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**A Revision of the Genus *Ephemerella*
(Ephemeroptera: Ephemerellidae)
I. The Subgenus *Timpanoga***

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Subgenus *Timpanoga* Needham

- 1927—Needham — Ann. Ent. Soc. Amer., 20: 108.
1935—Traver — Biol. Mayflies, 565 (*hecuba* group).
1954—Edmunds and Traver — Proc. Ent. Soc. Wash., 56: 238.
1954—Demoulin — Bull. Ann. Soc. Ent. Belg., 90: 324.

The subgenus *Timpanoga* of the genus *Ephemerella* contains but a single species, *Ephemerella hecuba* Eaton. Needham (1927) derived the name for this subgenus from Mt. Timpanogos in north central Utah, after collecting specimens of *Ephemerella hecuba* in the nearby Provo River. He based the subgenus on the nymph which shows remarkable morphological distinction with its broad entire frontal shelf and its extremely flattened body.

The subgenus may be characterized in the adult stages by (1) the retention of vestiges of the nymphal gills on abdominal segments four to seven, (2) the well developed postero-lateral projections on segments eight to nine, and (3) type of male genitalia (Fig. 4). The nymphal stages (Fig. 1) are characterized by (1) having gills on abdominal segments four to seven only, gill four operculate, (2) having a broad entire frontal shelf on the head, (3) having a wide, flat body, the width of the fifth abdominal segment being from 2/3 to 3/4 as long as entire abdomen, and (4) having femora prolonged apically into an acute spine.

***Ephemerella (Timpanoga) hecuba* (Eaton)**

There is some confusion concerning the authorship of this species. Eaton (1884:33) placed the nymph of this species as *Ephemerella, sedis incertae*, nymph No. 4; however, in his figures (Pl. 40) he cites the name "*Ephemerella hecuba* Hagen," which he refers to as a misapplied name. The authors find no published description by Hagen so the authorship is given to Eaton.

Male imago. Length: body 12-15; wing 12-14 mm.

Head light gray, smoky at base of ocelli; antennae yellow brown; upper portion of eye orange, lower portion gray. Prothorax pale, the pronotum yellow brown with smoky markings; mesonotum yellow brown, medium brown between the inner parapsidal furrows anterior to the transverse mesonotal groove and on the scutellum; metanotum medium brown, pleurae largely pale with some brown sclerites, especially the mesepisternum; thoracic sternum pale, furcisternal plates light brown, a dark stripe along the anterior margin of the mesosternum. Fore-legs medium brown, the base of the femora and the tarsi paler; middle and hind legs yellow brown; basal tarsal segment medium brown. Wings hyaline, clouded along the costal margin; venation medium brown. Tergites smoky brown to reddish brown, the anterior and posterior margins pale; near the pleural margin is a pale spot surrounded by an irregular darker marking; a broad pale median stripe present; pleural fold with a fuscous stripe attaining neither the anterior nor posterior margins of the segment. Sternites with a broad reddish irregular transverse stripe arising from the middle of the pleural margin of each sternite and arching forward to near the anterior margin, if extensive this reddish stripe may have a pair of oblique pale paramedian patches and a pair of pale submedian

