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The genus *Palaeagapetus* Ulmer (Trichoptera, Hydroptilidae, Ptilocolepinae) in North America

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Abstract

The genus *Palaeagapetus* Ulmer (Trichoptera, Hydroptilidae, Ptilocolepinae) is revised in North America. Descriptions of the western species, *P. nearcticus* Banks 1938, are provided with the first descriptions of the female, pupa, larva, egg and case and with notes on food, habitat and annual life cycle. The male and female of the eastern species, *P. celsus* Ross 1936, are described or redescribed with some ecological notes. Distributions of the two species are summarized.

Key words: adult, pupa, larva, case, food, habitat, annual life cycle, distribution

Introduction

Palaeagapetus Ulmer (Trichoptera, Hydroptilidae, Ptilocolepinae) is a small Holarctic genus containing 11 species: 2 living species in North America, 7 living species in the Asian Far East and 2 fossil species from Baltic and Turonian ambers (Ulmer 1912; Banks 1936; Ito & Hattori 1986; Botosaneanu & Levanidova 1987; Ito 1991a, 1991b, 2010; Ito *et al.* 1997; Botosaneanu *et al.* 1998). All known larvae live among liverworts (Hepaticae, Jungermanniales) just above the water in small streams in forests, making their bivalve cases of liverwort pieces and eating the liverworts (Flint 1962; Wiggins 1996; Ito 1998, 2010; Ito & Vshivkova 1999; Ito *et al.* 1997).

Two species of this genus are distributed in North America: *P. nearcticus* Banks 1936 in the west (from British Colombia to California) and *P. celsus* Ross 1936 in the east (reported previously from Quebec and New Brunswick south to Oklahoma, Tennessee and North Carolina) (Wiggins 1996; Morse 2013). In this paper, the descriptions of the adult and immature stages, including the first descriptions of some of these stages are provided along with notes on their distribution, habitat, food and annual life cycle.

Material and methods

Genitalia segments were figured after treatment in hot 10 % KOH solution. Terminology follows Botosaneanu & Levanidova (1987), Wiggins (1996) and Wiggins & Currie (1996). Repositories of specimens are shown in parentheses. Names of collectors, repositories and observers are abbreviated as follows: T. Ito (TI); Robert W. Wisseman (RWW); John C. Morse (JCM), Murray H. Colbo (MHC), John S. Weaver, III (JSW), D. E. Ruiter (DER), J. Lee (JL), O. S. Flint, Jr. (OSF), California Academy of Sciences (CAS), Christian Service University (CSU), Clarion University (CUP), Clemson University Arthropod Collection (CUAC), Illinois Natural History Survey (INHS), Smithsonian Institution National Museum of Natural History (NMNH), Oregon State University,

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Fisheries (OSAC-F), Oregon State University, Entomology (OSAC-E), Rhithron Associates Collection (RAI), Royal Ontario Museum (ROM), University of New Hampshire (UNHC), University of Montreal (QMOR). Specimens deposited in the TI Collection were used for the present descriptions, and adult specimens of *P. celsus* in the Clemson University Arthropod Collection were additionally used for measurements.

Palaeagapetus nearcticus Banks 1936

(Figs. 1–6, 8, Table 1)

Palaeagapetus nearcticus Banks 1936, 265, figs. 1–3, male; Frania & Wiggins, 1997, larva, 7, 13, 22, figs. 4, 7, 18; Schmid 1998, 31.

Palaeagapetus guppyi Schmid 1951, 1–2, figs. 1–2, male; Djernæs, 2011, adult, 19, 35, 49, fig. 23; synonymized by Botosaneanu & Levanidova1987, 43.

Adult (Fig. 1). Body black in life and dark brown in alcohol, 3.3 mm long in males (3.0–3.8 mm, n=17) and 4.0 mm long in females (3.1–4.4 mm, n=4). Antennae 27- or 28-segmented (n=2), 2.7 mm long, 0.77 times as long as body in male (2.6–2.8 mm, n=2); scape (1A, B) slightly thicker and longer than other segments. Maxillary palpi (1A) each 5-segmented, segment I short and round, segments II to V cylindrical; labial palpi (1A) each 3-segmented, all segments cylindrical; both pairs of palpi covered with fine setae. Head (1A, B): large anteromesal setal wart (am) and pair of small anterior setal warts (a) often fused, pair of posterior setal warts (p) round, pair of posterolateral setal warts (pl) large; numerous setae scattered on anterior 1/3. Pronotum with two pairs of round warts, mesoscutum with pair of long oblique warts, and mesoscutellum with single subtriangular wart.

Wings (1C) broad, black, covered with short black hairs, with few small white spots in middle of each forewing. Length of each forewing and hind wing, respectively: 4.0 mm and 3.5 mm in males (3.8–4.3 mm and 3.1–3.9 mm, n=17), 4.2 mm and 3.6 mm in females (4.1–4.5 mm and 3.4–3.9 mm, n=4). Forewings each with apical forks 1–5 and hind wings lacking fork 4; discoidal cell present in male and absent in female. Venation variable individually and even on opposite sides of same specimen; cross veins *r* and *s* absent in forewings of some male and female specimens; apex of *Sc* joined to *R1* in hind wings of some female specimens. Spurs 2, 4, 4.

Lateral bulges (gland) of sternum V (1D, J) round. Acute ventral process developed on segment VII in male (1D) and segment VI of female (1J).

Male genitalia (Figs. 1E–I). Segment IX short, anterolateral margins long, projecting to middle of segment VIII. Lateral appendages of tergite IX (la ap) developed from mid-lateral region of genital capsule, slightly variable individually (1E, H, I); long, 1.2 times as long as capsule, directed caudad and tribranched at middle; dorsal branches (db) longest, with many fine spines at apical half and each with single seta apically; middle branches (mb) as long as 1/2 of dorsal branches, thickest, each completely covered with fine spines and with single seta apically; ventral branches (vb) shortest, 1/4–1/5 length of dorsal branches, each with single seta and several spines apically. Tergite X (tX) depressed dorsoventrally, curved dorsad apically in lateral view (1E), semicircular in dorsal view (1F). Inferior appendages (1E, G, ia) short, each divided into dorsal lobe (dl) and ventral lobe (vl); lobes subequal in length, subacute apically; dorsal lobe curved mesad, ventral lobe directed caudad. Phallus (1E, G, ph) short, broad, membranous with small sclerotized structure inside.

Female genitalia (Figs. 1J, K). Segments I–VII very setose, each with sclerotized tergite and sternite, tergite VIII unpigmented at anterior half and slightly pigmented at posterior half. Segments IX–X very short, each segment about 1/6th as long as segment VIII, with somewhat developed cerci. Vaginal apparatus (1K) slender, lateral projections undeveloped, lateral bands round.

Pupa (Fig. 2). Body (2A) slightly depressed dorsoventrally; length up to 4.0 mm. Antennae and wing pads reaching to abdominal segment V or VI (2A). Mandibles (2B) triangular, each with numerous minute teeth and large tooth on inner edge. Pair of hook plates (2A, C, D) present near anterior margins of each of segments III–VII and near posterior margins of segments III–V, 10–18 hooks on each plate. Anal process (2A) thick and round apically.

Instars of larva (Fig. 3). Head widths of larvae reared from eggs in laboratory and collected on Mary's Peak, Oregon, 1982–1983 (see 'Habitat and specimens'), separating into 5 groups, suggesting 5 instars as follows: 1st instar 0.15–0.16 mm, 2nd instar 0.18–0.19 mm, 3rd instar 0.22–0.25 mm, 4th instar 0.28–0.32 mm, and 5th instar 0.36–0.39 mm, respectively.

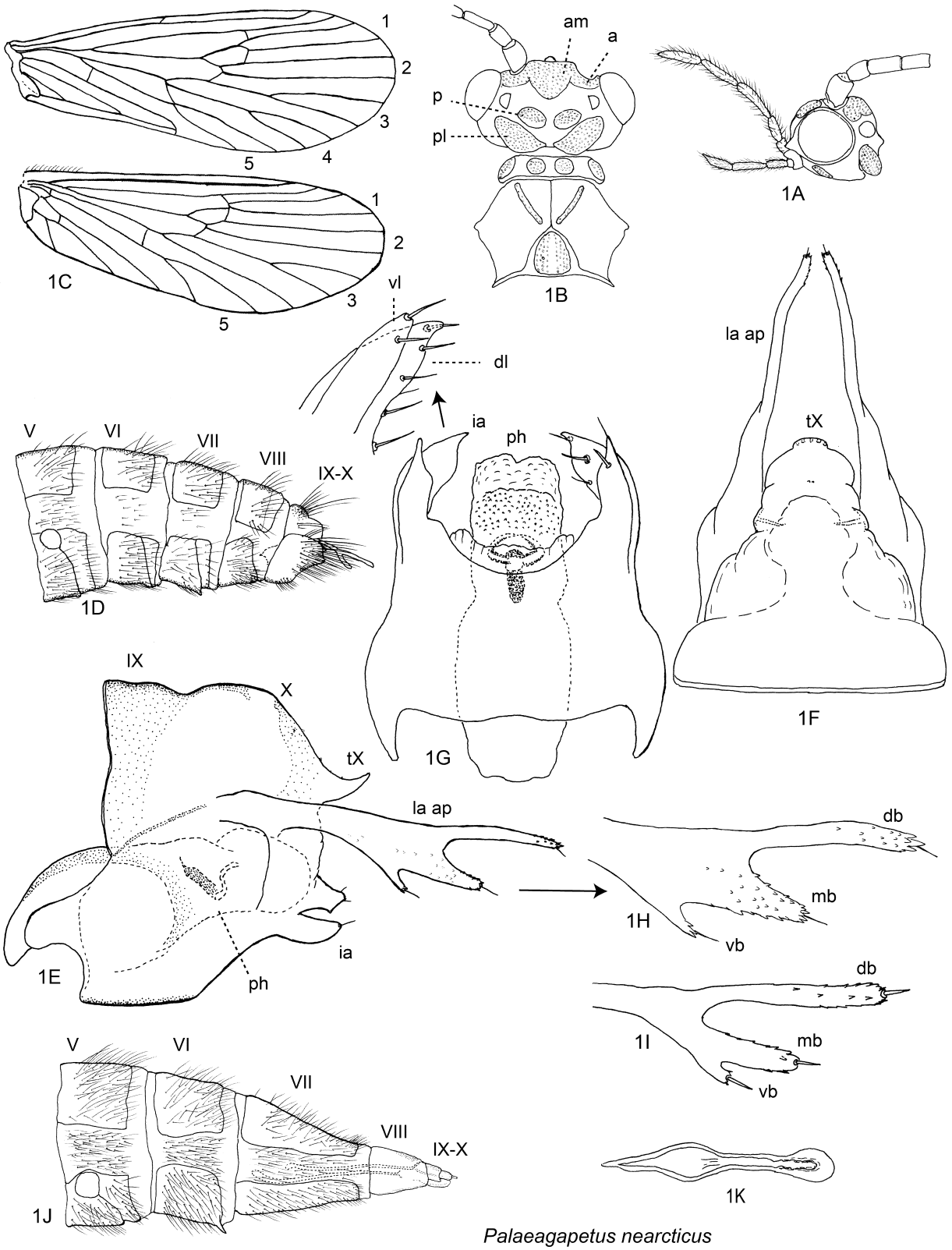

FIGURE 1. *Palaeagapetus nearcticus* male and female. Male (A–I): A, head, left lateral; B, head and thorax, dorsal; C, right wings, dorsal; D, abdominal segments V–X, left lateral; E, genitalia, left lateral; F, same, dorsal; G, same, ventral; H, I, lateral appendage, left lateral. Female (J, K): J, abdominal segments V–X, left lateral; K, vaginal apparatus, ventral. Abbreviations: 1–5=1st to 5th apical forks; V–X= abdominal segments V–X; tX= tergite X. Setal warts (B): a= anterior setal wart, am= anteromesal setal wart, p=posterior setal wart, pl=posterolateral setal wart. Genitalia: ia=inferior appendage (paired): dl=dorsal lobe of inferior appendage, vl=ventral lobe of inferior appendage; la ap=lateral appendage (paired): db=dorsal branch of lateral appendage; mb=middle branch of lateral appendage, vb=ventral branch of lateral appendage; ph, phallus.

