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A Revision of the Genus *Ephemerella* (Ephemeroptera, Ephemerellidae) VIII. The Subgenus *Ephemerella* in North America

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CONTENTS

A Revision of the Genus *Ephemerella* (Ephemeroptera, Ephemerellidae) VIII. The Subgenus *Ephemerella* in North America

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ABSTRACT

The 25 species of the genus *Ephemerella* Walsh in North America formerly placed in the subgenera *Ephemerella*, s. s. (=*invaria*-group auct.), and *Chitonophora* (Bengtsson) (=*needhami*-group auct.) are placed in the subgenus *Ephemerella*, s. s. Characters do not allow grouping of the nymphs and adults in concordant groups that correspond with the 2 subgenera previously recognized. Accounts are given for the nymph and male adult of each species including synonymies, synoptic descriptions, and distribution records and maps. Illustrated keys are given for the nymphs and male adults. *E. euterpe* Traver is regarded as a synonym of *E. maculata* Traver. *E.* **lacustris** is described from imagoes and nymphs from Wyoming, and *E.* **verruca** from Oregon, *E.* **simila** from West Virginia, *E.* **rossi** from Tennessee, and *E.* **crenula** and *E.* **hispida** from North Carolina and Tennessee are described from the nymphal stage only.

INTRODUCTION

Part I of this revision (Allen and Edmunds 1959) dealt with the subgenus *Timpanoga* Needham, Part II (Allen and Edmunds 1961a) with the subgenus *Caudatella* Edmunds, Part III (Allen and Edmunds 1961b) with the subgenus *Attenuatella* Edmunds, Part IV (Allen and Edmunds 1962a) with the subgenus *Dannella* Edmunds, Part V (Allen and Edmunds 1962b) with the subgenus *Drunella* Needham, Part VI (Allen and Edmunds 1963a) with the subgenus *Serratella* Edmunds, and Part VII (Allen and Edmunds 1963b) with the subgenus *Eurylophella* Tiensuu. This paper, Part VIII, concludes the revision of the North American species of this diverse and abundant genus.

TAXONOMY

Most of the North American species of the genus *Ephemerella* Walsh can be determined to subgenus with ease by employing the existing published keys (Traver 1935, Edmunds 1959). Because some species, especially those in the larger subgenera, are rather atypical members of the subgenus to which they are assigned, the presently published subgeneric keys may be difficult for those who have only a casual acquaintance with the Ephemeroptera. For this reason we include the following artificial key to the North American subgenera which will facilitate the subgeneric assignment of male adult and nymphal specimens of the genus *Ephemerella*.

In the following key the Roman numerals and figure numbers enclosed in parentheses refer to the previously published revisions of the genus. That is, Roman numeral III in couplet 2 makes reference to "A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). III. The subgenus *Attenuatella*. J. Kans. Entomol. Soc. 34: 161–73," and Fig. 3–4 indicate the figure numbers in that publication.

[1] The research on which this report is based was supported by grants from the National Science Foundation and the University of Utah Research Fund.

KEYS TO THE NORTH AMERICAN SUBGENERA OF *EPHEMERELLA*

MALE IMAGOES

1. Paired lateral cerci ¼–¾ as long as median terminal filament ..... **Caudatella**
   Paired lateral cerci and median terminal filament subequal in length 2

2(1). Terminal segment of genital forceps 6 times as long as broad (III, Fig. 3–4) ..... **Attenuatella**
   Terminal segment of genital forceps less than 4 times as long as broad (as in V, Fig. 2, 5–10, 20; or VI, Fig. 2–10) 3

3(2). Terminal segment of genital forceps more than twice as long as broad and inner margin of long 2nd segment of genital forceps distinctly incurved or strongly bowed (V, Fig. 2, 5–10, 20) ..... **Drunella**
   Terminal segment of genital forceps less than twice as long as broad and inner margin of long 2nd segment of genital forceps not strongly bowed (as in VI, Fig. 2–10) 4

4(3). Penes with spines (VIII, Fig. 2–15, 18–19) ..... **Ephemerella**, s.s, in part
   Penes without spines 5

5(4). Penes with long lateral apical lobes (as in I, Fig. 4; VIII, Fig. 17) 6
   Penes without long lateral apical lobes (as in VI, Fig. 2–10; VII, Fig. 3–13) 7

6(5). Vestigial nymphal gills retained on abdominal segments 4–7; well-developed postero-lateral projections on segments 8 and 9; penes constricted at base (I, Fig. 4); distribution restricted to Western North America (I, Fig. 16) ..... **Timpanoga, E. hecuba**
   Vestigial nymphal gills wanting; posterolateral projections wanting on segments 8 and 9; penes not constricted at base (VIII, Fig. 17); distribution restricted to Eastern North America (VIII, Fig. 81) ..... **Ephemerella**, s.s.; **E. needhami**

7(5). Abdominal sterna 2–7 with reddish-brown to dark brown medially notched rectangular markings (VIII, Fig. 28); subgenital plate

broad, penes small and genital forceps bowed (VIII, Fig. 16); distribution restricted to Western North America (VIII, Fig. 78) ..... **Ephemerella,** s.s.; **E. maculata**

Abdominal sterna without rectangular markings; subgenital plate narrow, penes variable and genital forceps nearly straight (as in VI, Fig. 2–10; VII, Fig. 3–13); widely distributed 8

8(7). Penes with lateral subapical projections (VI, Fig. 2–3; 6–10) ..... **Serratella,** in part

Penes without lateral subapical projections (as in IV, Fig. 2; VI, Fig. 4–5; VII, Fig. 3–13) . 9

9(8). Foretibia longer than foretarsus; male genitalia without a median tubercle on subgenital plate (VI, Fig. 4–5) ..... **Serratella,** in part

Foretibia shorter than foretarsus; male genitalia with a small median tubercle on subgenital plate (as in IV, Fig. 2; VII, Fig. 3–13) 10

10(9). Third foretarsus shorter than 2nd; penes united apically, swollen at base, and 2nd segment of genital forceps thick (VII, Fig. 3–13) ..... **Eurylophella**

Third foretarsus longer than 2nd; penes expanded apically, narrow at base, and 2nd segment of genital forceps thin (IV, Fig. 2) ..... **Dannella**

MATURE NYMPHS

1. Lamellate gills present on abdominal terga 3–7 (as in II, Fig. 1) 2

Lamellate gills present on abdominal terga 4–7 (as in I, Fig. 1) 8

2(1). Paired lateral cerci ¼–¾ as long as median terminal filament ..... **Caudatella**

Paired lateral cerci and median terminal filament subequal in length 3

3(2). Distinct tubercles present on ventral (leading) edge of forefemora (V, Fig. 42–49); tarsal claws with only 1–4 denticles . . **Drunella,** in part

Tubercles wanting on ventral (leading) edge of forefemora (as in V, Fig. 50, 62; VI, Fig. 26–37); tarsal claws usually with more than 4 denticles 4

4(3). Abdominal sterna 3–8 with an adhesive disc of long hair; distribution restricted to Western North America (V, Fig. 51) ..... **Drunella, E. pelosa**

Abdominal sterna may have long hair, but only sparse and not forming an adhesive disc; distribution not restricted to Western North America 5

5(4). Head, thorax, and abdomen with well-developed tubercles (V, Fig. 55–57, 68); distribution restricted to Western North America ..... **Drunella,** in part

Head, thorax, and abdomen without tubercles (as in VI, Fig. 1; VIII, Fig. 1) or with only small tubercles on the head, thorax, or abdomen as in III, Fig. 1); widely distributed 6

6(5). Abdominal terga 2–7 each with a small median tubercle; legs long and thin (VIII, Fig. 52); caudal filaments with whorls of long spines at apex of each segment; distribution restricted to Eastern North America (VIII, Fig. 81) ..... **Ephemerella,** s.s., **E. septentrionalis**

Abdominal terga without tubercles (as in VIII, Fig. 1) or with paired submedian tubercles (as in VI, Fig. 1); legs short and robust (as in VI, Fig. 26–37); caudal filaments without spines or with whorls of only short spines at apex of each segment; distribution not restricted to Eastern North America 7

7(6). Caudal filaments with whorls of spines at apex of each segment and with only sparse intersegmental setae or none (VI, Fig. 16); maxillary palpi absent or reduced in size (VI, Fig. 41) ..... **Serratella**

Caudal filaments with or without whorls of spines at apex of each segment and with heavy intersegmental setae (VIII, Fig. 27); maxillary palpi well developed (VIII, Fig. 20) ..... **Ephemerella,** s.s., in part

8(1). Tarsal claws without denticles 9

Tarsal claws with denticles 10

9(8). Apex of each femur terminating in a sharp spine (I, Fig. 1); distribution restricted to Western North America (I, Fig. 16) ..... **Timpanoga, E. hecuba**

Apex of each femur without such a spine (IV, Fig. 1); distribution restricted to Eastern North America ..... **Dannella**

10(9). Abdominal segment 9 distinctly longer than segment 8, and gills on tergum 4 semi-operculate (VII, Fig. 1) ..... **Eurylophella**

Abdominal segments 8 and 9 subequal, and gills imbricated (III, Fig. 1) ..... **Attenuatella**

In the following species accounts collections made by the authors are indicated by initials GFE and/or RKA. Abbreviations for collections in which specimens are deposited are: AMNH, American Museum of Natural History; CAS, California Academy of Sciences; CNC, Canadian National Collection; CU, Cornell University; GE, General Electric (Hanford Works, Richland, Wash.); INHS, Illinois State Natural History Survey; JRT, J. R. Traver personal collection; LL, J. W. and F. A. Leonard personal collection; MCZ, Museum of Comparative Zoology; OSU, Oregon State University; SGJ, S. G. Jewett, Jr. personal collection; UCSC, University of California (Sagehen Creek Station); UF, University of Florida; UMo, University of Missouri; UU, University of Utah; VKM, V. K. Mayo personal collection. Specimens without designation are deposited in the collection of the University of Utah.

Subgenus *Ephemerella* Walsh, s. s.

Ephemerella Walsh 1862, 377; McDunnough 1925b, 171; Needham 1927, 108; Walley 1930, 17 (=*Chitonophora*); Edmunds and Traver 1954, 238; Demoulin 1958, 10; Edmunds 1959, 544, type *excrucians* Walsh, first valid designation by Eaton 1884, 126.

Chitonophora Bengtsson 1908, 243; Bengtsson 1909, 8; Bengtsson 1913, 292; Ulmer 1914, 98; Lestage 1917, 361; Ulmer 1920, 119; Rousseau 1921, 236; Lestage 1924, 347; McDunnough 1925b, 171; Lestage 1925, 295; Schoenemund 1928, 158; Ulmer 1929, 15; Bengtsson 1930b, 3; Bengtsson 1930a, 10; Schoenemund 1930, 59;

McDunnough 1931b, 188; Ueno 1931, 224; Ulmer 1932a, 205; Ulmer 1932b, 214; Edmunds and Traver 1954, 238; Demoulin 1958, 10.

(Ephemerella) excrucians-group McDunnough 1925b, 169.

(Ephemerella) Section I (typical section) McDunnough 1931b, 192.

(Ephemerella) invaria-group Traver 1932, 144, 176; Traver 1935, 565; Berner 1950, 153; Burks 1953, 67.

(Ephemerella) needhami-group Traver 1935, 565; Berner 1950, 153.

The genus *Ephemerella* was established in 1862 by Walsh for the species *excrucians* and *consimilis* (now a nomen dubium); Eaton (1884: 126) designated the type as *excrucians*. *Chitonophora* was established as a genus by Bengtsson in 1908 for the species *aurivillii*. These species were described from adults only, and the nymphal stage of *E. aurivillii* was not known until 1930; the nymph of *E. excrucians* was not described until 1949.

Needham (1927) characterized the subgenus *Ephemerella* when he reduced *Drunella* Needham to subgeneric rank and described the subgenus *Timpanoga* and the nominal *Eatonella* (=*Drunella*). Walley (1930) technically synonymized *Chitonophora* with *Ephemerella* when he declared *Chitonophora aurivillii* to be a synonym of *Ephemerella aroni* Eaton.[2] McDunnough (1930) also noted that *Chitonophora* had no characters to reliably separate it from *Ephemerella*.

Traver (1935) did not follow Needham's (op. cit.) subgeneric categories but instead treated the genus *Ephemerella* as composed of 8 species groups. She stated that the proper application of these subgeneric names awaited a better definition of all stages, especially of the type, *E. excrucians*. Traver (op. cit.) recognized 2 distinct species groups for the species herein included in the *Ephemerella*, s. s., and placed *E. aurivillii* and closely related species in the *needhami*-group and *E. excrucians* and related species in the *invaria*-group. She separated the male adults of the *invaria*-group from the males of the *needhami*-group on the form of the penes. In the *invaria*-group the penis lobes are short with only a shallow notch between them (Fig. 2-15), while in the *needhami*-group the penis lobes are long with a deep apical notch (Fig. 17-19). According to Traver (op. cit.) the nymphs of the *invaria*-group have rather long spines along the posterior margins of the femora, and on the upper surface of the forefemora, where they are arranged in an irregular transverse band near the apical end, and the caudal filaments never have a whorl of spines at the base. The nymphs of the *needhami*-group were characterized as having only short and inconspicuous spines along the margins of the femora; usually no spines on the upper surface of the forefemora, but if present, generally distributed and not in an apical band; and the caudal filaments sometimes having whorls of spines in the basal half.

[2] Walley (op. cit.) mistakenly used the name *aroni* rather than the prior name *aurivillii*. Bengtsson (1930b) corrected this synonymy when he established that *E. aurivillii* had date priority over *E. aroni*.

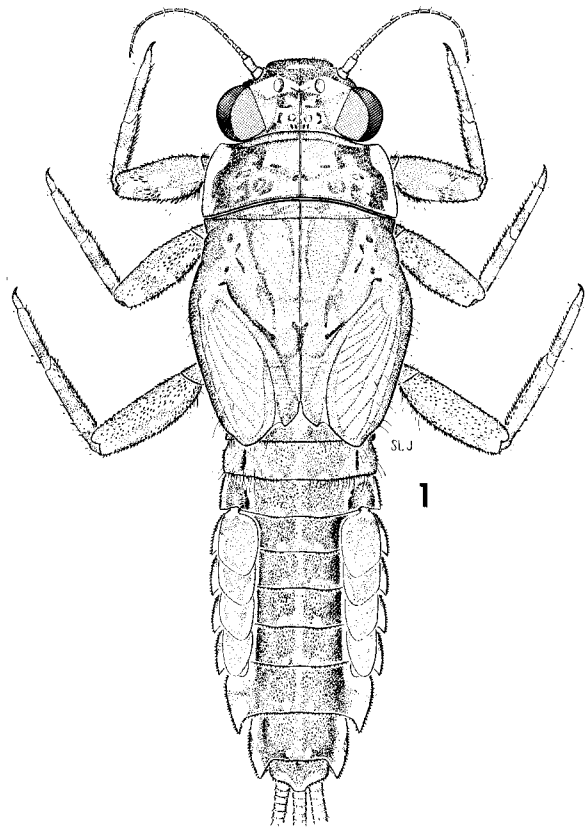


FIG. 1.—*Ephemerella inermis*, mature male nymph, dorsal view.

This arrangement was followed by Day (1956), but Burks (1953) treated all species included in Traver's *invaria*- and *needhami*-groups as the *invaria*-group. Edmunds and Traver (1954) reduced *Chitonophora* to subgeneric rank and Edmunds (1959) regarded *Chitonophora* as doubtfully separable from *Ephemerella*. Edmunds (op. cit.) stated that *Chitonophora* could not be maintained on the characters first suggested by Bengtsson (1908), but that Traver's (1935) separation may have merit for the North American fauna.

North American workers have generally considered *Chitonophora* and *Ephemerella* synonymous since Leonard's (1949) description of the nymphal stage of *E. excrucians*; however, most European workers still place *E. aurivillii*, *E. krieghoffi* (Ulmer), and *E. mucronata* (Bengtsson) in the genus *Chitonophora*.

We have found that there is no concordance of nymphal and adult characters in the North American species which will maintain *Chitonophora* and *Ephemerella*, s. s., even as subgenera. Only 3 North American species, *E. aurivillii*, *E. septentrionalis* McDunnough, and *E. needhami* McDunnough, can be included in the *needhami*-group (=*Chitonophora*), since the penes of the male imagoes all have long lateral apical processes with a deep median apical notch. On the other hand, only the nymphs of *E.*

septentrionalis could be placed in this species group as they alone lack subapical bands of spines on the forefemora (Fig. 52) and have whorls of spines on the proximal segments of the caudal filaments. *E. berneri* Allen and Edmunds, known only from the nymphal stage, also would be included in the *needhami*-group by the character of the forefemora (Fig. 53), but would be placed in the *invaria*-group by the character of the caudal filaments. It is our hope that this report will stimulate foreign workers to make a thorough study of the Eurasian species for further clarification of this problem.

At present, 25 species of the subgenus *Ephemerella* are known to occur in North America. These are: *catawba* Traver; *excrucians* Walsh; *ora* Burks; *argo* Burks; *dorothea* Needham; *inconstans* Travers; *subvaria* McDunnough; *rotunda* Morgan; *invaria* (Walker); *choctawhatchee* Berner; *fratercula* McDunnough; *mollitia* Seemann; *lacustris*, n. sp.; *inermis* Eaton; *infrequens* McDunnough; *maculata* Traver (=*euterpe* Traver 1934: 213, NEW SYNONYMY); *needhami* McDunnough; *aurivillii* (Bengtsson); *verruca*, n. sp.; *crenula*, n. sp.; *simila*, n. sp.; *rossi*, n. sp.; *hispida*, n. sp.; *berneri* Allen and Edmunds; and *septentrionalis* McDunnough.

The subgenus *Ephemerella* may be characterized in the male adult as follows: (1) the terminal segment of the genital forceps is less than twice as long as broad, (2) the lateral apical margins of the penes project apically as distinct processes or lobes, and (3) dorsal and/or ventral spines are usually present on the penes. The nymphal stages (Fig. 1) are characterized by (1) having imbricated gills on segments 3–7, (2) not having tubercles on the ventral (leading) margin of forefemora and without well developed paired tubercles on the head and thorax, (3) having numerous (3–14, usually more than 6) denticles on tarsal claws, (4) having well-developed 3-segmented maxillary palpi, and (5) having subequal caudal filaments usually with whorls of spines on segments in basal ⅔ and heavily setaceous apically (Fig. 27a-f).

The keys will serve to distinguish the species of the subgenus *Ephemerella*.

The male genitalic structures are for the most part distinctive for each species and, because of the lack of other characters, these structures are emphasized in the adult key. We have attempted to stress the general shape of the penes and forceps, and the usual number and arrangement of the dorsal and/or ventral spines when they are present. Adequate series of male genitalia have been examined for the western species and the included figures portray the usual shape, and average number and position of the spines. It is our regret that sufficient series have not been at hand for many eastern species, and our conclusions are based often on a single microscope preparation with reference to other descriptions and figures.

The nymphal stages of most species included in the subgenus *Ephemerella* are extremely variable. Well-defined morphological structures are used to define most species in the nymphal stage; however, in some cases this has been impossible. Those species without good structural characters have been found to exhibit distinctive but variable color characters. In distinguishing the species in the nymphal stage, especially those with only color characters, extreme caution must be exercised. Young or newly molted individuals are usually impossible to determine to species, and determinations are always more certain when a series of specimens is available for study.

KEYS TO THE NORTH AMERICAN SPECIES OF THE SUBGENUS *EPHEMERELLA*

MALE IMAGOES[3]

1. Western North American species, eastern limits in Alberta, Montana, South Dakota, Colorado, and New Mexico (Fig. 78) 2
   Eastern North American species, western limits in Ontario, Michigan, Illinois, Missouri, Oklahoma, and Florida (Fig. 79–81) 7

2(1). Abdominal sterna 2–7 with reddish-brown to dark brown postero-medially notched rectangular markings (Fig. 28); penes without spines (Fig. 16); 2nd segment of genital forceps bowed (Fig. 16) ..... **maculata**
   Abdominal sterna without rectangular markings; penes with spines; 2nd segment of genital forceps not bowed (Fig. 12–15, 18) 3

3(2). Penes with long apical lobes and a deep median notch; penis lobes with only dorsal and median spines (Fig. 18); forewing more than 11 mm long ..... **aurivillii**
   Penes with short apical lobes and a shallow median notch; penis lobes with dorsal and ventral spines (Fig. 12–15); forewing usually less than 10 mm long 4

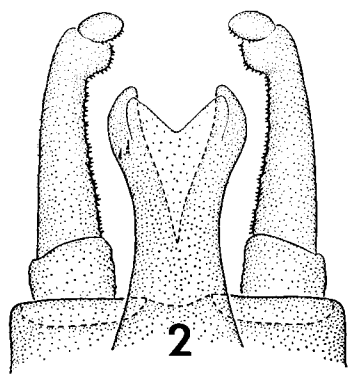
4(3). Penes with 15–20 dorsal and 15–20 ventral spines (Fig. 12) ..... **mollitia**
   Penes with 2–14 dorsal and 1–11 ventral spines (Fig. 13–15) 5

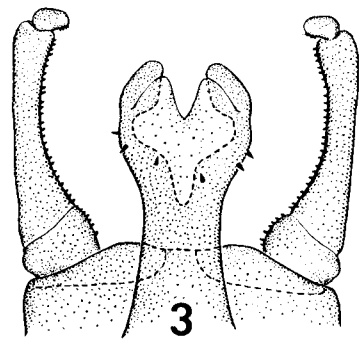
5(4). Lateral margins of penis lobes rather straight; 2nd segment of genital forceps swollen apically (Fig. 15) ..... **infrequens**
   Lateral margins of penis lobes distinctly incurved; 2nd segment of genital forceps with only a slight apical expansion (Fig. 13–14) . 6

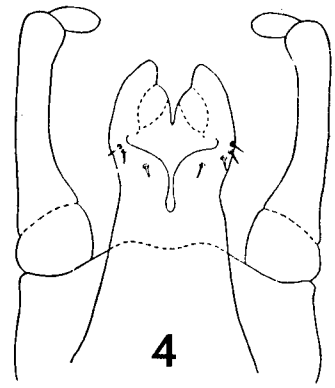
6(5). Foreleg as long or longer than forewing (forewing 8.5–9.5 mm, foreleg 9.0–9.5 mm); mesothoracic notum deep chocolate brown; abdominal terga light brown; penes with 8–12 dorsal and 1–4 ventral spines usually arranged as in Fig. 13 ..... **lacustris**
   Forelegs shorter than forewing (forewing 8–10 mm, foreleg 6.0–6.5 mm); mesothoracic notum olive brown; abdominal terga light brown to reddish brown; penes with 3–14 dorsal and 1–9 ventral spines usually arranged as in Fig. 14 ..... **inermis**

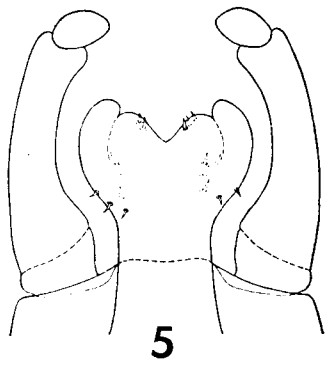
7(1). Penes with long apical lobes and a deep median notch; penes without spines or with only dorsal median spines (Fig. 17–19) 8

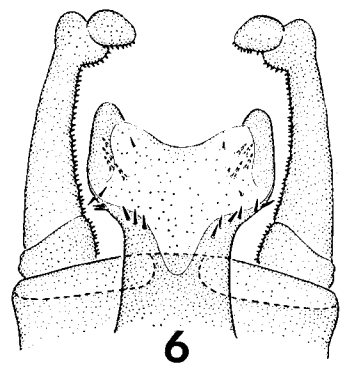
[3] Male imagoes of *E. crenula*, n. sp.; *E. simila*, n. sp.; *E. rossi*, n. sp.; *E. verruca*, n. sp.; *E. hispida*, n. sp.; *choctawhatchee* Berner; and *E. berneri* Allen and Edmunds are unknown.