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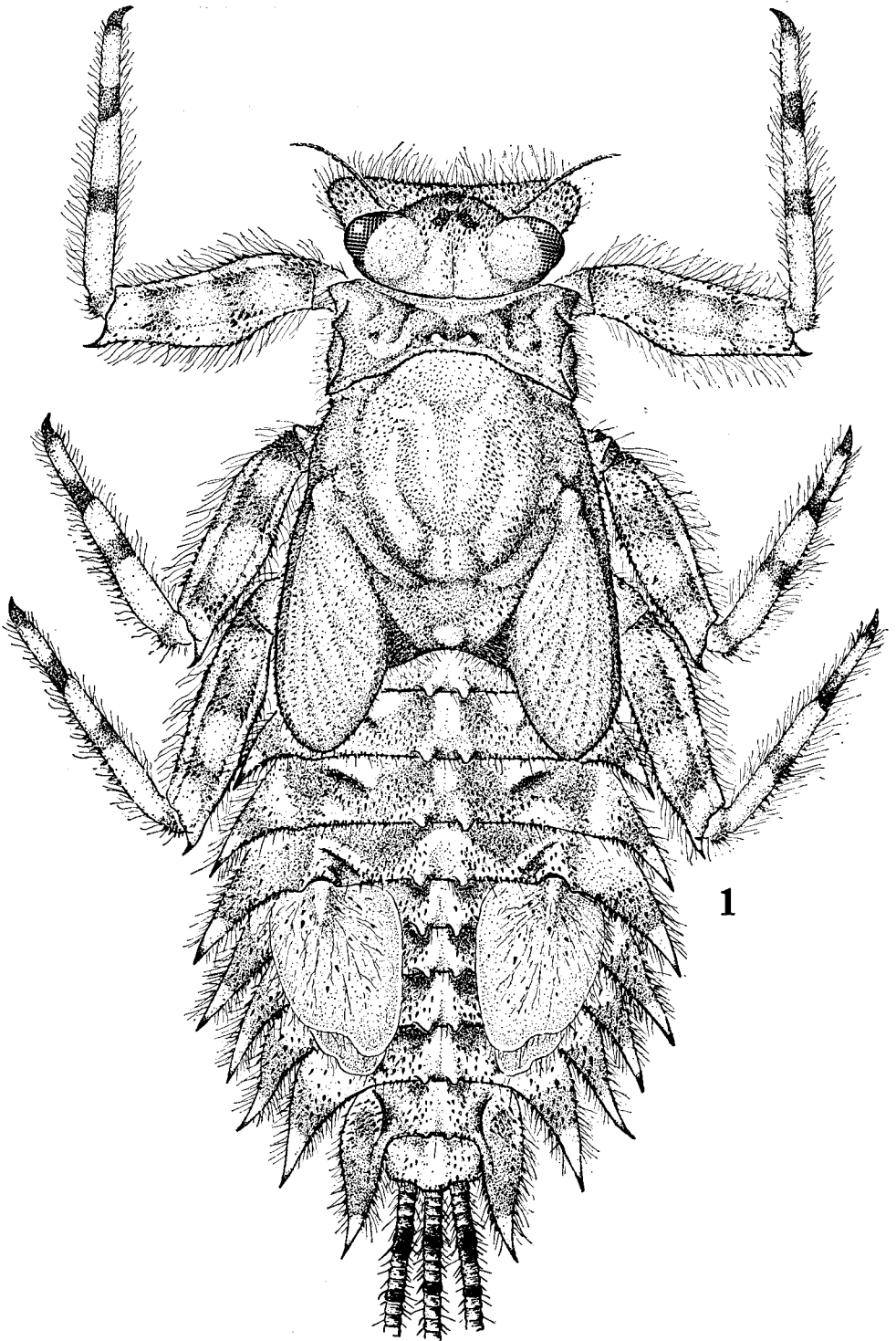
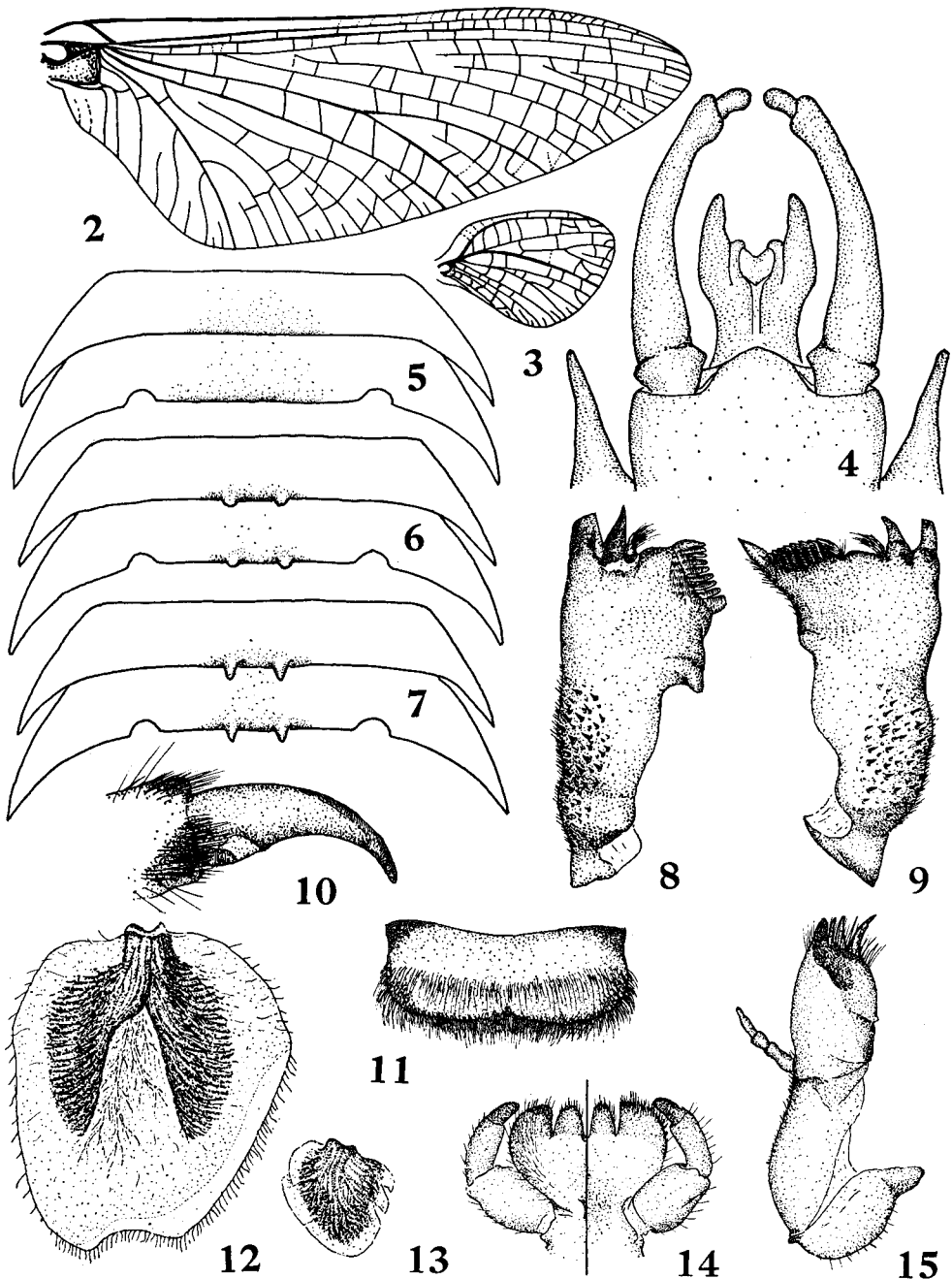