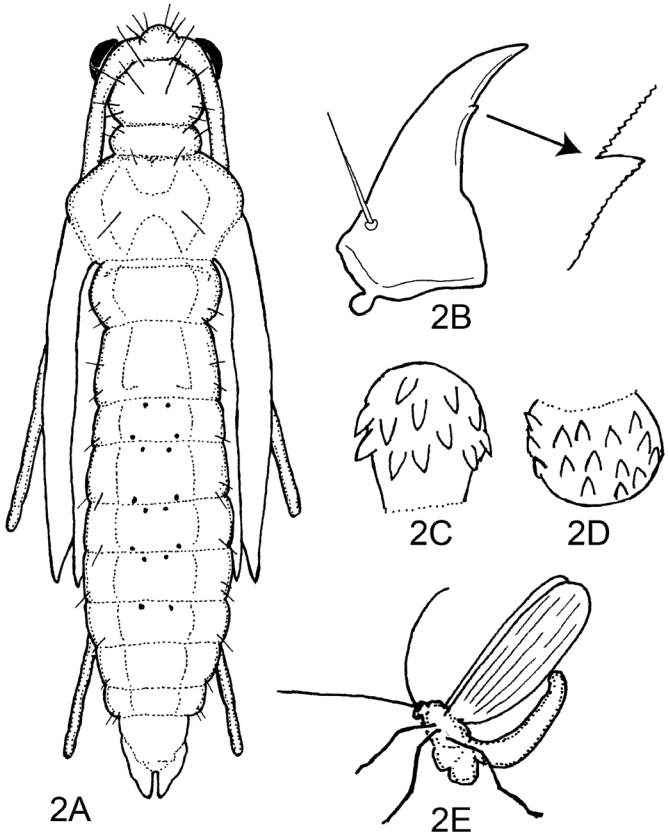

FIGURE 2. *Palaeagapetus nearcticus* pupa and newly emerged adult. Pupa (A–D): A, dorsal; B, left mandible, dorsal; C, anterior hook plate, dorsal; D, posterior hook plate, dorsal. Newly emerged adult: E, wing erection of newly emerged adult, left lateral, see text.

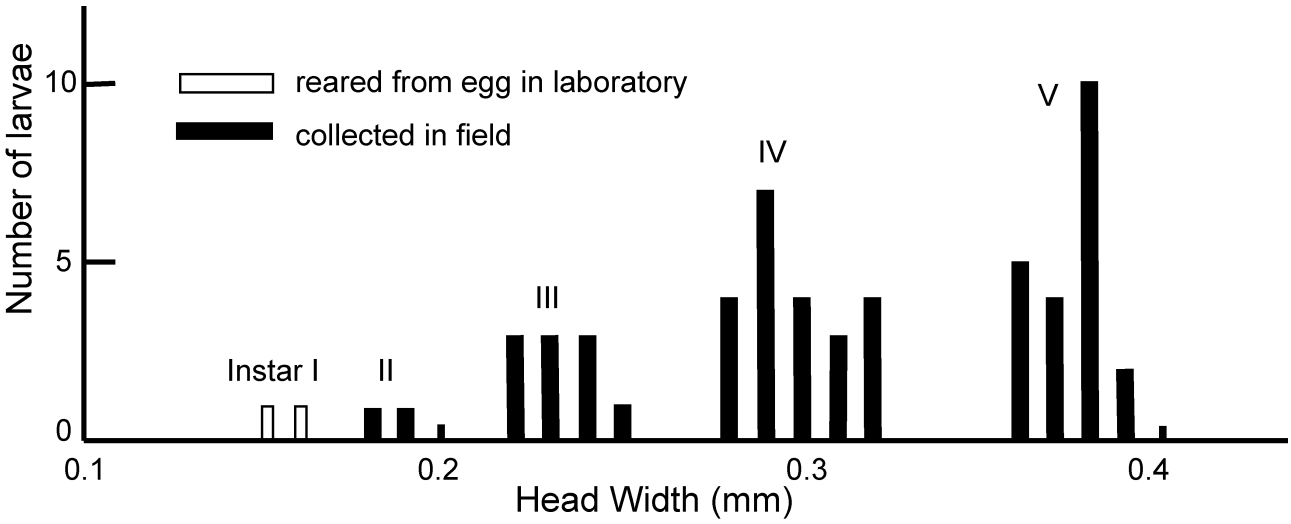

FIGURE 3. Instar analysis of *Palaeagapetus nearcticus* larvae by head-width distribution.

Final (5th) instar larva (Fig. 4). Body (4A) suberuciform, length up to 5 mm, flattened dorsoventrally, widest at abdominal segments III–V, membranous portion whitish yellow and sclerites deep brown. Head (4B, C): Width subequal to length, black to deep brown except light eye spot, 18 primary setae present, secondary setae or spines absent; antennae (4C inset) situated just beneath anterior corner of eye spot; anterior ventral apotome subtriangular with concave anterior margin, posterior ventral apotome indistinct. Mandibles (4E, F) deep brown, stout, each with

three teeth dorsally, mesal brush of left mandible with setae longer and more numerous than of right one, setae of brushes slightly serrate (4F inset). Labrum (4D) light brown, anterior margin deeply concave. Thorax (4A, G): Each segment dorsally covered by two, deep brown, square sclerites bearing about 55, 45 and 45 setae on each of pro-, meso- and metanotal plates; posterior margin of pronotum (4G) dark, posterior margins of meso- and metanota deep brown. Propleuron (4H, upper) rectangular with distinct pleural sutures separating it from foretrochantins; meso- and metapleura (4H, middle and lower) each crescentic with no distinct pleural sutures. Three thoracic legs (4H) brown, similar in structure, tarsi with two enlarged apical spurs, trochanter or femur with no ventral brush. Abdomen (4A): Segments I–VIII each with pair of truncate lateral tubercles, segment I with three small sclerites and about 40 setae, segments II–VIII each with 8–12 setae; dorsal tergite IX (4I) deep brown, semicircular with concave anterior margin and with about 30 long setae; lateral sclerites of anal prolegs (4J) rectangular, pale brown; anal claws (4J) strongly curved ventrad, deep brown without accessory hooks or denticles.

Early (1st–4th) instar larvae (Figs. 5A–G). Campodeiform (5A), sclerites brown in 4th instar larva and lighter in younger instar larvae, thorax and abdomen very setose.

Head (5A) length subequal to head width, with 18 primary setae; thoracic segments (5A) covered with two dorsal plates, each dorsal plate with 60–70 setae. Abdominal segments I–VIII (5A–D) each with rectangular dorsal sclerite, pair of lateral humps and lateral tubercles, lateral tubercles indistinct in earlier instar larvae, each segment with many setae and sensillae (5B–D). Dorsal sclerite IX (5E–G) with about 30 setae and several sensillae; anal legs (5A inset) extended caudad, without accessory hooks or denticles. Other characters as in final instar larva.

Egg (Fig. 5H). Eggs orange, spherical, about 0.2 mm in diameter, and separately deposited on leaves of liverworts.

Case (Fig. 5I). Case of final instar larva up to 7 mm long, depressed dorsoventrally and composed of two valves with slit-like openings at front and rear. Each valve consisting of roundish or oval pieces of liverwort.

Food and feeding behavior (Fig. 5J). Larvae eat leaves of the liverwort, *Scapania uliginosa* (Sw. ex Lindenb.) Dumort. (Jungermannidales, Scapaniaceae). They pierce cell walls and swallow contents of cells one at a time.

Emergence (Fig. 2E). Emergence was observed in the laboratory (Corvallis, Oregon,) in late July, 2009. Teneral adults emerged on leaves of liverwort in the morning (5:30–9:30 AM). The newly emerged adults stretch their wings and abdomens in an upright position like mayflies, which takes ca. 3 minutes (n=2).

Annual life cycle (Fig. 6). Occurrence of 5 development stages in British Columbia (B); Washington (W); Mary's Peak, Benton County, Oregon (M); other sites of Oregon (O); and California (C) were summarized in 10-day periods based on the collecting data in "habitat and biology" and Table 1 in Fig. 6. Collection records that did not specify early or final instar larvae were omitted from the figure.

Eggs and early instar larvae were found mainly in late July and September–early November, respectively. Final instar larvae were seen from September to the following July. Adults occurred mainly in June to September. Therefore, a univoltine life cycle with a summer emergence season was suggested as shown by the grey band in Fig. 6. However, another annual cycle could be supposed for a few populations, because some adults and early instar larvae were collected in April–May and June, respectively.

Habitat and biology. The larvae live in springs, spring brooks and seepage areas of forested mountain streams, often just above the water surface and in hygropetric habitats, and they are exclusively associated with moss and liverwort.

Observation at Mary's Peak, Benton County, **Oregon.** Many springs and seeps enter the stream around 1100–1200 m elevation where the channel is 1–2 m wide; moss and the liverwort *Scapania ulinosa* are abundant; cold year-round water regime. Many larvae and pupae of *P. nearcticus* were found in the liverwort and moss on cobbles and logs mainly just above water. Specimens were collected and deposited by RWW unless otherwise indicated: 21 August 1952, V. Roth, 1 male; 03 September 1982, many 5th and early instar larvae; 20 September 1981, 22 1st–4th instar larvae; 31 October 1981, 26 empty pupal cases, no larvae found; 30 May 1982, many 5th-instar larvae; 03 November 1982, 1st to 4th-instar larvae and many 5th-instar larvae with newly constructed cases; 27 April 1983, 15 5th-instar larvae; 09 August 1983, about 60 adults; 29 July 2009, 2 males, 2 females, 10 pupae, 2 5th-instar larvae, 5 eggs, RWW & TI (TI); 07 July 2010, no larvae or adults; 01 August 2010, 4 males, many adults seen.