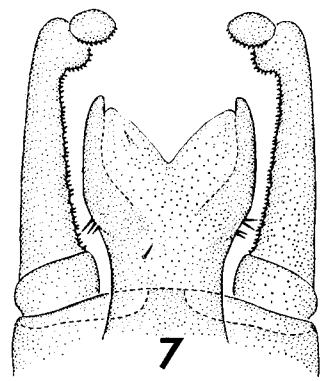


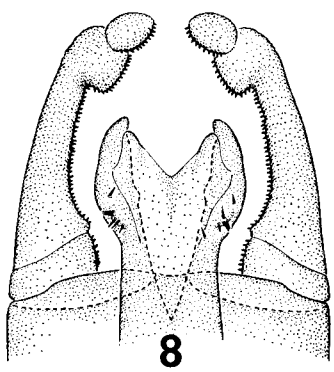


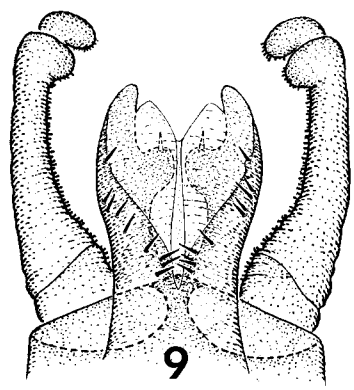


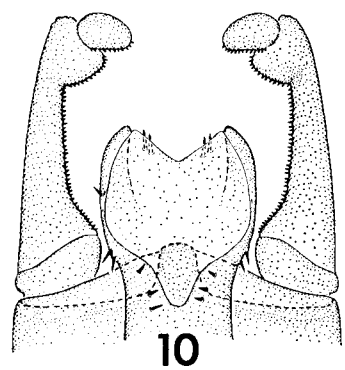


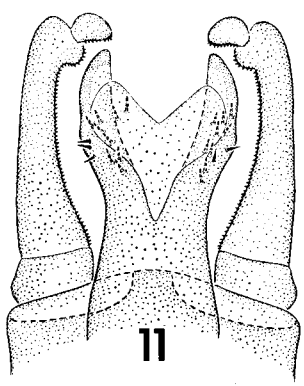


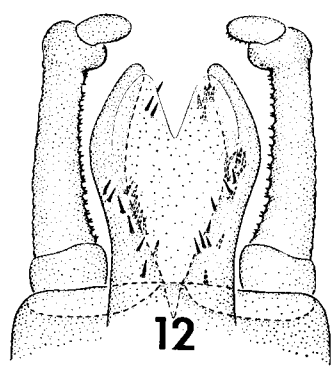












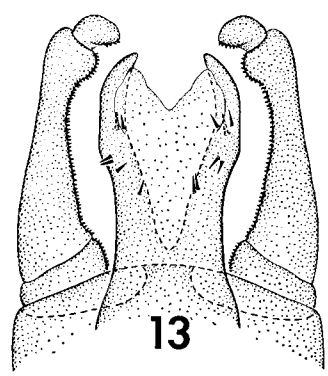


FIG. 2–13.—Subgenus *Ephemerella,* s. s., dorsal view male genitalia. Fig. 2, *E. catawba;* Fig. 3, *E. excrucians;* Fig. 4, *E. ora;* Fig. 5, *E. argo;* Fig. 6, *E. dorothea;* Fig. 7, *E. inconstans;* Fig. 8, *E. subvaria;* Fig. 9, *E. rotunda;* Fig 10, *E. invaria;* Fig. 11, *E. fratercula;* Fig. 12, *E. mollitia;* Fig. 13, *E. lacustris.*

Penes with short apical lobes and a shallow median notch; penes almost always with dorsal and/or ventral lateral spines (Fig. 2–11) .10

8(7). Penes without spines; 2nd segment of genital foreceps without apical expansion (Fig. 17) ..... **needhami**

Penes with dorsal and/or median spines; 2nd segment of genital forceps with a slight apical expansion (Fig. 18–19) 9

9(8). Penes with 1–5 median spines as in Fig. 19; foreleg much longer than forewing (forewing 9–10 mm, foreleg 12–13 mm) ..... **septentrionalis**

Penes with 12–14 dorsal and 12–14 median spines as in Fig. 18; foreleg shorter than or only equal to length of forewing (forewing 11–13 mm, foreleg 10–11 mm) ..... **aurivillii**

10(7). Second segment of genital forceps without a distinct meso-apical lobe (Fig. 3–5) 11

Second segment of genital forceps expanded into a distinct meso-apical lobe (Fig. 2, 6–11) 13

11(10). Penes with numerous (usually more than 10) ventral and apical spines (Fig. 5) ..... **argo**

Penes without ventral or apical spines, spines dorsal (Fig. 3, 4) 12

12(11). Thoracic notum tan and yellow; compound eyes of living insect pinkish tan; male genitalia as in Fig. 4 ..... **ora**

Thoracic notum deep reddish brown; compound eyes of living insect yellow; male genitalia as in Fig. 3 ..... **excrucians**

13(10). Penes with few or no dorsal and ventral spines (0, 1, or 2) as in Fig. 2 ..... **catawba**

Penes usually with more than 10 dorsal and ventral spines and not as above (Fig. 6–11) 14

14(13). Penis lobes short and broad with nearly parallel lateral margins; dorsal and ventral spines arranged as in Fig. 6; thorax and abdomen pale yellow ..... **dorothea**

Penis lobes not so short and broad, usually with round lateral margins; dorsal and ventral spines not arranged as preceding; thorax and abdomen brown or reddish brown, if yellow always shaded with brown or tan 15

15(14). Penes with numerous ventral spines (18–20) and 5–7 dorsal spines arranged as in Fig. 11 ..... **fratercula**

Penes without, or with only a moderate number of ventral spines (0–10) and 6–20 dorsal spines (Fig. 7–10) 16

16(15). Posterior margin of subgenital plate with a distinct median projection (Fig. 9–10); penes with 6–8 median basal spines on dorsal surface and with 1–4 apical or subapical spines (Fig. 9–10) 17

Posterior margin of subgenital plate gently rounded (Fig. 7–8); penes with only 1 or 2 or no basal spines on the dorsal surface, and without or with only 1 or 2 apical spines (Fig. 7–8) 18

17(16). Penes with *long* spines (Fig. 9); penes usually with more than 15 dorsal spines and with paired ventral subapical spines (Fig. 9); abdominal terga yellow with a brown transverse band ..... **rotunda**

Penes with *short* spines (Fig. 10); penes usually with less than 12 dorsal spines and with paired ventral apical spines (Fig. 10); abdominal terga reddish brown ..... **invaria**

18(16). Penes usually with 12 or more dorsal spines and without ventral spines (Fig. 8); forewings with light brown to reddish-brown primary longitudinal veins ..... **subvaria**

Penes usually with less than 10 dorsal spines and occasionally with ventral spines (Fig. 7); forewings with yellow primary longitudinal veins ..... **inconstans**

MATURE NYMPHS[4]

1. Western North American species, eastern limits in Alberta, Montana, South Dakota, Colorado, and New Mexico (Fig. 78) 2

Eastern North American species, western limits in Ontario, Michigan, Illinois, Missouri, Oklahoma, and Florida (Fig. 79–81) 8

2(1). Abdominal terga with well-developed paired submedian tubercles (Fig. 30–32), if small tubercles are present (Fig. 32), postero-lateral projections are present on segment 3 and nymph usually more than 11 mm long .. 3

Abdominal terga without well-developed paired submedian tubercles (Fig. 1); if small tubercles are present, postero-lateral projections are absent on segment 3 and nymph usually less than 9 mm long 4

3(2). Front of head with 3 spiculate wartlike tubercles (Fig. 71); abdominal terga 2–10 with small, sharp, paired submedian tubercles (Fig. 30) ..... **verruca**

Front of head without tubercles (Fig. 70); abdominal terga 1–9 with moderately long, sharp, heavily spiculated tubercles (Fig. 31), or abdominal terga 3–7 with small, blunt, heavily spiculated tubercles (Fig. 32) ..... **aurivillii**

4(2). Abdominal sterna 2–7 with reddish-brown to dark brown medially notched rectangular markings (Fig. 29); head much broader than long (Fig. 66); forefemora with numerous subapical spines (Fig. 49) .... **maculata**

Abdominal sterna without rectangular markings; head as long as broad (Fig. 65); forefemora with only a few subapical spines (Fig. 50–51) 5

5(4). Abdominal segments 3–9 with distinct postero-lateral projections (Fig. 35–36); tarsal claws usually with more than 11 denticles as in Fig. 72 and 74 6

Abdominal segments 4–9 with distinct postero-lateral projections (Fig. 1); tarsal claws usually with less than 8 denticles as in Fig. 73 7

6(5). Legs pale; femora thin and with a light brown macula near the middle (Fig. 50); abdominal

[4] The nymphal stage of *E. fratercula* McDunnough and *E. ora* Burks are unknown.

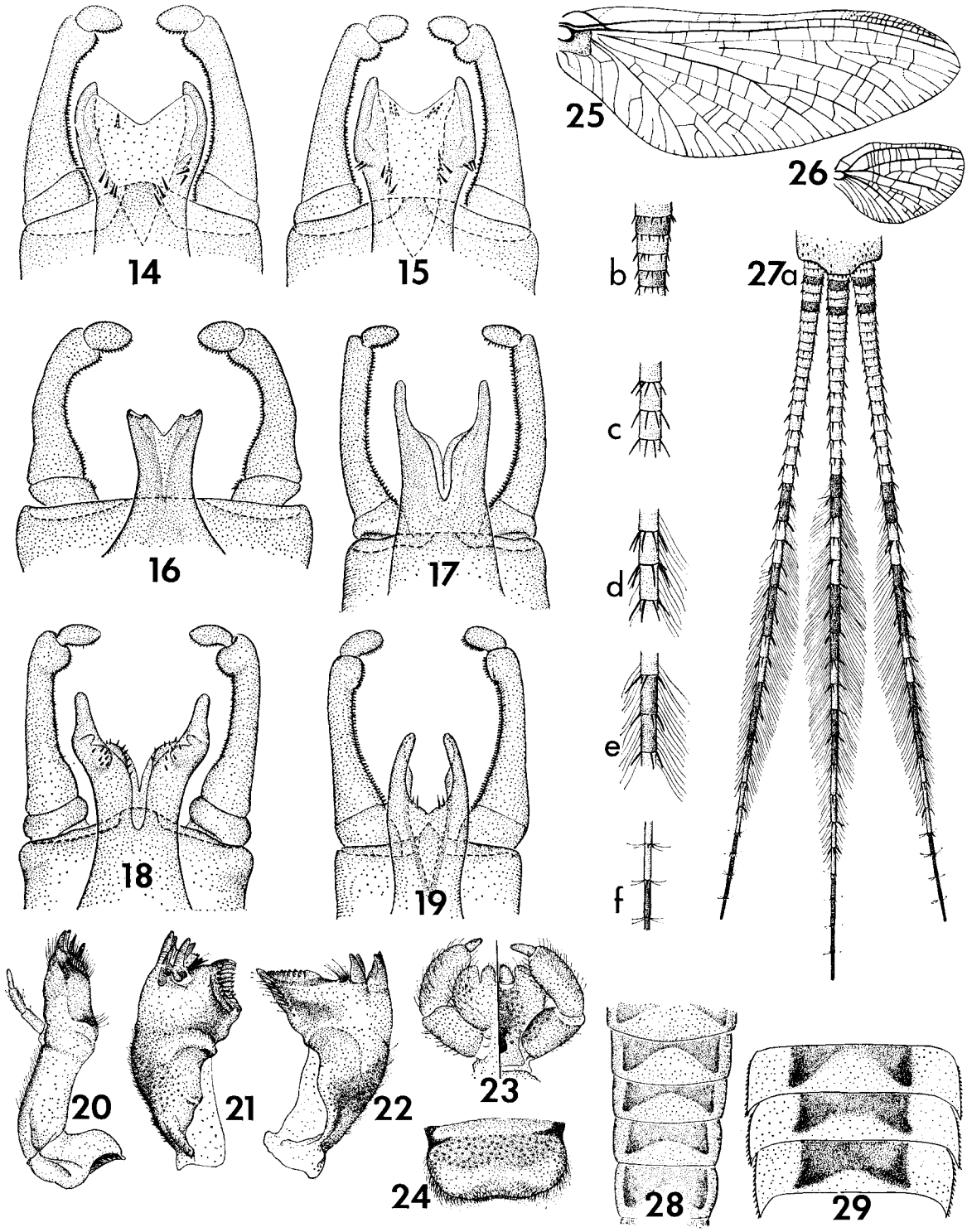


FIG. 14–19.—Subgenus *Ephemerella*, s. s., dorsal view male genitalia. Fig. 14, *E. inermis;* Fig. 15, *E. infrequens;* Fig. 16, *E. maculata;* Fig. 17, *E. needhami;* Fig. 18, *E. aurivillii;* Fig. 19, *E. septentrionalis.*

FIG. 20–26.—*Ephemerella subvaria.* Fig. 20, maxilla; Fig. 21, left mandible; Fig. 22, right mandible; Fig. 23, labium, dorsal and ventral; Fig. 24, labrum; Fig. 25, forewing; Fig. 26, hindwing.

FIG. 27a-f.—*Ephemerella rotunda,* caudal filaments of mature nymph.

FIG. 28–29.—*Ephemerella maculata.* Fig. 28, abdominal sterna 2–6 of male imago; Fig. 29, abdominal sterna 3–5 of mature nymph.

terga brown with large pale patches on middle and posterior segments (Fig. 35) . . **lacustris**

Legs brown; femora thick and with pale markings as in Fig. 51; abdominal terga brown usually with paired submedian pale spots on posterior margin of segments (Fig. 36) . . . . . **mollitia**

7(5). Abdominal terga usually dark brown to black with well-marked submedian pale spots and a pale median stripe (Fig. 1), terga occasionally with minute paired submedian tubercles on segments 2–8; body usually robust; postero-lateral projections comparatively short (Fig. 34); foreleg less than 3 mm long . . . . . **inermis**

Abdominal terga usually brown with variable pale markings, often indistinct paired submedian pale spots present, and without minute tubercles; body usually slender; postero-lateral projections comparatively long (Fig. 33); foreleg more than 3 mm long . . **infrequens**

8(1). Legs long and thin (Fig. 52); abdominal terga 2–7 each with a single small median tubercle; tarsal claws with 11–14 denticles (Fig. 75); caudal filaments with whorls of long spines at apex of each segment . . . . . **septentrionalis**

Legs short and robust (Fig. 53–64); abdominal terga without tubercles, or with paired submedian tubercles or protuberances (Fig. 37–48); tarsal claws with 4–11 denticles; caudal filaments with only short spines in basal ⅔ of filament or spines absent 9

9(8). Abdominal terga with paired submedian tubercles (Fig. 37–40, 42–48) or with paired submedian protuberances (Fig. 41), tubercles or protuberances always discernible on segments 4–7 10

Abdominal terga without tubercles or protuberances as in Fig. 35 22

10(9). Abdominal terga with long paired submedian tubercles on segments 1–10 (Fig. 42); forefemora without a subapical band of spines (Fig. 53); caudal filaments without whorls of spines on apex of basal segments . . . . **berneri**

Abdominal terga with protuberances or short to moderately developed tubercles and without tubercles on segment 10 (Fig. 37–41, 43–48); forefemora with a subapical band of spines (Fig. 54–64); caudal filaments with whorls of spines on apex of basal segments . . 11

11(10). Abdominal terga with paired submedian protuberances on segments 4–7 (Fig. 41); abdominal terga glabrous and lustrous; tarsal claws with 8–11 denticles (Fig. 77) . . . **catawba**

Abdominal terga with paired submedian tubercles (Fig. 37–40, 43–48); abdominal terga with scattered spicules; dentition of tarsal claws variable 12

12(11). Abdominal tubercles heavily spiculate (Fig. 32b), and usually as in Fig. 32a, tubercles sometimes better developed, approaching or similar to those in Fig. 31a; body usually more than 11 mm long; legs relatively long, hindleg more than 1.5 times longer than foreleg; foreleg as in Fig. 54 . . . . . **aurivillii**

Abdominal tubercles lightly to moderately spiculate (Fig. 37b–40b, 43b–48b); body usually less than 11 mm long; legs relatively short, hindleg less than 1.5 times longer than foreleg; forelegs as in Fig. 55–61, 63–64 13

13(12). Abdominal terga with moderately long, blunt paired submedian tubercles on segments 1–9 (Fig. 45) . . . . . **hispida**

Abdominal terga with variable paired submedian tubercles, tubercles absent on segments 1 and/or 9 (Fig. 37–40, 43–44, 46–48) . . 14

14(13). Abdominal terga with moderately long, sharp, paired submedian tubercles on segments 1–8 (Fig. 44); foreleg as in Fig. 56 . . . . . **needhami**

Abdominal terga with variable paired submedian tubercles, tubercles absent on tergum 1 (Fig. 37–40, 46–48); forelegs as in Fig. 55, 57–61, 63 15

15(14). Abdominal terga with moderately long, sharp, paired submedian tubercles on segments 2–9 (Fig. 43); tibial and tarsal bands dark brown to black (Fig. 55); head with small submedian occipital tubercles (Fig. 67) . . **subvaria**

Abdominal terga with variable paired submedian tubercles (Fig. 37–40, 46–48); tibial and tarsal bands lighter than above or absent (Fig. 57–61, 63); head without tubercles or with minute tubercles as in Fig. 69 . . 16

16(15). Abdominal terga with moderately long, blunt, paired submedian tubercles on segments 2–8 (Fig. 39a), tubercles on tergum 6 comparatively long (Fig. 39b); foreleg with long subapical femoral spines (Fig. 57); female with small submedian suboccipital tubercles (Fig. 69) . . . . . **simila**

Abdominal terga with variable paired submedian tubercles (Fig. 37a, 40a, 46a-48a); tubercles on tergum 6 comparatively short (Fig. 37b, 40b, 46b-48b); foreleg with short subapical femoral spines (Fig. 58–61, 63); head without tubercles 17

17(16). Abdominal terga with short blunt paired submedian tubercles on segments 4–9, and with paired submedian rows of spicules (Fig. 40); legs unicolorous (Fig. 59) . . . . . **rossi**

Abdominal terga with variable paired submedian tubercles and without rows of spicules (Fig. 37, 46–48); legs with dark tibial and tarsal bands (Fig. 58, 60–61, 63) 18

18(17). Head covered with fine spicules (Fig. 68); abdominal terga with short, blunt, paired submedian tubercles on segments 3–8 (Fig. 37); foreleg as in Fig. 58 . . . . . **crenula**

Head without fine spicules; abdominal terga with short, sharp, paired submedian tubercles (Fig. 46–48); forelegs as in Fig. 60–61, 63 . . 19

19(18). Abdominal terga with paired submedian tubercles on segments 2–9, tubercles small but discernible on terga 3–8, barely discernible on terga 2 and 9 (Fig. 47); forefemora with a moderately wide band of subapical spines (Fig. 60) . . . . . **rotunda**

Abdominal terga with paired submedian tubercles on segments 3–8 (rarely small tubercles on 2), tubercles small but discernible on

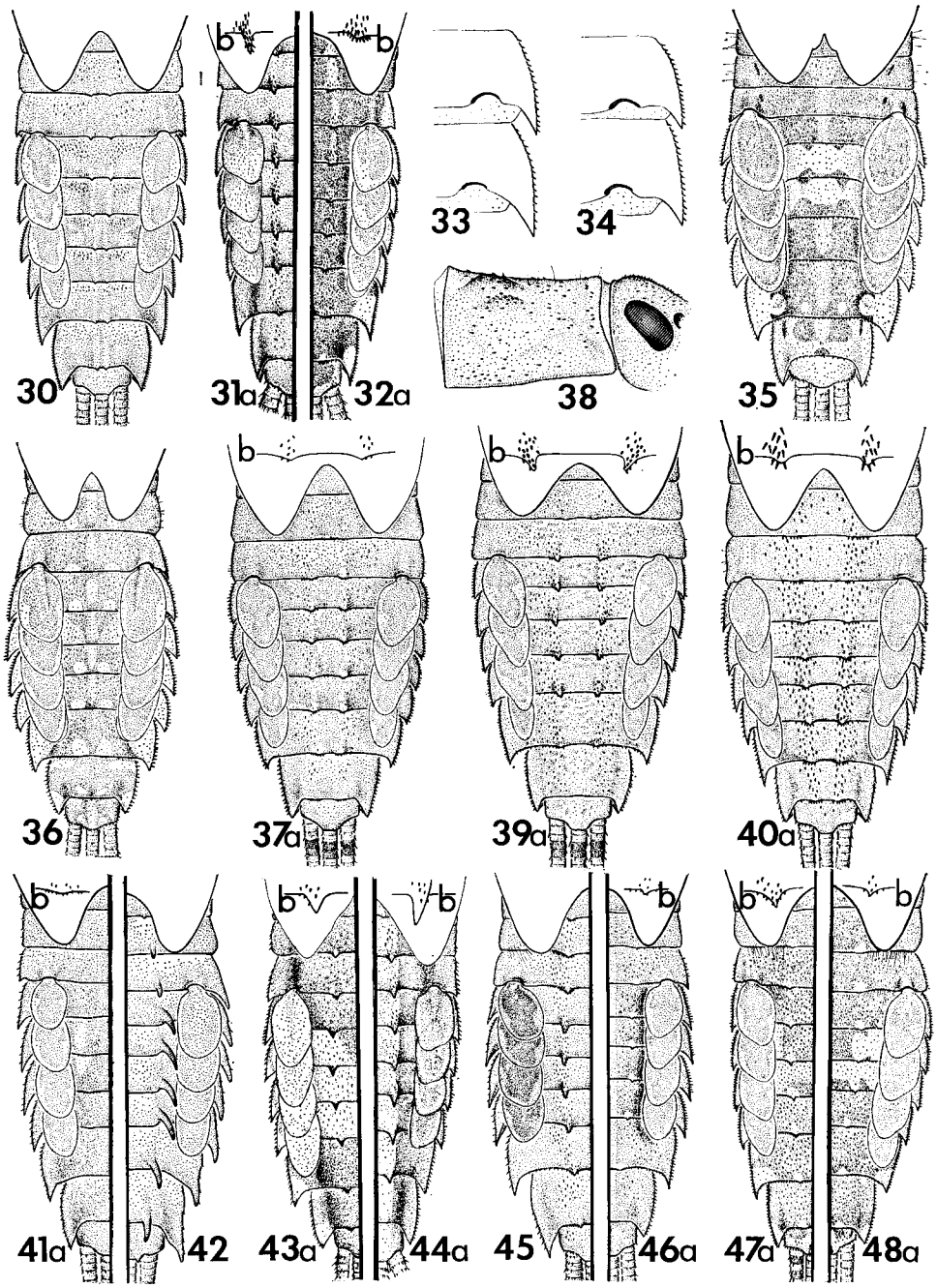


FIG. 30–32.—Subgenus *Ephemerella,* s. s., abdominal terga of mature nymph. Fig. 30, *E. verruca;* Fig. 31a, *E. aurivillii,* western population; 31b, tubercles, 6th abdominal tergum; Fig. 32a, *E. aurivillii,* eastern population; 32b, tubercles, 6th abdominal tergum.

FIG. 33–34.—Subgenus *Ephemerella,* s. s., postero-lateral projections of abdominal segments 4–5 mature nymph. Fig. 33, *E. infrequens;* Fig. 34, *E. inermis.*

FIG. 35–37.—Subgenus *Ephemerella,* s. s., abdominal terga of mature nymph. Fig. 35, *E. lacustris;* Fig. 36, *E. mollitia;* Fig. 37a, *E. crenula;* 37b, tubercles, 6th abdominal tergum.