Fig. 1. *Ephemerella hecuba pacifica* n. subsp., dorsal view of paratopotype ♂ nymph.



Figs. 2-3. *Ephemerebella hecuba hecuba* (from Grande Ronde River, Oregon); Fig. 2, forewing of ♀ subimago; Fig. 3, hindwing of ♀ subimago. Fig. 4, *Ephemerebella hecuba* subsp. ?, genitalia of ♂ imago (from Scott River, Northern California). Fig. 5, *Ephemerebella hecuba hecuba*, abdominal tergites 3-4 (John Day, Oregon). Figs. 6-15. *Ephemerebella hecuba pacifica*: Fig. 6, abdominal tergites 3-4 (from Alsea River, Five Rivers Area, Oregon); Fig. 7, abdominal tergites 3-4 (from Cummins Cr., near Neptune State Park, Oregon, Figs. 8-15 also from same series); Fig. 8, dorsal view left mandible; Fig. 9, dorsal view right mandible; Fig. 10, claw of right foreleg; Fig. 11, labrum; Fig. 12, first gill; Fig. 13, fourth gill; Fig. 14, labium, dorsal and ventral; Fig. 15, maxilla.

spots within it; segments eight and nine with large postero-lateral projections, segments four to seven with irregular twisted projections. Genitalia as in Fig. 4. Cerci and terminal filament dark brown at base, becoming paler distally.

Female imago. Length: body 12-15; wing 12-15 mm.

Similar to male except for usual sexual differences. All legs similar to middle and hind legs of male. Abdominal markings less conspicuous than in male. Apex of subanal plate rounded.

Mature nymph. Length: body 12-15; caudal filaments 5-7.5 mm.

