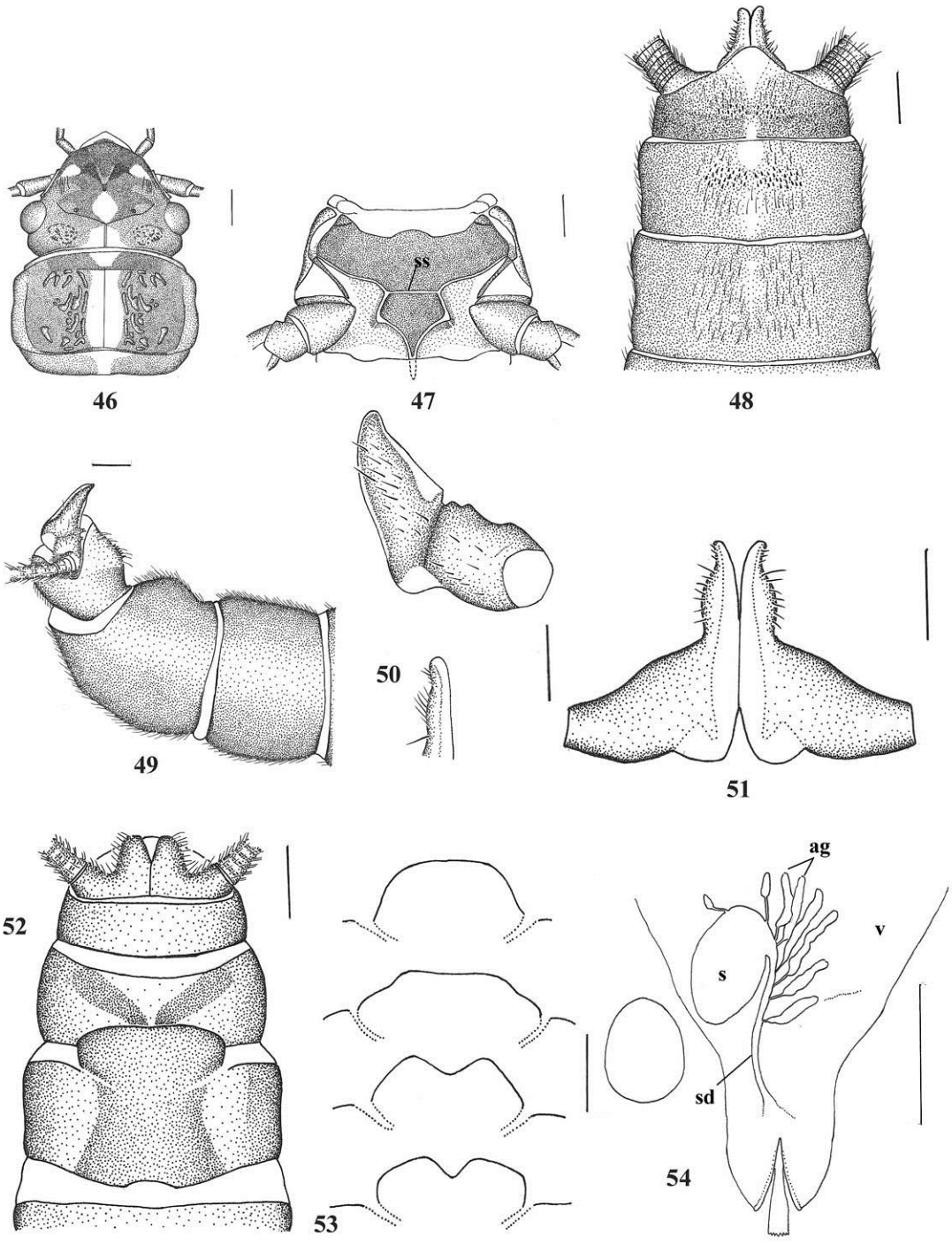
fig. 76) and nearly identical to *D. washingtoniana.*

***Diura bicaudata* (Linnaeus, 1758)**
Lapland Springfly
http://lsid.speciesfile.org/urn:lsid:Plecoptera.speciesfile.org:TaxonName:934
Figs. 46-60, 76-77

Phryganea bicaudata Linnaeus 1758: 548, type(s) not designated, Europe
Phryganea bicaudata Linnaeus 1767: 908
Diura bicaudata Billberg 1820: 96
Diura bicaudata Brinck 1949:61
Diura bicaudata Illies 1966: 381
Diura nanseni Raušer 1968: 357
Diura bicaudata Zwick 1973: 227
Diura bicaudata Judson and Nelson, 2012:42
Diura majuscula Judson and Nelson 2012:42
Diura bicaudata DeWalt et al. 2018