FIG. 38–39.—*Ephemerella simila.* Fig. 38, pronotum, lateral view; Fig. 39a, abdominal terga; 39b, tubercles, 6th abdominal tergum.

FIG. 40–48.—Subgenus *Ephemerella,* s. s., abdominal terga of mature nymph. Fig. 40a, *E. rossi;* 40b, tubercles, 6th abdominal tergum; Fig. 41a, *E. catawba;* 41b, tubercles, 6th abdominal tergum; Fig. 42, *E. berneri;* Fig. 43a, *E. subvaria;* 43b, tubercles, 6th abdominal tergum; Fig. 44a, *E. needhami;* 44b, tubercles, 6th abdominal tergum; Fig. 45, *E. hispida;* Fig. 46a, *E. inconstans;* 46b, tubercles, 6th abdominal tergum; Fig. 47a, *E. rotunda;* 47b, tubercles, 6th abdominal tergum; Fig. 48a, *E. invaria;* 48b, tubercles, 6th abdominal tergum.

terga 4–7 barely discernible on terga 3 and 8 (Fig. 46, 48); forefemoral spines variable (Fig. 61, 63) 20

20(19). Distinct postero-lateral projections on segments 3–9 (Fig. 46); forefemora usually with a broad band of numerous spines (Fig. 63); body usually more than 9 mm long. **inconstans**

Distinct postero-lateral projections on segments 4–9 (Fig. 48); forefemora usually with a narrow band of only a few spines (Fig. 61); body usually less than 9 mm long 21

21(20). Body 6.5 mm long; distribution restricted to Florida (Fig. 80) ..... **choctawhatchee**

Body 7.0–9.5 mm long; widely distributed in Eastern North America but not known from Florida ..... **invaria**

22(9). Caudal filaments unicolorous, without brown bands ..... **excrucians**

Caudal filaments with alternating pale and brown bands 23

23(22). General color yellow with brown markings; pronotum yellow with brown sublateral longitudinal stripes and mesonotum with a brown transverse stripe; abdominal terga 5–6 usually yellow ..... **argo**

General color brown to dark brown and sprinkled with fine pale dots; thoracic nota brown to dark brown; abdominal terga 5–6 brown to dark brown ..... **dorothea**

The following verification table will allow rapid comparison of some of the important specific characters used in the preceding keys. Abbreviations given under the distributions of the species are as follows: E, Eastern North America; W, Western North America; H, Holarctic. When the known distribution is restricted the States and Provinces are indicated by standard abbreviations.

In the nymphal table, under the heading "ABDOMINAL TUBERCLES" and subheading "SEGMENTS," the numbers are listed for all segments that have been found to possess tubercles, even though the tubercles are barely discernible or even absent in some specimens. The development of the postero-lateral projections on the 3rd segment is variable in some species, and occasionally one which possesses distinct projections on only segments 4–9 will be found with a small projection on segment 3. Then only those segments are listed which possess distinct postero-lateral projections.

Ephemerella catawba Traver

(Fig. 2, 41, 62, 77, 79)

Ephemerella catawba Traver 1932, 153, 176, 2 Fig.; Traver 1935, 585, 1 Fig.; Traver 1937, 68; Wright and Berner 1949, 295.

E. catawba was described in the *needhami*-group from male imagoes and nymphs collected in North Carolina.

Male Imago (in alcohol).—Length: body 6–7; forewing 6–7 mm. Compound eyes orange. Thorax reddish brown; prothorax yellow laterally; mesothorax with yellow markings; foreleg reddish brown; length of segments of foreleg in millimeters: femur = 1.5; tibia = 2.3; tarsus I = 0.2; tarsus II = 1.0; tarsus III = 1.1; tarsus IV = 0.8; tarsus V = 0.3; middle and hind legs pale; wings hyaline; primary longitudinal veins tinged with yellow, crossveins and intercalaries hyaline. Abdominal terga brown with dark brown markings; abdominal sterna light brown. Penes

VERIFICATION TABLE—MALE IMAGOES

Species	Distribution	Wing size	Foreleg length	Forceps type	Penes type	Spines on penes
1. *catawba*	N.C., Tenn., Ga.	6–7	7.2	*invaria*	*invaria*	0–2 dorsal, 0–2 ventral
2. *excrucians*	E	7–9	7.5	*excrucians*	*excrucians*	6–10 dorsal, no ventral
3. *ora*	Ill.	8	?	*excrucians*	*excrucians*	7 dorsal, no ventral
4. *argo*	Ill., Ind.	9	?	*excrucians*	*excrucians*	5 dorsal, 11 ventral
5. *dorothea*	E	7.5–8.5	9.7	*invaria*	*dorothea*	15–17 dorsal, 8–10 ventral
6. *inconstans*	N.C., Ky., Va.	8–10	9.8	*excrucians*	*dorothea*	6–8 dorsal, 0–2 ventral
7. *subvaria*	E	9–10	11.5	*invaria*	*invaria*	10–12 dorsal, no ventral
8. *rotunda*	E	9–11	10.1	*invaria*	*invaria*	14–20 dorsal, 1–3 ventral
9. *invaria*	E	8–10	10.4	*invaria*	*invaria*	10–16 dorsal, 2–4 ventral
10. *choctawhatchee*	Fla.	.....	.....	Undescribed	.....	.....
11. *fratercula*	Que.	7–8	?	*invaria*	*invaria*	5–7 dorsal, 18–20 ventral
12. *mollitia*	Calif.	10	?	*invaria*	*invaria*	15–20 dorsal, 15–20 ventral
13. *lacustris*	Wyo.	8.5–9.5	9.5	*inermis*	*invaria*	8–10 dorsal, 1–4 ventral
14. *inermis*	W	8–10	6.6	*inermis*	*invaria*	3–14 dorsal, 1–9 ventral
15. *infrequens*	W	9.0–10.5	8.9	*invaria*	*dorothea*	2–11 dorsal, 4–11 ventral
16. *maculata*	Calif.	10–11	?	*inermis*	*maculata*	without
17. *needhami*	E	7–8	9.0	*excrucians*	*needhami*	without
18. *aurivillii*	H	11–13	11.2	*invaria*	*needhami*	12–14 dorsal, 12–14 medial
19. *verruca*	Ore.	.....	.....	Undescribed	.....	.....
20. *crenula*	N.C., Tenn.	.....	.....	Undescribed	.....	.....
21. *simila*	Va.	.....	.....	Undescribed	.....	.....
22. *rossi*	Tenn.	.....	.....	Undescribed	.....	.....
23. *hispida*	N.C., Tenn.	.....	.....	Undescribed	.....	.....
24. *berneri*	Ga., Va.	.....	.....	Undescribed	.....	.....
25. *septentrionalis*	E	9–10	12.4	*inermis*	*needhami*	1–5 medial, no dorsal or ventral

VERIFICATION TABLE—NYMPHS

Species	Distribution	Body size	Abdominal tubercles		Postero-lateral projections	Caudal filaments banded	Denticles	Tibial & tarsal bands
			Segments	Size & shape				
1. *catawba*	N.C., Tenn., Ga.	7–8	3–8	protuberances	3–9	No	8–11	No
2. *excrucians*	E	6–7	absent		4–9	No	5–7	Yes
3. *ora*	Ill.	.....	.....	Undescribed	.....	.....	.....	.....
4. *argo*	Ill., Ind.	7–9	absent		4–9	Yes	6–9	Yes
5. *dorothea*	E	6–8	absent		4–9	Yes	6–9	Yes
6. *inconstans*	N.C., Ky., Va.	8–11	2–8	small & sharp	3–9	Yes	6–10	Yes
7. *subvaria*	E	8.5–9.5	2–9	moderate & sharp	3–9	Yes	4–6	Yes
8. *rotunda*	E	10–11	2–9	small & sharp	4–9	Yes	5–7	Yes
9. *invaria*	E	7.0–9.5	3–8	small & sharp	4–9	Yes	5–7	Yes
10. *choctawhatchee*	Fla.	6.0–6.5	3–8	small & sharp	4–9	Yes	6–8	Yes
11. *fratercula*	Que.	.....	.....	Undescribed	.....	.....	.....	.....
12. *mollitia*	Calif.	10–11	absent		3–9	Yes	9–13	Yes
13. *lacustris*	Wyo.	7–9	absent		3–9	Yes	10–13	Yes
14. *inermis*	W	7–9	absent		4–9	Yes	6–9	Yes
15. *infrequens*	W	8–11	absent		4–9	Yes	7–10	Yes
16. *maculata*	Calif.	7.5–11.0	absent		2–9	No	4–5	No
17. *needhami*	E	7–8	1–8	moderate & sharp	3–9	Yes	6–11	Yes
18. *aurivillii*	H	10.0–13.5	1–9	variable	3–9	Yes	6–10	Yes
19. *verruca*	Ore.	12–14	2–10	small & sharp	3–9	?	10–12	Tarsal only
20. *crenula*	N.C., Tenn.	6–7	3–8	small & round	4–9	Yes	4–6	Yes
21. *simila*	W. Va.	8–9	2–8	small & round	4–9	Yes	4–6	Tarsal only
22. *rossi*	Tenn.	6.0–7.5	4–9	small & round	4–9	No	3–5	No
23. *hispida*	N.C., Tenn.	8–12	1–9	moderate & blunt	4–9	No	8–10	No
24. *berneri*	Ga., Va.	11–13	1–10	long & blunt	3–9	No	8–10	No
25. *septentrionalis*	E	9–10	2–7 median	small & round	4–9	Yes	11–14	Yes

with 0–2 dorsal and 0–2 ventral spines (Fig. 2); penis lobes short; lateral margins of penis lobes rounded; 2nd segment of genital forceps swollen apically (Fig. 2). Caudal filaments pale with dark annulations at apex of each segment.

Mature Nymph.—Length: body 7–8; caudal filaments 4–5 mm. General color brown with dark brown and light brown or pale markings. Head brown with pale vermiculate markings on the vertex; without paired occipital tubercles. Thoracic notum brown with irregular dark brown maculae, lateral margins of pronotum sometimes pale or partly pale; legs brown; femora brown with variable markings, often with pale markings near middle of segment, darker apically; forefemora with a narrow subapical band of long spines; tibiae and tarsi brown, often darker at apices (Fig. 62); tarsal claws with 8–11 denticles (Fig. 77). Abdominal terga without paired submedian tubercles, but terga 3–8 with small rounded paired submedian protuberances (Fig. 41a); terga with fine spicules (Fig. 41b); terga brown, often with pale patches mediad of gills on middle segments; terga glabrous and lustrous; distinct postero-lateral projections on segments 3–9, usually small or barely discernible on segment 3; abdominal sterna brown. Caudal filaments unicolorous brown or with faint pale bands.

Type-Locality.—Catawba River at Andrews Geyser, N. C.

Type.—No. 1094.1, Cornell University Collection, Ithaca, N. Y.

DISTRIBUTION

This species is known from Virginia, North Carolina, Tennessee, and Georgia (Fig. 79). We have examined specimens from:

GEORGIA: Brook, Neels Gap, 3 mi. S Vogel State Park, 10-VI-58, W. L. Peters. NORTH CAROLINA: Catawba River 21-V-29, J. R. Traver (Paratype) (CU); Cascades, Danbury, 3-V-30, J. R. Traver (Paratype, nymphs) (CU); Watanga River, Valle Crucis, 30-V-36, 10-VI-36, J. R. Traver (JRT); Conestee Creek nr. Brevard, 25-VI-36, "L.E.T." and J. R. Traver (JRT); Glen Falls on E. Fork, Blue Valley, 7-VII-57, S. and D. Mulaik; Bryson City, 8-VII-30, H. T. Spieth (AMNH); Nr. Grandfather Mountain W. Blowing Rock, 23-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS). TENNESSEE: Little River, Elkmont, 14-V-39, T. H. Frison and H. H. Ross (INHS); LaConte Creek, Gatlinburg, 14-V-39, 14-VI-40, T. H. Frison and H. H. Ross (INHS); Cades Cove, 13-VI-49, T. H. Frison et al. (INHS). VIRGINIA: Crooked River, Madison, 1-I-39, T. H. Frison and B. D. Burks (INHS).

TAXONOMY

E. catawba is a distinctive species in both the male adult and the nymphal stages.

The nymphs are distinguished by characters of the forelegs and abdomen, but are variable in the character of the caudal filaments. Most specimens examined possess only sparse setae on the caudal filaments, whereas, most species of the subgenus *Ephemerella* have filaments that are heavily setaceous. The absence of setae on these structures superficially makes it difficult to distinguish them from *E.* (*Serratella*) *deficiens* Morgan. The abdominal terga of *E. catawba* are glabrous and lustrous and this character, plus the rounded submedian protuberances on the middle abdominal terga, serves to distinguish this species from *E. deficiens* and all other *Ephemerella*.

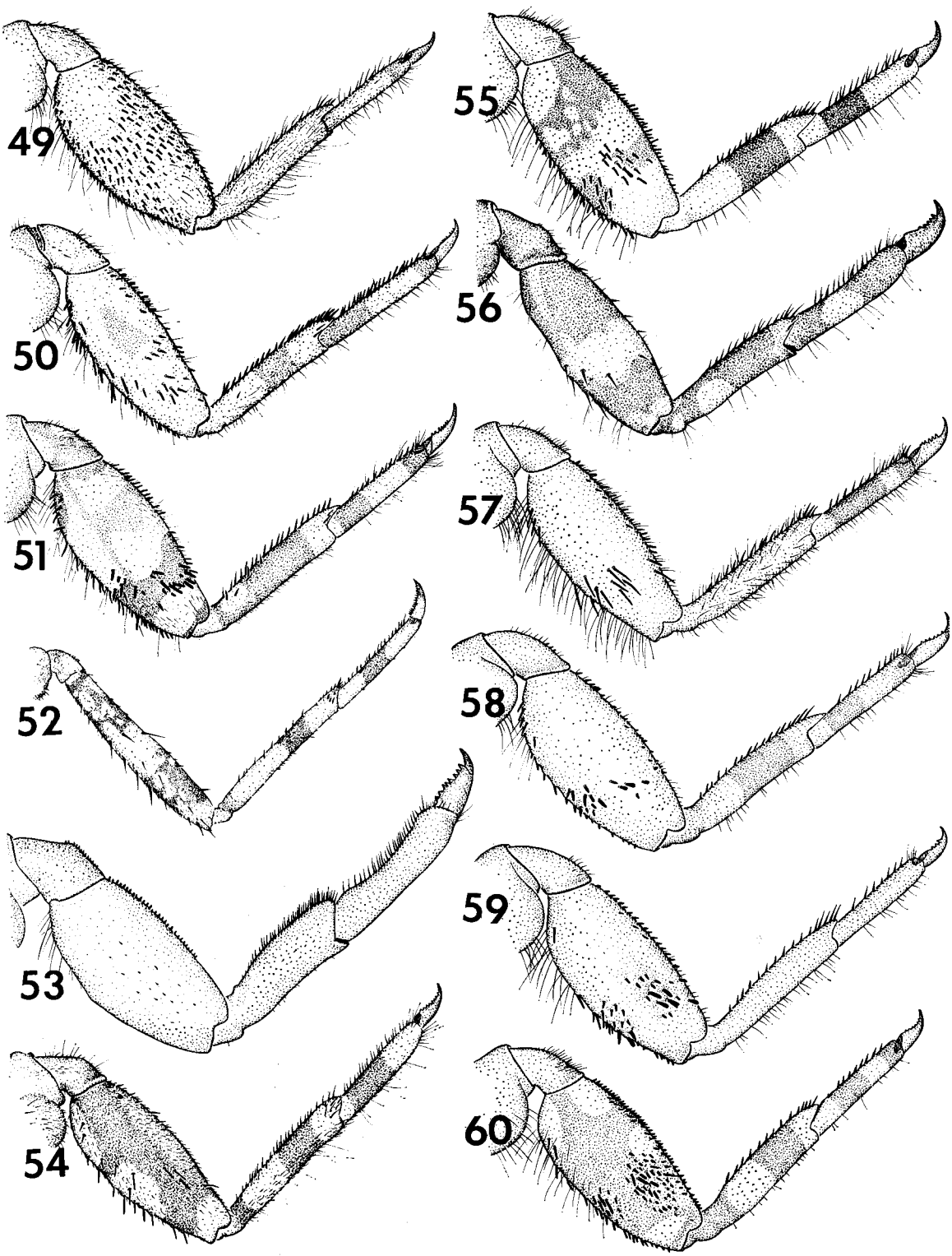


FIG. 49–60.—Subgenus *Ephemerella*, s. s., right nymphal forelegs. Fig. 49, *E. maculata;* Fig. 50, *E. lacustris;* Fig. 51, *E. infrequens;* Fig. 52, *E. septentrionatis;* Fig. 53, *E. berneri;* Fig. 54, *E. aurivillii;* Fig. 55, *E. subvaria;* Fig. 56, *E. needhami;* Fig. 57, *E. simila;* Fig. 58, *E. crenula;* Fig. 59, *E. rossi;* Fig. 60, *E. rotunda.*

Dorsal and ventral spines are usually absent on the penes of the males of *E. catawba,* but occasionally specimens are found with 1 or 2 dorsal and/or ventral spines.

Ephemerella excrucians Walsh

(Fig. 3, 79)

Ephemerella excrucians Walsh 1862, 377; Eaton 1873, 385; Banks 1892, 347; Eaton 1884, 130; Banks 1907, 17; Smith 1909, 37; Morgan 1913, 400, 1 Fig.; Ulmer 1920, 119; McDunnough 1925b, 169, 1 Fig.; Ide 1930, 211; McDunnough 1931b, 192; Traver 1935, 596; Leonard 1949, 158, 3 Fig. (nymph); Burks 1953, 70 (=*semiflava*); Leonard and Leonard 1962, 52, 2 Fig.

Ephemerella invaria Eaton 1868, 87 (nec Walker 1853, 568); Eaton 1871, 100.

Ephemerella semiflava McDunnough 1926b, 300; McDunnough 1931b, 192; Traver 1935, 617; Leonard 1950, 19.

Walsh (1862) described this species from male imagoes collected in Illinois. Eaton (1868) synonymized this species with *E. invaria* (Walker), but in 1873 he treated it as a valid species. The nymphal stage was not known until 1949, when a description was published by Leonard.

Male Imago (in alcohol).—Length: body 5.5–7.5; forewing 7–9 mm. Compound eyes pale orange, lower portion gray. Thorax light brown; forelegs pale yellowish brown, foretarsal segments darkened at tips; length of segments of foreleg in millimeters: femur = 1.5; tibia = 2.6; tarsus I = 0.2; tarsus II = 1.2; tarsus III = 1.2; tarsus IV = 0.8; tarsus V = 0.4; middle and hind legs pale yellowish brown; wings hyaline; longitudinal veins near costal margin yellowish, other primary longitudinal veins, crossveins, and intercalaries hyaline. Abdominal segments light yellowish brown, sterna pale. Penes with 6–10 dorsal spines, position of spines usually as in Fig. 3; lateral margin of penis lobes rounded; second segment of genital forceps not expanded at apex (Fig. 3). Caudal filaments white with reddish brown annulations at apex of each segment.

Mature Nymph.—Length: body 6–7; caudal filaments 3–4 mm. General color dark brown to nearly black with pale maculae on head, thorax, and abdomen. Head dark brown to nearly black with pale maculae; without paired occipital tubercles. Thoracic notum dark brown to black with pale maculae, pronotum pale at corners; femora brown with pale maculae; forefemora with a subapical band of spines; tibiae and tarsi with alternating pale and dark bands; tarsal claws with 5–7 denticles. Abdominal terga without paired submedian tubercles; terga dark brown to nearly black, anterior margin of terga 4–8 usually pale, pale paired submedian spots on posterior margin of segments and postero-lateral areas pale; distinct postero-lateral projections on segments 4–9; abdominal sterna dark brown to black with pale sublateral maculae on each segment. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments unicolorous light brown.

Type-Locality.—Rock Island, Ill.

Type.—Museum of Comparative Zoology, Cambridge, Mass. Lectotype ♂ 11213. Burks (1953:15) published a table of the "lectotypes designated by Nathan Banks from specimens collected by Walsh and deposited by Herman A. Hagen in the Museum of Comparative Zoology, . . ." Banks did not publish his "type" designations, so they therefore have no application. As there is doubt that Burks (loc. cit.) intended to designate lectotypes in his publication, we hereby designate the lectotype ♂, Type 11213, to insure stability of the application of the name.

DISTRIBUTION

E. excrucians is a boreal Eastern North American species known from New Brunswick to Michigan and austrad to New Jersey and Oklahoma (Fig. 79). We have examined male imagoes from Mt. Fork River, Hachatown, Okla., 6-V-38 (INHS), and male imagoes and nymphal cast skins from Au Sable River, Crawford Co., Mich., 12/13-VI-48, J. W. and F. A. Leonard (LL).

TAXONOMY

The male adult stage of *E. excrucians* is separable from *E. ora* Burks only by color characters, as the male genitalia of the 2 species are nearly identical (Fig. 3, 4). The nymphal stage of *E. ora* is unknown but, of the known nymphs of the subgenus *Ephemerella, E. excrucians* is most similar to *E. dorothea* Needham.

The male imagoes of this species were described as dark; however, those we have examined are all preserved in alcohol and are very light. It is apparent that the color pigments of this species are very unstable in preserving media and the dark color characters are present only in fresh or pinned specimens.

Ephemerella ora Burks

(Fig. 4, 80)

Ephemerella ora Burks 1949, 235, 2 Fig.; Burks 1953, 70, 2 Fig.

This species was described from 1 ♂ imago and 1 ♀ imago.

Male Imago.—Length: body 7; forewing 8 mm. Compound eyes pinkish tan. Prothorax yellow with tan shading; mesothorax mostly tan, yellow at anterior tip of scutellum; legs yellow, with apices of foretibiae and basal 3 foretarsal segments darkened; wings hyaline; venation hyaline except anterior 2 veins and stigmatic area yellowish. Abdominal terga yellow, basal and middle terga brown dorsally, apical terga pinkish tan; abdominal sterna yellow, postero-lateral margin of sternum 8 pink. Penes with 7 dorsal spines, positioned as in Fig. 4; lateral margin of penis lobes rounded; 2nd segment of genital forceps not expanded at apex (Fig. 4). Caudal filaments yellow with black annulations at apex of each segment (abstracted from Burks 1949).

Nymph.—Unknown.

Type-Locality.—Mt. Carmel, Ill.

Type.—Illinois State Natural History Survey, Urbana, Illinois.