Observation at Flynn Creek, Lincoln County, Oregon. Oregon Coast Range, Flynn Creek, 44.53°N, 123.87°W, 150–300 m, 3rd-order stream and tributaries, 0.3–3 base flow width, mean monthly water temperature

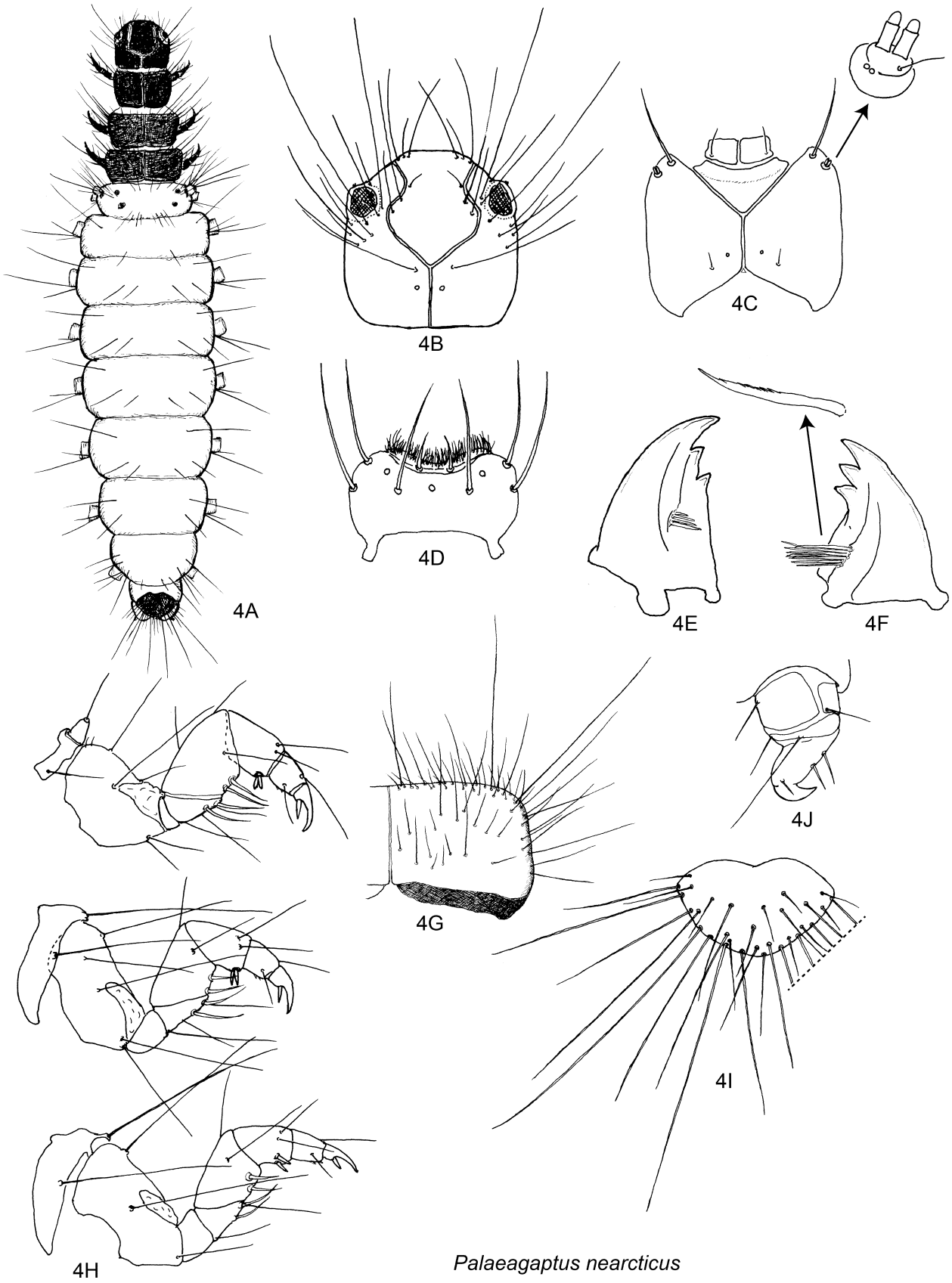

FIGURE 4. *Palaeagapetus nearcticus* final instar larva. A, larva, dorsal; B, head, dorsal; C, same, ventral; D, labrum, dorsal; E, right mandible, ventral; F, left mandible, ventral; G, right pronotal plate, dorsal; H, right pleura and legs on thorax, right lateral; I, dorsal tergite on segment IX, dorsal; J, right anal leg, right lateral.

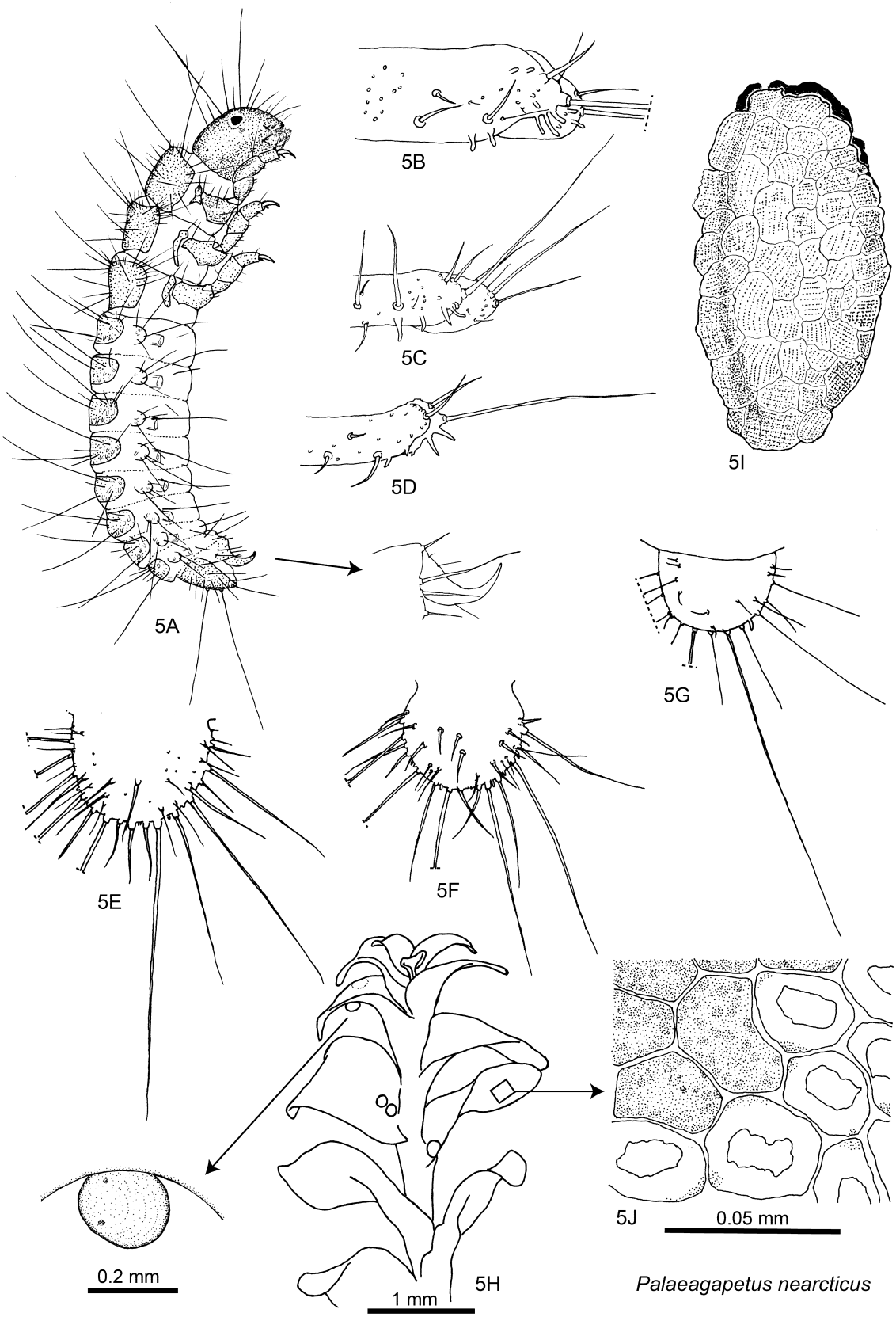

FIGURE 5. *Palaeagapetus nearcticus* early instar larva, eggs on liverwort, case of final instar larva and feeding trace. Early instar larva (A–G): A, 4th instar larva, right, lateral; B–D, right lateral parts of abdominal segment II of 4th (B), 3rd (C) and 2nd (D) instar larvae, dorsal; E–G, dorsal tergites of segment IX of 4th (E), 3rd (F) and 2nd (G) instar larvae, dorsal. Eggs (H and inset): eggs on liverwort. Case (I), dorsal. Feeding trace (J): cells of the liverwort showing feeding trace, see text.

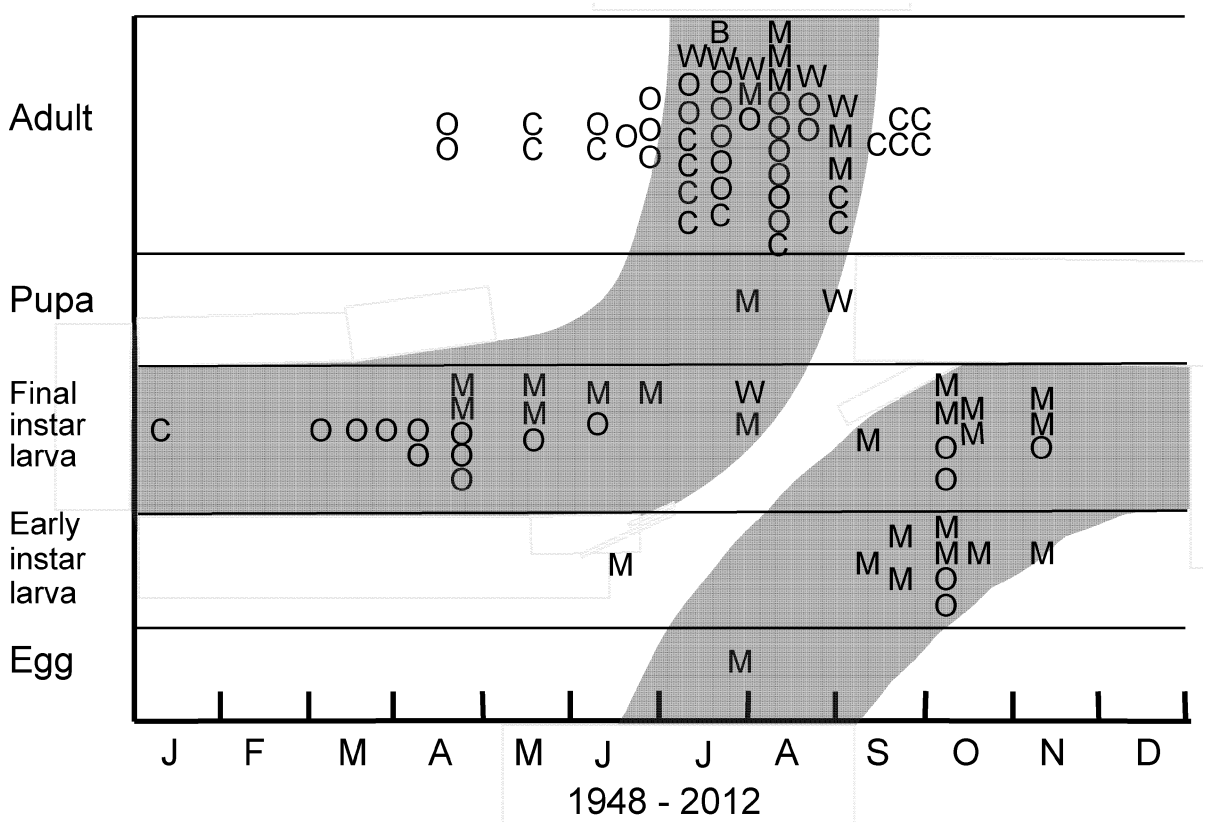

FIGURE 6. Occurrence of 5 development stages of *Palaeagapetus nearcticus* in British Colombia (B), Washington (W), Mary's Peak in Oregon (M), other localities in Oregon (O), and California (C) in 1948–2012. Grey bands indicate the supposed main annual life cycle in all study sites.

varies from 7.5 to 12.5°C, mature second growth Douglas fir forest on slopes, red alder and big leaf maple overstory in riparian. Many larvae and pupae were found in moss and liverwort on logs and bedrocks. All specimens were collected and deposited by RWW: 09 December 1981, 3 4th instar and 21 5th-instar larvae; 09 December 1981, 2 old pupal cases; 29 January 1982, no larvae found; 05 March, 1982, 8 5th-instar larvae; 07 April 1982, 4 5th-instar larvae; 07 April 1982, 3 5th-instar larvae; 26 April 1982, 9 5th-instar larvae; 05 May 1982, 20 5th-instar larvae; 05 May 1982, 4 5th instar larvae; 22 May 1982, 20 5th-instar larvae; 02 June 1982,7 5th-instar larvae; 20 June 1982, 23 5th-instar larvae; 20 June 1982, 1 male; 07 July 1982, no larvae or pupae found; 19 July 1982, 1 male; 05 August 1982, no larvae or pupae found; 04 October 1982, 2 probably 4th-instar larvae without cases, 1 5th-instar larva; 06 April 1983, 4 5th-instar larvae.