General color variable, light brown to medium brown. Head light brown and hairy, subquadrate in shape, and widest across the frontal shelf; antennae brown; eyes black. Pronotum widest at posterior margin; antero-lateral corner developed into a spine; a short spine on each side near the middle of the lateral margin; paired sub-median spines near the posterior margin. Mesonotum without spines. Coxae and trochanters reddish with long hairs and spicules on anterior surface; femora broad and prolonged apically into an acute spine; anterior and posterior margins lined with long hairs and spicules, with spicules on dorsal surface; tibiae light brown with dark band near middle; anterior and posterior margins lined with long hairs with a few spicules on dorsal surface; tarsi pale with wide dark band at proximal end and a dark spot on the distal end; claws dark and without denticles (Fig. 10). Abdomen extremely flattened, with or without paired spines on the tergites; lateral extensions prolonged into sharp sawtooth-like postero-lateral spines (Fig. 11), color reddish-brown with lateral extensions pale and tips of postero-lateral spines black. Sternites marked with wide reddish bands occupying the anterior half of the segment, postero-lateral spines two to nine with a wide dark oblique band. Cerci and terminal filament fringed with long hairs, color dark reddish-brown at base, paling distally, interrupted by a narrow dark basal band and a wide dark transverse band in the apical third.

Type Locality. "Colorado"

Type. Museum of Comparative Zoology, Cambridge, Massachusetts.

After careful study of material from throughout the known range, we have divided the species into two subspecies, *E. h. hecuba* and *E. h. pacifica*, new subspecies. The nymphs of the latter may be readily distinguished by the presence of paired dorsal abdominal spines, which are totally lacking in *E. h. hecuba*. Where the ranges of the forms meet in Oregon and California, the two races are seen to intergrade (see Fig. 16). The description of the nymph above is drawn from specimens of both races.

Until such time as imagos of typical *E. h. hecuba* and *E. h. pacifica* have been reared or collected and compared, we are unable to say if the adults of the two races can be as easily distinguished as the nymphs. The descriptions of the adults which we have given are of an intergrading population from the Scott River, Siskiyou County, Northern California, collected by W. C. Day. The description given by McDunnough (1935) applies to the imago of *E. h. hecuba*, but the description of adult *E. h. pacifica* by Shepherd (1929) applies to the subimago.

***Ephemerella (Timpanoga) hecuba hecuba* Eaton**

1874—Hagen — Ann. Rept. U.S. Geol. & Geog. Surv. Terr., (1873): 582 (*Heptagenia pudica* Hagen, 1874, *nec* Hagen, 1861).

1884—Eaton — Trans. Linn. Soc. London, Sec. Ser. Zool., 3: 133. (Nymph #4), Pl. XL, figs. 1-17 (*Ephemerella hecuba* Hagen).

1905—Needham — N.Y. State Mus. Bull., 86: 46, 1 fig. (*Ephemerella sp.*).

- 1925—Lestage — Ann. Biol. Lacust., 13: 236, 287 (*Ephemerella* sp., larvae) 289, 1 fig. (? *Ephemerella* sp.).
- 1927—Needham — Ann. Ent. Soc. Amer., 20: 115.
- 1927—Needham & Christenson — Utah Agric. Exp. Sta. Bull., 201: 9, 1 fig.
- 1930—Walley — Canad. Ent., 62: 14, 1 fig.
- 1935—McDunnough — Canad. Ent., 67: 99, 1 fig. (adult).
- 1935—Traver — Biol. Mayflies, 602, 629, (nymph *nec* adult).
- 1941—Spieth — Ann. Ent. Soc. Amer., 34: 87.
- 1954—Edmunds — Proc. Utah Acad. Sci., Arts and Letters, 31: 66.
- 1956—Day — Aquatic Insects of Calif., 98, 1 fig.
- 1956—Allen & Edmunds — Proc. Utah Acad. Sci., Arts and Letters, 33: 87 (in part).
- 1957—Edmunds & Allen — Ann. Ent. Soc. Amer., 50: 322.