Material examined. Photographs of the dorsal aspect of the Linnaean collection pinned specimen of this species are available at the Linnean Society of London (2017). The specimen is macropterous and is likely a female as European males are usually micropterous. Specimens of *D. bicaudata* examined for this study are consistent with previous descriptions and illustrations of this species (Klapálek 1909, 1912 (as *Dictyopterygella recta*, *Dictyopterygella septentrionis* – *vide* Brinck 1949), Hanson 1940 (as *Dictyopterygella hudsonica* - *vide* Brinck 1949), Hynes 1940 (as *Dictyopterygella recta* – *vide* Brinck 1949), 1941, Brinck 1949, 1954, Koponen 1949 (as *Dictyopterygella recta* – *vide* Brinck 1949), Illies 1955, Raušer 1966, Lillehammer 1974, 1988, Stewart & Oswood 2006). In the following listing macropterous males are indicated, otherwise micropterous: **Canada**; *Nunavut*; Baker Lake, 64°N, 95°W, Dutilly, 10 August 1936, 1♂ [Holotype *Dictyopterygella hudsonica*] (USNM). **Germany**; Rhön, Upper reaches of Ulster River, P. Zwick, 9 May 1971 (PZC) **Isle of Man**; Llergyrhemy, Headwaters of Sulby River, N.S. Jones & H.B.N. Hynes, 7 June 1951, 1♂ (USNM). Headwaters of Sulby River, H.B.N. Hynes & N.S. Jones, 26 July 1949 & 7 June 1951, 14 larvae (USNM). Silver Burn, N.S. Jones, 3 May 1951, 1♀ (USNM). River Neb, Glen Hellen, 220, H.B.N. Hynes, 10 April 1949, 3 larvae (USNM). Ballaguine stream, G67, H.B.N. Hynes, 25 July 1949, 2 larvae (USNM). **Mongolia**; *Arkhangay*: Bulgan Soum, Gol braid upstream of bridge ~63 km SW of Tsetserleg, N47.11192°, E101.01048°, elev. 2066 m, Selenge River Project Team, 13-15 July 2004, 1♂ [macropterous] (BYU) [CRN laboratory photo voucher D11]. Bulgan Soum, Urd Tamir Gol braid upstream of bridge ~63 km SW of Tsetserleg, N47.11192°, E101.01048°, elev. 2066 m, Selenge River Project Team, 13-15 July 2004, 1♂ [macropterous] (BYU).Bulgan Soum, Urd Tamir Gol ~50 km SW of Tsetserleg, N47.21109°, E101.07947°, elev. 1962 m, Selenge River Project Team, 13 July 2004, 2♀ (BYU) [CRN laboratory photo voucher D22]. Chuluut Soum, Khuurmen/Davaat Gol 15 km SSE of Chuluut/Jargalant N47.42580°, E100.30130°, elev. 2104 m, Selenge River Project Team 15-16 July 2004, 2♀ (BYU), [CRN laboratory photo voucher D21]. Chuluut Soum, Chuluutin Gol ~45 km SW of Chuluut/Jargalant N47.21768°, E99.92824°, elev. 2471 m, 16 July 2008, Selenge River Project Team SRP2004071602, 1♀(BYU) [CRN laboratory photo voucher D14]. *Bayankhongor*: Gurvanbulag Soum, Khokh Nuur (Blue Lake) N47.53° E 97.53°, 2600m, Yu Marusik, 7-10 June 1997, 2♂, 2♀ (RASC). *Bayan Olgiy*; Bulgan Soum, "Ulaagchiny Davaa Gol", unnamed stream, ~50 km SSE Deluun N 47.45456° E 90.92342°, 2631 msl, 6 July 2009, S.W. Judson & C.R. Nelson #9234, 2♀, MAIS2009070601, (BYU) [CRN laboratory photo voucher D13]. Bulgan Soum, Khar Nuur (Black Lake), ~50 km NNW Bulgan N 47.24133° E 90.75316°, 2563 msl, 7 July 2009, S.W. Judson & C.R. Nelson #9239, 2♂ 4♀, MAIS2009070703, (BYU). [CRN laboratory photo voucher D23]. Bulgan Soum, Bulgan Gol, ~15 km N Bulgan N47.03954° E91.03448° elev. 2010 m, 8 &9 July 2009, S.W. Judson, Mongolian Aquatic Insect Survey, MAIS2009070803, 1♀ (BYU), [CRN laboratory photo voucher D29]. Bulgan Soum, Turgen Gol, ~40 km NNW Bulgan, N47.18333° E91.77660° elev. 2492 m, Mongolian Aquatic Insect Survey, 7-8 July 2009, 1♂ 2♀, MAIS2009070705 (BYU), [CRN laboratory photo voucher D17]. Bulgan Soum, Turgen Gol, ~40 km NNW Bulgan, N47.18333° E90.77660° elev. 2492 m, S.W. Judson, Mongolian Aquatic Insect Survey, 7-8 July 2009, 5♀ (BYU), [CRN laboratory photo voucher D26].

Deluun Soum, Gantsmodi Gol 27 km S Deluun, N47.66395° E90.7181°, elev. 2196 m, 5 - 6 July 2009, S.W. Judson & C.R. Nelson #9231 & MAIS Team MAIS2009070502, 3♂ 1♀ (BYU), [CRN laboratory photo voucher D15]. Deluun Soum, Gantsmodi Gol 33 km S Deluun, N47.62447°, E90.67194°, elev. 2241, 5 July 2009, S. W. Judson & C.R. Nelson #9230, Mongolian Aquatic Insect Survey, MAIS2009070501, 1♂, 2♀ (BYU), [CRN laboratory photo voucher D18]. Deluun Soum, Gantsmodi Gol 33 km S Deluun, N47.62447° E90.67194°, elev. 2241 m, 5 July 2009, S. Chuluunbat, Mongolia Aquatic Insect Survey MAIS2009070501, 1♀ (BYU), [CRN laboratory photo voucher D25]. Deluun Soum, Buyant Gol 46 km SE Deluun, N47.60915°, E91.13574°, elev. 1947 m, 4 July 2009, S.W. Judson & C.R. Nelson # 9227, Mongolian Aquatic Insect Survey, MAIS2009070404, 1♂ (BYU), [CRN laboratory photo voucher D27]. Tsengel Soum, Syrgali Gol, Bagakhatuugiin Lake junction Ikh Khatuugiin Gol N49.04586° E88.50939° elev. 2385 m, 13 July 2008, C.R. Nelson #8993, 1♀ (BYU), [CRN laboratory photo voucher D3]. Tsengel Soum, Khoton Lake, 15 km NW of Syrgal, N48.66718° E88.29908°, elev. 2090 m, C.R. Nelson, 14 July 2008 1♀ (BYU), [CRN laboratory photo voucher D7]. Tsengel Soum, Khoton Lake, 15 km NW of Syrgal, N48.66718° E88.299908°, elev. 2090 m, C.R. Nelson, 14 July 2008, 1♂, 1♀ (BYU), [CRN laboratory photo voucher D4]. Tsengel Soum, Khoton Lake, 15 km NW of Syrgal, N48.66718° E88.29908°, elev. 2090 m, C.R. Nelson, 14 July 2008 1♀ (BYU), [CRN laboratory photo voucher D5]. Tsengel Soum, Syrgali Gol, bridge over outflow between Khoton Nuur and Khurgen Nuur at Syrgal, N49.59925° E88.43707°, elev. 2095m, 16 July 2008 P. Sigitas, MAIS 2008071603, 2♂ (BYU), [CRN laboratory photo voucher D8]. Tsengel Soum, Syrgali Gol, bridge over outflow between Khoton Nuur and Khurgen Nuur at Syrgal, N49.59925° E88.43707° elev. 2095 m, 16 July 2008, C.R. Nelson #9005, MAIS 2008071603, 1♂, 2♀ (BYU), [CRN laboratory photo voucher D2]. *Hovsgol:* Ulaan Uul Soum, Gunain Gol, 12 km SW of Ulaan Uul, N 50.61826° E 99.12094°, elev. 1761 m, 29 June 2006, C.R. Nelson #8465, Selenge River Project Team SRP2006062903, 1♂ {macropterous} (BYU), [CRN laboratory photo voucher D12]. Ulaan Uul Soum, Hugin Gol at toll bridge, 46.8km N of Ulaan Uul town, N 51.09845° E 99.32051°, elev. 1557 m, 1 July 2006, C.R. Nelson #8475, Selenge River Project Team SRP 2006070101, 1♂ {macropterous} (BYU), [CRN laboratory photo voucher D28]. Renchinlhumbe Soum, Jarin Gol 32.8 km N of Renchinlhumbe N51.39852°, E99.75011° elev. 1575 m, C.R. Nelson #8481, 3 July 2006, 1♀ (BYU), [CRN laboratory photo voucher D6]. *Ovorhangay:* Bat-Olziy Soum, Orkhon Gol ~34 km W of Khujirt N46.89303°, E102.39457°, elev. 1610 m, Selenge River Project Team, 06 July 2004, 1♀ (BYU) [CRN laboratory photo voucher D19]. *Tov*: Erdene Soum, Gorkhi Terelj National Park, Gultain Gol at road crossing 19.1 km upstream of Tuul River Bridge, N48.09720°, E107.9199° elev. 1551 m, 1 July 2002, Suvdaa Chuluunbat, E. Sanaa, 1♂ {macropterous} (BYU), [CRN laboratory photo voucher D9]. Erdene Soum, Gorkhi Terelj National Park, Tuul River 10.1 km upstream of Tuul River Bridge N48.09549°, E107.84265°, elev. 1531m, 8 July 2003, Selenge River Basin Insect Survey Team, SRBIS03070801 Gelhaus #903 1♂ {macropterous} 1♀ (BYU), [CRN laboratory photo voucher D10]. Erdene Soum, Gorkhi Terelj National Park, unnamed tributary of Tuul River on its E side 8.5 km downstream of Galtain Gol N48.09720° E107.84928°, elev. 1542m, E. Sanaa., 8 July 2003, 1♀ (BYU), [CRN laboratory photo voucher D 20]. Erdene Soum, Gorkhi Terelj National Park, Terelj River, just above Terelj, N47.99158° E107.46717°, elev. 1516 m, 28 June 2008, C.R. Nelson #8949, 1♀ (BYU), [CRN laboratory photo voucher D24]. *Zavkhan*; Ider Soum, Dogshin/Nogoon Nuur ~21 km SE of Zuummod/Ider N48.06257° E97.55064°, elev. 2054m, Selenge River Project Team, 23=24 July 2004, 2♀ (BYU), [CRN laboratory photo voucher D16]. **Sweden**; Torne Träsk, Abisko, H.B.N. Hynes, 30 July 1968, 7♂, 11♀ (USNM). **United Kingdom**; *England*; Fisher Gill, 1300 – 1500′ [400 – 461 m], H.B.N. Hynes, 13 May 1940, 1♂, 1♀ (USNM). Cumberland, Whelpside Gill, 2000′ [616 m], T.T. Macon, 20 May 1940, 2♂, 1♀ (USNM). Cumberland, Whelpside Gill, 2000 – 2800′ [616 – 862m], T.T.M. & J.M., May 1940 & May & June 1953, 37 larvae (USNM). Cumberland, Wastwater,