Remarks. The male of this species is characterized by tri-branched lateral appendages of tergite IX, which are never seen in other congeneric species. On the other hand, the female, pupa, final instar larva, early instar larva, egg and case are very similar to those of other congeneric species, including Nearctic *P. celsus* (Ulmer 1912; Ross 1938; Flint 1962; Ito & Hattori 1986; Botosaneanu & Levanidova 1987; Ito 1991a, 1991b, 1997, 1998, 2010; Ito *et al.* 1997).

The habitat, feeding behavior and emergence behavior of this species are also very similar to those of other species studied (Ito 1998; Ito & Vshivkova 1999). The female pupal weights, used for an indicator of fecundity in the subfamily Ptilocolepinae (Ito 1998), were 1.43–2.00 mg (n=4, average 1.73 mg), suggesting *P. nearcticus* resembles *P. parvus* in terms of fecundity (Ito 1998). The liverwort used for food and case materials by *P. nearcticus* is *Scapania uliginosa* (Sw. ex Lindenb.) Dumort., which is the first report of this host for a *Palaeagapetus* species. Another congeneric liverwort host, *Scapania undulata* (L.) Dumort., was reported for a population of Japanese species, *P. parvus* (Ito 1991a).

Life cycles have been studied for five Far East Asian species; three of them, *P. flexus*, *P. parvus* and *P. kyushuensis*, are distinctly univoltine with a short summer emergence period (Ito 1991b, 1998; Ito *et al.* 1997), and

the fourth species, *P. finisorientis*, has 3–4 generations in 2 years with a long flight period from March–October (Ito & Vshivkova 1999). For the fifth species, *P. ovatus*, two sorts of life cycles have been reported: 3–4 generations in 2 years with a long emergence period (from March to October) at many sites (Ito 1988, 1998; Kuhara 2011), but univoltine with a short summer flight period in a very cool headwater stream at high elevation (Kuhara 2011). According to the collecting data (Fig. 6), the annual cycle of *P. nearcticus* may be 1 generation per year at many sites, but with a more complicated life cycle and long emergence period at a few sites (similar to *P. ovatus*), and probably depending on local water temperature regimes.

Distribution and specimens (Fig. 8). The species has been reported from the following states and provinces: **CANADA: British Columbia** (Williams & Williams 1987; and as *P. guppyi* by Schmid 1951; Schmid & Guppy 1952; Blickle 1979), **USA: Washington** (Banks 1936; Ross 1944; Blickle 1979; Ruiter *et al.* 2005), **Oregon** (Anderson & Wold 1972; Anderson 1976; Blickle 1979; and as *P. guppyi* by Anderson 1976; Blickle 1979), and **California** (Denning 1956; Blickle 1979).

The species is patchily distributed in mountain ranges along the western coast of North America from British Columbia (about 100–200 km north of the U.S. –Canadian border), southward in the Cascade and Sierra Nevada Mountains to Sequoia National Park in the southern Sierras; and southward in the Olympic Mountains and coastal ranges of Oregon and California to Mendocino County (Table 1). Most of the Cascade Mountain sites are on the wetter west slopes, though it has been found at several sites on the more xeric east slope of the Cascades. The majority of the springs and spring-streams where it occurs are in mature or old-growth coniferous forests. In the Cascade and Coastal Mountains in the northern part of its range, it is generally found at elevations <1200 m, below the alpine and subalpine zone. In The Sierra Nevada Mountains in the southern part of its range, it has been found in coniferous forests between 1265–2134 m elevation.

TABLE 1. Annotated collection data for *Palaeagapetus nearcticus* Banks 1936.

British Columbia (BC): Mount Benson, 19 August 1949, R. Guppy, holotype male for *Palaeagapetus guppyi* Schmid, 1951; recorded as *P. guppyi* by Nimmo & Scudder (1978) and Schmid & Guppy (1952); but recorded as *P. nearcticus* by Scudder (1994) (Canadian National Collection). Mount Benson is in the maritime coastal ranges about 9.6 km west of Nanaimo, BC, on the southern end of Vancouver Island.
Coastal Mountains, tributary to Lillooet River at the Tenquilla Lake Trailhead; 100–200 km NNE of Vancouver, 16 July 1988, R.W. Baumann, Wells & Whiting, 18 males, 7 females (DER). This is the northern most record for *P.nearcticus*.

California (CA): Sierra County, Rock Creek, 39.5986°N, 120.9972°W, watershed area 6.46 km^2, record extracted from US EPA national database and supplied by A. Herlihy, 24 June 2009, 6 larvae.
Del Norte County, California Coastal Ranges: Crescent City Fork of Blue Creek, 396 m, 41.532°N, 123.827°W, watershed area 26.98 km^2, record extracted from US EPA national database and supplied by A. Herlihy, 19 July 2000, 5 larvae; Clarks Creek, 58 m, watershed area 4.61 km^2, 41.8082°N, 124.1122°W, record extracted from US EPA national database and supplied by A. Herlihy, 30 July 2003, 4 larvae; Clarks Creek above Highway 199, 55 m, 41.8083°N, 124.1122°W, record extracted from the California SWAMP database and supplied by A. Rehn, 30 July 2003, larvae; South Fork Smith River Road, spring creek at mile 1.26, 27 September 2008, JL, 2 males (JL); South Fork Smith River Road, spring creek at mile 12.69, 04 April 2009, JL, 1 larva (JL).
Humboldt County, Squaw Creek: 335 m, watershed area 2.47 km^2, 40.3167°N, 123.9976°W, for an EPA study, 08 August 2002, record supplied by A. Herlihy, 1 larva; about 1 km upstream from Grasshopper Creek, 341 m, 40.3167°N, 123.996°W, record extracted from the California SWAMP database and supplied by A. Rehn, 08 August 2002, larvae. California Coastal Ranges: North Fork Tectah Creek, north of Bald Hills Road, 27 June 2011, JL, 3 males (JL); Godwood Creek, about 0.3 km above Prairie Creek, 49 m, 41.3679°N, 124.0243°W, record extracted from the California SWAMP database and supplied by A. Rehn, 15 September 2010, larvae; Arcata Community Forest, Jolly Giant Creek, about 200 m, 23 April to 14 June 1994, reared, JL, 2 males (JL); 06 September, 2011, JL, 1 male, 1 female (JL & RWW); Dragsaw Spring at Forest Service Road 13N01, tributary of Red Mountain Creek near Fish Lake, 10 July 2005, JL, 1 male (JL); 30 September 2008, JL, 2 males (JL & TI); Red Mountain Creek at Forest Service Road 10N12, near Fish Lake, 10 July 2005, JL, 4 males (JL); 17 September 2009, JL, 8 males, 4 females (JL); 30 September 2008, JL, 6 males, 4 females (JL & TI); unnamed creek 1.6 km north of Trinidad, 03 June 1972 & 08 August 1973, adults (Burdick personal communication 1999, 2013); upper Willow Creek, below Berry Summit, 29 August 2012, JL, 4 males (JL); Sixes Rivers National Forest, Slide Creek, Highway 13, south of Fish Lake Campground, 31 May 1991, R. Baumann and B. Stark, 1 female (Brigham Young University). Redwoods National Park: California Coastal Ranges, benthic biomonitoring samples collected by park personnel, Godwood Creek, 22 June 2012, larvae; Little Lost Man Creek, 05 July 2012, larvae.
Madera County, Sierra Nevada Mountains, Nelder Creek, about 1.6 km above California Creek, 1535 m, 37.4249°N,

119.5957°W, record extracted from the California SWAMP database and supplied by A. Rehn: 05 May 2009, larvae; 15 June 2009, larvae; 15 October 2009, larvae.
Mariposa County, Sierra Nevada Mountains, 11.3 km ENE of Fish Camp, 2134 m, 11 July 1946, H.P. Chandler, 2 males (CAS).
Mendocino County, California Coastal Ranges, Wages Creek, Highway 1, 30 August 2009, JL, 2 males (JL).
Plumas County, Sierra Nevada Mountains, Rice Creek, north arm, 1814 m, 40.4002°N, 121.4390°W, record extracted from the California SWAMP database and supplied by A. Rehn, 16 June 2009, larvae.
Sierra County, Sierra Nevada Mountains, Rock Creek, 1.9 km upstream of Little Rock Creek, 1265 m, 39.5986°N, 120.9978°W, record extracted from the California SWAMP database and supplied by A. Rehn, 24 June 2009, larvae.
Siskiyou County, Klamath-Siskiyou Mountains, Big Springs, Mount Shasta, City of Mount Shasta, Mount Shasta Park, about 1000 m, 25 May 2007, B. Kondratieff and R. Baumann, 2 males (CSU).
Tulare County, Sierra Nevada Mountains, Sequoia National Park, 1829 m, , 20 July 1946, D.G. Denning, adults (CAS) (Burdick personal communication 1999, 2013).