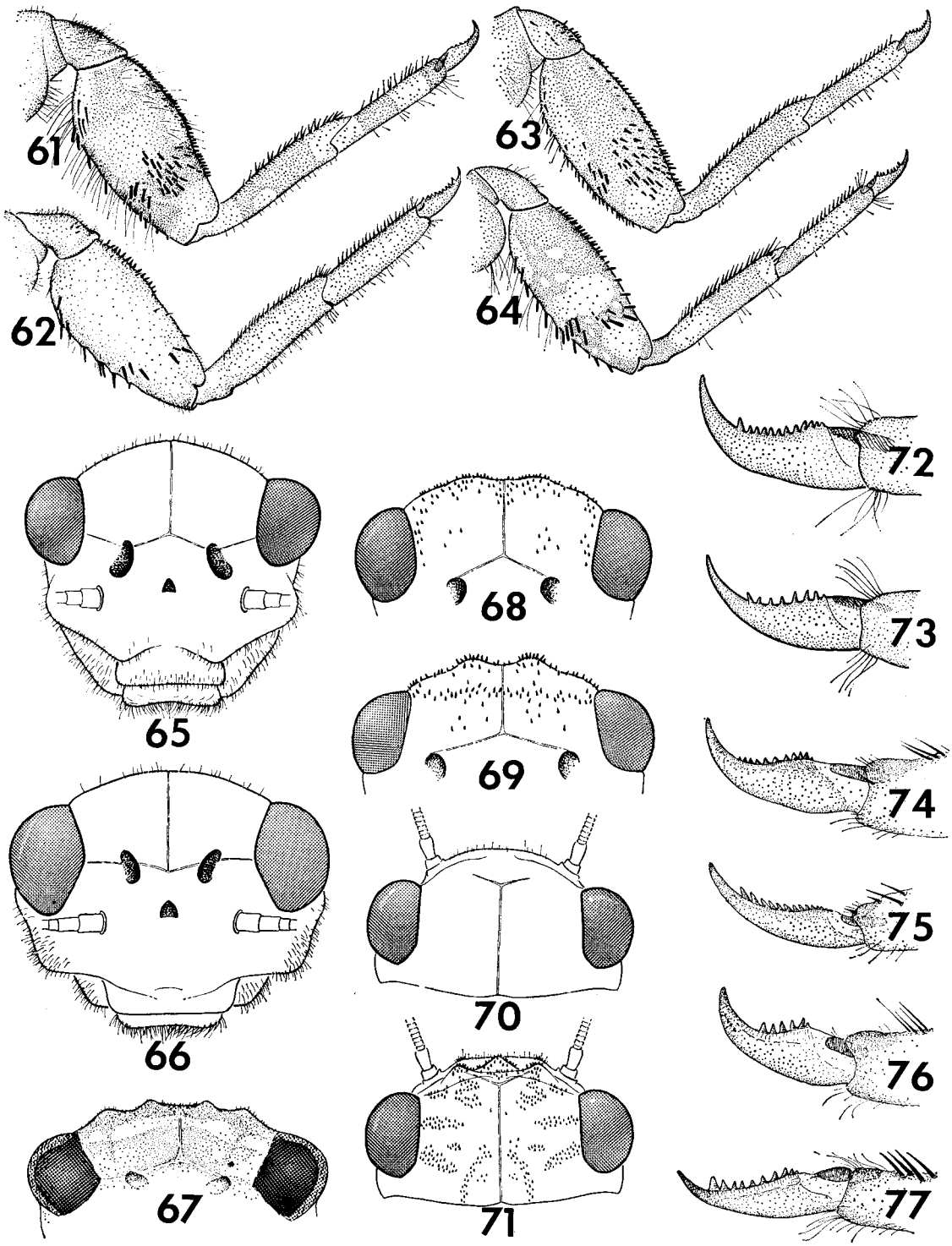


FIG. 61–64.—Subgenus *Ephemerella*, s. s., right nymphal forelegs. Fig. 61, *E. invaria;* Fig. 62, *E. catawba;* Fig. 63, *E. inconstans;* Fig. 64, *E. dorothea.*

FIG. 65–71.—Subgenus *Ephemerella* s. s., nymphal heads. Fig. 65, *E. mollitia,* front view; Fig. 66, *E. maculata,* front view; Fig. 67, *E. subvaria,* front view; Fig. 68, *E. crenula,* front view; Fig. 69, *E. simila,* front view; Fig. 70, *E. aurivillii,* dorsal view; Fig. 71, *E. verruca,* dorsal view.

FIG. 72–77.—Subgenus *Ephemerella,* s. s., right foretarsal claw. Fig. 72, *E. lacustris;* Fig. 73, *E. infrequens;* Fig. 74, *E. mollitia;* Fig. 75, *E. septentrionalis;* Fig. 76, *E. invaria;* Fig. 77, *E. catawba.*

DISTRIBUTION

This species is known only from the type locality in Southeastern Illinois (Fig. 80).

TAXONOMY

Burks (1949) based this species on 2 adults. He stated it was related to *E. excrucians* Walsh on the basis of the 2nd segment of the genital forceps of the male imago, by the presence of stout spines on the penes, and the dark brown shading of the abdominal terga. He distinguished *E. ora* from *E. excrucians* by the number and distribution of the spines on the penes, the color of the thorax, and the color of the eyes in the living adult.

We have examined the male genitalia of a topotype male imago of *E. excrucians* (Fig. 3), compared it with the figure of *E. ora* presented by Burks (Fig. 4), and find that they are comparable in general shape as well as the number and the position of the dorsal spines. The color patterns of most species of *Ephemerella,* s. s., are variable (1 western species is known to vary from light brown to brick red) and eye color in living specimens, which Burks (op. cit.) used to distinguish *E. ora* from *E. excrucians,* varies in response to light. The morphological and color characters used to distinguish *E. ora* Burks indicate to us that it may eventually be considered a synonym of *E. excrucians.*

Ephemerella argo Burks

(Fig. 5, 81)

Ephemerella argo Burks 1949, 232, 2 Fig.; Burks 1953, 69, 3 Fig.

Burks (1949) described this species from male imagoes and nymphs collected in Indiana and Illinois.

Male Imago.—Length: body 8; forewing 9 mm. Compound eyes yellowish tan. Thorax light yellowish tan, vaguely tinted with brown on dorsal area of pronotum, at apex of mesoscutellum and on basal area of metanotum; legs deep cream colored; apices of tibiae and of 2nd and 3rd tarsal segments of foreleg slightly darkened; wings hyaline, stigmatic area milky; venation hyaline except anterior veins and anastomosed stigmatic crossveins yellow. Abdominal terga light yellowish tan and shaded with brown; abdominal sterna light yellowish tan with a vague brown stripe at lateral margins. Penes with 5 dorsal and 11 ventral spines, positioned as in Fig. 5; lateral margin of penis lobes rounded; second segment of genital forceps with a slight apical expansion (Fig. 5). Caudal filaments yellowish tan with brown annulations at apex of each segment (abstracted from Burks 1949).

Mature Nymph.—Length: body 7–9; caudal filaments 4–5 mm. General color yellow brown with brown markings. Head brown with irregular yellow-brown markings on the vertex; a yellow-brown transverse stripe crossing the face at the lower margin of the eyes; without paired occipital tubercles. Thoracic notum yellow brown with brown markings; pronotum yellow brown with 2 wide brown sublateral longitudinal stripes; mesonotum with an irregular wide brown transverse stripe, apex of wing pads often brown; femora brown with variable yellow-brown markings at apex and base; forefemora with subapical band of spines; tibiae and tarsi with alternating pale and brown bands; tarsal claws with 6–9 denticles. Abdominal terga without paired submedian tubercles; terga brown with pale markings; terga 2–4 and 7–9 brown, often with a pale median stripe and paired pale submedian spots on posterior margin; terga 5–6 and 10 pale, lateral margins usually entirely pale; distinct postero-lateral projections on segments 4–9; abdominal sterna brown and sprinkled with fine pale dots, margins usually entirely pale. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments pale with brown bands.

Type-Locality.—White River, Rogers, Ind.

Type.—Illinois State Natural History Survey, Urbana, Ill.

DISTRIBUTION

This species is known only from a small area on the Illinois-Indiana State line (Fig. 81). We have examined specimens from:

ILLINOIS: Wabash River, Mt. Carmel, 2-V-32, T. H. Frison and H. H. Ross (INHS). INDIANA: White River, Rogers, 4-IV-40, C. O. Mohr and B. D. Burks (INHS); White River, Rogers, 16-IV-36, H. H. Ross and C. O. Mohr (INHS); Rogers, 19-IV-40, C. O. Mohr and B. D. Burks (INHS).

TAXONOMY

The nymphal stage of this species is easily distinguished from all other *Ephemerella,* s. s., by the unique yellow-brown color pattern. The male imago also appears to be distinct by the character of the number and arrangement of the dorsal and ventral spines on the penis lobes.

Ephemerella dorothea Needham

(Fig. 6, 64, 79)

Ephemerella dorothea Needham 1908, 190, 1 Fig.; Morgan 1911, 94; Ulmer 1920, 119; Lestage 1925, 279; McDunnough 1925a, 212; Steger 1931, 31; McDunnough 1931b, 194; Traver 1932, 177; Traver 1935, 594, 1 Fig.; Traver 1937, 66; Wright and Berner 1949, 295; Burks 1953, 70, 1 Fig.; Pugh 1956, 26; Leonard and Leonard 1962, 52, 2 Fig.

Ephemerella dorothea (Variety A) Traver 1937, 67, 1 Fig.

Needham (1908) described *E. dorothea* from male imagoes and nymphs collected in New York.

Male Imgao (dry).—Length: body 7–8; forewing 7.5–8.5 mm. Compound eyes reddish brown, lower portion darker. Thorax yellow; legs yellow; length of segments of forelegs in millimeters: femur = 1.5; tibia =3.0; tarsus I = 0.2; tarsus II = 1.5; tarsus III = 1.6; tarsus IV = 1.4; tarsus V = 0.5; wings hyaline; venation hyaline. Abdominal terga yellow, hind margins slightly darker. Penes with 15–17 dorsal and 8–10 ventral spines, position of spines usually

as in Fig. 6; penis lobes short; lateral margin of penis lobes parallel; 2nd segment of genital forceps swollen apically (Fig. 6). Caudal filaments pale.

Mature Nymph.—Length: body 6–8; caudal filaments 4–5 mm. General color light brown to dark brown and sprinkled with fine pale dots. Head brown with pale vermiculate markings on vertex; a pale transverse stripe crossing the face at the anterior margin of the eyes, stripe sometimes interrupted medially; without paired occipital tubercles. Thoracic notum light brown to dark brown and sprinkled with fine pale dots and variable pale blotches; lateral margins of pronotum pale; femora light brown to brown with variable pale markings; forefemora with only a few subapical spines (Fig. 64); tibiae and tarsi brown with pale bands; tarsal claws with 6–9 denticles. Abdominal terga without paired submedian tubercles; terga brown and sprinkled with fine pale dots, often with a pale median stripe and with submedian paired pale spots on posterior margin; distinct postero-lateral projections on segments 4–9; abdominal sterna brown and sprinkled with fine pale dots. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments, filaments light brown with brown to dark brown bands.

Type-Locality.—Beaver Meadow Brook, Old Forge, N. Y.

Type.—Cornell University Collection, Ithaca, N. Y.

DISTRIBUTION

E. dorothea occurs from Michigan to Nova Scotia and austrad to Missouri and South Carolina (Fig. 79). Specimens have been examined from:

DELAWARE: Newark, T. Dolan (no other data) (JRT). ILLINOIS: Wabash River, Mt. Carmel, 2-IV-32, T. H. Frison and H. H. Ross (INHS); Golconda, 13-V-32, C. O. Mohr, T. H. Frison, and H. H. Ross (INHS). INDIANA: White River, Rogers, 16-IV-36, H. H. Ross and C. O. Mohr (INHS). KENTUCKY: Cumberland Falls, 12-V-39, T. H. Frison and H. H. Ross (INHS); Quicksand, 8-V-47, P. O. Ritcher and M. W. Sanderson (INHS); Jackson, 8-V-47, P. O. Ritcher and M. W. Sanderson (INHS); Slade, 8-V-47, P. O. Ritcher and M. W. Sanderson (INHS). MARYLAND: Piney Grove, 19-IV-38, H. H. Ross and B. D. Burks (INHS). MASSACHUSETTS: Amherst, 19-V-39, J. R. Traver (JRT); S. Hadley, 27-V-39, J. R. Traver (JRT). MICHIGAN: Pere Marquette River, Baldwin, 28-V-39, T. H. Frison and H. H. Ross (INHS); Platte River, Honor, 27-V-39, T. H. Frison and H. H. Ross (INHS); Little Manistee River nr. Irons, 28-V-39, T. H. Frison and H. H. Ross (INHS). MISSOURI: James River, Virgin Bluff, Cape Fair, 23-II-57, R. M. Matter (UMo). NEW BRUNSWICK: NW Miramichi River nr. Newcastle, 7/13-VII-61, T. Dolan; SW branch long Creek nr. Sussex, 26-VI-60, B. V. Peterson. NEW HAMPSHIRE: Warren, 21-VI-41, T. H. Frison and H. H. Ross (INHS); Colebrook nr. Stewartstown, 11-VI-52, E. I. Coher. NEW YORK: Schoharie River, Lexington, 3-V-38 (no other data); Slaterville, 6-VII-27, P. R. Needham (JRT); East Islip, 16-VII-36, H. T. Spieth (AMNH); Au Sable River, 23-VI-34, P. S. Jennings (JRT); Beaverkill, 2-VI-35, H. T. Spieth (AMNH); Tuxedo Park, 4-VI-39, H. T. Spieth (AMNH). NORTH CAROLINA: Nr. Greensboro, 4-V-44, T. H. Frison and H. H. Ross (INHS); Valle Crucis, 25-V-36, J. R. Traver (JRT); Balsam, 3-I-39, T. H. Frison and B. D. Burks (INHS); Statesville, 23-IV-38, H. H. Ross and B. D. Burks (INHS). NOVA SCOTIA: Nr. Five Islands, 20-VI-50, E. L. Bousefield; Nr. Amherst, 9-VII-50, E. L. Bousefield; Baddeck River, 6-VII-50, E. L. Bousefield; Nr. Margaree, Cape Breton Island, 6-VII-50, E. L. Bousefield; Long Creek nr. Sussex, 26-VI-60, B. V. Peterson. OHIO: Waterloo State Forest, Athens Co., 3-VII-37, John Herman. PENNSYLVANIA: Scranton, summer 1945, H. K. Townes (JRT); E. Hopwood, 19-IV-38, H. H. Ross (INHS). QUEBEC: Mont Tremblant, 15-VII-59, B. V. Peterson; Grand Lac Jacques-Cartier, 6-VIII-38, "C. G."; Covey Hill, 17-VI-24, G. S. Walley (CNC); Penneys Brook, Knowlton, 14-VI-29, L. J. Milne (CNC). TENNESSEE: Cumberland Falls State Park, 12-V-39, T. H. Frison and H. H. Ross (INHS); LaConte Creek, Gatlinburg, 14-V-39, T. H. Frison and H. H. Ross (INHS); Fighting Gap Creek, Gatlinburg, 15-V-39, T. H. Frison and H. H. Ross (INHS); Cades Cove, 13-VI-40, T. H. Frison (INHS); Cates Landing, Mississippi River, 22-III-40, G. T. Riegel (INHS); Jellico, 13-VII-39, T. H. Frison and H. H. Ross (INHS). VERMONT: Starkshore, 4-VI-52, E. I. Coher. VIRGINIA: Lydia, 4-V-44, T. H. Frison and H. H. Ross (INHS).

TAXONOMY

E. dorothea is one of the most distinctive species in the subgenus. It is not highly variable in the adult stage, and the nymphal stage varies only in color. The nymphs are usually light brown with extensive pale markings, but in some populations they are brown to dark brown with restricted pale markings. The nymph of *E. dorothea* suggests that the species is closely allied to *E. excrucians* Walsh as both species lack paired dorsal abdominal tubercles; however, the male adult stages of these species are noticeably different in color and genitalic characters.

Ephemerella inconstans Traver

(Fig. 7, 46, 63, 80)

Ephemerella inconstans Traver 1932, 194, 2 Fig.; McDunnough 1938, 24; Howell 1941, 314; Edmunds 1959, 544.
Ephemerella vernalis Traver 1935; 626 (nec Banks 1914).

Traver (1932) described this species in the *invaria*-group from all stages, collected in North Carolina. In 1935 she placed *E. inconstans* as a junior synonym of *vernalis* Banks (=*rotunda* Morgan). McDunnough (1938) refuted this synonymy and Edmunds (1959) substantiated McDunnough's view after examining the type of *vernalis*.

Male Imago (in alcohol).—Length: body 8–9; forewing 8–10 mm. Upper portion of compound eye tan, lower portion black. Thorax brown; legs pale; length of segments of forelegs in millimeters: femur = 1.8; tibia = 3.1; tarsus I = 0.3; tarsus II = 1.5; tarsus III = 1.5; tarsus IV = 1.2; tarsus V = 0.4; wings hyaline; primary longitudinal veins yellow, crossveins and intercalaries hyaline. Abdominal terga brown; abdominal sterna light brown. Penes with 6–8 dorsal and 0–2 ventral spines, position of spines usually as in Fig. 7; penis lobes short; lateral margin of penis lobes nearly parallel; 2nd segment of genital forceps swollen apically (Fig. 7). Caudal filaments pale with light brown annulations at apex of each segment.

Mature Nymph.—Length: body 8–11; caudal filaments 5–6 mm. General color brown with dark brown markings and often sprinkled with fine pale dots. Head brown with numerous pale dots; a partially developed pale transverse stripe crossing the face at the anterior margin of the eyes, interrupted medially; without paired occipital tubercles. Thoracic notum brown, often sprinkled with fine pale dots and some maculae; legs brown; femora brown with scattered dark brown markings; forefemora usually with an interrupted subapical broad band of spines (Fig. 63); tibia brown, with a pale basal macula or band and a pale apical band; tarsi pale with a brown band in basal half; tarsal claws with 6–10 denticles. Abdominal terga with small paired submedian tubercles on segments 2–8; tubercles barely discernible or absent on segments 2–3 and 8, small on segments 4–7 (Fig. 46a), terga with fine spicules (Fig. 46b); terga brown with pale median stripe and sublateral dark brown longitudinal streaks, terga often with paired submedian pale spots on posterior margin of segments; distinct postero-lateral projections on segments 3–9, projection on segment 3 variable in length (Fig. 46a); abdominal sterna brown with fine pale spots, sterna 2–8 often with paired sublateral dark brown streaks and dark submedian spots and oblique dashes. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments light brown with alternating brown bands.

Type-Locality.—Hamburg Lake, N. C.

Type.—No. 1093.1, Cornell University Collection, Ithaca, N. Y.

DISTRIBUTION

E. inconstans is known from Kentucky, North Carolina, and Virginia (Fig. 80). We have examined specimens of this species from:

KENTUCKY: 2 mi. SW Holston River Bridge, Washington Co., 20-VI-58, W. L. Peters; Pine Mtn. State Park, Bell Co., 18-VI-58, W. L. Peters. NORTH CAROLINA: Hamburg Lake, 15/18-III-30, J. R. Traver (Paratype) (CU); Big Alamance Creek, 21-III-29, J. R. Traver (JRT); Polecat Creek nr. Greensboro, 11-IV-30, J. R. Traver (JRT); Rainbow Gap, 24-IV-38, H. H. Ross and B. D. Burks (INHS); Balsam, 3-I-39, T. H. Frison and B. D. Burks (INHS). VIRGINIA: Crooked River, Madison, 1-I-39, T. H. Frison and H. H. Ross (INHS); Afton, 22-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Robinson River, Madison, 21-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Gatlinburg, 24-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Hedge Creek, Auburn, Power Co., 3-II-39 (no other data) (JRT).

TAXONOMY

E. inconstans may be confused with *E. invaria* (Walker) and *E. choctawhatchee* Berner in the nymphal stage by the character, degree of development, and the position of the paired dorsal abdominal tubercles. The nymphs of *E. inconstans* may be distinguished from these species, however, by the pattern of the forefemoral spines and by possessing a distinct postero-lateral projection on abdominal segment 3. The color pattern and the degree of development of the postero-lateral projections on the 3rd segment may vary within a given population.

The male imagoes are morphologically similar to *E. invaria*, but are distinguished from this species by the shape and position of the spines of the penes (Fig. 7).

Ephemerella subvaria McDunnough

(Fig. 8, 20–26, 43, 55, 67, 79)

Ephemerella invaria (dark form) McDunnough 1925a, 213; Ide 1930, 211.

Ephemerella subvaria McDunnough 1931a, 84; McDunnough 1931b, 194, 1 Fig. (nymph); Ide 1935b, 13, 43; Ide 1935a, 457, 1 Fig..; Traver 1935, 622; Britton 1938, 12; Sprules 1947, 75; Leonard 1950, 19; Burks 1953, 71, 2 Fig.; Schwiebert 1955, 118, 2 Fig.; Davis 1956, 117, 145; Leonard and Leonard 1962, 54, 4 Fig.

E. subvaria was first reported in the literature by McDunnough (1925a) as a dark form of *E. invaria* (Walker). In 1931 he named these imagoes as new, and later the same year he presented a description of the nymphal stage.

Male Imago (dry).—Length: body 8–9; forewing 9–10 mm. Compound eye reddish brown, lower portion gray. Thorax brown, a dark median area on mesonotum, pleural membranes pale; forelegs brown; length of segments of foreleg in millimeters: femur = 2.2; tibia = 3.5; tarsus I = 0.2; tarsus II = 1.9; tarsus III = 1.8; tarsus IV = 1.4; tarsus V = 0.5; middle and hindlegs yellow to yellow brown; wings hyaline; primary longitudinal veins medium or light brown, intercalaries and crossveins light brown or yellowish brown (Fig. 25–26). Abdominal terga brown, lateral margins pale, terga 1–9 with dark brown lateral maculae; abdominal sterna brown, posterior margin paler. Penes with 10–12 dorsal spines, position of spines usually as in Fig. 8; lateral margins of penis lobes rounded; 2nd segment of genital forceps swollen apically (Fig. 8). Caudal filaments pale with black anulations at apex of each segment.

Mature Nymph.—Length: body 8.5–9.5; caudal filaments 5–6 mm. General color light brown to brown with dark brown to black markings and sprinkled with fine pale dots. Head brown with irregular pale markings on vertex; both sexes with small paired occipital tubercles; mouthparts as in Fig. 20–24; thoracic notum brown with dark brown and black markings; femora brown with variable dark brown markings; forefemora with a subapical band of spines; tibiae and tarsi with dark brown to black bands (Fig. 55); tarsal claws with 4–6 denticles. Abdominal terga with sharp paired submedian tubercles on segments 2–9 (Fig. 43a); terga with fine spicules (Fig. 43b); terga brown with variable light and dark brown to black markings; terga 5–7 often pale; distinct postero-lateral projections on segments 3–9; abdominal sterna brown, usually sprinkled with fine pale dots. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments brown, sometimes with darker brown bands.

Type-Locality.—Cascades Point, St. Lawrence River, Quebec, Canada.

Type.—No. 3272, Canadian National Collection, Ottawa, Ontario.

DISTRIBUTION

E. subvaria is a boreal Eastern North American species and is known from northern Ontario austrad to Wisconsin and Pennsylvania (Fig. 79). Specimens have been examined from:

MASSACHUSETTS: N. Amherst, 26-XI-38, J. R. Traver (JRT); S. Hadley, 4-V-38, J. R. Traver (JRT); S. Deerfield, 1-IV-39, J. R. Traver (JRT). MICHIGAN: N. St. Ignace, 11-V-40, T. H. Frison and H. H. Ross (INHS); Crawford Co., Au Sable River, 20/29-V-45, J. W. and F. A. Leonard (LL). NEW YORK: Sloatsburg, 24-IV-38, H. T. Spieth (AMNH); Green Lake, 6-V-31, J. R. Traver (JRT); Beaverkill, 26-IV-41, "Webster" (JRT); Ithaca, 12-VI-32, "Sadler" (JRT). ONTARIO: Moosonee, mi. 176 B, 31-V-61, B. V. Peterson and E. Bond; Artemis Road 15, Fleherton, Shighampton Co., 6-IV-61, E. Bond; Speed River nr. Fergus, 17-IV-59, B. V. Peterson; 2 mi. S Campbellville, 17-I-61, E. Bond; Blair, 30-III-61, E. Bond; Credit River Forks, Credit, 16-I-61, E. Bond; N Madawaska River, Algonquin Park, 2-V-61, B. V. Peterson; 2 mi. S Elmira, 16-I-61, E. Bond; 2 mi. E Durham, 18-I-61, E. Bond; Puslinch, 18-V-60, B. V. Peterson. QUEBEC: Gatineau River, 12-XI-50, E. L. Bousefield. WISCONSIN: Manitowish River, Boulder Junction, 2-X-37, T. H. Frison (INHS).

TAXONOMY

E. subvaria is a distinctive species with little variability. The nymphs have well-developed paired submedian abdominal tubercles which are very similar in shape and production to those of the nymphs of *E. needhami* McDunnough; however, the structure of the male genitalia suggests that the imagoes are closely allied to *E. invaria* (Walker) and *E. rotunda* Morgan.