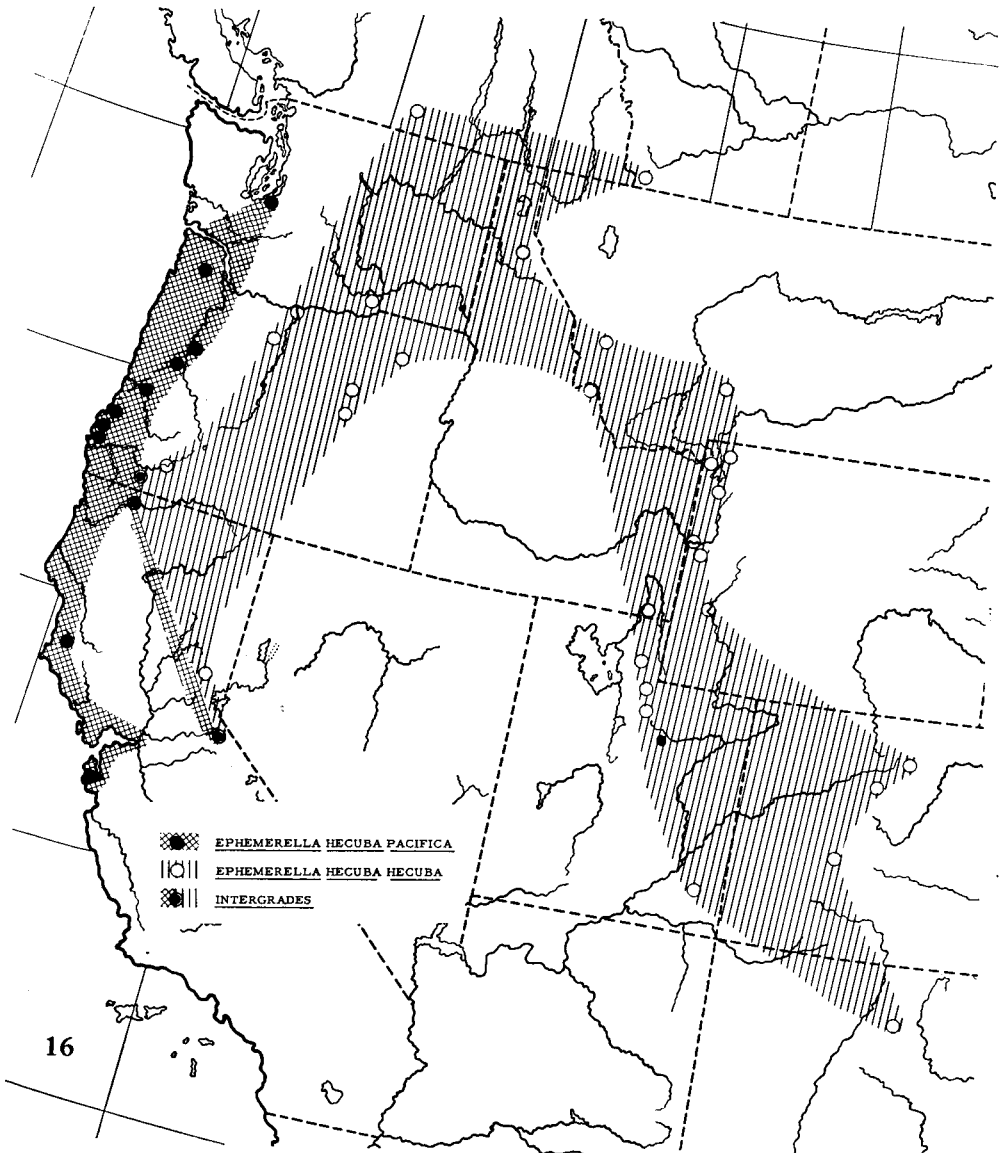


Fig. 16. Distribution of the subspecies of *Ephemerella* (*Timpanoga*) *hecuba*.

Nymph. The nymph of this race is distinguishable by the complete absence of paired abdominal spines on the abdominal tergites (Fig. 5).

Distribution

Ephemerella hecuba hecuba is an inland western form and known to range from the eastern slope of the Rocky Mountains to the eastern slope of the Cascades and Sierra Nevadas. It has been collected in suitable habitats from northern New Mexico to southern British Columbia and Alberta, Canada. It is known from every western state in the United States except Nevada and Arizona. It seems likely that this subspecies will eventually be collected in western Nevada and northern Arizona. We have examined specimens from the following localities; collections made by the authors are indicated by initials, GFE and RKA. The abbreviations for collections in which the specimens are located are as follows: Illinois State Natural History Survey (INHS); personal collection of Jay R. Traver (JRT); Oregon State College (OSC); University of Utah (UU); and personal collection of W. C. Day (WCD).