Figs. 46-54. *Diura bicaudata*, adult. 46. Head and pronotum, dorsal. 47. Mesothorax, ventral. ss = sternacostal suture. 48. Male terminalia, dorsal. 49. Male terminalia, lateral. 50. Paraproct caudal projections, lateral and frontal. 51. Paraprocts, ventral. 52. Female terminalia, ventral. 53. Examples of female subgenital plate variation. 54. Spermatheca and vagina. ag = accessory glands, s = spermatheca, sd = spermathecal duct, v = vagina. Scale bars = 0.5 mm.

H.B.N. Hynes, 7, 12 May 1940, 2♂, 2♀ (USNM). Cumberland, Ennerdale, H.B.N. Hynes, April 1939, 14♂, 12♀, 11 exuviae (USNM). Cumberland, Ennerdale water, collector unknown, 17 April 1939, 14 larvae (USNM). Cumberland, Stake Pass, 1540′ [474m], W.E. Frost, 4 May 1940, 1♀ (USNM). Cumberland, Derwent Water, 15, H.B.N. Hynes, 2 October 1939, 7 larvae (USNM). Cumberland, Ullswater, H.B.N. Hynes, 1939, 28 larvae (USNM). Westmoreland, Windermere, H.B.N. Hynes, 22 April 1939, 23 May 1940 & 2 June 1941, 26♂, 18♀ (USNM). Westmoreland, Scandale Beck, 1400′ [431m], 71, H.B.N. Hynes, 30 April 1940, 1♂, 1♀ (USNM). Westmoreland, Brothers Water, H.B.N. Hynes, 8 August 1939, 10 larvae (USNM). Westmoreland, Rydal Beck, 2000′ [616m], 102, H.B.N. Hynes, 12 August 1940, 4 larvae (USNM). *Scotland*; Argyle; L. Triochatan (Pass of Glencoe), W.D.W., 24 May 1959, 1♂, 2♀ (USNM). Caithness, Loch Shurrery, W.E. Frost, 3 May 1939, 1♂, 2♀, 2 exuviae (USNM). Selkirk, St. Mary's Loch, 22 March 1955, H.B.N. Hynes, 36 larvae (USNM). Mid Perth, Loch Rannoch, H.B.N. Hynes, 30 March 1955, 29 larvae (USNM). North Sutherland, Allt na a Bhathaich, Quinag, 1500 – 1750′ [461 – 539m], 28 August 1957, 224294, H.B.N. Hynes, 3 larvae (USNM). East Ross, L. Garve, H.B.N. Hynes, 25 March 1955, 16 larvae (USNM). *Scotland*, South Sutherland, "L. Assynt & L. Borralan" or *England*, South Somerset, H.B.N. Hynes, 28 March 1955, 6 larvae (USNM). *Wales;* Caernarvon, Llyn Idwal, 225, H.B.N. Hynes, 1 July 1949, 9 larvae (USNM). Merioneth, Afon Hirnant, H.B.N. Hynes, 1955/1956, 132 larvae (USNM).

Adult habitus. General color in alcohol similar to that of *D. washingtoniana*. Markings on head, pronotum, and meso- and metaeusterna (Figs. 46, 47, 55) similar to *D. washingtoniana.* However, Brinck (1949) reports that head coloration is variable. A well-developed sternacostal suture (Fig. 47 ss), as observed in *D. washingtoniana* (Fig. 3) and *D. nanseni* (Fig. 32), is present in *D. bicaudata*.

Male. Body length (Lillehammer 1974, Stewart and Oswood 2006) similar to that of *D. washingtoniana*. Typically micropterous (Lillehammer 1974) but Brinck (1949) concluded that several populations with macropterous males are actually this species. In this study Mongolian populations with micropterous males exhibiting wings terminating prior to the 2nd abdominal segment or reaching the mid-section of the abdomen as well as populations with macropterous males exhibiting wings reaching the abdominal apex or beyond are considered to be this species as well. Tergum 8 (Fig. 48) bearing a narrow, longitudinal, lightly sclerotized median strip; setose but lacking short, stout sensilla basiconica. Tergum 9 similar to that of *D. nanseni* in that the hind margin (Fig. 48) exhibits a broad, lightly sclerotized, median U-shaped area separated by a short distance from a more anteriorly located narrow, longitudinal, lightly sclerotized median band; presence of mesal patches of short, stout sensilla basiconica similar to *D. washingtoniana*. Tergum 10 with median, pale, longitudinal lightly sclerotized strip interrupted mesally by darkly sclerotized band connecting the adjacent tergal halves (Fig. 48); distribution of setae and sensilla basiconica similar to that of *D. washingtoniana* and *D. nanseni*. Epiproct also absent. Paraproct caudal projections in dorsal and ventral view (Figs. 48, 50, 51, 56) with outer surfaces somewhat flattened, not robustly convex as are those in *D. washingtoniana* and *D. nanseni*, setal lengths variable but generally shorter than those of preceding species; in lateral view (Figs. 49, 50, 57, 59, 60) subtriangular, tapering to narrowly rounded apical margins

Female. Body length (Lillehammer 1974) similar to *D. washingtoniana*. Macropterous, forewing length (Lillehammer 1974) similar to *D. washingtoniana*. Sternum 9 bearing two oblique brown bands (Figs. 52). Subgenital plate shape variable (Figs. 53, 58) (Brinck 1949, Lillehammer 1974); plate width overlaps that of *D. nanseni* but can be wider, ca 2.3 – 6.5X wider than long. Vagina and spermatheca membranous; spermatheca (Fig. 54 s) ovoid or egg-shaped, nearly as long as wide (1.3x longer than wide); spermathecal duct (sd) 0.5x length of vagina; spermatheca and duct bearing accessory glands (ag).