Oregon (OR): Benton County, Oregon Coast Range, unnamed perennial tributary to Crooked Creek, tributary of the Alsea River, Oregon Coast Range, 348 m, 44.4374°N, 123.4900°W, early August, year unknown, J. Banks, 1 adult (OSAC-F); Oak Creek, tributary of the Mary's and Willamette River near Corvallis, 213 m, densely forested, cobble/gravel substrates, emergence trap, 5–9 June 1969, J. Wold, 1 male (Anderson & Wold 1972, Anderson 1976).
Clackamas County, Western Cascade Mountains: Dinger Creek near mouth at Timothy Lake, 1484 m, old-growth conifer watershed, snow-melt and spring-fed stream, 4–5 m wide channel, cold year-round temperature regime, moderate gradient, cobble substrates, 5–10% coverage with moss and liverwort, 04 June 2000, RWW,2 5th-instar larvae (TI); Mount Hood, Hidden Lake outlet stream, 1219 m, 23 July 1953, collector unknown, 1 male (INHS); Mount Hood, Still Creek Forest Camp, 10 August 1955, S.G. Jewett, 1 male, 1 female (NMNH); Mount Hood, Still Creek near Swim, mid-elevation, 20 July 1947, S. Jewett, males, females (1 male, OSAC-E; others INHS); Last Creek, 1219 m, 45.0009°N, 121.8152°W, watershed area 3.76 km^2, record extracted from US EPA national database and supplied by A. Herlihy, 1997, larvae.
Douglas County, Western Cascade Mountains: tributary to Emile Creek at river mile 0, 1274 m, 43.2454°N, 122.7943°W, watershed area 2.67 km^2, record extracted from US EPA national database and supplied by A. Herlihy, 1999 larvae; upper Emile Creek, Umpqua National Forest biomonitoring site, 1189 m, 2–4 m wide channel, relatively open canopy, moderate gradient, meadow/wetland above site, cold year-round water temperature, spring-fed with low seasonal discharge amplitude, 50–60% coverage of substrates with moss and liverwort, mostly sand and gravel substrates, 21 October 1997, RWW, 13 larvae (RWW); Umpqua National Forest, headwater tributaries of Bulldog Creek, tributary to Big Bend Creek, Steamboat Creek, & North Umpqua River, Western Cascades, 1183–1561 m, 43.40°N, 122.50°W, Forest Service road 3850 and spur roads, Site 1, 1561–1573 m, 1st-order stream and ponds in subalpine meadow, 18–19 June 1998, RWW, 10 5th-and two -early instar larvae (TI); headwaters of Little River, tributary to the South Umpqua River, about 1000 m, 18 April 1998, RWW, 1 male (RWW).
Jackson County, Klamath/Siskiyou Mountains, East Fork Ashland Creek, Rogue River National Forest, 914 m, 100–200 m above Reeder Reservoir, City of Ashland water supply, mature 2nd growth conifer/hardwood forest, 2–4 m-wide channel, moderate gradient, cobble/boulder substrate with abundant decomposed granitic sand, primarily spring-fed, cold year-round water temperature, 2 November 1999, RWW, 3 5th-instar larvae (RWW). Western Cascade Mountains: North Fork Little Butte Creek 0–50 m below Camp Creek, site NBB6, 884 m, Medford Bureau of Land Management biomonitoring site, spring-fed stream with low seasonal hydrograph amplitude, 2nd-growth conifer/hardwood forest, high logging and roading intensity, cool-cold year-round water temperatures, 3–5 m wide channel, moderate gradient, gravel/cobble substrates, siltation high, high coverage of substrates with aquatic moss and liverwort, 03 October 2001, RWW, 8 larvae (RWW and TI); Clark Creek, site CLK9, tributary of Butte Creek and the Rogue River, about 915 m, spring-fed stream with cold year-round water temperatures and low seasonal hydrograph amplitude, 2nd-growth mixed conifer/hardwood forest with high logging and roading intensity, moderate gradient, 1–5 m-wide channel, sand/gravel/cobble/boulder substrates, high siltation, high coverage of substrates with aquatic moss and liverwort, Medford Bureau of Land Management biomonitoring site, 01 October 1992, 194 larvae; 06 October 1993, 1 larva; 03 October 2001, many larvae, RWW (RWW).
Josephine County, Klamath/Siskiyou Mountains, Oregon Caves National Park, Cave Creek, benthic biomonitoring samples, 13 June 2012, collected by park service personnel, larvae (RAI).
Klamath County, Eastern Cascade Mountains: Cold Creek, 2.4 km upstream mouth, tributary to Johnson Creek, 1509 m, high gradient, moss, liverwort and woody debris abundant, coarse, embedded substrate, spring-fed, cold, year-round water temperature, biomonitoring sample, 16 June 1992, Klamath Bureau of Land Management perspnnel, 178 larvae/m^2 (RWW); Irving Creek, Winema National Forest, mid-elevation, open coniferous forest, 1.2–1.8 m-wide channel, spring-fed, cold year-round water temperature, benthic biomonitoring sample, 22 September 1992, Chemult Ranger District personnel, 24 larvae (RWW).

Lane County, Western Cascade Mountains: South Fork McKenzie River, side channel, about 600 m, considerable cold water upwelling in this shaded side channel mimics spring conditions, biomonitoring sample, 01 April 2010, the McKenzie Watershed Council personnel, 2 5th-instar larvae (RWW); Roney Creek 1.6 km up horse trail, 792 m, 44.1077°N, 122.0187°W, watershed area 4.77 km^2, record extracted from US EPA national database and supplied by A. Herlihy, 1999, larvae; Cullen Creek at river mile 0.3, 408 m, 44.2032°N, 123.9491°W, record extracted from US EPA national database and supplied by A. Herlihy, 1996 larvae; Salt Creek Falls near Willamette Pass, mid-elevation, 07 August 1948, H.H. Ross, 1 male (INHS); HJ Andrews Experimental Forest, Nostoc Creek, mid-elevation, 29 April 1982, Greg Courtney, 1 5th-instar larva (OSAC-E); HJ Andrews Experimental Forest, emergence trap, mid-elevation, Site 2, 44.2145°N, 122.2493°W, 21–25 June 2010, B. Gerth, 1 male (OSAC-F); Iko Spring, tributary to Indigo Creek, Middle Fork Willamette River basin, about 915 m, dense old-growth coniferous forest; large spring with pools and channels, 6.7–8.9° C water temperature in late summer, sand dominant substrate, large woody debris, moss and liverwort abundant, September 1997, Forest Service personnel, larvae common (RWW); Huckleberry Creek above 7th-Creek, 2.4 km east of the Middle Fork of the Willamette River, 9.6 km NE of Oakridge, EPA fertilization study, 11 March 1976, 3 5th-instar larvae (OSAC-E); Quartz Creek, mid-elevation, 22 March 1974, OSF, 1 5th-instar larva (OSAC-E).
Lane County, H.J. Andrews Experimental Forest, Shorter Creek, tributary to Lookout Creek, 19 June 1978, N.H. Anderson, life stage unknown (ROM).
Lincoln County, Oregon Coast Range, Needle Branch Creek, Alsea River watershed, adjacent to the Flynn Creek watershed, about 200 m, 44.5151°N, 123.8545°W, 24 May 2010, B. Gerth, 3 larvae (OSAC-F).
Linn County, Western Cascade Mountains: Pyramid Creek tributary, 1203 m, watershed area 0.70 km^2, 44.5493°N, 122.0741°W , record extracted from US EPA national database and supplied by A. Herlihy, 31 July 2002, 7 larvae; Suttle Camp Creek, 790 m, watershed area 2.84 km^2, 44.4398°N, 122.2795°W, record extracted from US EPA national database and supplied by A. Herlihy, 08 July 2003, 1 larva; Monument Peak Campground near waterfall, mid-elevation, 02 August 1969, 1 male, K. Goeden (Anderson 1976); Big Meadows, North Santiam Highway, Western Cascades, about 1200 m, 03 August 1948, collector unknown, 1 male (INHS); 1.6 km west of Marion Forks, North Santiam Highway, mid-elevation, 09 August 1952, collector unknown, male, female (INHS); Willis Creek, North Santiam Highway, mid-elevation, 17 July 1947, 1 female, collector unknown (INHS).
Multnomah County, Western Cascade Mountains, Columbia River Gorge, Wahkeena Creek headwater spring, 450 m, large volume spring, 6°C year-round water temperature, dense forest canopy, 21 June 1989, RWW, 2 males; 05 July 1989, RWW, 2 males, 1 female; 19 July 1989, RWW, 2 males, 3 females; 16 August 1989, RWW, 4 males, 2 females, RWW (TI).
Tillamook County, Oregon Coast Range, headwater tributary of the Trask River, 45.3678°N, 123.464°W, emergence trap, 10 August 2009, B. Gerth, 1 male (OSAC-F).

Washington (WA): Chelan County, Eastern Cascade Mountains, Middle Shaser Creek, near Cashmere, tributary of Peshastin Creek, about 900–1200 m, 09 July 2008, benthic biomonitoring samples, larvae (RAI).
Mount Rainier National Park, Western Cascade Mountains: Longmire Springs, about 900 m, 25 July 1953, K.M. Fender, 9 males (CAS); boggy stream 2.7 km north of Highway 706 on Westside Road, 17 August 1999, Kondratieff, Lechleitner & Zuellig, 2 females (CSU) (Ruiter et al. 2005); large spring-fed stream 3.06 km north Highway 706, west side of road, 13 July 2004, Kondratieff, Lechleitner & Zuellig, 1 male (CSU) (Ruiter et al. 2005); Falls Creek at Carbon River, 16 August 1999, Kondratieff, Lechleitner & Zuellig, 1 male (CSU) (Ruiter et al. 2005); Ohanapecosh River at oil spill, site o29–00a, benthic sample, 23 August 2010, B. Samora, 7 immature pupae (RWW).
Olympic National Park, unnamed small stream at about mile 3 on Queets River Road, 30 m, 47.7880°N, 124.1977°W, 03 June 2013, JL, 10 males, 2 females (JL).
Pierce County, Mount Rainier, White River, 20 to 24 July (no year given), A.L. Melander, holotype male for *Palaeagapetus nearcticus* Banks, 1936. The White River flows north from the flanks of Mount Rainier. Highway 410 parallels the river from its mouth to near the headwaters on the NW side of Mount Rainier, so the collection probably was made somewhere along this highway.
Thurston County, Puget Sound Lowlands, Thompson Creek, about 100 m, forested streams and springs, benthic biomonitoring sample, 23 July 2011, Thurston County Stream Team, 1 5th-instar larva (RWW).
Whatcom County, Western Cascade Mountains, Mount Baker, small stream, 1829 m, 29 August 1946, collector unknown, 1 male (INHS).

Palaeagapetus celsus **Ross, 1938**
(Figs. 7, 8, Table 2)

Palaeagapetus celsus Ross, 1938, 111–112, fig. 16, male, female, North Carolina; Flint, 1962, 40–44, figs. 1–9, larva, pupa, case, North Carolina, Tennessee.

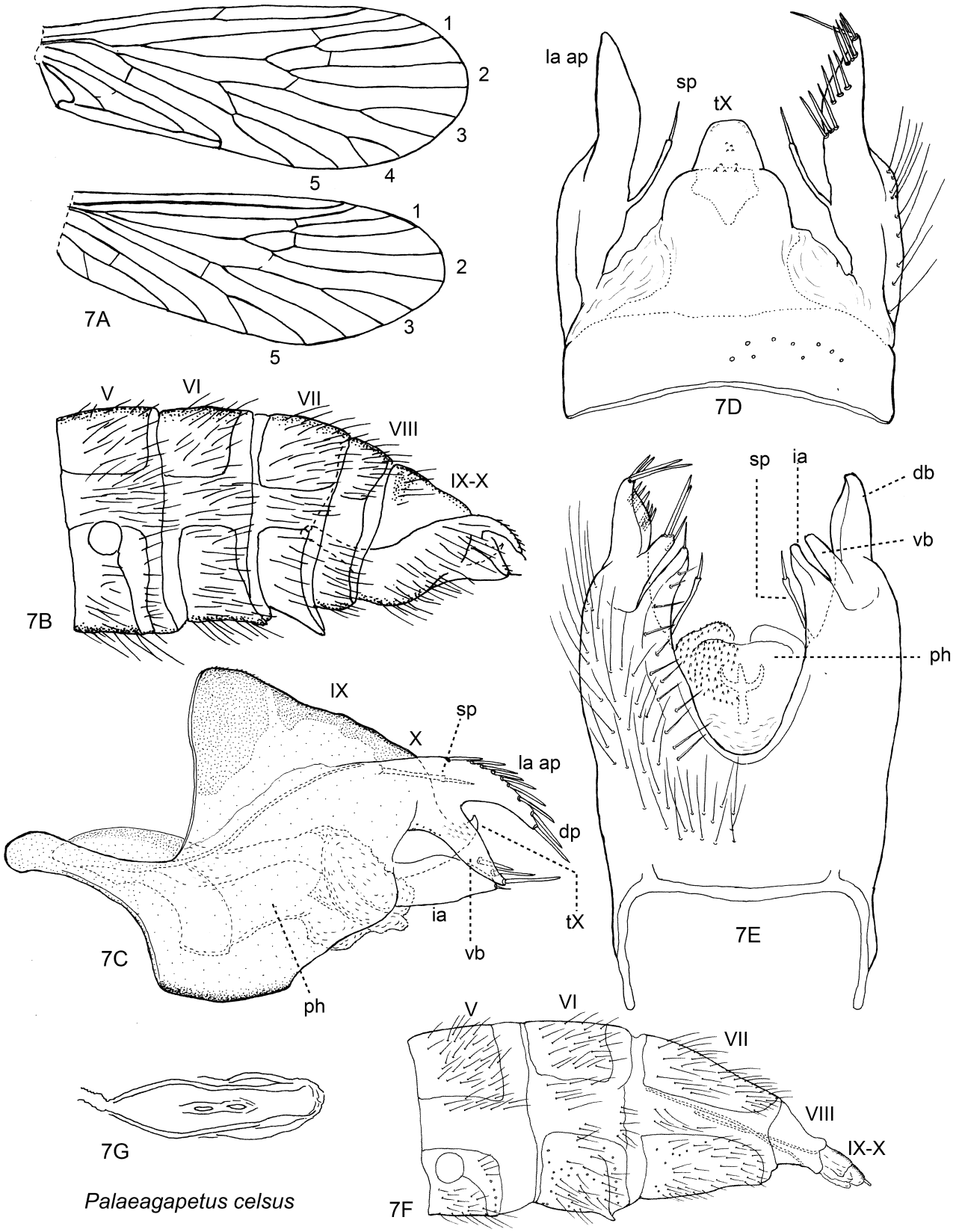

FIGURE 7. *Palaeagapetus celsus* male and female. Male (A–E): A, right wings, dorsal; B, abdominal segments V–X, left lateral; C, genitalia, left, lateral; D, same, dorsal; E, same, ventral. Female (F, G): F, abdominal segments V–X, left lateral; G, vaginal apparatus, ventral. Abbreviations: 1–5=1st to 5th apical forks; V–X=5th to 10th abdominal segments; tX=tergite X; ia=inferior appendage; la ap=lateral appendage: db=dorsal branch of lateral appendage, vb=ventral branch of lateral appendage, sp=slender process of lateral appendage; ph=phallus.