California. Sierra Co., 4 mi. W. Sierra City on California Route No. 49, 20-IX-1946, H. G. Nelson (INHS). *Colorado.* Gunnison Co., Gunnison River, Iola, 16-VIII-1949, H. Higgins (UU); Larimer Co., Granby, Fraser River, 24-VII-1938, H. H. Ross and J. A. Ross (INHS); Big Thompson River, Estes Park, 14-VIII-1940, T. H. Frison and T. H. Frison, Jr. (INHS). *Idaho.* Shoshone Co., Wallace, 3-IX-1949, S. and D. Mulaik (UU); Idaho Co., Salmon River at North Fork, 20-VIII-1949, L. T. Nielsen (UU); Franklin Co., Cub River, Mapleton, 15 mi. NE Franklin, 12-VIII-1951, A. R. Gaufin (UU). *Montana.* Granite Co., W. Fk. Rock Creek, Phillipsburg, 27-VIII-1934, Tarzwell (INHS). *New Mexico.* San Miguel Co., Pecos River, 10 mi. above Pecos, 30-VII-1943 (JRT). *Oregon.* Clackamas Co., Salmon River, Mt. Hood National Forest, 15-VIII-1932, R. E. Dimick (OSC); Umatilla Co., Grande Ronde River, 6 mi. W. LaGrande, 27-VIII-1954, GFE and RKA. (UU); Jackson Co., Rogue River near McLeod, 24-VIII-1954, GFE and RKA (UU); Grant Co., Canyon Creek, John Day, 21-VIII-1954, GFE and RKA (UU); Silvies River near Bear Valley Rangers Station, 21-VIII-1954, GFE and RKA (UU); Hood River Co., Hood River at Hood River, 27-VIII-1954, GFE and RKA (UU). *Utah.* Wasatch Co., Provo River at Midway, 24-VII-1949, W. A. Dunstan (UU); Summit Co., Weber River near Glendale Ranch, 19-VIII-1945, GFE (UU); San Juan Co., Abajo Mountains above Monticello, 24-VIII-1948, A. W. Grundmann (UU). *Wyoming.* Sublette Co., Snake River, 7 mi. E. Alpine, 8-IX-1957, GFE (UU); Green River, Big Piney, 9-IX-1949, H. Higgins (UU); Yellowstone National Park, Gibbon River, 3 mi. N. Morris Jct., 21-VI-1949, GFE (UU); Teton Co., Cottonwood Creek, Grand Teton Nat'l Park, 5-VIII-1940, T. H. Frison and T. H. Frison, Jr. (INHS); Hoback, 13-VIII-1940, T. H. Frison and T. H. Frison, Jr. (INHS).

Biology

This subspecies is found at elevations between 1,400 and 7,000 feet. It usually inhabits large, clear or silted, moderately flowing warmer trout streams with rocky bottoms. The nymphs are found near the edge of the stream in slow currents crawling over rocks, boards and debris. The slow moving nymphs are extremely flattened and are always covered with a heavy coating of debris. In addition to these camouflage devices the nymphs have distinctive dark bands on the legs and lateral margins of the abdomen which break their outlines. Although the flattened form suggests an adaptation to current, the flattening is another adaptation for camouflage. *Ephemerella h. hecuba* has never been found

to be abundant at any particular locality. The nuptial flight has not been observed.

Ephemerella (Timpanoga) hecuba pacifica n. subsp.

1929—Shepherd — Canad. Ent., 61: 260, 16 figs.

1935—McDunnough — Canad. Ent., 67: 99 (in disc. of *E. b. hecuba*).

1935—Traver — Biol. Mayflies, 602 (adult, nec nymph).

1956—Allen & Edmunds — Proc. Utah Acad. Sci., Arts and Letters, 33: 87 (in part).

Nymph. The race is distinguished by the presence of paired abdominal spines on tergites one to eight (Fig. 1), distinct on tergites one to seven, much smaller on tergite eight. These abdominal spines are sharp pointed on specimens from the coastal streams of Oregon (Fig. 7), but forms from further inland in the coast range have the spines with blunted apices (Fig. 6).