Larva. Originally described by Hynes (1941), other

Figs. 55-60. *Diura bicaudata* adult. 55–58 (Bayan Olgiy, Mongolia). 55. Head and pronotum, dorsal. 56. Male (micropterous) terminalia, dorsal. 57. Male (micropterous) paraprocts, lateral. 58 Female terminalia, ventral. 59. (Arkhangay, Mongolia). Male (macropterous) lateral. 60. (Rhön, Germany). Male (micropterous) paraprocts, lateral.

information provided by Brinck (1949, 1952), Illies (1955), Hynes (1958) and Lillehammer (1988). Closely similar to *D. washingtoniana*, except that the lateral pronotal margins are lined with a row of short spinulae and a few longer hairs at the posterolateral corners (Fig. 77).

Egg. First illustrated by Lillehammer (1988) and nearly identical to *D. washingtoniana* and *D. nanseni* (Fig. 78).

***Diura knowltoni* (Frison, 1937)**
Nearctic Springfly
http://lsid.speciesfile.org/urn:lsid:Plecoptera.speciesfile.org:TaxonName:932
Figs. 61–73, 79–81

Dictyopterygella knowltoni Frison 1937:89. Holotype ♂, Logan, Utah.
Diura (*Dolkrila*) *knowltoni* Ricker 1952:138
Diura knowltoni Illies 1966:383
Diura knowltoni Zwick 1973:228
Diura knowltoni DeWalt et al. 2018

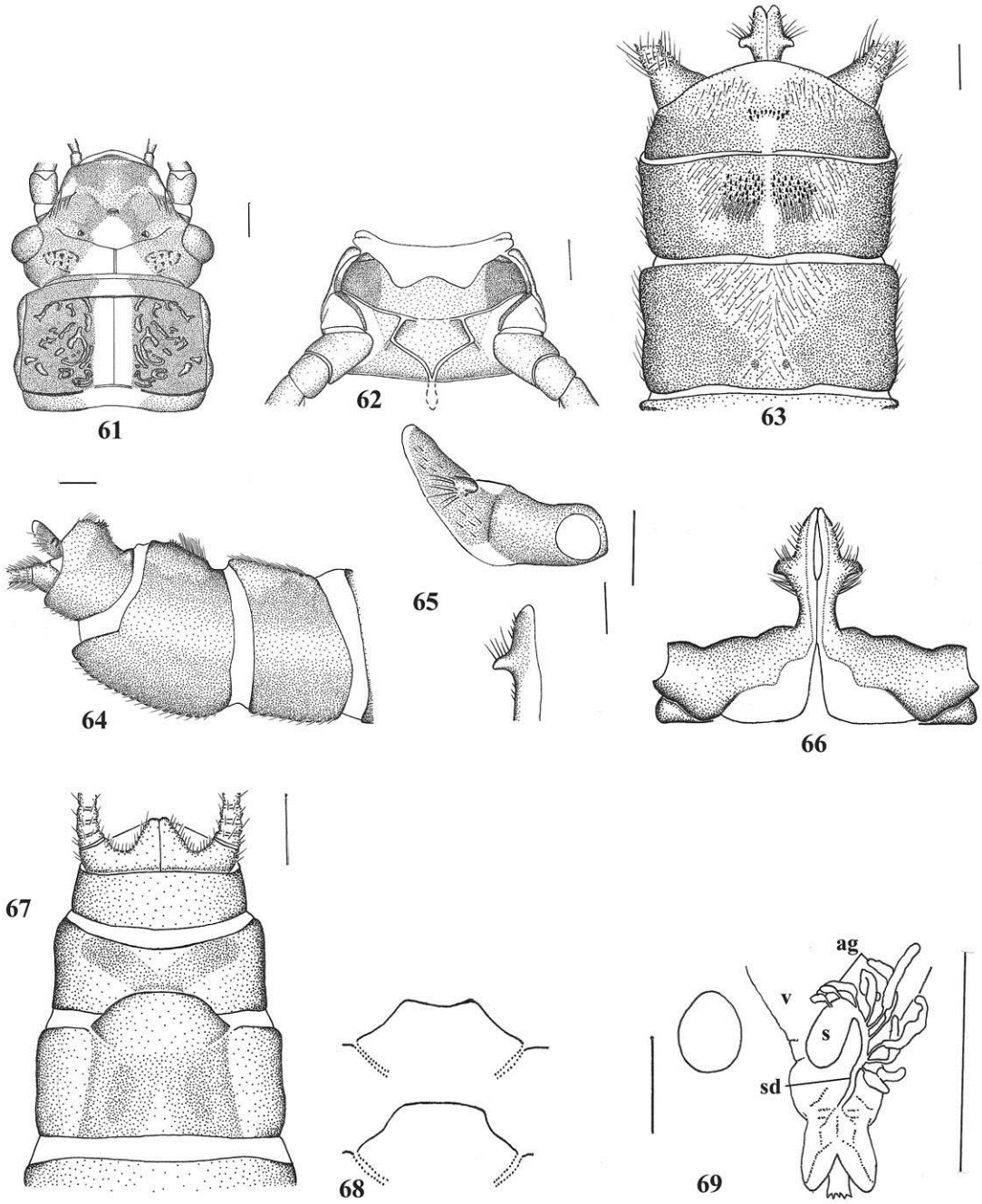
Material examined. Specimens of *D. knowltoni* examined for this study conform with previous descriptions and illustrations of this species (Frison 1937, 1942, Jewett 1959, Gaufin et al. 1966, Gaufin et al. 1972, Baumann et al. 1977, Stark and Szczytko 1984, Stark et al. 1988, Stewart and Oswood 2006): **Canada**; *Alberta*: Oldham River, Highway 22 north of Lundbreck, Baumann & Liu, 4♂, 3♀ (BYU). **USA;** *Colorado;* Mineral County, Pass Creek, 46° F, elev. 3048 m, Ross & Ross, 14 June 1954, 4♂, 5♀ (BYU), [CRN laboratory photo voucher D33]. Summit Co., Blue River, S. of Breckenridge, B.C. Kondratieff, 5 June 1990, 2♂, 3♀, 2 larvae (CHNC). Larimer Co., Fall River Pass, near Estes Park, C.P. Alexander, 19 August 1934, 1♀ (CHNC). *Montana;* Ponderosa Co., South Fork of Sun River, Lewis and Clark National Forest, R. M. Duffield, 15 July 2000, 1♀ (CHNC). *Utah*; Cache Co., Logan Canyon, R. E. Nye, 23 April 1938, 1♂ (CHNC). Emery Co., Huntington Creek, Stewart Stn, 6 June 1975, 5♂, 4♀ (BYU), [CRN laboratory photo voucher D34] *Wyoming*; Grand Teton National Park, Pilgrim Creek at junction US Highway 89&287, 1 mile S Colter Bay 6800′, J.W. Richardson & S.L. Jensen, 1♂, 3♀ (BYU), [CRN laboratory photo voucher D35].