Ephemerella rotunda Morgan

(Fig. 9, 27, 47, 60, 80)

Ephemerella sp?, near *ignita* Needham 1905, 45, 1 Fig.

Ephemerella rotunda Morgan 1911, 113; Morgan 1912, Fig. 21, 22; Morgan 1913, Fig. 41; Ulmer 1920, 119; McDunnough 1926a, 188 (=*feminina*); McDunnough 1931b, 195 (=*vernalis*); Steger 1931, 32; Traver 1932, 176; Traver 1935, 616; Traver 1937, 67; Howell 1941, 314; Burks 1953, 71, 2 Fig.; Edmunds 1959, 544, 1 Fig.; Leonard and Leonard 1962, 56, 2 Fig.

Ephemerella vernalis Banks 1914, 614; McDunnough 1925a, 213; McDunnough 1938, 24; Wright and Berner 1949, 295.

Chitonophora vernalis Ulmer 1920, 120, 1 Fig.; Lestage 1925, 298.

Ephemerella feminina Needham 1924, 309.

Morgan described *E. rotunda* from nymphs and female imagoes collected in New York. Banks (1914) described male imagoes collected in North Carolina as *E. vernalis* and Needham (1924) named a series of nymphs, which he described as *"Ephemerella* sp?, near *ignita"* in 1905, as *E. feminina*. McDunnough synonymized *feminina* (in 1926a) and *vernalis* (in 1931b) with *E. rotunda*.

On the basis of examination of a paratype of *vernalis*, Traver (1935) disagreed with McDunnough's synonymy of *vernalis* with *E. rotunda*, resurrected the name *vernalis* and placed *E. inconstans* Traver as a synonym of it. McDunnough (1938) refuted Traver's action, insisted that the original synonymy was based on examination of another paratype and re-established the validity of *E. inconstans*. Edmunds (1959) examined the holotype of *vernalis* and stated that *vernalis* is a junior synonym of *E. rotunda* rather than a senior synonym of *E. inconstans*. The confusion resulted from the fact that the original series of *E. vernalis* included both *E. rotunda* and the species later named by Traver as *E. inconstans*.

Male Imago (in alcohol).—Length: body 9–11; forewing 9–11 mm. Upper portion of compound eye orange, lower portion black. Thorax light brown; legs pale yellowish brown; length of segments of foreleg in millimeters: femur = 2.0; tibia = 3.0; tarsus I = 0.2; tarsus II = 1.5; tarsus III = 1.6; tarsus IV = 1.4; tarsus V = 0.4; wings hyaline; primary longitudinal veins pale yellowish brown; crossveins and intercalaries hyaline. Abdominal terga reddish brown with a paler transverse band near the anterior margin of each segment; abdominal sterna pale. Penes with 14–20 dorsal and 1–3 ventral long spines, position of spines usually as in Fig. 9; penis lobes short; lateral margins of penis lobes rounded; 2nd segment of genital forceps swollen apically (Fig. 9). Caudal filaments pale with dark brown annulations at apex of each segment.

Mature Nymph.—Length: body 10–11; caudal filaments 5–6 mm. General color light brown to dark brown, usually sprinkled with fine pale dots and with pale markings. Head brown with irregular pale markings on the vertex; a pale transverse stripe crossing the face at the anterior margin of the eyes, stripe

may be interrupted medially; both sexes with very small paired occipital tubercles. Thoracic notum brown, sprinkled with fine pale dots and maculae and sometimes with dark brown markings, postero- and antero-lateral corners of pronotum often pale; femora brown with variable pale markings; forefemora with a broad subapical band of spines (Fig. 60); tibiae and tarsi with alternating pale and brown bands; tarsal claws with 5–7 denticles. Abdominal terga with paired submedian tubercles, tubercles usually present on segments 2–9, tubercles may be absent, small or barely discernible on segments 2 and 8, often absent on segment 9 and moderately developed and always discernible on segments 3–7 (Fig. 47a); terga with fine spicules (Fig. 47b); terga 1–4 and 8–10 usually brown and sprinkled with fine pale dots and maculae; terga 5–7 usually brown with pale markings; terga often with paired submedian pale spots on posterior margin of segments and postero-lateral angles pale; distinct postero-lateral projections on segments 4–9, rarely with a small projection on 3; abdominal sterna brown and sprinkled with fine pale dots and maculae. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments, filaments pale brown with alternating brown bands (Fig. 27).

Type-Locality.—Pleasant Brook, Ithaca, N. Y.

Type.—Destroyed.

DISTRIBUTION

E. rotunda is a boreal Eastern North American species known from Northern Ontario to Nova Scotia austrad to North Carolina and Tennessee (Fig. 80). Specimens we have examined are from:

KENTUCKY: Slade, 8-V-47, P. O. Ritcher and M. W. Sanderson (INHS). MASSACHUSETTS: Amherst (no date), J. R. Traver (JRT); Deerfield, 1-VI-39, J. R. Traver (JRT). MICHIGAN: Nr. Lansing, 30-V-26, J. G. Needham (JRT); Baldwin, 28-V-39, T. H. Frison and H. H. Ross (INHS); Sanborn Creek, Nirvana, 28-V-39, T. H. Frison and H. H. Ross (INHS); Boardman River, Mayfield, 28-V-39, T. H. Frison and H. H. Ross (INHS); Little Manistee River nr. Peacock, 10-V-40, T. H. Frison and H. H. Ross; Great Sable River, Peacock, 28-V-39, T. H. Frison and H. H. Ross (INHS); Manistee River, 27-V-48, J. W. and F. A. Leonard (LL). NEW JERSEY: Ringwood, 27-V-37, J. R. Traver (JRT). NEW YORK: Beaverkill, 2-VI-35, H. T. Spieth (AMNH); McLean, 29-V-31, J. R. Traver (JRT); Brewster, 15-VI-37, H. T. Spieth (AMNH); Tenafly, 30-V-35, Herbert Johnson (AMNH); Westbill, 30-V-38, H. T. Spieth (AMNH); Beebe Lake, Ithaca, 31-V-32, "C. N. H." (JRT); Slaterville, 20-V-31, J. R. Traver (JRT). NORTH CAROLINA: Sylva, 23-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Scotts Creek, 8-IV-30, T. S. Gutsell (JRT); Woodlawn, 23-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Smokemont, 11-V-44, T. H. Frison and H. H. Ross (INHS); Dillsboro, 23-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Willetts, 23-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS). NOVA SCOTIA: Nr. Parrsboro, 20-VI-50, E. L. Bousefield; Nr. Five Islands, 20-VI-50, E. L. Bousefield; McLeod Stream, Cape Breton Island, 6-VII-50, E. L. Bousefield. ONTARIO: Moosonee, 30-V-61, B. V. Peterson and E. Bond; N. Madawaska River, Algonquin Park, 27-V-60, E. Bond; Rideau River, Ottawa, 17-V-28, "Adams" and W. J. Brown (CNC); Forks of Credit River, 4 mi. NE Belfountain, 27-V-59, B. V. Peterson and E. Bond. PENNSYLVANIA: Scranton, summer 1945, H. K. Townes (JRT); E. Hopwood, 19-IV-38, H. H. Ross (CNC). VERMONT: Moscow, 15-V-52, E. I. Coher; Lee River above Four Corners, 23-IV-38 (no other data). VIRGINIA: North River, Port Republic, 21-III-40, T. H. Frison (INHS); Roanoke River, Elliston, 22-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS). WEST VIRGINIA: Seneca Creek, 30-IV-44, T. H. Frison and H. H. Ross (INHS); Red Creek nr. Dry Creek, 30-IV-44, T. H. Frison and H. H. Ross (INHS). WISCONSIN: Totopatic River, Cable, 29-IV-39, T. H. Frison and B. D. Burks (INHS); Namakegon River, Spooner, 29-IV-39, T. H. Frison and B. D. Burks (INHS); St. Croix River, Gordon, 20-IV-39, T. H. Frison and B. D. Burks (INHS).

TAXONOMY

E. rotunda is closely allied to *E. invaria* (Walker) and they are difficult to distinguish morphologically. The difficulty is further complicated as these species occur in the same geographic area and often occur in the same streams.

The male imagoes of *E. rotunda* are usually larger and lighter hued than *E. invaria*, but the only reliable character which can be used to differentiate them is the form of the penes. The penis lobes of *E. rotunda* have more numerous and longer dorsal spines than those of *E. invaria*.

The nymphal stages of these 2 species are usually separable; however, some populations of *E. rotunda* are variable in the development of the paired dorsal abdominal tubercles. The tubercles of *E. rotunda* are usually present on terga 2–9 and are always discernible on terga 3–7. In *E. invaria* they are present on terga 3–8 and usually discernible on terga 4–6. The description and figure of the whole nymph by Leonard and Leonard (1962) show that the paired dorsal abdominal tubercles of *E. rotunda* from Michigan are smaller and present on fewer terga than on specimens from the Southeastern States. Reared nymphs from Michigan, sent to us by J. W. Leonard, corroborate this difference. A re-examination of all our nymphal material has revealed that most specimens from Wisconsin, Michigan, Ontario, and New York have smaller abdominal tubercles than other eastern and southeastern populations. Nymphs from this geographic area have tubercles on only terga 3–8 and they are often barely discernible on 3 and 8. Extreme caution should be used in the determination of these species in this area, and reared specimens are needed in some localities.

Ephemerella invaria (Walker)

(Fig. 10, 48, 61, 76, 80)

Baetis invaria Walker 1853, 568; Hagen 1861, 48.

Ephemerella invaria Eaton 1868, 87; Eaton 1871, 100; Eaton 1884, 129, 1 Fig.; Banks 1907, 17; Clemens 1915, 114; Ulmer 1920, 119; Lestage 1925, 282; McDunnough 1925a, 212, 1 Fig.; Ide 1930, 211; McDunnough 1931b, 196, 1 Fig. (nymph); Traver 1935, 607; Ide 1935b, 43; McDunnough 1938, 24; Sprules 1947, 44, 61, 75; Spieth 1940, 335; Leonard 1950, 19; Burks 1953, 71, 1 Fig.; Leonard and Leonard 1962, 54, 5 Fig.

Walker described this species from male imagoes as *Baetis invaria,* and Eaton (1868) transferred it to the genus *Ephemerella.* McDunnough (1931b) described the nymphal stage, thus making both stages known.

Male Imago (dry).—Length: body 8–9; forewing 8–10 mm. Compound eyes purplish brown, lower portion gray. Thorax reddish brown; pleurae yellow; forelegs light brown to smoky brown; length of segments of foreleg in millimeters: femur = 1.9; tibia = 3.1; tarsus I = 0.2; tarsus II = 1.6; tarsus III = 1.8; tarsus IV = 1.4; tarsus V = 0.4; middle and hind legs yellow; wings hyaline; primary longitudinal veins light brown, crossveins and intercalaries hyaline. Abdominal terga dark reddish brown, pleural margins paler; abdominal sterna light brown, paler posteriorly. Penes with 10–16 dorsal and 2–4 ventral spines, position of spines usually as in Fig. 10; penis lobes very short; lateral margins of penis lobes nearly parallel; 2nd segment of genital forceps swollen apically (Fig. 10). Caudal filaments pale with dark brown annulations at apex of each segment.

Mature Nymph.—Length: body 7.0–9.5; caudal filaments 4–5 mm. General color exceedingly variable, light brown to dark brown with pale and dark brown markings and often sprinkled with fine pale dots. Head brown with irregular pale markings on the vertex, or vertex entirely pale; a pale transverse stripe crossing the face at the anterior margin of the eyes, stripe may be interrupted medially in some specimens; without occipital tubercles. Thoracic notum brown and often sprinkled with fine pale dots and with irregular dark brown markings or pale with brown bands; femora pale with variable light brown to brown markings; forefemora with a narrow band of subapical spines (Fig. 61); tibiae and tarsi pale with broad dark brown bands near the middle, apex of tarsi often brown; tarsal claws with 5–7 denticles. Abdominal terga with small to minute paired submedian tubercles on segments 3–8, tubercles barely discernible or absent on segment 3 and 7–8, and small on segments 4–6 (Fig. 48a); terga with fine spicules (Fig. 48b); terga usually light brown and often sprinkled with fine pale dots, terga 3 and 7–9 usually dark brown with variable pale markings, and terga 1, 4–6 and 10 usually predominantly pale with dark brown markings; some specimens with pale paired submedian spots on posterior margin of segments; lateral margins pale, often with a brown band near the middle; postero-lateral projections on segments 4–9; abdominal sterna brown and sprinkled with fine pale dots, apical segments the darkest. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments light brown with several darker brown bands.

Type-Locality.—St. Martins Falls, Albany River, Ontario, Canada.

Type.—British Museum (Natural History), London, England.

DISTRIBUTION

E. invaria is known from Wisconsin to Northern Ontario and Nova Scotia austrad to Missouri, Alabama, and Georgia (Fig. 80). We have examined specimens from:

ALABAMA: Hedge Creek, Auburn, 18–II–39, Reed Christenson (JRT). GEORGIA: Pine Log Creek, 5 mi. S Fair Mount, 9–IV–39, P. W. Fattig (INHS). ILLINOIS: Rock River, Rockford, 4–V–26, D. H. Thompson (INHS); Rock River, Dixon, 22–V–25, D. H. Thompson (INHS); Oregon, 15–V–30, T. H. Frison and H. H. Ross. MICHIGAN: Hunt Creek, Montmorency Co., 14–IV–39, J. W. Leonard (INHS); Sanborn Creek, Nirvana, 28–V–39, T. H. Frison and H. H. Ross (INHS); Great Sable River, Peacock, 28–V–39, T. H. Frison and H. H. Ross (INHS); Little Manistee River, Peacock, 10–V–40, T. H. Frison and H. H. Ross (INHS); Rapid River, Rapid River, 12–V–40, T. H. Frison and H. H. Ross (INHS); Sturgeon River, Nahma Junction, 12–V–40, T. H. Frison and H. H. Ross (INHS); Platte River, Honor, 27–V–39, T. H. Frison and H. H. Ross (INHS); Boardman River, Mayfield, 28–V–39, T. H. Frison and H. H. Ross (INHS); Little Manistee nr. Irons, 28–V–39, T. H. Frison and H. H. Ross (INHS); Pere Marquette River nr. Baldwin, 9/10–V–40, T. H. Frison and H. H. Ross (INHS); Manistique River, Germfask, 11–V–40, T. H. Frison and H. H. Ross (INHS); Au Sable River, Crawford Co., 14–VI–48, J. W. Leonard and F. A. Leonard (LL). MISSOURI: White River, Viola, 30–III–57, "Fajen" (UMo); Cassville, 22–IV–55, R. D. Turner (UMo); Forsyth, 10–III–57, M. Milonski (UMo); Cape Fair, 23–II–57, R. M. Matter (UMo). NEW BRUNSWICK: Carding Mill Stream, Nelson, 31–V–51 (no other data). NEW YORK: Six Mile Creek, Ithaca, 9–IV–33, J. R. Traver (JRT); Condor, 10–V–26 (no other data); Beaverkill, 2–VI–35, H. T. Spieth (AMNH); Westbill, 30–V–38, H. T. Spieth (AMNH). NORTH CAROLINA: Blowing Rock, 23–III–40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Woodlawn, 23–III–40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Nr. Greensboro, 4–III–44, T. H. Frison and H. H. Ross (INHS); Boone, 23–III–40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS). NOVA SCOTIA: Margaree Harbor, Cape Breton Island, 6–VII–50, E. L. Bousefield. ONTARIO: Madawaska River, Algonquin Park, 1–VI–59, B. V. Peterson; Madawaska River, Whitney, 1–VI–59, B. V. Peterson. PENNSYLVANIA: Scran-

ton, summer 1945, H. K. Townes (JRT). PRINCE EDWARD ISLAND: West Wood Island, 28-VI-60, B. V. Peterson. QUEBEC: LaPeche River, Wakefield, 28-V-30, G. S. Walley and J. McDunnough (CNC); Lac Aigneau, 25-VI-55, D. R. Oliver (CNC); Kazubazua River, 10-VI-27, J. McDunnough (CNC); Grand Lac Jacques-Cartier, 6-VII-38, "C. G." (INHS). TENNESSEE: Jellico, 13-VII-39, T. H. Frison and H. H. Ross (INHS). VERMONT: Starkshore, 4-VI-52, E. I. Coher; Lee River above Four Corners, 23-IV-38 (no other data). VIRGINIA: Crooked Run, Madison, 1-I-34, T. H. Frison and B. D. Burks (INHS); Robinson River, Madison, 21-II-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Rapidan River, Ruckersville, 21-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Indian Run Creek, Vienna, 13-II-38, B. D. Burks (INHS); Speedwell, 22-III-40, T. H. Frison, C. O. Mohr, and "Hawkins" (INHS); Great Falls, 10-IV-36, B. D. Burks (INHS). WISCONSIN: St. Croix River, Gordon, 20-IV-39, T. H. Frison and H. H. Ross (INHS); Totopatic River, Gable, 29-IV-39, T. H. Frison and B. D. Burks (INHS).

TAXONOMY

E. invaria is closely allied to *E. choctawhatchee* Berner and *E. rotunda* Morgan. The male imago of *E. choctawhatchee* is presently unknown and the nymphal stage is separable from *E. invaria* only by body size and color characters of the legs. When the male imago of *E. choctawhatchee* becomes known these species may be found to be synonymous or geographic races of a single species.

E. invaria is difficult to distinguish from *E. rotunda*. The male imagoes of *E. rotunda* are usually separable from this species by the number and size of the dorsal and ventral spines on the penes. The nymphs are usually distinguished by the number and development of the paired dorsal abdominal tubercles. In *E. invaria* small to barely discernible tubercles (Fig. 48b) are usually present on segments 3-8 (Fig. 48a), while in *E. rotunda* they are usually better developed (Fig. 47b) and present on segments 2-9 (Fig. 47a); however, some populations of *E. rotunda* from Northeastern North America often have smaller tubercles than those from the Southeastern United States, thus being more similar to *E. invaria*. Great care must be exercised in identifying these species in this critical area and specimens considered questionable should be reared.

Ephemerella choctawhatchee Berner

(Fig. 80)

Ephemerella choctawhatchee Berner 1946, 71; Berner 1950, 164, 1 Fig.

Berner (1946) described this species in the *needhami*-group from nymphs only and the adult stages are still undescribed.

Mature Nymph.—Length: body 6.0-6.5; caudal filaments 4-5 mm. General color brown with dark brown markings and often sprinkled with fine pale dots. Head brown with pale vermiculate markings and pale dots; without paired occipital tubercles. Thoracic notum brown, often sprinkled with fine pale dots; legs brown; femora brown with scattered pale spots; forefemora with a narrow band of subapical spines; tibiae brown, sometimes with a pale apical band; tarsi pale with a brown band in basal half; tarsal claws with 6-8 denticles. Abdominal terga with small to minute paired submedian tubercles on segments 3-8, tubercles barely discernible or sometimes absent on segments 3 and 7-8, and small on segments 4-6 as in Fig. 48; terga brown with a pale median stripe and dark brown longitudinal streaks mediad of gills, postero- and antero-lateral angles pale, variable; distinct postero-lateral projections on segments 4-9; abdominal sterna brown with fine pale spots, sterna 2-8 often with paired sublateral dark brown streaks and dark submedian spots and oblique dashes. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments light brown with several brown bands on distal half.

Type-Locality.—5.1 mi. W Walton Co. line on Highway no. 10, Olaloosa Co., Fla.

Type.—Museum of Comparative Zoology, Cambridge, Mass.

DISTRIBUTION

Known only from Northern Florida (Fig. 80). We have examined nymphs from Gadsden Co., Fla., presented to us by Lewis Berner of the University of Florida.

TAXONOMY

E. choctawhatchee is very closely allied to *E. invaria* (Walker). The nymphs of these species are identical in the number and development of the paired dorsal abdominal tubercles, and are nearly the same in general color pattern, leg structure, and dentition on the tarsal claws. They may be distinguished from *E. invaria* by the coloration of the tibiae and by total body length; however, when the male imago of this species is described it may be found to be a subspecies or a synonym of *E. invaria*.

Ephemerella fratercula McDunnough

(Fig. 11, 81)

Ephemerella fratercula McDunnough 1925a, 213, 1 Fig.; McDunnough 1931b, 197; Traver 1935, 598, 1 Fig.; Burks 1953, 71, 1 Fig.

Ephemerella fratercula ? Traver 1937, 67, 1 Fig.

McDunnough (1925a) described this species from male and female imagoes collected in southern Quebec. The nymphal stage is presently unknown.

Male Imago (dry).—Length: body 7-8; forewing 7-8 mm. Compound eyes reddish brown, lower portion black. Thorax brown; forelegs light brown; length of segments in millimeters: femur = 1.6; tibia = 2.8; tarsus I = 0.1; tarsus II = 1.5; tarsus III = 1.1; tarsus IV = ?; tarsus V = ?; middle and hind legs yellowish brown; wings hyaline; venation hyaline. Abdominal terga 1-7 dark brown, anterior

area paler, terga 8–10 light brown; abdominal sterna yellowish brown, sterna 1–7 translucent, sterna 8–10 opaque. Penes with 5–7 dorsal and 18–20 ventral spines, position of spines usually as in Fig. 11; penis lobes moderately long; lateral margins of penis lobes rounded; 2nd segment of genital forceps swollen apically (Fig. 11). Caudal filaments pale with dark annulations at the apex of each segment.

Type-Locality.—Covey Hill, Quebec, Canada.

Type.—No. 1320, Canadian National Collection, Ottawa, Ontario.

DISTRIBUTION

Ephemerella fratercula is known only from the type-locality in Quebec (Fig. 81). We have examined a male paratype and a female topotype.

TAXONOMY

McDunnough (op. cit.) considered this species "closely allied" to *E. invaria* (Walker). However, *E. fratercula* is readily distinguished from *E. invaria* and all other *Ephemerella*, s. s., by the number and position of dorsal and ventral spines on the penes (Fig. 11).

Ephemerella mollitia Seemann

(Fig. 12, 36, 65, 74, 78)

Ephemerella mollitia Seemann 1927, 44, 2 Fig.; Traver 1935, 613, 1 Fig.; Day 1956, 98, 1 Fig.

This species was described from a male imago, subimagoes, and nymphs collected in Southern California.

Male Imago.—Only male genitalia examined. Penes with 15–20 dorsal and 15–20 ventral spines, position of spines as in Fig. 12; penis lobes short, lateral margins of penis lobes rounded; 2nd segment of genital forceps expanded apically (Fig. 12).

Mature Nymph.—Length: body 10–11; caudal filaments 6–7 mm. General color brown with pale markings. Head brown with irregular pale markings on vertex; a pale transverse stripe crossing the face at the anterior margin of the eyes, stripe often interrupted medially or absent in some specimens; without paired occipital tubercles. Thoracic notum brown with irregular pale markings, lateral margins of pronotum pale; femora brown with variable pale markings and with long hair and spines; forefemora with a subapical band of spines; tibiae and tarsi with alternating pale and light brown bands; tarsal claws with 9–13 denticles (Fig. 74). Abdominal terga without paired submedian tubercles; terga brown, typically with a pale median stripe and paired submedian pale spots on posterior margin of segments, lateral margins pale (Fig. 36); distinct postero-lateral projections on segments 3–9; abdominal sterna light brown, sterna 2–8 often with paired sublateral brown maculae and dark submedian spots and oblique dashes. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments pale with brown basal annulations and several brown transverse bands.

Type-Locality.—San Antonio, San Dimas, and Cucamonga Canyons, Calif.

Type.—Cornell University Collection, Ithaca, N. Y.

DISTRIBUTION

Traver (1935) reported this species from several localities in California and from Farmington, N. Mex. The record from Farmington is quite possibly based on nymphs of *E. inermis*. We have collected large numbers of this species from the San Juan River upstream and downstream from Farmington. We have not seen the Farmington specimens. We have examined specimens (Fig. 78) from:

CALIFORNIA: San Dimas, 10–II–23, (no other data) (CU); Cucamonga Canyon, 4–VII–23 (no other data) (JRT); San Antonio Canyon, 9–V–23, "T. M. R." (CU); Fall River, 19–III–49, W. C. Day.