Holotype. Nymph. Cape Creek near Sealion Point, Lane Co., Oregon, 25-VIII-1954, G. F. Edmunds, Jr., and R. K. Allen, in collection of University of Utah, Salt Lake City. Paratopotypes. 3 nymphs (UU). Paratypes. California. Mendocino Co., 1 nymph, Baechtel Creek, 3 mi. W. Willits, 15-VI-1948, H. B. Leech (UU). Oregon. Washington Co., 1 nymph, Wilson River, Glenwood, 7-VII-1945, V. E. Shelford (INHS); Linn Co., 1 nymphal cast skin, Santiam River, 8 mi. N. Albany, 26-VIII-1954, GFE and RKA (UU); Lincoln Co., 2 nymphs, Alsea River, Five Rivers Area, 11-V-1940, W. E. Pitney (OSC); 1 nymph, Five Rivers Area, 2-V-1940, O. Luelf (OSC); Benton Co., 1 nymph, Rock Creek, 18-IV-1945, C. R. Hess (OSC); Lane Co., 13 nymphs, Cummins Creek near Neptune State Park, 25-VIII-1954, GFE and RKA (UU); 1 nymph, Rock Creek near Heceta Head Lighthouse, 25-VIII-1954, GFE and RKA (UU); Curry Co., 1 nymph, Sixes River, Siskiyou Forest, 13-VII-1935, F. Zeisenhenne (UU). Washington. King Co., 1 nymph, Green River, 18-VIII-1939, B. L. Lambuth, in collection B. L. Lambuth. Some paratypes will be deposited in the collections of California Academy of Sciences, personal collection of J. R. Traver, Canadian National Collection, and University of Florida.

Distribution

Ephemerella hecuba pacifica is known on the Pacific Coast from Palo Alto, California, to Seattle, Washington. It primarily inhabits the Coast Range but an interbreeding population is known from the east slope of the Sierra Nevada Mountains. Future collections may extend its range southward in California and north into British Columbia.

Biology

Ephemerella (Timpanoga) hecuba pacifica has been found in clear, rocky, moderate flowing streams from sea-level to about 1,400 feet. The nymphal habitat and habits are very similar to those of *E. b. hecuba*. The adults of both races emerge from July to September depending on locality. The eggs apparently hatch within a month. The nymphal life is therefore approximately 11 months.

Taxonomy

In the coastal streams of Oregon, *E. b. pacifica* nymphs show development of sharp-pointed abdominal spines (Fig. 7), but in the streams further inland on the coast range the apices of spines are blunted (Fig. 6). Intergradation of the two subspecies undoubtedly occurs wherever suitable streams allow exchange of populations between the Coast Range and interior mountains. Collections from the Klamath region of Northern California and Southern Oregon show considerable intergradation. Of 12 specimens collected in the Rouge River at

Jackson Falls, Medford, Oregon, 17-VIII-1937 by Mote (OSC, UU), one specimen totally lacked spines, nine specimens had weak spines and two specimens had well developed blunt spines. Of 34 specimens collected by Mr. W. C. Day in the Scott River, Roxbury, Siskiyou County, California, VIII-1949 (WCD), none totally lacked spines, 20 had only weak spines and 14 had well developed blunt spines.

The range of the intergrading populations also extends along the eastern slope of the Sierra Nevada Mountains as seen in specimens collected by W. C. Day in the West Fork of the Carson River, 10 miles above Woodfords, California, VII-1949 (WCD). Of 23 nymphs, five totally lacked spines, 23 had weak spines and 14 had well developed blunt spines. The writers collected four additional nymphs nearby (West Fork Carson River, 3 miles NE Woodfords, California, 21-IX-1957 (UU)), of these, one totally lacked spines and three had weak spines.

The population from the Sierra Nevada Range needs further study to determine its origin and nature. Our record of *E. b. hecuba* from near Sierra City is based on a single specimen, and hence its subspecific assignment has little value. Intergradation of *E. b. hecuba* and *E. b. pacifica* in the Sierras might be explained by any of three hypotheses: (1) migration across the central valley, (2) migration of the coastal form into the interior via the Tehachepi Mountains, or (3) the southward migration of the intergrading population from the Klamath region. Of our hypotheses, the first is highly improbable under present day conditions, and seems unlikely in the past. Of the remaining hypotheses our data favors the last named, but additional series from the Sierra Nevada are essential for a clarification of the problem.

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