Adult habitus. General color dark brown to black in life (Stark et al. 1998). Markings on head and pronotum similar to *D. washingtoniana* and *D. bicaudata*, except that the sub-triangular yellow interocellular spot is broadly continuous with the longitudinal, yellow median band of the vertex and occiput (Figs. 61, 70). Meso- and metaeusterna yellow with lateral areas dark brown (Fig. 62). Mesothoracic sternum with an incomplete sternacostal suture separating the basisternum from the furcasternum (Fig. 62).

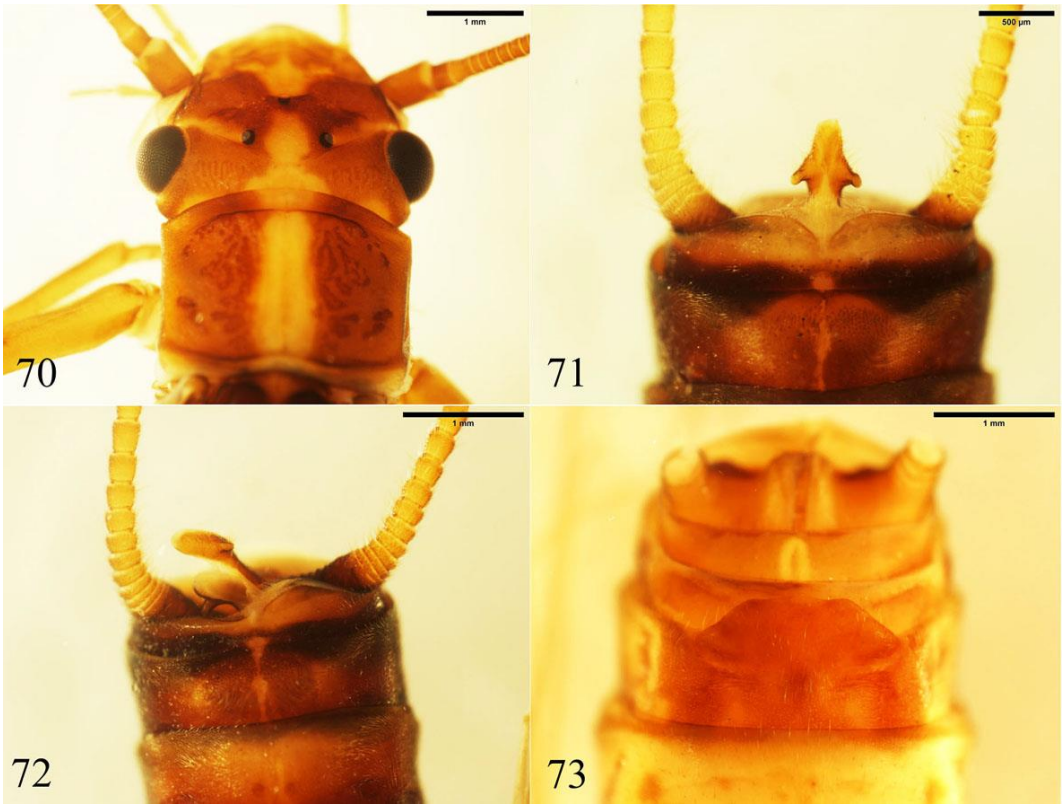
Male. Body length longer than *D. nanseni*, similar to *D. washingtoniana* and *D. bicaudata*. Macropterous, forewing length similar to *D. washingtoniana* and *D. nanseni*. Tergum 8 (Fig. 63) exhibits a broad chalice-shaped light-colored area; setose, lacking short, stout sensilla basiconica. Tergum 9 (Fig. 63) similar to that of *D. washingtoniana* in that it is nearly divided by a longitudinal, lightly sclerotized median band that extends from the posterior margin to near the anterior margin; setose and on each side of the mesal band exhibits a semicircular area of short, stout sensilla basiconica; immediately laterad of each sensilla basiconica patch there is a broad light-colored band. Tergum 10 pattern of sclerotization similar to *D. bicaudata* – the median pale, longitudinal, lightly sclerotized strip is interrupted mesally by a darkly sclerotized band connecting the adjacent darkly sclerotized tergal halves; setose with a single, mesal patch of a few short, stout sensilla basiconica. Epiproct also absent. Each paraproct caudal projection in dorsal and ventral views with its outer surface exhibiting a bluntly pointed protuberance (Figs. 63, 65, 66, 71); setal lengths generally less than those of *D. washingtoniana* and D. *nanseni*; in lateral view (Figs. 64, 65, 72) the caudal projection of each side is somewhat sub-triangular and tapers to a bluntly pointed apical margin.

Female. Body length longer than *D. nanseni*, similar to *D. washingtoniana* and *D. bicaudata*. Macropterous, forewing length similar to preceding species. Sternum 9 bearing two oblique brown bands (Fig. 67). Subgenital plate similar to preceding species by exhibiting variable shapes (Figs. 68. 73), ca. 3.8 – 4.6x wider than long. Vagina and spermatheca membranous; spermatheca (Fig. 45 s), similar to that of *D. bicaudata*, ovoid or egg-shaped, nearly as long as wide (1.3x longer than wide); spermathecal duct (sd) 0.5x length of vagina (v); spermatheca and duct bearing accessory glands (ag).

Larva. Originally described by Frison (1942), other information provided by Stewart and Stark (1984,



Figs. 61-69. *Diura knowltoni*, adult. 61. Head and pronotum, dorsal. 62. Mesothorax, ventral. 63. Male terminalia, dorsal. 64. Male terminalia, lateral. 65. Paraproct caudal projections, lateral and frontal. 66. Paraprocts, ventral. 67. Female terminalia, ventral. 68. Examples of female subgenital plate variation. 69. Spermatheca and vagina. ag = accessory glands, s = spermatheca, sd = spermathecal duct, v = vagina. Scale bars = 0.5 mm.



Figs. 70–73. *Diura knowltoni* adult (Alberta, Canada). 70. Head and pronotum, dorsal. 71. Male terminalia, dorsal. 72. Male paraprocts lateral. 73. Female terminalia, ventral.