TAXONOMY

The nymph of *E. mollitia* is similar in appearance to the other Western North American species which lack paired dorsal submedian abdominal tubercles. It may be distinguished from these species by leg and abdominal characters and by its biology. The male adults are readily distinguished from all known Western North American species by the number of dorsal and ventral spines on the penes (Fig. 12).

BIOLOGY

Seemann (1927) states that this species was collected in cold, swift-flowing streams.

Ephemerella lacustris, new species

(Fig. 13, 35, 50, 72, 78)

Ephemerella inermis Walley 1930, 15 (nec Eaton 1884, 127); Traver 1935, 605 (in part).

In reviewing the *Ephemerella* nymphs of Western North America, Walley (1930) based the identification of *E. inermis* Eaton on a series of fully grown nymphs from Yellowstone Lake, Wyo. These specimens have been examined and found to be *E. lacustris*.

Male Imago (in alcohol).—Length: body 8–9; forewing 8.5–9.5 mm. Upper portion of compound eye dull orange, lower portion gray. Thoracic notum dark chocolate brown, pleural sutures pale; forelegs medium brown, tarsi paler, especially the distal segments; length of segments of foreleg in millimeters: femur = 2.4; tibia = 3.0; tarsus I = 0.2; tarsus II = 1.2; tarsus III = 1.3; tarsus IV = 1.0; tarsus V = 0.4; middle and hind legs pale brown; wings hyaline; primary longitudinal veins brown, crossveins and intercalaries hyaline. Abdomen clay colored; segments 1–7 semihyaline, 8–10 opaque; pleural and posterior margins of terga washed with brown, darkest on the anterior terga; abdominal sterna lightly washed with brown, sternum 9 darker; trachea inside abdominal segments clearly visible, smoky gray. Penes with 8–10 dorsal and 1–4 ventral spines, position of spines usually as in Fig. 13; penis lobes short, lateral margins rounded; second segment of genital forceps with a slight apical expansion (Fig. 13). Caudal filaments brown with dark brown annulations at apex of each segment.

Female Imago (in alcohol).—Length: body 8–9; forewing 9–10 mm. Thorax chocolate brown, but lighter than in male. Abdominal segments clay colored, darker than in male. Caudal filaments pale with light brown annulations at apex of each segment. Other characters as in male except for usual sexual differences.

Mature Nymph.—Length: body 7–9; caudal filaments 4–6 mm. General color light brown to dark brown and occasionally red, with highly variable light brown to pale markings. Head brown with irregular light brown markings on the vertex; a pale transverse stripe crossing the face at the anterior margin of the eyes, stripe often widest at midline; pale areas so ex-

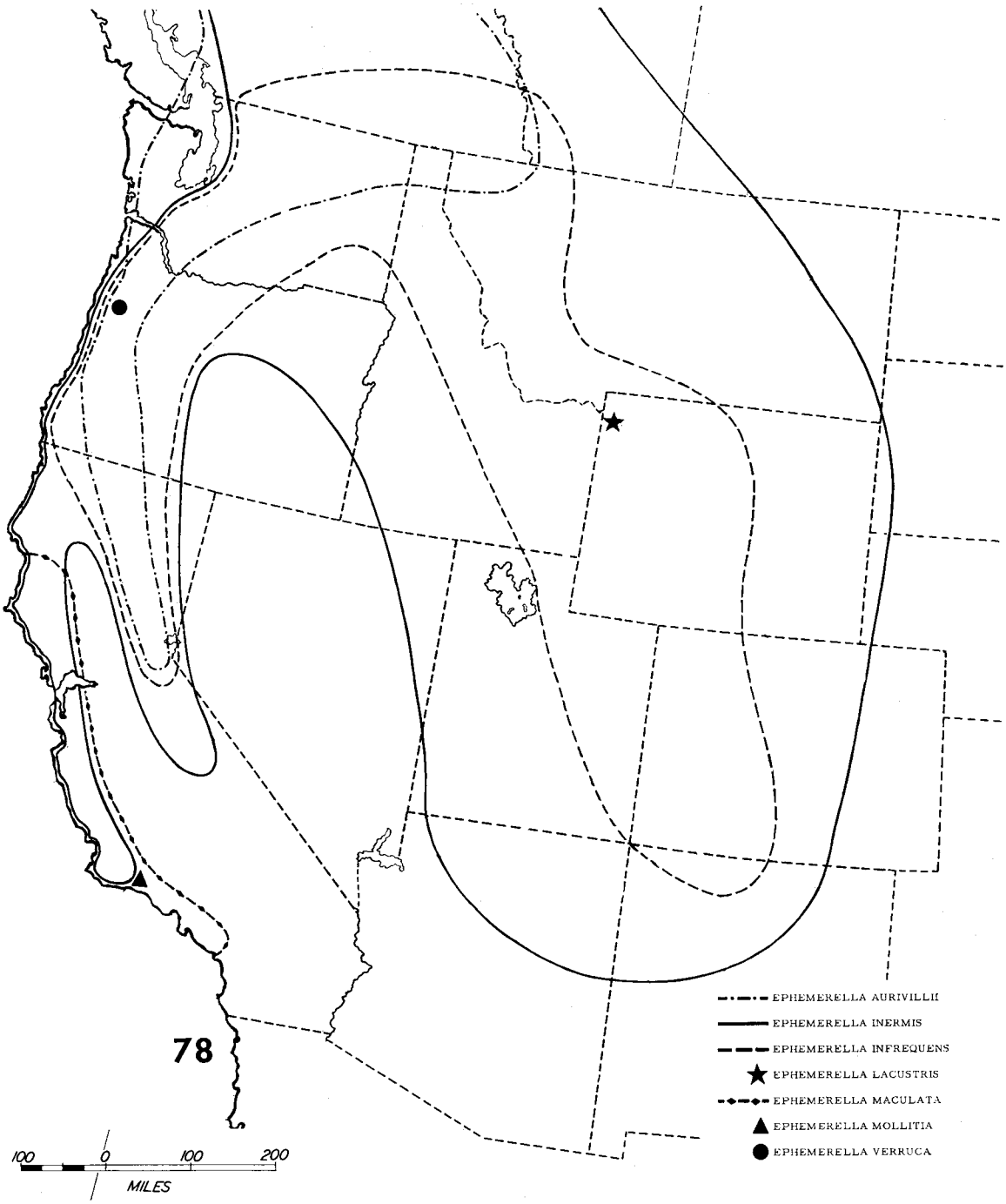


FIG. 78.—Distribution map of *E. aurivillii, E. inermis, E. infrequens, E. lacustris, E. maculata, E. mollitia,* and *E. verruca.*

tensive in some specimens that head is mostly pale; without paired occipital tubercles. Thoracic notum brown with irregular light brown or pale markings, pale areas sometimes so extensive in some specimens that brown markings persist only on pronotum and central area of mesonotum and at base of wing pads; lateral margins of pronotum pale; legs pale; femora pale, usually with 1 or 2 light brown maculae; forefemora with a subapical band of spines; tibiae and tarsi pale, occasionally with light brown transverse bands (Fig. 50); tarsal claws with 10–13 denticles (Fig. 72). Abdominal terga without paired submedian tubercles; terga brown, often with a pale continuous or interrupted median stripe; terga 5–10 with variable large pale patches, patches may be present on all these segments or only on segments 5 and 6 (Fig. 35); distinct postero-lateral projections on segments 3–9; lateral margins pale; abdominal sterna brown, lateral margins pale; sterna 2–8 often with brown sublateral maculae and dark submedian spots and oblique dashes, some specimens with a brown median stripe, most pronounced on posterior sterna. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments light brown or pale, usually with darker brown annulations.

Holotype.—Male imago, Yellowstone Lake, West Thumb, Yellowstone National Park, Wyo., 17-VIII-1959, G. F. Edmunds, Jr. and W. L. Peters, in collection of University of Utah, Salt Lake City.

Allotype.—Female imago, same data. Paratopotypes: 5 ♂ imagoes, 3 ♀ imagoes, 81 ♂ and 93 ♀ nymphs, 8 ♂ subimagoes, 12 ♀ subimagoes and 3 cast skins in collection of University of Utah. Paratypes: 1 ♂ imago, 2 ♂ and 1 ♀ nymphs, Yellowstone Lake nr. Pumice Point, Yellowstone National Park, 1-VIII-1940, T. H. Frison and T. H. Frison, Jr., in collection Illinois Natural History Survey, Urbana; 2 ♂ subimagoes, 2 ♂ and 3 ♀ nymphs, Yellowstone National Park, 19-VII-1945, V. E. Shelford, in collection Illinois Natural History Survey; 5 ♂ nymphs, Yellowstone Lake, Wyo., 23-VII-28, J. McDunnough, in collection Canadian National Collection, Ottawa, Ontario.

Remarks.—Ephemerella lacustris is most closely related to *E. inermis* Eaton but may be distinguished from it in both the nymphal and male adult stages by morphological and biological characteristics.

The male imagoes may be distinguished from all other known species by the combination of the deep chocolate brown thorax, the length of the foreleg in relation to the total length of the body, and by the form and spining of the penes. The nymphal stage is recognizable by the characteristic abdominal color pattern, the relative length of the thoracic legs, and by the dentition on the tarsal claws. This species is biologically distinct because it is the single species in the subgenus that is known only from lakes.

BIOLOGY

The nymphs are abundant under rocks near the shore of Yellowstone Lake, especially under large flat rocks. They were found to be commonest in water 18–24 in. deep. Subimagoes were emerging in numbers during midafternoon on a cloudy day in mid-August. The subimagoes molted about 24 hr later. The nymphs also were observed in great numbers in the stomachs of cutthroat trout (*Salmo clarkii* Richardson) taken at Steamboat Point in early June.

Ephemerella inermis Eaton

(Fig. 1, 14, 34, 78)

Ephemerella inermis Eaton 1884, 127; Banks 1907, 17; Ulmer 1920, 119; McDunnough 1925b, 169; Needham and Christenson 1927, 9; Walley 1930, 15; Traver 1935, 604; Linduska 1942, 27; Edmunds 1954, 66; Day 1956, 98; Allen and Edmunds 1956, 87.

Eaton (1884) described this species from a male and a female imago collected in central Colorado. In 1927 Needham reported as this species nymphs and adults from Utah. The nymphal material may be a composite of *E. inermis* and *E. infrequens* McDunnough; however, as McDunnough (1928) declared, the male genitalia which Needham figured were those of *E. infrequens.*

Male Imago (in alcohol).—Length: body 8–10 forewing 8–10 mm. Upper portion of compound eye orange, lower portion black. Thorax light brown to brownish black; pleural sutures pale; forelegs olive brown to light brown, tarsi paler; length of segments of foreleg in millimeters: femur = 1.5; tibia = 2.0; tarsus I = 0.2; tarsus II = 1.0; tarsus III = 0.9; tarsus IV = 0.7; tarsus V = 0.3; middle and hind legs paler than forelegs, often marked with brown or red; wings hyaline; primary longitudinal veins yellow, crossveins and intercalaries hyaline. Abdominal terga light brown, brown, or red; pleural margins pale, on the mdidle segments posterior margins pale, anterior margins sometimes pale; abdominal sterna light brown to red, much paler than terga. Penes with 3–14 dorsal and 1–9 ventral spines, position of spines usually as in Fig. 14; penis lobes short; lateral margins of penis lobes rounded; 2nd segment of genital forceps with a slight apical expansion or none (Fig. 14). Caudal filaments pale with dark brown annulations at apex of each segment.

Mature Nymph.—Length: body 7–9; caudal filaments 4–5 mm. General color light brown to dark chocolate brown with extremely variable pale markings (Fig. 1). Head brown with irregular light brown or pale markings on vertex; a pale transverse stripe crossing the face at the anterior margin of the eyes, stripe may be interrupted medially in some specimens; without paired occipital tubercles. Thoracic notum brown with irregular light brown or pale markings, occasionally with 3 pale longitudinal stripes; lateral margins of pronotum pale; femora brown with variable pale markings; forefemora with a subapical band of spines; tibiae and tarsi with alternating pale and brown bands (Fig. 1); tarsal claws with 6–9 denticles. Abdominal terga usually without paired submedian tubercles, occasionally very small tubercles or protuberances present on middle segments, some-

times from 2 to 8; terga brown, typically with a pale median stripe (sometimes absent) and paired submedian pale spots on posterior margin of segments, spots may fuse to form a large pale median patch or paired submedian longitudinal stripes, lateral margins pale; distinct postero-lateral projections on segments 4–9; abdominal sterna brown; sterna 2–8 often with paired sublateral pale maculae and dark submedian spots and oblique dashes. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments light brown with several brown transverse bands.

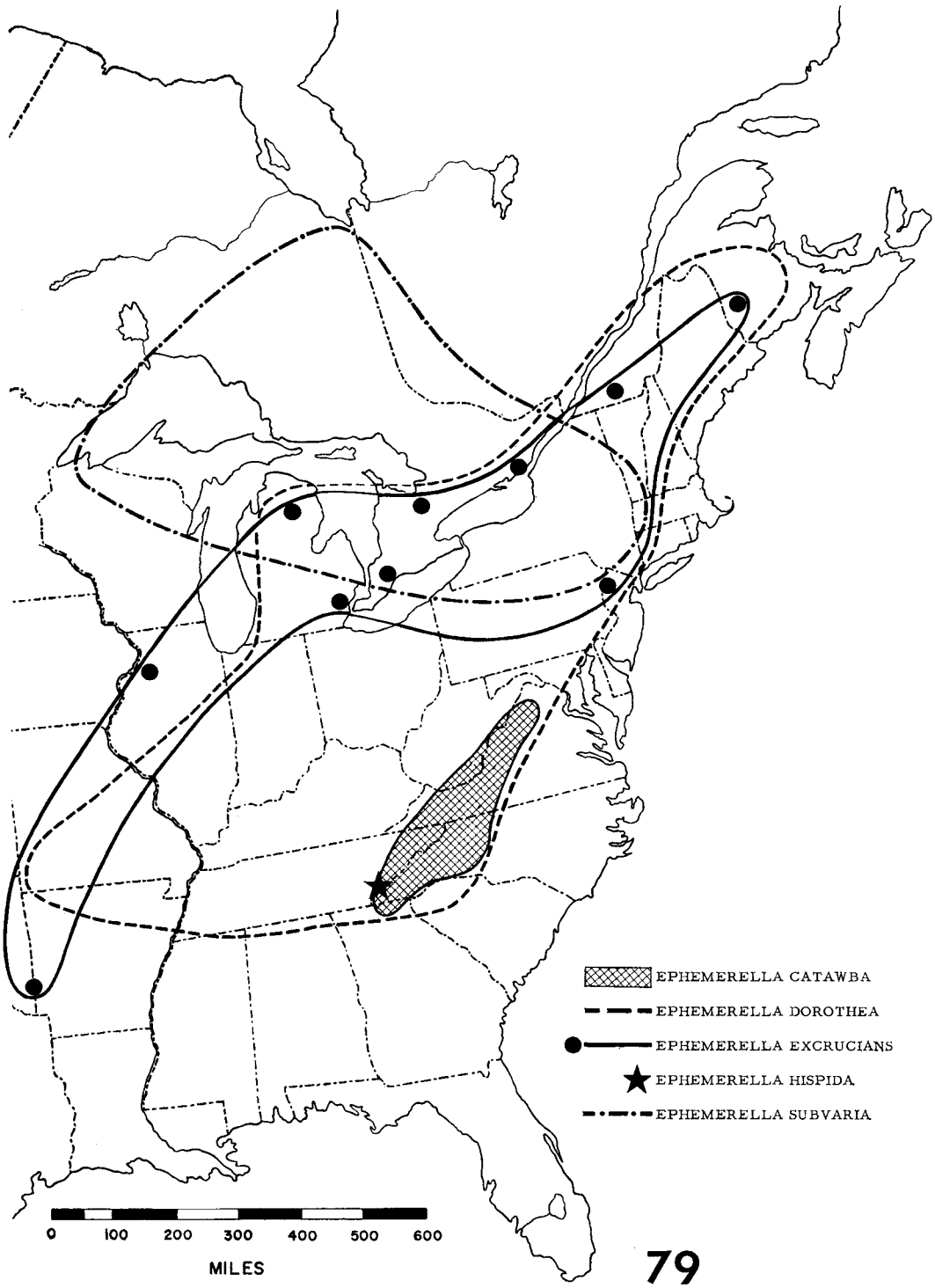


FIG. 79.—Distribution map of *E. catawba, E. dorothea, E. excrucians, E. hispida,* and *E. subvaria.*

Type-Locality.—Arkansas Canyon and Denver, Colo.

Type.—Museum Comparative Zoology, Cambridge, Mass.

DISTRIBUTION

E. inermis is a Western North American species and is known from Central Alaska austrad to California, Arizona, and New Mexico (Fig. 78). We have examined specimens from the following localities (many records are omitted when collection sites are numerous for one area):

ALASKA: Anan Creek, SE Alaska, 26-VI-58, G. L. Miller; Mosman Creek, Etolin Island, 25-V-58, G. L. Miller; Beaver Creek nr. Swede Boys Camp, 66°15′ N, 147°25′ W, 26-VIII-62, John Varley. ARIZONA: Graham Co., White River, 4 mi. N White River, 25-V-51, S. J. Preece, Jr.; Gila Co., Horton Creek, Tonto Natl. Forest, 1-VI-37, C. M. Tarzwell; Greenlee Co., Black River, Apache Natl. Forest, 19-VI-37, C. M. Tarzwell. CALIFORNIA: Pescadero Creek, 7-V-50, H. B. Leech; Alpine Co., Markleeville, 4-VII-49, W. C. Day; W. Fork Carson River, 2 mi. NE Woodfords, 21-IX-57, GFE and RKA; Sequoia Natl. Park, Marble Fork, Keweah River, 18-VI-59, RKA; Yosemite Natl. Park, Merced River at Highway Jct. 140-120, 19-VI-59, RKA; Inyo Co., S Fork Bishop Creek, 25-VI-34, V. K. Mayo (VKM); Sierra Natl. Forest, Stream 0.8 mi. up road to Soquele, 19-VI-59, RKA; Chilacoot Creek, 1 mi. above Bass Lake, 19-VI-59, RKA; Tehama Co., Mill Creek, 5 mi. N Childs Meadow, 3-VII-59, RKA; Shasta Co., Hat Creek at Sandy Public Camp, 2 mi. N Old Station, 3-VII-59, RKA. COLORADO: Grove Creek, Parry Park, 13-II-43, T. H. Frison (INHS); S. Platte River, Littletown, 13-II-43, T. H. Frison (INHS); Gunnison Co., Tomichi Creek, Hwy 114, 11-VII-61, D. W. Argyle; Gunnison Creek Jct. Stauben Creek, 5-VII-61, D. W. Argyle; Myers Gulch Jct. Gunnison River, 8-VI-61, A. R. Gaufin; Curecanti Creek Jct. Gunnison River, 8-VI-61, A. R. Gaufin; Soap Creek Jct. Gunnison River, 1/12-VII-61, A. R. Gaufin; Beaver Creek Jct. Gunnison River, 7-VI-61, A. R. Gaufin; Montrose Co., Cimarron Creek, Cimarron, 8-VI-61, A. R. Gaufin; Larimer Co., Poudre River, Fort Collins, 20-III-37 (INHS); Estes Park, Thompson River, 26-VII-38, H. H. and J. A. Ross (INHS); Boulder Co., St. Vrains Creek, E. Lyons, 18-II-43, T. H. Frison and H. Rodeck (INHS); Boulder Creek, Boulder, 19-II-43, T. H. Frison and H. Rodeck (INHS); Archuleta Co., Piedra River, 8-VII-60, L. D. Jensen and W. L. Peters; San Juan River, 5-VII-60, W. L. Peters; El Paso Co., Green Mountain Falls, 19-VII-38, H. H. and J. A. Ross. IDAHO: Cub Creek, Mapleton, 25-VI-55, A. R. Gaufin; Blaine Co., Big Wood River, 5-IX-45, GFE; Custer Co., Mackay, 30-VI-58, GFE; Ada Co., Boise River, Boise, 29-XII-51 (no other data). MONTANA: Whitefish River, Whitefish, 6-IV-52, T. N. Wilson; Polson, 7-VIII-10, R. T. Young (JRT); Beaverhead Co., Dillon, 7-VI-55, RKA; Missoula Co., Jct. E and W Forks Bitterroot River, 30-VI-59, GFE; Mineral Co., Clark Fork, 12 mi. W St. Regis, 30-VI-59, GFE; Glacier Natl. Park, 12-VII-40, H. H. and J. A. Ross (INHS). NEVADA: Elko Co., Columbia Creek, Bull Run Mountains, 20-IX-57, GFE and RKA; Secret Creek, 8 mi. NW Arthur, 19-IX-57, GFE and RKA. NEW MEXICO: Taos Co., La Junta Creek, Carson Natl. Forest, 15-VII-37, C. M. Tarzwell; San Juan Co., San Juan River, 29-VI/16-VIII-60, L. D. Jensen and W. L. Peters. OREGON: Rock Creek, 10-V-41, H. E. Mastin (OSU); McKenzie River, 9-III-39, "J. E. D." (OSU); Benton Co., Siletz River, Corvallis, 3-V-47, E. P. Hughes; Klamath Co., Little Deschutes River, Crescent, 23-VIII-54, GFE and RKA; Lincoln Co., Alsea River, Five Rivers Area, 2-V-35 (OSU); Grant Co., John Day River, John Day, 13-VI-54, GFE; Deschutes Co., Deschutes River, Cline Falls State Park, 18-VI-54, GFE; Curry Co., Mussel Creek, Ophir, 15-V-48, H. B. Leech; Jefferson Co., Lake Creek, Camp Sherman, 20-VI-54, GFE; Malheur Co., Camp Creek, 68 mi. N Vale, 20-VIII-54, GFE and RKA. SOUTH DAKOTA: Lawrence Co., Spearfish Creek, 9-VI-61, GFE and W. L. Peters; Pennington Co., Rapid Creek, 8-VI-61, GFE and W. L. Peters. UTAH: Morgan Co., Weber River nr. Devils Slide, 10-IX-50, GFE; Salt Lake Co., Red Butte Canyon, V-54, GFE and RKA; Murray, 5-IV-45, GFE; Utah Co., Provo River on U. S. Hwy 91, Provo, 8-VII-45, GFE; Thistle, 7-VII-45, GFE; Springville, 6-IX-44, GFE; Castilla, 8-VII-45, GFE; Uintah Co., Brush Creek, 2 mi. N Jensen, 24-V-59, G. G. Musser and GFE; Daggett Co., Green River, Hideout Canyon, 11-IX-52, GFE; Duchesne Co., Deep Creek, 30-V-47, GFE; Uintah River, Ft. Duchesne, 2-VII-45, GFE; Emery Co., Colorado River at Dewey Bridge, V-53, GFE; Sanpete Co., Ephraim Canyon, 7-VII-45, GFE; Fairview, 7-VII-45, GFE; Garfield Co., Sevier River, Spry, 7-II-47, GFE; Sevier River, Hatch, 4-V-47, D. R. Merkley; Zions Natl. Park, Virgin River, 19-III-56, L. E. Bitner; Kane Co., Asay Creek, between Orderville and Cedar Breaks (no other data); Washington Co., Pine Valley Gorge, 13-VII-47, GFE. WASHINGTON: Stevens Co., Loon Lake, VI-55, GFE; Spokane Co., Little Spokane River, Chattaroy, 23-VI-40, H. H. and J. A. Ross (INHS); Little Spokane River, Dartford, 13-VI-55, RKA; Benton Co., Columbia River, Hanford, 9-VI-51, J. J. Davis and C. L. Cooper (GE); Richland, 19-VI-55, J. J. Davis (GE). WYOMING: Sweetwater Co., Green River, Green River, 11/12-VI-61, GFE and W. L. Peters; Uinta Co., Bear River, head of Chalk Creek Road, 16-VII-48, L. T. Nielsen; Bear River, Evanston, 6-VI-61, GFE and W. L. Peters; Carbon Co., N. French Creek, 7-VI-61, GFE and W. L. Peters; N Brush Creek, 7-VI-61, GFE and W. L. Peters; N Platte River, Saratoga, 6-VI-61, GFE and W. L. Peters; Albany Co., Little Laramie River, 6 mi. E Centennial, 7-VI-61, GFE and W. L. Peters; Platte Co., N. Platte River, Guernsey, 7-VI-61, GFE and W. L. Peters; Sibylle