Adult (Fig. 7). Body dark brown in alcohol, 2.8 mm long in male (2.5–3.3 mm, n=7) and 3.5 mm long in female (3.1–3.9 mm, n=8). Antennae each 25-segmented, 2.3 mm long in male (2.2–2.5 mm, n=4); 23- or 24-segmented, 1.8 mm long in female (1.6–2.0 mm, n=8); scape slightly thicker and longer than other segments. Maxillary palpi, labial palpi and warts on head and thorax as in *P. nearcticus*.

Wings (A). Length of each forewing and hind wing 3.4 mm and 3.0 mm in male (3.1–3.6 mm, 2.6–3.2 mm, n=6); 3.4 mm and 2.9 mm in female (3.0–3.6 mm and 2.7–3.0 mm, n=9). Color and venation as in *P. nearcticus*.

Lateral bulges of sternum V (7B, F) round. Ventral process developed on segment VII in male (7B) and segment VI of female (7F).

Male genitalia (Figs. 7C–E). Segment IX (IX) short, anterolateral margins long, strongly projecting to anterior of segment VIII. Lateral appendages (la ap) of segment IX developed from mid-lateral region of genital capsule and directed caudad; thick and bilobed into dorsal and ventral branches at basal 1/3; dorsal branches (db) gently curved and tapered apically, each with slender process (sp) at basal 1/3 of mesal surface and many thick setae at apical half of dorsal surface, slender process directed mesocaudad with seta apically; ventral branches (vb) emerging near ventral bases of dorsal branches, directed ventrocaudad, each with 3 thick setae apically. Tergite X (tX) depressed dorsoventrally, curved dorsad apically in lateral view (7C), semicircular in dorsal view (7D). Inferior appendages (ia) each thick, short, twice as long as basal width, tapered at apical half with seta apically. Phallus (ph) short and broad, membranous with small forklike structure inside (7C, E).

Female genitalia (Figs. 7F, G). Segments I–VII each with sclerotized tergite and sternite, very setose, tergite VIII unpigmented. Segments IX–X very short, each segment about 1/2 as long as segment VIII, with somewhat developed cerci. Vaginal apparatus (7G) slender, lateral projections undeveloped, lateral bands round.

Pupa. Unknown.

Final (5th)instar larva. Described by Flint (1962).

Early(1st–4th) instar larva. Unknown.

Egg. Unknown.

Case. Described by Flint (1962).

Food and feeding behavior. Unknown.

Emergence. Unknown.

Annual life cycle. Unknown.

Habitat and biology. The larvae of this species also live in springs, spring brooks and seepage areas of forested mountain streams and exclusively associated with moss and liverwort.

Observation at Maul Spring, Westmoreland County, Pennsylvania

(1) Population. A high population was observed at Maul Spring, Powdermill Nature Reserve of the Carnegie Museum of Pittsburgh, near the town of Rector, Westmoreland County (Weaver 1974). The origin (eucrenon) of Maul Spring is a sandy-bottom pool (about 12 m in diameter). Adults were collected from April to November, 1974, inclusively. The water temperature of the spring is relatively constant, ranging from 8°C in the winter to 10°C in the summer. This mild temperature regime supported an abundant growth of aquatic bryophytes which consequently supported aquatic herbivores, including *P. celsus* Ross and *Adicrophleps hitchcocki* Flint (Brachycentridae).

Three benthic samples were collected each month from January to August of 1974, inclusively, in the riffle area of the springbrook (hypocrenon, about 12 m wide) just below the source of the spring, using a Modified Hess sampler (Merritt *et al.* 2008, fig 3.6). The number and density of *P. celsus* larvae collected each month are depicted in the followings: January (65 larvae collected, larval density 233.2/ m^2), February (24 larvae, 86.1/ m^2), March (27 larvae, 96.9/ m^2), April (23 larvae, 82.5/ m^2), May (4 larvae, 14.4/ m^2), June (6 larvae, 21.5/ m^2), July (4 larvae, 14.4/ m^2), August (35 larvae, 125.6/ m^2). The number and density of larvae were highest in January, lower in February, March and April, lowest in May, June and July, and then increased in August. The decline in numbers and density between January and February correlated with the phenology of the dominate aquatic liverwort in the springbrook, tentatively identified as *Chiloscyphus pallescens* (Ehrh. Ex Hoffm.) Dum. JSW observed that the liverwort was abundant and green in January, but in February less abundant and its leaves and stems had turned brown, including that sporulation had occurred.

(2) Living Larvae. While examining live larvae under the microscope, JSW observed that the lateral processes of abdominal segments I–VIII do not resemble truncated fleshly tubercles of dead specimens as described by Flint (1962), but are actually much larger, membranous spheres. JSW also observed when a larva was prodded, to force

it to exit its case, that the individual would sometimes turn 180° while staying completely inside its case. Then its head and thorax would emerge from the other end of its case and the larva would proceed to craw away in the opposite direction (in respect to its previous position). The larva had the ability to use either end of its case as an opening for its head and thoracic legs, and the two ends of the case seemed to be rather similar in structure and function, similar in these ways to the larval behavior and case structure of distantly related *Glossosoma* spp. (Glossosomatidae) and *Setodes* spp. (Leptoceridae) (Wiggins 1996). Could it be that the "anterior" and "posterior" ends of the larval case are only relative to the current orientation of the occupant?

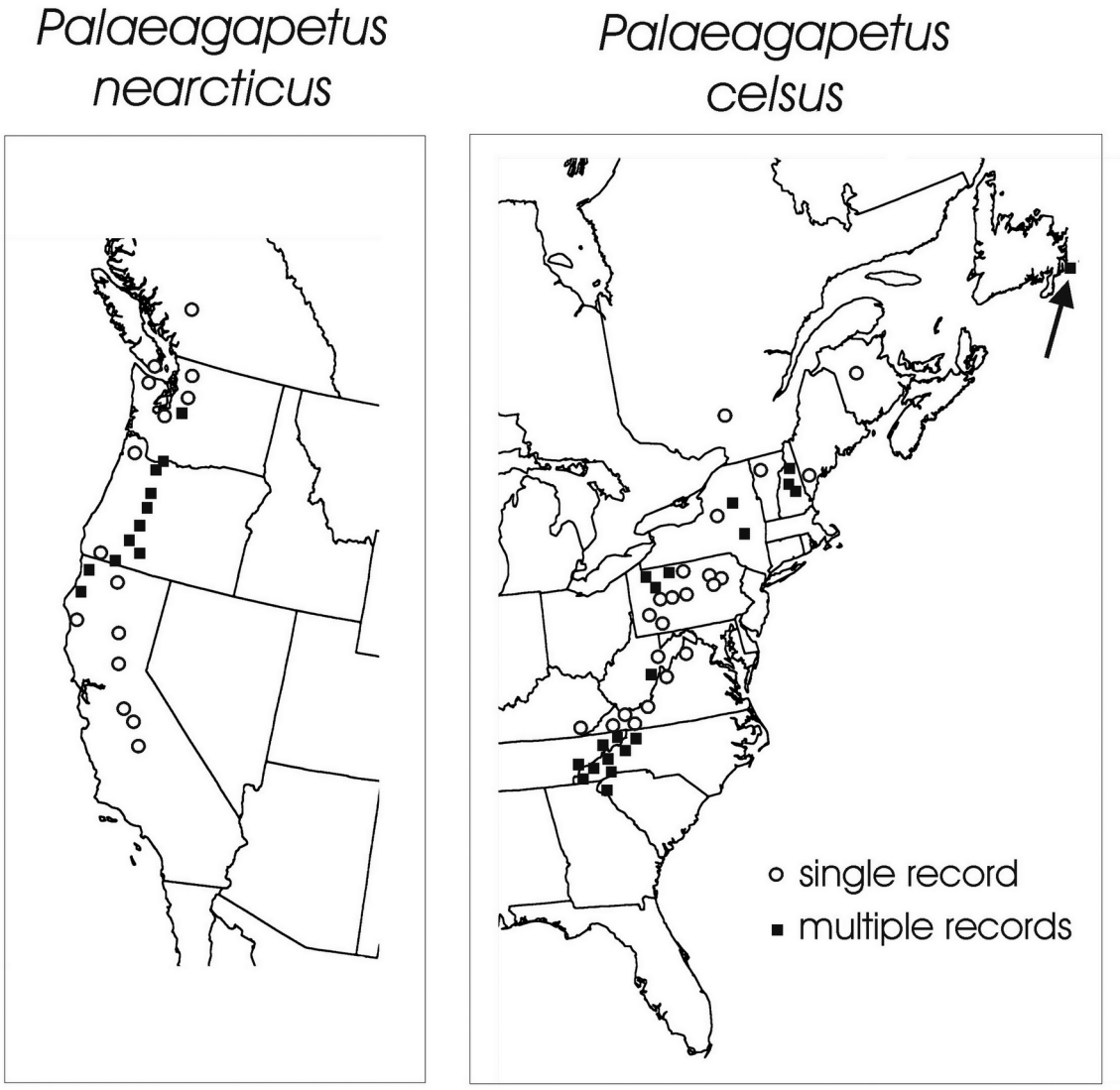

FIGURE 8. Distribution map. The arrow indicates that the new records from Newfoundland should not be overlooked.

(3) Habitat of larvae. At Maul Spring there were massive amounts of aquatic mosses and leafy liverworts attached to rocks in the brook. In the winter the greenery of the springbrook made a striking contrast to the surrounding brown dead leaves and white snow. The aquatic mosses dominated in the higher areas of the rocks that were often exposed above the surface of the water and the leafy liverworts were more common in the lower areas that were usually submerged and covered by water; the larvae of *P. celsus* were usually found among the liverworts. JSW hypothesizes that the mosses flourished on the tops of the stones because they were well protected from erosional forces and ice accumulations that were minimized at Maul Spring, allowing them to flourish on the tops of the rocks. The leafy liverworts on the other hand, appeared to be more opportunistic in occupying lower areas where the mosses could not maintain their dominance. At other locations, this might explain why the larvae occur in marginal lotic erosional areas, sprawling above the water where the leafy liverworts can flourish. Perhaps

the adaptation of lateral abdominal spheres of the abdomen of *Palaeagapetus* evolved so that the larvae could become better sprawlers - a mode of locomotion well suited to marginal lotic microhabitats.