2002, 2008) and Stark et al. (1998). Similar to preceding species except that abdominal tergites have broad areas of light color giving the impression that the larva is yellow to light brown with dark brown markings, spinulae pattern of pronotal margins (Fig. 79) similar to *D. washingtoniana* and *D. nanseni.*

Egg. Initially described by Knight et al. (1965). Collar forms a Y-shaped, triradiate ridge (Stark & Szczytko 1984). Anchor uniquely comprised of three rounded mushroom-shaped plates each located between the arms of the ridged collar (Figs. 80, 81). Chorionic surface similar to preceding three species (Figs. 80, 81).

Key to the adults of *Diura*
(*D. majuscula* not included)

Males

1 Light medial band of tergum 10 complete (Figs 4, 33); apical half of paraproct caudal projections in profile appearing somewhat finger-like (Figs. 5, 6, 34, 35) 2

1′ Light medial band of tergum 10 incomplete, mesally interrupted by a darkly sclerotized transverse strip connecting the adjacent tergal halves (Figs. 48, 63); paraproct caudal projections in profile appearing as a right triangle, apical halves not appearing finger-like (Figs. 49, 50, 57, 59, 60, 64, 65, 72) ……..... 3

2 Paraproct caudal projections in profile with apical frontodorsal margins not excavated, terminate in abruptly upturned, slightly bulbous tips that provide a boot-like appearance (Figs. 5, 6, 13, 24); tergum 9 with a noticeable mesal patch of sensilla basiconica (Fig. 4, 23); known distribution northeastern Nearctic realm, New Hampshire and

possibly Quebec …… *D. washingtoniana*
2′ Paraproct caudal projections in profile resemble a Bowie knife blade in that the apical frontodorsal margins are noticeably 'clipped out' or excavated, terminate in broadly rounded tips that are not bulbous or so sharply upturned as to appear boot-like (Figs. 34, 35, 42, 45, 75); tergum 9 lacks a mesal patch of sensilla basiconica (Figs. 33, 74); known distribution Palearctic realm .....… *D. nanseni*
3 Paraproct caudal projections in dorsal or ventral view lack a bluntly pointed protuberance at midlength (Figs. 48, 49, 50, 51, 56); mesothoracic sternum with a complete sternacostal suture separating the basisternum from furcasternum (Fig. 47 ss); known distribution northern Holarctic ……..... *D. bicaudata*
3′ Paraproct caudal projections in dorsal or ventral view each with a bluntly pointed protuberance at midlength (Figs. 63, 65, 66, 71); mesothoracic sternum with an incomplete sternacostal suture (Fig. 62); known distribution higher elevations of western North America……...……*D. knowltoni*

Females

1 Spermatheca elongate, somewhat sausage-link-shaped (Figs. 10, 39 s), length greater than 2X width ..……...2
1′ Spermatheca ovoid, somewhat egg-shaped (Figs. 54, 69 s), length approximately 1.3X width ..…….…… 3
2 Known distribution eastern Nearctic realm, New Hampshire and possibly Quebec …… ……..……. *D. washingtoniana*
2′ Known distribution Palearctic realm . *D. nanseni*
3 Mesothoracic sternum with a complete sternacostal suture separating the basisternum from furcasternum (Fig. 47 ss); egg collar ring-shaped and stalked (Fig. 78) …… *D. bicaudata*
3′ Mesothoracic sternum with an incomplete sternacostal suture (Fig. 62); egg collar in dorsal view a Y-shaped triradiate ridge (Figs. 80, 81) ……..... *D. knowltoni*

Comments

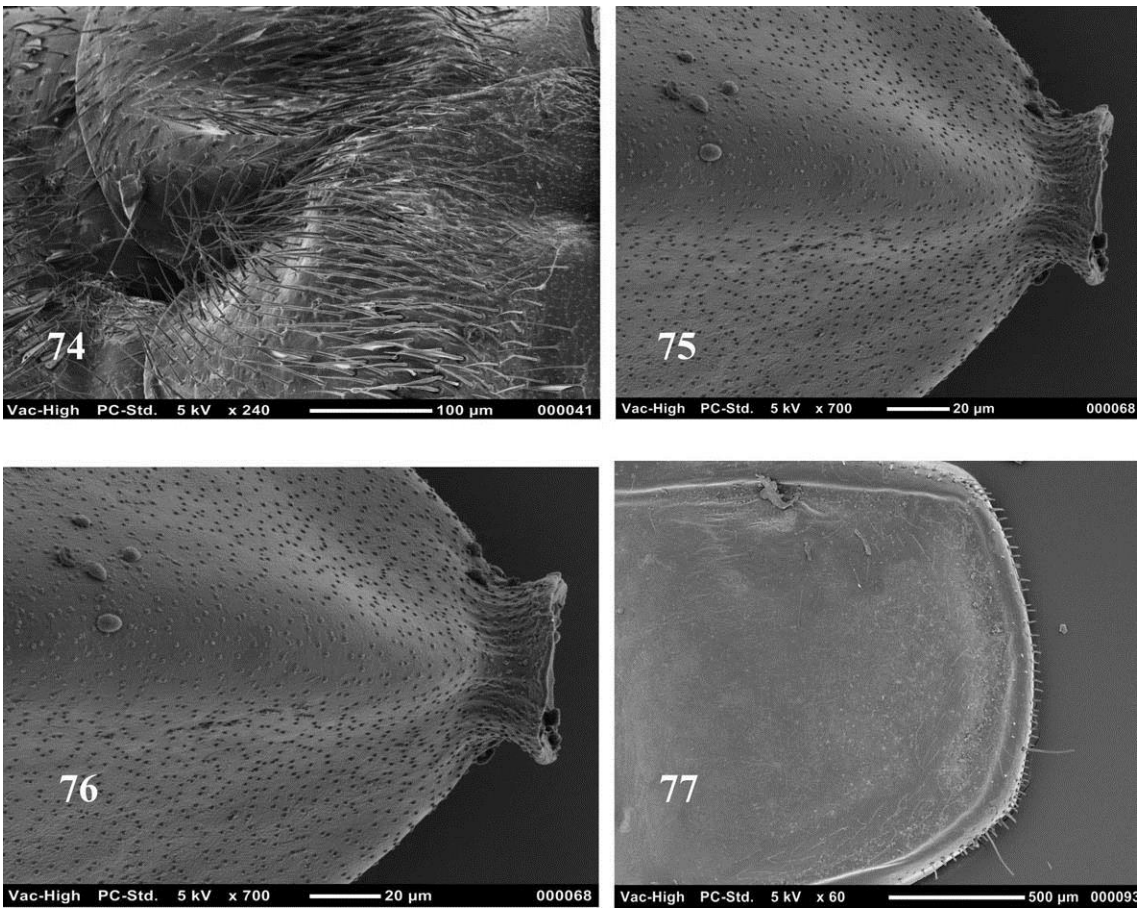
The species *D. washingtoniana* inhabits the northeastern Nearctic and is morphologically similar to *D. nanseni* of the Palearctic. This can be considered an example of a formerly continuous trans-Atlantic distribution (Hynes 1988, Sanmartin et al. 2001). Disruption of this distribution resulted from the opening of the North Atlantic that completely severed land connections between North America and Europe by the Eocene (50 million years ago). A similar north-Atlantic pattern was noted for the genus *Leuctra* (Harper and Harper 2003).