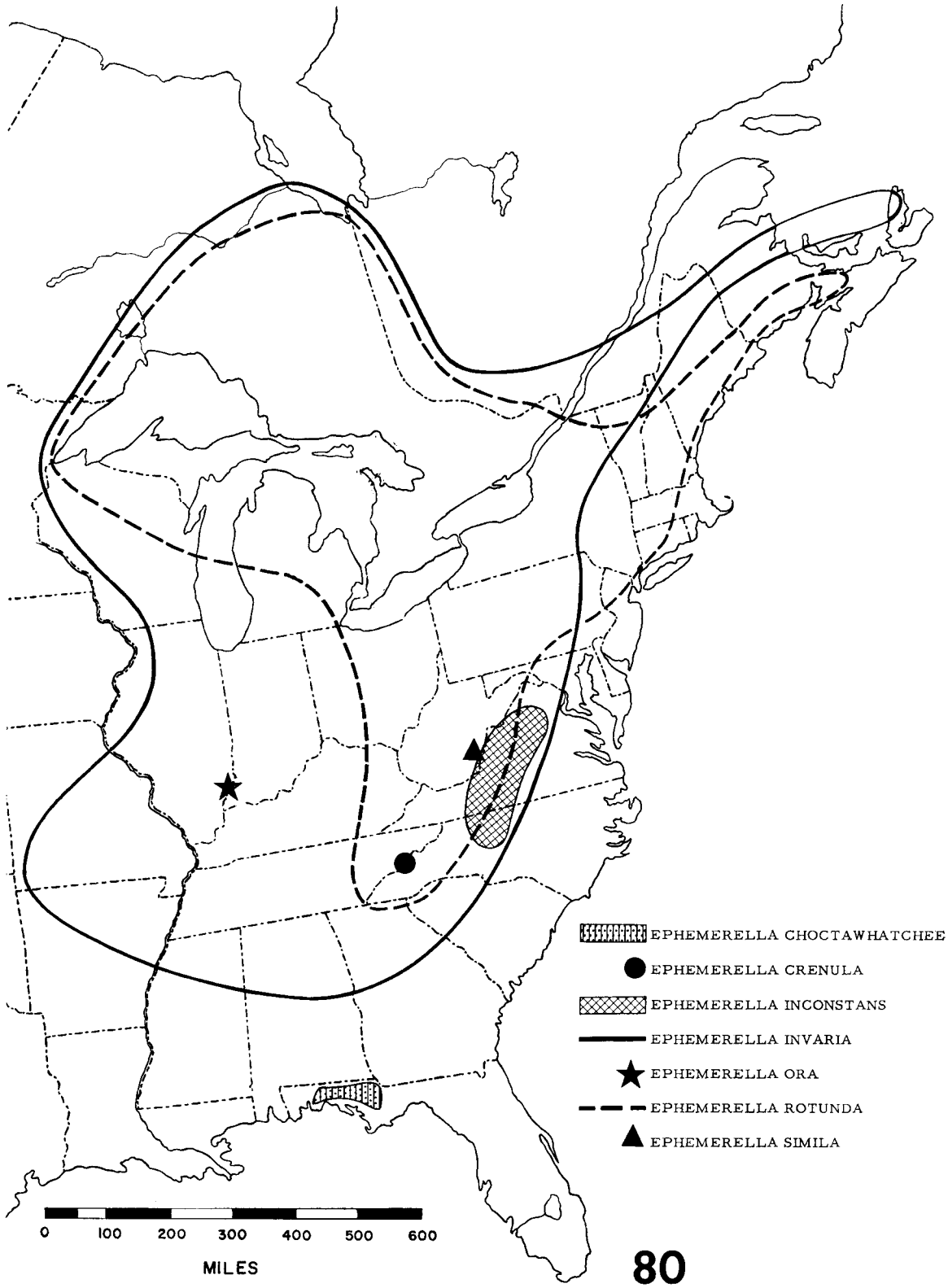


FIG. 80.—Distribution map of *E. choctawhatchee, E. crenula, E. inconstans, E. invaria, E. ora, E. rotunda,* and *E. simila.*

Creek, nr. Wheatland, 19-VI-47, D. G. Denning; Fremont Co., Little Popo Agie River, 10 mi. S Lander, 11-VI-61, GFE and W. L. Peters; Hornecker Creek, 2 mi. SW Lander, 11-VI-61, GFE and W. L. Peters; Rock Creek, Atlantic City, 11-VI-61, GFE and W. L. Peters; Yellowstone Natl. Park, Firehole River, Biscuit Basin 21-VI-49, GFE; Hayden Valley, 10-VI-46, GFE; Johnson Co., Clear Creek, Buffalo, 9/10-VI-61, GFE and W. L. Peters; Sourdough Creek, 10-VI-61, GFE and W. L. Peters; Washakie Co., Tensleep Creek, 4 mi. NE Tensleep, 10-VI-61, GFE and W. L. Peters; Sheridan Co., Sheridan, 10-VII-47, R. E. Pfadt (INHS).

TAXONOMY

E. inermis is closely related to *E. infrequens* McDunnough and *E. lacustris,* new species.

The nymphal stage is difficult to distinguish from *E. infrequens*. *E. inermis* are usually darker than *E. infrequens* or *E. lacustris,* and characteristic abdominal color patterns are usually evident in both *E. inermis* (Fig. 1) and *E. lacustris* (Fig. 35) while the abdominal terga of *E. infrequens* are usually unicolorous. Morphological characters to distinguish this species from *E. lacustris* are present. However, well-defined morphological characters have not been found to distinguish *E. inermis* from *E. infrequens* and young or faded specimens usually cannot be assigned to species.

The male adult stage of *E. inermis* and *E. infrequens* are readily distinguished from each other by the shape of the penes and the genital forceps; however, the male genitalia of *E. inermis* and *E. lacustris* are nearly identical.

BIOLOGY

E. inermis is one of the commonest mayflies in Western North America. The nymphs live in a wide variety of streams with summer stream temperatures of 50–64°F, and from sea level to 10,000 ft elevation but usually below 7,000 ft. They are more abundant in clear than in silted streams, but often form a higher percentage of the total number of mayflies present in silted streams, owing to the paucity of other species. They occupy a wide variety of microhabitats in the stream where they are found on various sized rocks and gravel in mid-stream riffles, and on exposed roots, vegetation, and debris at streamside.

The adults swarm in very late evening and the females have been observed ovipositing during mid-morning, about 9:00 to 11:00 AM. Adults have been collected throughout the summer from late May to early September. Numerous broods seem to occur throughout the summer months, but the population in the Green River consists of a single brood that emerges in June and early July. It is possible that 2 or more sibling species are still included under the name *E. inermis*.

Ephemerella infrequens McDunnough

(Fig. 15, 33, 51, 73, 78)

Ephemerella infrequens McDunnough 1924, 223; McDunnough 1925b, 169; McDunnough 1928, 238 (*inermis* Needham 1927 nec Eaton = *infrequens*); Traver 1935, 605 (nymph); Edmunds 1954, 66; Day 1956, 98; Allen and Edmunds 1956, 87.

Ephemerella inermis Needham 1927, 114 (nec Eaton 1884, 127).

E. infrequens was described from male imagoes collected in Alberta, Canada, and Central California

Male Imago (in alcohol).—Length: body 8.5–10.0; forewing 9.0–10.5 mm. Upper portion of compound eye orange, lower portion black. Thorax light brown to reddish brown, pleural sutures pale; forelegs light to medium brown; length of segments of foreleg in millimeters: femur = 1.6; tibia = 2.8; tarsus I = 0.2; tarsus II = 1.5; tarsus III = 1.4; tarsus IV = 1.1; tarsus V = 0.3; middle and hind legs light brown to yellowish brown; wings hyaline; primary longitudinal veins light brown to yellowish brown, crossveins and intercalaries hyaline. Abdominal terga reddish brown, the postero-lateral and lateral margins of terga 7–9 often paler or yellowish, terga 1–7 often semihyaline, 8–10 opaque; abdominal sterna light reddish brown. Penes with 2–11 dorsal and 4–11 ventral spines, position of spines usually as in Fig. 15; penis lobes short; lateral margins of penis lobes parallel; 2nd segment of genital forceps swollen apically (Fig. 15). Caudal filaments pale with dark brown annulations at apex of each segment.

Mature Nymph.—Length: body 8–11; caudal filaments 5–6 mm. General color light brown to reddish brown with pale markings. Head brown with irregular pale markings on vertex; an interrupted pale transverse stripe crossing the face at the anterior margin of the eyes, stripe may be complete in some specimens; without paired occipital tubercles. Thoracic notum brown with irregular pale markings; lateral margins of pronotum sometimes pale; femora light brown with variable pale markings; forefemora with a narrow subapical band of spines; tibiae and tarsi with alternating pale and brown bands (Fig. 51), bands frequently faint; tarsal claws with 7–10 denticles (Fig. 73). Abdominal terga without paired submedian tubercles or projections; terga usually brown, often with variable pale markings, and occasionally with an indistinct pale median stripe and paired submedian pale spots on posterior margin of segments, lateral margins light brown; distinct postero-lateral projections on segments 4–9; abdominal sterna brown. Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments; filaments light brown, occasionally with brown transverse bands.

Type-Locality.—Waterton Lakes, Alberta, Canada.

Type.—No. 816, Canadian National Collection, Ottawa, Ontario.

DISTRIBUTION

Ephemerella infrequens is a Western North American species and is known from British Columbia and Alberta austrad to California and New Mexico (Fig. 78). We have examined specimens from:

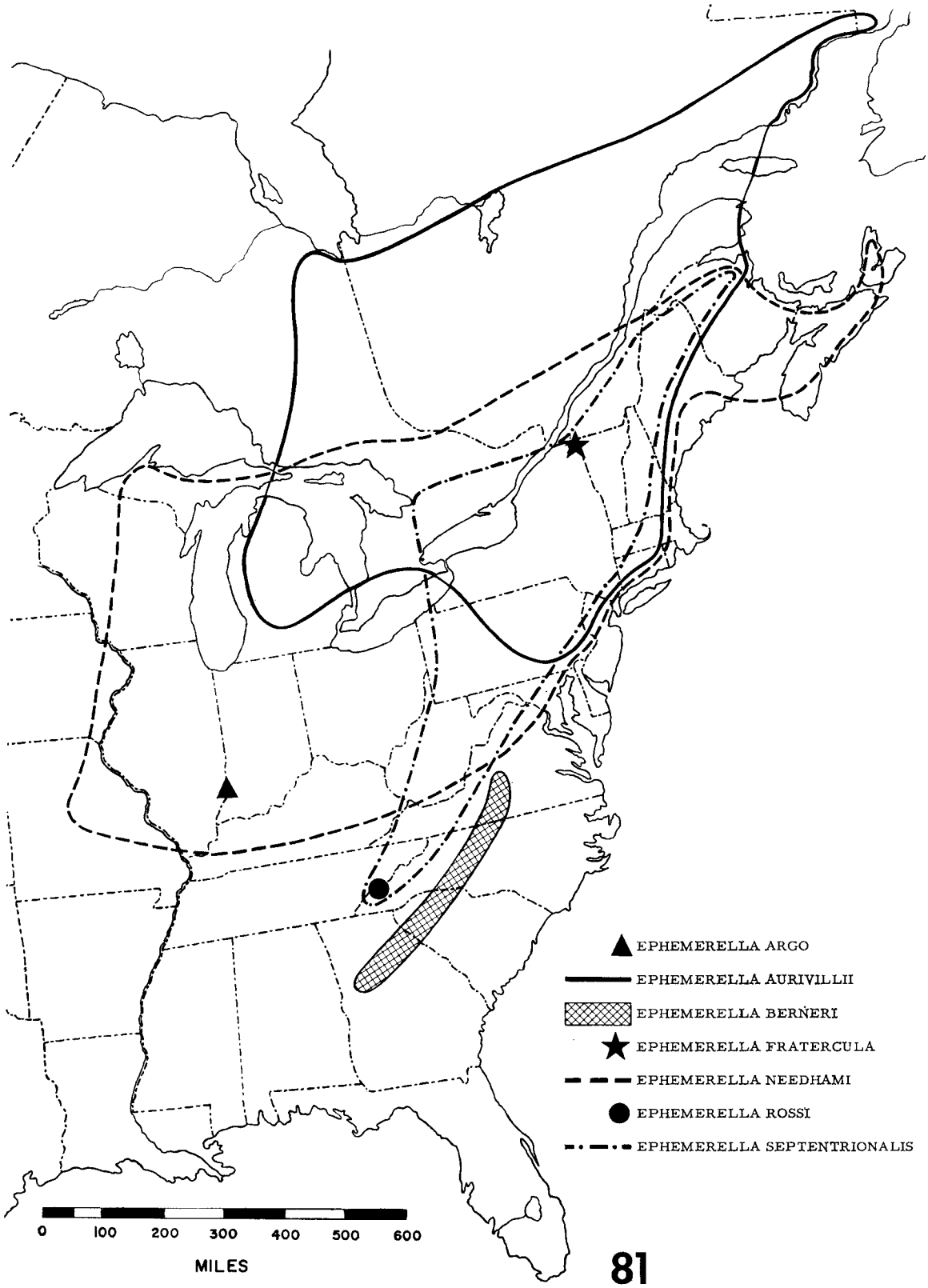


FIG. 81.—Distribution map of *E. argo, E. aurivillii, E. berneri, E. fratercula, E. needhami, E. rossi,* and *E. septentrionalis.*

BRITISH COLUMBIA: Napta Lake, Yoho Natl. Park, 2-IX-54, L. T. Nielsen; Trepanier Creek, Peachland, 22-VI-35, A. N. Gartrell (CNC); Shingle Creek, Penticton, 20-VII-35, A. N. Gartrell (CNC); nr. Vancouver, 18-VII-46, H. H. Ross (INHS). CALIFORNIA: Hat Creek, Old Station, Shasta Co., 21/22-VI-60, S. G. Jewett, Jr. (SGJ); Eure Valley, 7-VII-48, W. C. Day; W. Fork Carson River, 1-IV-50, W. C. Day. COLORADO: Delta Co., Surface Creek nr. Eckert, 28-VI-38, "Lanham" and "Bauer" (INHS); Estes Park, Thompson River, 28-VII-38, H. H. and J. A. Ross (INHS); El Paso Co., Monument Creek, Monument, 13-II-43, T. H. Frison (INHS); Green Mountain Falls, 23-VI-38, J. A. Ross (INHS); Gilpin Co., Tolland, 30-V-36 (CNC). IDAHO: Wood River, Sawtooth Natl. Forest, 9-IV-44, GFE; Warm River, 13-VI-46, GFE; Big Lost River, Mackay, 15-VII-57, GFE. MONTANA: Beaverhead Co., Dillon, 3-VIII-47, F. C. Harmston; Pipestone Pass, 20 mi. SE Butte, 21-VI-49, L. T. Nielson and S. J. Preece, Jr. NEW MEXICO: Taos Co., Carson Natl. Forest, Red River, 28-VII-37, C. M. Tarzwell; LaJunta Creek, 15-IV-37, C. M. Tarzwell. OREGON: McKenzie River, 5-V-37 (OSU); Rock Creek, 10-V-41, J. W. Joyce (OSU); Fall Creek, 4-V-40, N. L. Sieg (OSU); Bull Run River, 22-VI-33, R. Dimick (OSU); Tumalo State Park, Deschutes River, 25-VI-54, GFE; Jefferson Co., Spring Creek, 19/20-IV-52, V. Roth; Tributary of Metolius River, Sherman Camp, 20-VI-54, GFE; Benton Co., Marks Creek, Corvallis, 26-II-38, B. White (OSU); Woods Creek, 2 mi. W Philomath, 24-III-37, "N. G. R."; Lane Co., Odell Creek, 8 mi. from Highway 50, 7-VI-58, M. L. Johnson; Middle Fork Willamette River, Shady Dell Forest Camp, 17-VI-58, M. L. Johnson; McKenzie River, Ben and Kay Doris State Park, 15-VI-58, M. L. Johnson. UTAH: Huntington Canyon, 14-VII-45, I. B. McNulty; Paradise Park Creek, 21-VII-47, GFE; Provo River, Bridal Veil Falls, 26-VII-45, GFE; Box Elder Co., Brigham Canyon, 18-V-46, F. C. Harmston; Weber Co., Ogden, 22-VI-51, H. Knight; Salt Lake Co., Spring Run, Salt Lake City, 9-IV-50, W. J. Arnold; Utah Co., Thistle, 7-VII-45, GFE; Provo River on U. S. Highway 91, Provo, 8-VII-45, GFE; Duchesne Co., Deep Creek, 30-V-47, GFE; Uintah Co., Merkley Park nr. Vernal, 6-VI-46, D. R. Merkley; Mouth Dry Fork Canyon, Vernal, 6-VI-46, D. R. Merkley; Wasatch Co., Provo River, Heber, 7-VII-47, GFE; Sanpete Co., Fairview, 7-VII-45, GFE; Mt. Pleasant, 7-VII-45, GFE. WASHINGTON: Little Spokane River, Dartford, 13-VI-55, RKA; Peone Creek at Bruce Road, Spokane, 19-VI-55, RKA; Wenatchee River, Cashmere, 23-VI-40, H. H. and J. A. Ross (INHS). WYOMING: Yellowstone Natl. Park, Madison Junction, 12-VII-50, GFE; Crawfish Creek, 5-VI-46, GFE; Yellowstone River Canyon, 17-VI-49, GFE; Nez Perce Creek, 10-VI-46, GFE; Tributary Pine Branch River, Boulder, 6-VI-36, H. H. Ross (INHS); Sheridan; 29-VII-48, D. G. Denning.

TAXONOMY

E. infrequens and *E. inermis* are closely related and are difficult to distinguish from each other in the nymphal stage. Nymphs of *E. infrequens* do not appear to have any unique characters which will separate them from *E. inermis*. They are often larger than *E. inermis* and their postero-lateral projections appear to be longer and sharper than the latter species. The male imagoes of *E. infrequens* may be distinguished from all other known species by the shape of the penes and genital forceps (Fig. 15).

BIOLOGY

E. infrequens occurs in the same streams as *E. inermis*, but it is neither as abundant nor as widely distributed. Adults have been collected from June to September, but the nuptial flight has not been observed.

Ephemerella maculata Traver

(Fig. 16, 28, 29, 49, 66, 78)

Ephemererlla maculata Traver 1934, 216, 1 Fig.; Traver 1935, 610, 2 Fig.; Day 1956, 97.

Ephemerella euterpe Traver 1934, 213, 1 Fig.; Traver 1935, 595, 1 Fig.; Day 1956, 97, 1 Fig. NEW SYNONYMY.

E. maculata was described from male and female imagoes and nymphs collected in Southern California, and the nominal species *euterpe* was named from all stages from West-central California.

Male Imago (in alcohol).—Length: body 9–11; forewing 10–11 mm. Upper portion of compound eyes dull orange, lower portion black. Thorax chocolate brown; legs brown, forelegs darker than middle and hind legs; wings hyaline; primary longitudinal veins brown, intercalaries and crossveins light brown, except cross veins in cubital area and in hind wing hyaline. Abdominal terga brown; abdominal sterna pale, sterna 2–7 with reddish brown to dark brown medially notched rectangular markings and brown ganglionic spots (Fig. 28). Penes without dorsal or ventral spines (Fig. 16); penis lobes short; 2nd segment of genital forceps bowed and with a slight apical expansion (Fig. 16). Caudal filaments pale with brown basal annulations.

Mature Nymph.—Length: body 7.5–11.0; caudal filaments 4–5 mm. General color light brown to dark brown with darker brown markings. Head brown with irregular dark brown markings on vertex; without a pale transverse stripe between the eyes; without paired occipital tubercles; genae expanded laterally (Fig. 66). Thoracic notum brown; femora pale and with long hair and spines; forefemora with a broad subapical continuous or interrupted band of spines (Fig. 49); tibiae and tarsi pale with dark brown markings; tarsal claws with 4–5 denticles. Abdominal terga without tubercles or protuberances; terga with fine spicules; terga brown occasionally with pale submedian patches; distinct postero-lateral projections on segments 2–9, those on segment 2 rather small; abdominal sterna with reddish brown to dark brown

postero-medially notched rectangular markings (Fig. 29). Caudal filaments with whorls of spines on apex of segments in basal ⅔ and heavily setaceous on distal segments, filaments brown.

Type-Locality.—San Gabriel Canyon, San Gabriel Mountains, Calif.

Type.—No. 1284.1, Cornell University Collection, Ithaca, N. Y.

DISTRIBUTION

Ephemerella maculata is known from only the Coast Ranges of California (Fig. 78). Specimens have been examined from:

CALIFORNIA: San Gabriel Canyon, San Gabriel Mountains, 9-VI-32, C. D. Michener (Holotype) (CU); Waddell Creek, Rancho del Oso (no date), D. Shepherd (Holotype, *euterpe*) (CU); Mendocino Co., Eel River at Bell Glen nr. Leggett, 2-VII-59, RKA; Broaddus Creek on Highway 20, 1.3 mi. W Willits, 2-VII-59, RKA; Baechtel Creek, 3 mi. W Willits, 15-VI-48, H. B. Leech; San Gregorio Creek, 17-VI-50, W. C. Day.

TAXONOMY

Traver (1934) described *E. maculata* and *E. euterpe* from all stages and presented adequate descriptions for both species. In describing the nymph of *E. euterpe* she made an occasional note, "as in *maculata*," but failed to give an adequate comparison of the 2 newly named forms.

We have examined the types, and find no characters that will distinguish them. The unique head shape (Fig. 66), supposedly a character of both "species" is different from heads of other species in the subgenus (Fig. 65), and both *E. maculata* and the nominal *euterpe* have identical ventral abdominal color patterns in both the nymphal and adult stages, and identical male genitalia. These evidences leave little doubt that *euterpe* is synonymous with *E. maculata.*

Ephemerella needhami McDunnough

(Fig. 17, 44, 56, 81)

Ephemerella bispina Needham 1905, 43, 1 Fig. (nymph nec adult).

Ephemerella excrucians Needham (nec Walsh 1862; 377) 1905, 47, 1 Fig. (adult nec nymph).

Ephemerella needhami McDunnough 1925b, 171, 1 Fig.; McDunnough 1931b, 202, 2 Fig. (nymph); Traver 1932, 147; Traver 1935, 614, 1 Fig.; Ide 1935b, 44; Britton 1938, 12; Leonard 1950, 19; Burks 1953, 67, 6 Fig.; Leonard and Leonard 1962, 50, 3 Fig.