Remarks. The male of this species is distinguished by the branched lateral appendages of segment IX from other congeneric species. On the other hand, the female, pupa, final instar larva and case are very similar to those of other congeneric species including the other Nearctic species, *P. nearcticus* (Ulmer 1912; Ross 1938; Ito & Hattori 1986; Botosaneanu & Levanidova 1987; Ito 1991a, 1991b, 2010; Ito *et al.* 1997; Ito & Vshivkova 1999).

The liverwort used for food and case materials was tentatively identified as *Scapania nemorosa* (L.) Dum. The life cycle of this species has also been studied (Flint 1962).

Distribution and specimens (Fig. 8). This species has been reported from Quebec and New Brunswick south to Oklahoma, Tennessee, and North Carolina (Table 2), including the following states and provinces: **CANADA**: **New Brunswick** (Harris & Lawrence 1978); **Quebec** (Roy & Harper 1975, 1979; Wiggins 1977, 1996; Blickle 1979; Williams & Williams 1987). **USA**: **Maine** (Bilger 1986); **North Carolina** (Ross 1938; Wray 1950; Wiggins 1977, 1996; Blickle 1979; Huryn & Wallace 1988; Lenat *et al.* 2010; Zhou *et al.*, 2011; and from NC/SC Unzicker *et al.* 1982); **New York** (Myers *et al.* 2011); **New Hampshire** (Ross 1944; Blickle 1979); **Oklahoma** (Blickle 1979; Bowles & Mathis 1992); **Pennsylvania** (Blickle 1979; Masteller & Flint 1980, 1992); **Tennessee** (Ross 1944; Wiggins 1977, 1996; Etnier & Schuster 1979; Blickle 1979; Etnier *et al.* 1998; DeWalt & Heinold 2005); **Vermont** (Wimmer 1979); **Virginia** (Parker & Voshell 1981; Flint *et al.* 2004); and **West Virginia** (Tarter 1990; Griffith & Perry 1992).

The new material from Newfoundland represents a new record of *P. celsus* from that Canadian province and the northernmost record for the species. In addition, students of JCM have studied a population of this species in **South Carolina** (Oconee County, unnamed tributary of Wash Branch, 16 km NW of Walhalla, 34.9144°N, 083.1071°W, 664 m). JCM confirmed the identity of these students' specimens, but no voucher specimens are in the Clemson University Arthropod Collection. We have been unable to find specimens of the species at this locality in recent years, suggesting that this southernmost population may no longer exist, possibly as a result of climate change as the ranges of cool-adapted species shift northward (Sheldon 2012; Comte & Grenouillet 2013).

TABLE 2. Annotated collection data for *Palaeagapetus celsus* Ross 1938.

Kentucky (KY): Bell County, Cumberland Gap National Historical Park, Martins Fork Cumberland River at road access, site code CUGA Martins Fork at road, 36.6786°N, 83.4645°W, 07 April 2007, J.L. Robinson, 1 larva (C.R. Parker & J.L. Robinson personal communication).

Maine (ME): Checklist of New England species with no collection data (Bilger 1986).
Androscoggin County, Androscoggin River, 44.46919°N, 70.18932°W, 91 m, Omernik Ecoregion 82, EPA stream ID ME, 222, rock basket samples, summer 2000, 1 larva (record extracted from US EPA national database and supplied by A. Herlihy).

New Brunswick (**NB):** Listed as occurring but with no collecting information (Harris & Lawrence 1978).

Newfoundland (NF): St. Johns, Southside Hills, MHC (CUAC): 15 May 2006, 26 larvae, 1 pupa, from which 3 larvae and the pupa were preserved on that date and the remaining specimens were reared and preserved, with emergence of adults as follows: 22 June, 1 male, 1 pupa; 23 June, 1 male; 24 June, 1 male; 27 June, 2 males, 1 pupa; 30 June, 2 females, 1 pupa; 01 July, 2 females, 2 pupae; 03 July, 22 females, 1 pupa; 07 July, 2 females, 2 pupae; 1 larva had died without maturing. These emergence data clearly indicate that males emerge before females.

New Hampshire (NH): Checklist of species and states/provinces in which they occur, but with no collecting information (Blickle 1979).
Carroll County, Highway 112, Livermore Trail near Passaconaway, 29 June 1967, S.W. Hitchcock, 1 male (NMNH); Albany, 43.9582°N, 71.1612°W, 177 m, uv light trap, 4 August 1959, R.L. Blickle, 2 adults (UNHC); Slippery Brook, 8.3 km E Jackson, 44.1588°N, 71.0992°W, 366 m, 27 April 1980, D.P. Mason, life stage unknown (UNHC).
Coos County, Pinkham Notch near Mount Washington, White Mountain National Forest, 44.25762°N, 71.25372°W, 23 June 1941, T.H. Frison & H.H. Ross, 1 male (INHS); Abenaki Brook, 6 km E Fabyans on Mount Clinton Road, 44.25343°N, 71.39185°W, 595 m, kick-net sample, 20 May 2009, D.S. Chandler & E. Wolff, 7 larvae (UNHC); Assaquam Brook, 6 km E Fabyans on Mount Clinton Road, 44.24822°N, 71.39159°W, 617 m, kick-net sample, 4 June 2009, B. Krause & E. Wolff, 4 larvae (UNHC); East Branch Mill Creek, 5 km SE Meadows, 44.33648°N, 71.43399°W,

516 m, kick-net sample, 4 June 2009, B. Krause & E. Wolff, 2 larvae (UNHC); 1st order stream on Mill Brook Road, 3.5 km S Stark, 44.5766°N, 71.3977°W, 444 m, 28 April 2009, D.S. Chandler & E. Wolff, 1 larva, (UNHC).
Grafton County, Underhill Brook, 2nd order stream 8.5 km S Easton, Highway 112, 44.07564°N, 71.79514°W, 404 m, 18 May 2010, D.S. Chandler, 1 larva (UNHC); West Branch Mad River, 43.9728°N, 71.5182°W, 507 m, 7 October 1980, D.P. Mason, life stage unknown (UNHC).

New York (NY): Greene County, Haines Falls, 42.1958°N, 74.0969°W, 518 m, 2 July 1956, J.F. Hanson, 1 male (NMNH); black light trap, Shingle Kill, off Maple Lawn Road, 23 June 2007, L. Myers, 1 male, (CSU).
Hamilton County, Adirondack Park, Upper Hudson River basin, small seep to Catlin Lake, Huntington Forest Newcomb, 43.9999°N, 74.2597°W, 28 June 2007, 21 males, 8 females (CSU); same data, 11 males, 7 females [New York State Museum (NYSM)] (Myers et al. 2011); same data, L. Myers & B. Kondratieff, 2 males, 1 female (TI).
Oneida County, Adirondack Park, northeastern Lake Ontario basin, Purgatory Creek, Rt. 28 nr. Otter Lake, 43.5775°N, 75.1259°W, 29 June 2007, 7 females (CSU). Purgatory Creek, Route 28 near Otter Lake, 29 June 2007, L. Myers & B.C. Kondratieff, 7 females (CSU).

North Carolina (NC)/South Carolina (SC): Listed as occurring in mountainous regions of the states; adult emergence from mid-May to mid-June; found in spring seeps, springs, spring-brooks, in moss and liverworts on rocks in current. No locale information is given (Unzicker et al. 1982).

NC/Tennessee (TN): Great Smoky Mountains National Park, species used for DNA barcoding project were collected from the park, with no collecting information provided (Zhou et al. 2011).

NC: Checklist of species and states/provinces in which they occur with no collecting information (Blickle 1979); checklist of species from the state with no collecting information, known from the mountains and in springs and streams (Lenat et al. 2010); listed as occurring but with no collecting information (Harris & Lawrence 1978).
Alleghany County, Big Sandy Creek, Stone Mountain Road, 36.39455°N, 81.03341°W, 29 May 2006, Kondratieff, Kirchner, Zuellig & Lenat, 1 male (CSU).
Avery County, unknown tributary, 36.09694°N, 81.80778°W, 1433 m, Omernik Ecoregion 66g, EPA stream ID NC:3318, benthic sample, record extracted from US EPA national database and supplied by A. Herlihy, collected 1984, 1 larva.
Buncombe County, Blue Ridge Parkway (National Park Service), small seep run at mile post 357.6 right, 35.73067°N, 82.30969°W, site code BLRI, 11 June 2007, J.L. Robinson & C.R. Parker, 1 male (J.L. Robinson & C.R. Parker personal communication); Blue Ridge Parkway (National Park Service), road-cut seep at mile post 358.8 right, 35.73752°N, 82.32277°W, site code BLRI, 28 March 2007, J.L. Robinson & C.R. Parker, 1 larva (J.L. Robinson & C.R. Parker personal communication).
Haywood County, Great Smoky Mountains National Park (National Park Service), Bunches Creek, 10 km NW Maggie Valley, Balsam Mountain Road, 35.5737°N, 83.1743°W, 1615 m, sweep net, 02 June 2002, R.E. DeWalt, 15 males (INHS); Blue Ridge Parkway (National Park Service), Mount Pisgah SW of Asheville, Pisgah National Forest, Frying Pan Campground, 1524 m, station 52, 24 June 1957, J.F. Hanson, 1 male (NMNH).
Jackson County, Blue Ridge Parkway (National Park Service): upper Woodfin Falls, 35D27MN, 83D06MW, 17 May 1994, OSF [O.S. Flint], 2 males (NMNH); Blue Ridge Parkway (National Park Service), road-cut seep Woolyback Overlook at mile post 452.3 right, 35.46766°N, 83.1418°W, site code BLRI 452.3 Sp052007, 01 May 2007, D. Lenat, 1 individual (J.L. Robinson & C.R. Parker personal communication). Clear Creek near Highlands, 6 June 1961, OSF, 1 male (NMNH).
Macon County; Coweeta Hydrologic Laboratory, Upper Ball Creek, watershed 27, 0.388 km^2 watershed, minimally disturbed mountainous reference watershed, 1035–1417 m, mixed hardwood forest, cool year-round water temperature with 2800–3300 annual degree day accumulation; berock-outcrop, riffle and pool sequences, monthly benthic samples acquired from 500 m reach upstream of Watershed 27 weir from July 1983 to June 1984, malaise and emergence trap collections, rare in samples, listed only with a biomass of >1 mg AFDW/m^2, and not discussed in publication (Huryn & Wallace 1988); Wayah Bald, Rattlesnake Spring, 26 March 1992, P.W. Schefter & R. MacCulloch, life stage unknown (ROM #920014).
Swain County, Deep Creek, Bryson City, 35.43083°N, 83.4475°W, 26–27 August 1930, N. Banks & Darlington, 3 males, 1 female (INHS). Great Smoky Mountains National Park (National Park Service): Newfound Gap, along Pigeon River, 35.61016°N, 83.4261°W, 13 June 1935, H.H. Ross, holotype male, allotype female, 54 males and 10 females paratypes (1 male paratype in NMNH, others in INHS) (Ross 1938); ATBI Plot, Andrews Bald, 35.5388°N, 83.4942°W, site code ATBI Plot, Andrews bald, malaise trap, 24 May 2001, I.C. Stocks, 2 females (J.L. Robinson & C.R. Parker personal communication); Indian Gap, 7 June 1961, OSF, 4 males, 1 female (NMNH) (Flint 1962); Indian Gap Trail, 1 July 1958, J.F. Hanson, 1 male (NMNH); locality unknown, 11–14 May 1970, 2 males (NMNH).