The Palearctic-western Nearctic distribution of *D. bicaudata* suggests a dispersal event across the Bering land bridge. Three separate Bering land bridges have occurred during the past 70 million years (Sanmartin et al. 2001), the most recent being disrupted at the Pleistocene-Holocene boundary (11,700 years ago). Although considered to just inhabit Western North America, the recent reporting of *D. knowltoni* in the Russian Far East (Teslenko 2009), suggests that this species, as Hynes (1988) noted, is also an example of trans-Beringian distribution.

Ricker (1964) and Ricker et al. (1968) recorded females purported to be *Diura nanseni* from Mt. Albert in the Gaspé Peninsula of Quebec. These may be *D. washingtoniana*. However, collection of additional material, especially males, is needed to establish the identity of this Canadian population.

Illies (1966), Zwick (1973), and DeWalt et al. (2018) list page 908 of the 10th edition of *Systema Naturae* (Linnaeus 1758) as the original citation for *Diura bicaudata*. The actual page, however, is 548. A description of this species does appear on page 908 of the 12th edition of this work (Linnaeus 1767). The source of this incorrect page citation may have been erroneous copying by Ricker (1952) of the more accurate information provided by Brinck (1949).

D. knowltoni was considered by Ricker (1952) to be distinct enough to warrant placement in a separate subgenus, *Dolkrila*. Distinguishing characteristics included the incomplete sternacostal ridge and the unusual protuberances of the male paraproct caudal projections. Add to these features the unusual structure of the egg collar (Stark &



Figs. 74-77. 74-76. *Diura nanseni*, adult (Fulufjället National Park, Sweden). 74. Male tergum 9 lacking sensilla basiconica, dorsal. 75. Male paraprocts, biased lateral. 76. Egg collar and anchor, lateral. 77. *Diura bicaudata* (Cumberland, England, United Kingdom). 77. Larval pronotal margins, dorsal.

Szczytko 1984) and presence of multiple anchors (this study). Illies (1966) synonymized this subgenus with *Diura* probably on the basis of Brinck's (1954) conclusion that *D. knowltoni* is less distinct from other members of *Diura* than is *D. nanseni*. Resolution of the subgenus status will have to await a cladistic analysis of the relationships of the species comprising this genus to determine whether *D. knowltoni* is a sister taxon to a clade comprising the three other *Diura* species. For now, a single genus is sufficient.

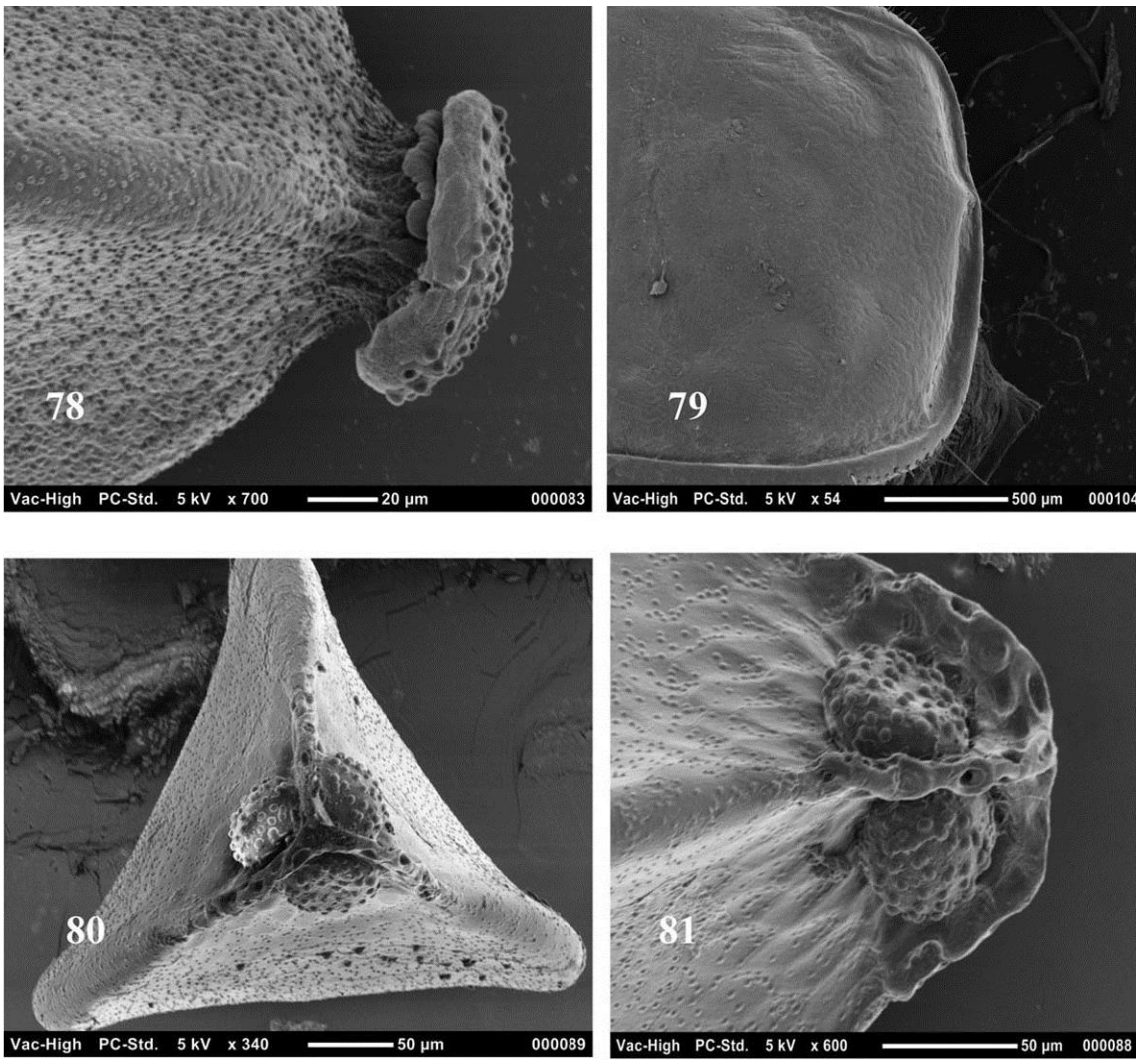
Specimens of *D. majuscula* Klapálek, 1912 were not available for examination. Judson and Nelson (2012) note that this species has been the source of some confusion. Klapálek (1912) reported in his description of *D. majuscula* that the genitalia of the male entirely correspond to that of *D. nanseni* and that of the female to *D. recta* (=*D. bicaudata*). Koponen (1949) then questioned the status of this species concluding that the male was nothing more than *D. nanseni*, a species that Klapálek had seen from only a few individual representatives. However, in the same study where Klapálek (1912) described *D. majuscula*, he also provided a description and illustrations of *D. nanseni*. Koponen concluded that the status of the female of *D. majuscula* was doubtful as he regarded the shape of the subgenital plate as being similar to that of *D. bicaudata*. Based on Koponen's (1949) observations, Brinck (1949) determined that *D. majuscula* was a

composite species and synonymized the male with *D. nanseni* and the female with *D. bicaudata*. Zhiltzova (1975) disagreed and reinstated this species but did not include additional illustrations to those provided earlier by Klapálek (1912). She distinguished males of *D. majuscula* from those of *D. nanseni* by (1) their larger body size (up to 50% larger), and (2) the shape of the paraprocts which when viewed dorsally lack the distinctly convex sides associated with those of the latter species. Additionally, Zhiltzova distinguished *D. majuscula* males from *D. bicaudata* males by the former's (1) macropterous condition, and (2) the presence of setose paraprocts. *Diura majuscula* was also distinguished from D. *bicaudata* by the former's (1) longer subgenital plate with a truncate posterior border, and (2) a bright M-band region in front of the distinct black M-line of the heads of both sexes.

Concerns remain. While Zhiltzova cast doubt on Brink's composite synonymy, especially that part pertaining to *D. nanseni*, from the perspective of the phylogenetic species concept she failed to satisfactorily differentiate *D. majuscula* from *D. bicaudata*. First, Brinck (1949) earlier noted the existence of both macropterous and micropterous male forms of *D. bicaudata* and during this study we observed that both forms of this species are present in Mongolia. Indeed, the many Mongolia *Diura* specimens we examined are variable with respect to overall size, wing length, and details of genitalia. Judson and Nelson (2012) recognized two species of this genus in Mongolia, *D. bicaudata* and *D. majuscula*. Our examination of this material led us to lump this variation into a single species, *D. bicaudata.* However, we suggest that this conclusion be reassessed in comparison to a stabilized nomenclature as to what *D. bicaudata* is based on examination of all relevant western Eurasian material. This is beyond the scope of the present study. Second, the male paraprocts of *D. bicaudata*, like those of the other species examined in this study are not bare but are actually setose (our Figs. 48-51, 56, 57, 59, 60), and with variable setal lengths. Third, Zhiltzova (1975) notes that Klapálek's (1912) illustration (his Fig. 43C) of the lateral view of the *D. majuscula* male paraproct depicts a blunt apex. Zhiltzova reports that this is apparently a distortion resulting from drying and that the apical margin has a typically rounded shape. If correct, when viewed in profile, the shape of *D. majuscula* male paraprocts, like those of *D. bicaudata* (our Figs. 49, 50, 57, 59. 60*)*, would appear to exhibit a right triangle shape. Unfortunately, Klapálek's (1912) illustration of this structure is partially obscured by the cercus. Lastly, the known variation of the head coloration (Brinck 1949) and subgenital plate shape (Brinck 1949, Lillehammer 1974) of *D. bicaudata* seemingly encompass those features exhibited by *D. majuscula.*

Clarification of the status of *D. majuscula* based on a careful redescription coupled with detailed line illustrations and photomicrographs is warranted. Until that study is completed we consider the valid species in the genus *Diura* to consist of *D. washingtoniana*, *D. nanseni*, *D. bicaudata*, and *D. knowltoni*.

Diura belongs to the *Perlodes*-group of the Family Perlodidae Klapálek, 1909 (Perlodini: Perlodinae) (Zwick 1997). The other members are the genera *Perlodes* Banks, 1903, *Filchneria* Klapálek, 1908 (1907), *Perlodinella* Klapálek, 1912, *Rauserodes* Zwick, 1999 and *Zhiltzovaia* Özdikmen, 2008. Zwick (1997) observed that the *Perlodes*-group is characterized by the absence of a well-developed male epiproct, a male tergum 10 that is entire and not divided into hemitergites, and eggs that are triangular in cross-section. *Diura* was considered by Zwick to be distinctive owing to the presence of a complete sternacostal suture separating the mesothoracic basisternum from the furcasternum as well as eggs that are circular in cross-section. However, an incomplete sternacostal suture is exhibited by *D. knowltoni* (Fig. 62) and oval eggs that are triangular in cross-section are exhibited by the four species of this genus examined in this study (Figs. 29, 76, 78, 80). Although definitive diagnostic differences that separate all the *Perlodes*-group genera will have to await careful comparative studies, *Diura* appears to be distinguished by the following combination of features; (1) head with the frontoclypeus bearing a small oval-shaped, light spot near the base of each



Figs. 78-81. 78 *Diura bicaudata* (Cumberland, England, United Kingdom). Egg collar and anchor, lateral. 79-81. *Diura knowltoni* (Summit County, Colorado, USA). 79. Larval pronotal margins, dorsal. 80. Egg, dorsal. 81. Egg collar and anchors, lateral.

antenna and mandible (Figs. 2, 11, 31, 40, 46, 55, 61, 70), (2) interocellular area with a light sub-triangular spot; vertex and occiput with a transverse light median band just posterior to the interocellular spot, (3) only abdominal segments 1 & 2 are divided on each side by a pleural membrane, (4) male tergum 9 in dorsal view with a mesal U- or V-shape pale lightly sclerotized area arising at the hind margin and that is continuous with (Figs. 4, 63), or is separated by a short distance from (Figs. 33, 48), a pale, narrow, longitudinal band that extends to but not quite reaches the front margin, (5) male tergum 10 in dorsal view produced posteriorly (Figs. 4, 12, 33, 41, 44, 48, 56, 63, 71, 72) (Ricker 1952), with a triangular shaped membranous area (Ricker 1952) that arises from the mesal area of the hind margin and that is continuous with a median pale, thin, longitudinal membranous median strip that is uninterrupted as it extends to the front margin (Figs. 4, 33) or is interrupted mesally by a darkly sclerotized band connecting the adjacent tergal halves (Figs. 48, 63), (6) male tergum 10 in lateral

view somewhat meso-posteriorly convex (Figs. 5, 34, 49, 64) but not arcuate or with the posterior area distinctly elevated, (7) male paraprocts extend from the cercus of each side to meet along the mesal line where they abruptly project caudally and are appressed or lie close together for the remainder of their length (Ricker 1952) (Figs. 7, 36, 41, 51, 66), (8) in dorsal view the paraproct caudal projections appear digitate (Figs. 4, 12, 33, 41, 44, 48, 56, 63, 71), (9) in lateral view the surfaces of the paraproct caudal projections are almost entirely sclerotized (Figs. 6, 13, 24, 35, 42, 45, 50, 57, 59, 60, 63, 72), and (10) membranous eversible paraproct lobes, reported for species of *Perlodes* and *Filchneria* (Zwick 1997), are absent.

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