Watauga County, unknown tributary, 36.12556°N, 81.7575°W, 1067 m, Omernik Ecoregion 66g, EPA stream ID NC: 6607, benthic sample, record extracted from US EPA national database and supplied by A. Herlihy, collected 1994, 1 larva.
Yancey County, Mount Mitchell, Camp Alice, 1764 m, 09 June 1961, OSF, 3 larvae, 1 pupa (NMNH) (Flint 1962); near Mount Mitchell, 1067 m, 29 May 1946, J.F. Hanson, adults (Wray 1950); lower creek, Commissary Trail/Old Mt. Mitchell Trail, Mt. Mitchell State Park, 12 July 2008, Kondratieff, Zuellig & Lenat, 14 males, 6 females (CSU).

Oklahoma (OK): Checklist of species and states/provinces in which they occur, but with no collecting information (Blickle 1979); checklist of species found in Oklahoma that cited Blickle's (1979) publication, but with no collection data provided (Bowles & Mathis 1992). Don Chandler at the University of New Hampshire checked the Blickle collection in July 2013 and could find no specimens from Oklahoma. OSF checked the NMNH Collection July 2013 and could find no OK specimens.

Pennsylvania (PA): Checklist of species and states/provinces in which they occur, but with no collecting information (Blickle 1979); checklist only with no new records (Masteller & Flint 1992).
Cameron County, Dark Hollow Creek, 41.27589ºN, 78.09132ºW, 579 m, Omernik Ecoregion 62d, watershed area 2.6784 km^2, EPA stream ID MAIA97-067, riffle habitat, record extracted from US EPA national database and supplied by A. Herlihy, summer 1997, 10 larvae.
Centre County, Pine Grove Mills, Schalls Gap, 20 June 1974, R.K. Markarian, life stage unknown (INHS).
Clearfield County, Montgomery Creek, 41.0367°N, 78.5316°W, 457 m, Omernik Ecoregion 69b, watershed area 11.0446 km^2, EPA stream ID PA794S, riffle habitat, record extracted from US EPA national database and supplied by A. Herlihy, summer 1994, 5 larvae.
Columbia County, West Branch Fishing Creek, just south of Benton, 40.573°N, 76.4836°W, 281 m, watershed area 6.91 km^2, EPA site ID OWW04440-PA04, benthic sample, record extracted from US EPA national database and supplied by A. Herlihy, 10 August 2004, 1 larva.
Forest County, Coleman Run, 41.3546°N, 79.1763°W, 457 m, Omernik Ecoregion 62d, watershed area 11.1951 km^2, EPA stream ID PA833S, composite habitat benthic sample, record extracted from US EPA national database and supplied by A. Herlihy, summer 1994, 1 larva; Little Salmon Creek headwaters, 41.518444°N, 79.145417°W, Allegheny National Forest, just north of Marienville, headwater springs, Surber sampler collections on 4 April 2002 by Joe Brancato, Pennsylvania Department of Environmental Protection, larval densities ranged from 11-3282/m^2.
Jefferson County, Shippen Run, 41.2697°N, 79.0984°W, 516 m, watershed area 0.9 km^2, EPA site ID OWW04440-0474, benthic sample, record extracted from US EPA national database and supplied by A. Herlihy, 19 August 2004, 11 larvae.
Luzerne County, Shades Creek, 41.16558°N, 75.7122°W, 585 m, Omernik Ecoregion 62a, watershed area 19.3238 km^2, EPA stream ID PA777S, riffle habitat, record extracted from US EPA national database and supplied by A. Herlihy, summer 1994, 1 larva.
McKean County, Hemlock Run; 41.8330°N, 78.8885°W, 12 August 2008, S. Harris, 2 larvae (CUP); 41.8407°N, 78.8857°W, 12 August 2008, S. Harris, 1 larva (CUP).
Potter County, Right Fork Reed Run, 41.72501°N, 78.15726°W, 671 m, Omernik Ecoregion 62d, watershed area 0.23 km^2, EPA stream ID PA056S, composite habitat benthic sample, record extracted from US EPA national database and supplied by A. Herlihy, summer 1995, 1 larva.
Somerset County, Tub Mill Run, collected by Jim Wassell, 29 May 1979, 1 larva (DER).
Sullivan County, Bloody Run, 41.3273°N, 76.44073°W, 640 m, Omernik Ecoregion 62C, watershed area 0.9568 km^2, EPA stream ID PA548S, riffle habitat, record extracted from US EPA national database and supplied by A. Herlihy, summer 1993, 1 larva; summer 1995, 2 larvae.
Warren County, Hedgehog Run, 41.78934°N, 79.24826°W, 518 m, Omernik Ecoregion 62d, watershed area 2.0526 km^2, EPA stream ID PA589S, composite habitat benthic sample, record extracted from US EPA national database and supplied by A. Herlihy, summer 1994, 3 larvae; Cherry Grove Township, Allegheny National Forest, Little Arnot Run, tributary of Tionesta Creek and the Allegheny River, about 41.75°N, 79.08°W, study site in 1st order reach, 500 m, mixed mesophytic forest with hemlock dominant, gravel dominant substrate, not found in 2nd and 3rd order Hemlock Run study site,; emergence trapping from May 15 to September 30, 1978 (Masteller & Flint 1979, on checklist only; Masteller & Flint 1980, complete record), 2–8 July 1978, 1 female; 9–15 July 1978, 1 female; Fluent Run, 41.8214°N, 79.0126°W, 20 August 2008, S. Harris, 4 larvae (CUP); Fluent Run, 41.8141°N, 79.0328°W, 30 July 2008, S. Harris, 1 larva (CUP); Allegheny National Forest, Minister Creek Trail, 25 June 1987, OSF, 1 male (NMNH).
Westmoreland County, Maul Spring, Powdermill Nature Reserve, 49.14028°N 79.26111°W, 506 m, 10 September 1975, J.S. Weaver & J.L. Sykora, 1 pupa, 3 larvae (NMNH).

Quebec (QC): Checklist of species and states/provinces in which they occur, but with no collecting information (Blickle 1979).
Mount Tremblant Provincial Park, 46.32°N, 74.50°W; basin 14a, Outaouais River, tributary of the Saint Lawrence River; about 90 km NW of Montreal, 17 June year unknown, 1 male (QMOR) (Roy & Harper 1975, 1979; Williams & Williams 1987).

TN: Checklist of species and states/provinces in which they occur, but with no collecting information (Blickle 1979); listed as occurring, but with no collecting information (Harris & Lawrence 1978).
Monroe and Sevier Counties, known from high elevation seeps in May–July, adults; no other collecting data provided (Etnier et al. 1998).
Great Smoky Mountains National Park:
Blount County, Forge Creek tributary of Abrams Creek (Abrams Creek is the westernmost drainage in the park, source at 1300 m along the NC/TN border and empties into Lake Chilhowee at 320 m, tributary of the Little Tennessee River), 9 sites repeatedly collected in summer 2001, found only at Site 6 (Forge CG12), 35.5472°N, 83.8321°W, 733 m, sweep net, 25 May 2001, 2 males, 1 female (INHS) (DeWalt & Heinold 2005); Forge Creek at Campground 12, Gregory Ridge Trail, 35.54089°N, 83.715°W, site code WLFB01I&M, 01 July 2001, I & M Aquatics Crew, 1 larva (J.L. Robinson & C.R. Parker personal communication); Flint Branch, 35.6452°N, 83.8341°W, site code INHS 1239, 25 May, 2001, R.E. DeWalt & B.D. Heinold, 2 males, 1 female (J.L. Robinson & C.R. Parker personal communication).
Sevier County, Indian Gap, 1 July 1958, collected by OSF, 3 males, 2 females; 7 June 1961, collected by OSF, 55 adults (NMNH); [Sevier County], Indian Gap Trail, station 26, 1554 m, collected by J.F. Hanson, 1 July 1957, 3 males, 4 females; 8 July 1957, 50 adults; 3 August 1957, 15 adults; 1 July 1958, 5 adults (NMNH); Sevier County, Indian Gap, collected by OSF: 19 May 1959, 60 larvae, 2 pupae; 7 June 1961, 37 males, 9 females, 8 pupae, 95 larvae; 01 July 1958, 6 adults (NMNH or OSF) (Flint 1962; Etnier & Schuster 1979); checklist of species, but with no collecting information (Parker et al. 2007); Sevier County, Surry Creek, LeConte Mountain on Brushy Mountain Trail, 35.6701°N, 83.4397°W, 1354 m, site code REDeW Surry Creek, sweep net, 03 June 2002, R.E. DeWalt, 1 male (INHS); Sevier County, Chimneys Campground, 35.6371°N, 83.4879°W, 01 September 1948, H.H. Ross & L.J. Stannard, 1 female (INHS); Sevier County, stream 1.3 km W Newfound on Highway 441, 29 May 1970, G.B. Wiggins & T. Yamamoto, life stage unknown (ROM #700359); Sevier County, stream 1.3 km N Newfound Gap on Newfound Gap Road, 22 May 1991, J. Kerr & R. Vineyard, life stage unknown (ROM #912014).

Vermont (VT): Chittenden County, Gleason Brook, Winooski River tributary near Camel's Hump, 1143 m, uv light trap, 18 July (year unknown) (Wimmer 1979).
Lamoille County, Ranch Brook, 44.5022°N, 72.7758°W, about 10 km NW of Stowe, 378 m, watershed area 9.9 km^2, benthic sample, record extracted from US EPA national database and supplied by A. Herlihy, 07 September 2004, 3 larvae.

Virginia (VA): Preliminary checklist from records in the Virginia Polytechnic Institute and State University, but with no collection data (Parker and Voshell 1980); "In Virginia it is known from the Blue Ridge and Alleghenian regions. Giles, Grayson, Highland, Shenandoah, Tazewell and Washington" counties. Adults were collected from May–October (Flint et al. 2004).
Giles County, Little Stoney Creek, emerged in lab rearing chamber, 14 June 1972, G.M. Simmons, 3 males (NMNH).
Grayson County: Whitetop Mountain, Forest Service road 89, 1.9 km from Highway 600, 36D38.4MN, 81D35.8MW, 1487 m, 13 July 2006, OSF, 1 male, 2 females (NMNH); headwater of Fox Creek, 9.5 km W Troutdale, 11 June 1979, OSF, 1 male (NMNH).
Highland County, Washington National Forest, Locust Springs Picnic Area, 1–4 July 1972, OSF, 1 male (NMNH).
Shenandoah County, Little Sluice Mountain Trail, springs near Liberty Furnace, 21 July 1974, OSF, 12 adults (NMNH).
Tazewell County, Station Spring Creek, Route 666, MBC Ranch, Burkes Garden, 17 May 1994, B.C. Kondratieff & F. Kirchner, 3 females (CSU).

West Virginia (WV): Pocahontas County, unpublished records from Kirchner and the Smithsonian (NMNH), June & July, adults (Tarter 1990); Sugar Creek, tributary of Williams River, spruce forest with sphagnum moss, 1285 m, 10 June 1979, R.F. Kirchner & C.E. Rossmore, 25 adults (NMNH); Monongahela National Forest, Middle Fork Sugar Creek, Forest Service road 76, spruce forest, 1219 m, 4 July 1984, R.F. Kirchner, 30 adults (NMNH); Sugar Creek, Highway 150 at Forest Service road 76, 30 June 1982, OSF & W. Mathis, 12 adults (NMNH).
Tucker County, Fernow Experimental Forest, Monongahela National Forest, 5 km south Parsons, 39.05°N, 79.67°W, survey of 6, 2nd order tributaries of Elklick Run; emergence traps, uv lights, and hand collecting; June 1989–August 1991, watersheds 1, 3 &4, light and emergence trap collections, no other collecting information (Griffith & Perry 1992).

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