McDunnough (1925b) described *E. needhami* from male adults from Quebec, and noted that this was evidently the same species identified as *E. excrucians* by Needham (op. cit.). Needham (1905) described *E. bispina* from all stages collected in Indiana. McDunnough (1931b) noted that the type male imago of *E. bispina* was a synonym of *E. walkeri* Eaton, and further noted that the supposed nymph of *E. bispina* was the nymph of *E. needhami.*

Male Imago (dry).—Length: body 6.5–7.5; forewing 7–8 mm. Compound eyes dark brown, lower portion paler. Thorax dark brown; pronotum and lateral margin of mesothorax to base of forewing suffused with black; forelegs brown; length of segments of foreleg in millimeters: femur = 1.6; tibia = 3.0; tarsus I = 0.2; tarsus II = 1.4; tarsus III = 1.3; tarsus IV = 1.0; tarsus V = 0.5; middle and hind legs light yellow; wings hyaline, venation hyaline. Abdominal terga 1–7 purple, terga 8–10 brown; abdominal sterna pale, each sternum with 2 dark oblique dashes anteriorly and 2 dark dots posteriorly. Penes without spines; penes deeply emarginate with long lateral lobes (Fig. 17); 2nd segment of genital forceps not expanded apically (Fig. 17). Caudal filaments pale with light brown annulations at the apex of each segment.

Mature Nymph.—Length: body 7–8; caudal filaments 4–5 mm. General color brown to black, usually a broad pale median dorsal stripe on head, thorax, and abdomen, which may contain a dark median line or be modified into 2 pale submedian lines, broad pale stripe often bordered by 2 dark stripes. Head without paired occipital tubercles. Thoracic notum without distinct tubercles or ridges; legs brown with pale or light brown markings, forefemora usually with a pale median transverse band and an apical mark, tibiae with a pale subproximal transverse band and an apical mark or band, tarsi with a pale median transverse band (Fig. 56); tarsal claws with 6–11 denticles. Abdominal terga 1–8 with paired submedian tubercles, tubercles on tergum 1 small, often barely discernible, tubercles on terga 2–8 well developed (Fig. 44a); terga with fine spicules (Fig. 44b); distinct posterolateral projections on segments 3–9; abdominal sterna with 2 dark oblique dashes anteriorly, 2 dark dots posteriorly, and paired sublateral streaks. Caudal filaments with whorls of spines on apex of proximal segments and heavily setaceous on distal segments; filaments light brown with several brown bands.

Type-Locality.—Laprairie, Quebec, Canada.

Type.—No. 1328, Canadian National Collection, Ottawa, Ontario.

DISTRIBUTION

E. needhami is known from Michigan to Nova Scotia and austrad to Missouri and Virginia (Fig. 81). We have examined specimens from:

ILLINOIS: Kankakee River, Momence, 21-V-40, C. O. Mohr and B. D. Burks (INHS); Kankakee River, Kankakee, 17-V-35, H. H. Ross (INHS); Lust Creek, Eddyville, 16-V-47, B. D. Burks (INHS); Oakwood, 22-V-42, H. H. Ross and B. D. Burks (INHS). KENTUCKY: Quicksand, 8-V-47, P. O. Ritcher and M. W. Sanderson (INHS). MICHIGAN: Platte River, Honor, 27-V-39, T. H. Frison and H. H. Ross (INHS); Great Sable River, Free Soil, 26-V-39, T. H. Frison and H. H. Ross (INHS); Pere Marquette River, Baldwin, 28-V-39, T. H. Frison and H. H. Ross (INHS); Crawford Co., Au Sable River, 26-IV-48, J. W. and F. A.

Leonard (LL); Tributary Manistee River, Wellston, 28-V-39, T. H. Frison and H. H. Ross (INHS); Little Manistee River nr. Iron, 28-V-39, T. H. Frison and H. H. Ross (INHS). MISSOURI: Maries River, Westphalia, 12-V-57, L. E. Vogele (UMo). NEW BRUNSWICK: NW Miramichi River, 6-VI-51, E. L. Bousefield; NW Miramichi River nr. Newcastle, 7/13-VII-61, T. Dolan. NEW YORK: Keene Valley, Tributary Au Sable River, 20-VI-41, T. H. Frison and H. H. Ross (INHS). NOVA SCOTIA: Annapolis River, 25-VI-50, E. L. Bousefield; nr. Springhill, 9-VII-50, E. L. Bousefield; nr. Margaree Harbor, Cape Breton Island, 6-VII-50, E. L. Bousefield. ONTARIO: Speed River, 7 mi. N Guelph, 17-V-60, B. V. Peterson. QUEBEC: Laprairie, 8-VII-24, G. S. Walley (Holotype) (CNC); Mississquoi River, S. Bolton, 19-VI-30, G. S. Walley (CNC); Lapeche River, Wakefield, 6-VI-30, 13-VI-30, J. McDunnough (CNC); Fulford, 13-VI-30, L. J. Milne (CNC); St. Lambert, 3-VII-27, W. J. Brown (CNC); Cascade Point, 4-VII-30, J. McDunnough (CNC). VIRGINIA: Shenandoah River, Berryville, 14-IV-38, E. Surber (JRT).

TAXONOMY

E. needhami is readily distinguished from all other species in the *Ephemerella*, s. s., in both the male adult and nymphal stages. Numerous specimens have been examined and morphological characters appear to be quite constant.

Ephemerella aurivillii (Bengtsson)

(Fig. 18, 31, 32, 54, 70, 78, 81)

Ephemerella (sp. n.) Eaton 1903, 35.

Chitonophora aurivillii Bengtsson 1908, 243; Bengtsson 1909, 8; Bengtsson 1913, 292, 1 Fig.; Lestage 1917, 362; Ulmer 1920, 119; Rousseau 1921, 238; Lestage 1925, 297; Bengtsson 1930b, 3 (=*aroni*), 5 (nymph); Bengtsson 1930a, 10; Lestage 1938, 248; Brekke 1938, 66; Tiensuu 1939, 121; Tshernova 1941, 215; Tshernova 1949, 156.

Ephemerella aroni Eaton 1908, 149; Aro 1910, 29, 1 Fig.; Walley 1930, 17 (=*aurivillii, norda*); McDunnough 1930, 55 (=*norda*); Ide 1930, 211; Kimmins 1960, 303.

Chitonophora aroni Bengtsson 1909, 9; Ulmer 1914, 98; Esben-Peterson 1916, 12; Lestage 1917, 363; Ulmer 1920, 120; Lestage 1925, 297; Ulmer 1943, 340.

Chitonophora sp ? Lestage 1917, 363, 13 Fig.; Rousseau 1921, 238; Lestage 1925, 297.

Ephemerella norda McDunnough 1924, 223, 1 Fig.; Walley 1930, 17.

Chitonophora aurivilliusi Lestage 1930, 204. Emended Name.

Ephemerella aurivillii McDunnough 1931b, 197; McDunnough 1932, 79; Traver 1935, 582; Ide 1935b, 43; Burks 1953, 69 (=*concinnata*); Allen and Edmunds 1956, 87.

Ephemerella concinnata Traver 1934, 219; Traver 1935, 586.

E. aurivillii was described from adults collected in Sweden, and was designated as the type species of the newly established genus *Chitonophora* (Bengtsson, February, 1908). In November, 1908, Eaton described *E. aroni* from adults collected in Finland. Bengtsson (1909) redescribed *E. aurivillii* and transferred *aroni* to the genus *Chitonophora* and in 1930 Walley placed *E. aurivillii* as a junior synonym of *aroni* and transferred *aroni* back into the genus *Ephemerella*. This same year, Bengtsson (1930b) established that *E. aurivillii* had date priority and reversed the synonymy, and described the nymphal stage; however, he retained the species in the genus *Chitonophora*. McDunnough described *E. norda* in 1924 and Traver (1934) described *E. concinnata* from North America; these nominal species were synonymized with *E. aurivillii*, respectively, by Walley (1930) and Burks (1953).

Male Imago (dry).—Length: body 10–11; forewing 11–13 mm. Compound eyes dark purple brown. Thorax chocolate brown, light brown at bases of wings and legs; forelegs smoky brown, femora with a brown apical macula; length of segments of foreleg in millimeters: femur = 2.2; tibia = 3.5; tarsus I = 0.3; tarsus II = 1.6; tarsus III = 1.6; tarsus IV = 1.4; tarsus V = 0.6; middle and hind legs yellowish brown, femora with a brown apical macula; wings smoky; primary longitudinal veins brown, crossveins and intercalaries hyaline. Abdominal terga 1–7 dark chocolate brown, terga 8–10 dark reddish brown, pleural margins paler, the anterior margins somewhat paler on middle segments; abdominal sterna light yellowish brown, anterior segments with a tinge of purple, sterna 1–5 with 2 dark oblique dashes anteriorly and 2 dark dots posteriorly. Penes with 12–14 dorsal and 12–14 medial spines, position of spines usually as in Fig. 18; penes deeply emarginate with long lateral lobes; 2nd segment of genital forceps expanded apically (Fig. 18). Caudal filaments smoky brown, with apex of each segment only faintly darker.

Mature Nymph.—Length: body 10.0–13.5; caudal filaments 10–11 mm. General color brown, often with a wide pale median stripe, or 2 narrow pale submedian stripes, occasionally with only paired pale submedian spots on posterior margin of abdominal terga; body and legs often with short black setae and usually with numerous spicules on abdominal terga. Head brown, usually with irregular pale markings; usually without a pale transverse stripe crossing the face; occiput and face smooth (Fig. 70). Thoracic notum brown with variable pale markings; femora brown with pale markings; forefemora with a subapical band of spines; tibiae and tarsi with alternating pale and brown bands (Fig. 54); tarsal claws with 6–10 denticles. Abdominal terga with tubercles covered with fine spicules (Fig. 31–32); tubercles may be small on segments 3–7 and barely discernible on segments 2 and 8 (Fig. 32), or tubercles may be well developed on segments 2–8 and small or barely discernible on segments 1 and 9 (Fig. 31); terga with numerous fine spicules (Fig. 31b and 32b); terga brown with pale stripes or spots, postero-lateral projections usually pale; distinct postero-lateral projections on segments 3–9, very small projection may be present on segment 2; abdominal sterna brown, with dark spots and streaks. Caudal filaments with

whorls of spines on apex of segments in basal ⅔; filaments light brown, usually with several brown bands.

Type-Locality.—"Provinz of Dalarne, Lappland" (Dalecarlia Province, Sweden).

Type.—Unknown.

DISTRIBUTION

E. aurivillii is the only known species in the genus with a Holarctic distribution, occurring in Northwestern Europe, Central and Northeastern Asia, and North America. We have examined 2 male imagoes from Europe. These specimens are part of the Zoology Museum of the University, Helsinki, and were presumably collected in Finland.

The North American populations have a disjunct distribution with eastern and western components. The eastern population is known from Ontario to Labrador and austrad to Pennsylvania and Michigan (Fig. 81). The western population is known from the Pribilof Islands in the Bering Sea and Southeast Alaska austrad to Montana and Central California (Fig. 78). We have examined specimens of this species from:

ALASKA: Southeast Alaska, Anan Creek, 17-V-58, G. L. Miller. CALIFORNIA: Nevada Co., Eure Valley, 4-VII-48, W. C. Day; Sagehen Creek, 19-II-55, R. Gard (UCSC). LABRADOR: 1 mi. E Wishart Lake outlet, 19-VI-60, B. V. Peterson. MASSACHUSETTS: Cambridge, "Hagen" (no other data) (MCZ). MICHIGAN: Benzie Co., Platte River, Honor, 27-V-39, T. H. Frison and H. H. Ross (INHS); Lake Co., Sanborn Creek, Nirvana, 28-V-39, T. H. Frison and H. H. Ross (INHS); Ottawa Co., Pigeon River, West Olive, 9-V-40, T. H. Frison and H. H. Ross (INHS). NEW HAMPSHIRE: Brook nr. Pinkham Notch Camp, Mt. Washington, 22-VI-41, T. H. Frison and H. H. Ross (INHS); Grafton Co., Pemigewasset River nr. Woodstock, 22-VI-41, T. H. Frison and H. H. Ross (INHS). ONTARIO: Stream at Moosonee, 30-V-61, B. V. Peterson and E. Bond. OREGON: Benton Co., Colorado Lake, 2-IV-38, S. G. Jewett, Jr. (OSU); Corvallis, 30-III-41, Fred A. Glover (OSU); Woods Creek, 2 mi. W Philomath, 24-III-37, D. C. Mote (OSU); Oak Creek nr. Corvallis, 17-II-34, E. E. Ball (OSU); Lincoln Co., Alsea River, Alsea, 5-I-42, T. H. Frison (INHS); Cresent Creek, 22-III-41, M. Cummings (OSU). QUEBEC: Pearce Lake inlet, Schefferville, 20-VI-60, B. V. Peterson; Key Lake outlet, 20-VI-60, B. V. Peterson; Great Jacques-Cartier Lake, 13-VI-38, "C. G." (INHS); Bradore Bay, 13-VII-29, W. J. Brown (JRT). WASHINGTON: Quinalt River above Quinalt Lake, 22-V-42, J. G. Needham (JRT).

TAXONOMY

The nymphal stage of *E. aurivillii* varies in the character of the paired dorsal abdominal tubercles. The populations from Eastern North America usually have very small blunt abdominal tubercles and on many specimens they are barely discernible (Fig. 32), whereas specimens from populations in Northwestern North America have longer and sharper abdominal tubercles (Fig. 13). Only 2 exceptions to this feature are known in the several collections we have examined. Mature nymphs from Honor, Mich., have tubercles which approach the development of the western populations, while mature nymphs from Cresent Creek, Ore., have very small blunt tubercles identical to those of eastern populations.

The relatively high percentage of nymphs showing the differences between the eastern and western populations indicates that *E. aurivillii* is probably polytypic. *E. aurivillii* was described from Northern Europe, but we have not examined nymphal material from this geographic area, nor does the literature reveal the shape and degree of development of the abdominal tubercles of the nymphs from this region. Tshernova (1949) states that nymphs from Lake Telotskoy and vicinity have sharp paired dorsal abdominal tubercles. This fact would indicate that the Northeastern Asian populations have their affinities with the Northwestern North American populations. Additional data are needed to clarify the geographic variation.

Ephemerella verruca, new species

(Fig. 30, 71, 78)

Mature Nymph.—Length: body 12–14 mm; caudal filaments broken. General color brown with light brown markings. Head brown with pale vermiculate markings on the vertex; a pale or light brown transverse stripe crossing the face at the anterior margin of the eyes; occiput with small rounded paired tubercles; face with 3 ocellar warts covered with fine spicules (Fig. 71). Thoracic notum brown, with variable ornate darker markings; femora brown with variable pale markings and with numerous spines; forefemora with a narrow subapical band of spines; tibiae and tarsi brown, tarsi with dark brown basal and apical bands; tarsal claws with 10–12 denticles. Abdominal terga with small sharp paired submedian tubercles on segments 2–10 (Fig. 30); terga brown with variable interrupted pale stripes, stripes developed primarily on terga 5–10, pale patches mediad of gills on segments 5–6; distinct postero-lateral projections on segments 3–9; abdominal sterna brown, sterna 2–8 often with paired sublateral brown maculae and dark submedian spots and oblique dashes, sterna 5–8 with a variable interrupted stripe. Extreme base of caudal filaments brown with whorls of spines at the apex of each segment (remainder missing from all specimens).

Holotype.—Mature male nymph, Marys Peak, Ore., 30-III-41, B. Borovicko, in collection of California Academy of Sciences, San Francisco. Paratopotypes: 2 ♀ and 1 ♂ nymphs, same data; 1 ♀ nymph in collection of Oregon State University, Corvallis, others in collection of University of Utah, Salt Lake City.

Remarks.—*E. verruca* is known from only the nymphal stage and appears to be most closely related

to *E. aurivillii* (Bengtsson). It differs from *E. aurivillii* and all other known species in the subgenus by possessing ocellar warts (Fig. 71), and by the number, placement, and shape of the paired dorsal abdominal tubercles (Fig. 30).

Ephemerella crenula, new species
(Fig. 37, 58, 68, 80)

Mature Nymph.—Length: body 6–7; caudal filaments 3.5–4.5 mm. General color brown to dark brown with light brown to pale markings. Head brown to dark brown with pale vermiculate markings on vertex; a pale transverse stripe crossing the face at the anterior margin of the eyes, stripe may be interrupted or absent; occiput without tubercles, but with spicules. Thoracic notum brown to dark brown with pale markings, pronotum with lateral margins or corners pale; pronotum with paired submedian tubercles covered with spicules as in Fig. 38; mesonotum with spicules and with a small median tubercle at base of wing pads; femora light brown with indistinct brown markings; forefemora with a subapical band of short spines (Fig. 58); tibiae and tarsi brown with brown bands near the middle; tarsal claws with 4–6 denticles. Abdominal terga with small paired submedian tubercles on segments 3–8, tubercles barely discernible on terga 3 and 8, small on segment 4 and better developed on segments 5–7 (Fig. 37a); terga with fine spicules (Fig. 37b); terga brown to dark brown with pale markings, terga often with paired submedian spots on posterior margin of segments, lateral margins pale; distinct short postero-lateral projections on segments 4–9; abdominal sterna brown, often sprinkled with fine pale dots. Caudal filaments with whorls of spines at apex of segments in basal ⅔, distal segments setaceous; filaments light brown with several brown bands.

Holotype.—Mature male nymph, Little River, Elkmont, Tenn., 14-V-39, T. H. Frison and H. H. Ross, in collection of Illinois State Natural History Survey, Urbana. Paratopotypes: 2 ♀ nymphs, same data, in collection Illinois State Natural History Survey. Paratypes: 1 ♀ nymph, Smoky Mountain, Tenn., 11-VI-31, J. G. Needham, in collection J. R. Traver, Amherst, Massachusetts; 4 ♀ and 5 ♂ nymphs, LaConte Creek, Gatlinburg, Tenn., 14-V-39, T. H. Frison and H. H. Ross, 1 ♀ and 1 ♂ nymphs in collection University of Utah, Salt Lake City, all others in collection Illinois State Natural History Survey; 2 ♀ and 1 ♂ nymphs, Gatlinburg, Tenn., 19-VI-40, T. H. Frison et al.; 8 ♀ and 14 ♂ nymphs, Hazelwood, N. C., 24-IV-38, H. H. Ross and B. D. Burks, 3 ♀ and 2 ♂ nymphs in collection University of Utah, all others in collection Illinois State Natural History Survey; 2 ♀ and 2 ♂ nymphs, Black Gap, N. C., 24-IV-38, H. H. Ross and B. D. Burks; 3 ♀ and 5 ♂ nymphs, Smokemont, N. C., 11-V-44, T. H. Frison and H. H. Ross, 1 ♀ and 1 ♂ nymphs in collection University of Utah, all others in collection Illinois State Natural History Survey.

Remarks.—*E. crenula* appears to be most closely allied to *E. simila*, n. sp., as they both possess small paired submedian tubercles on the prothorax (Fig. 38), have small round paired abdominal tubercles (Fig. 37, 39), brown bands on the caudal filaments, and both are known from the Southeastern United States. *E. crenula* is readily distinguished from *E. simila* because it lacks paired suboccipital tubercles, possesses short femoral spines and has bands on tibiae and tarsi (Fig. 58), and has paired abdominal tubercles only on segments 3–8 (Fig. 37).

E. crenula appears to be variable in the degree of development of the thoracic and abdominal tubercles. The thoracic tubercles vary in size within specific populations, but they are always present. The paired dorsal abdominal tubercles are variable in size and shape. Some populations have comparatively longer and sharper tubercles than others.

The relationships of *E. crenula* and *E. simila* to the other species of the subgenus are not clear. In some respects they are similar to *E. aurivillii* but in others are rather similar to the *E. invaria* complex. The relationships will probably be clarified only when the adults are known.

Ephemerella simila, new species
(Fig. 38–39, 57, 69, 80)

Mature Nymph.—Length: body 8–9; caudal filaments 4.5–5.5 mm. General color brown with numerous light brown or pale markings. Head brown with pale vermiculate markings on the vertex; with or without a pale transverse stripe crossing the face at the anterior margin of the eyes; females with small suboccipital tubercles covered with spicules (Fig. 69). Thoracic notum brown with light brown vermiculate markings, lateral margins of pronotum pale; pronotum with small paired submedian tubercles covered with spicules (Fig. 38); mesonotum with spicules; femora light brown or pale with indistinct brown markings; forefemora with a subapical band of long spines (Fig. 57); tibiae light brown or pale; tarsi light brown with a brown band near the middle; tarsal claws with 4–6 denticles. Abdominal terga with paired submedian tubercles on segments 2–8, tubercles barely discernible or absent on segment 2 and small on segment 8, tubercles better developed and sharp on segments 3–7 (Fig. 39a); terga with spicules (Fig. 39b); terga brown with light brown markings; postero-lateral projections on segments 4–9; abdominal sterna light brown. Caudal filaments with whorls of spines at apex of segments in basal ⅔, distal segments setaceous; filaments light brown with several brown bands.

Holotype.—Mature female nymph, Fellowsville, W. Va., 30-IV-44, T. H. Frison and H. H. Ross, in collection Illinois State Natural History Survey, Urbana. Paratopotypes: 5 ♀ and 9 ♂ nymphs, same data, 2 ♀ and 2 ♂ nymphs in collection University of Utah, Salt Lake City, all others in collection Illinois State Natural History Survey.

Remarks.—*E. simila* is allied to *E. crenula* but may be differentiated as noted in the remarks on the latter species.

Ephemerella rossi, new species
(Fig. 40, 59, 81)

Ephemerella sp. no. 5 Traver 1937, 70.

Mature Nymph.—Length: body 6.0–7.5; caudal filaments 3.0–4.5 mm. General color brown with light brown markings. Head brown with pale vermiculate markings on the vertex; without a pale transverse stripe crossing the face; occiput without tubercles, but with spicules. Thoracic notum brown with ornate darker markings, without tubercles, but with scattered spicules; legs unicolorous light brown; forefemora with a subapical band of short spines (Fig. 59); tarsal claws with 3–5 denticles. Abdominal terga with small blunt paired submedian tubercles on segments 4–9, tubercles barely discernible or absent on terga 9, small on segments 5–8 (Fig. 40a); terga with paired submedian bands of spicules, spicules on tubercles and posterior margin of segments (Fig. 40b); terga brown with pale patches mediad of the gills on segments 5–8; distinct long postero-lateral projections on segments 4–9; abdominal sterna light brown. Caudal filaments with whorls of heavy spines at apex of segments in basal ⅔, distal segments setaceous; filaments unicolorous brown.

Holotype.—Mature female nymph, Fighting Creek Gap, Gatlinburg, Tenn., 15-V-39, T. H. Frison and H. H. Ross, in collection of Illinois State Natural History Survey, Urbana. Paratopotypes: 2 ♀ and 1 ♂ nymphs, same data, in collection Illinois State Natural History Survey. Paratypes: 8 ♀ and 6 ♂ nymphs, Smoky Mountain, Tenn., 11-VI-31, J. G. Needham, 1 ♀ and 1 ♂ nymphs in collection University of Utah, Salt Lake City, all others in collection J. R. Traver, Amherst, Mass.; 1 ♀ and 1 ♂ nymphs, Mt. LaConte, Tenn., 14-VIII-29, J. R. Traver, in collection J. R. Traver; 4 ♀ nymphs, LaConte Creek, Gatlinburg, Tenn., 14-V-39, T. H. Frison and H. H. Ross, in collection Illinois State Natural History Survey; 6 ♀ and 3 ♂ nymphs, Gatlinburg, Tenn., 19-VI-40, T. H. Frison et al., 3 ♀ and 1 ♂ nymphs in collection University of Utah, all others in collection Illinois State Natural History Survey; 7 ♀ and 1 ♂ nymphs, LaConte Creek, Gatlinburg, Tenn., 14-VI-40, T. H. Frison et al., in collection Illinois State Natural History Survey.

Remarks.—*E. rossi* is similar to *E. crenula* and *E. simila* in some respects but in others appears nearer to *E. aurivillii.* These species are known from the same geographical area and the paired dorsal abdominal tubercles are similar in shape, position, and number. *E. rossi* may be distinguished from these species and all other species of *Ephemerella,* s. s., by the following combination of characters: They have (1) heavily spiculated paired dorsal abdominal tubercles on segments 4–9 (Fig. 40), (2) a short narrow band of subapical spines on the fore-femora (Fig. 59), (3) long postero-lateral projections on segments 4–9, and they lack (4) thoracic tubercles and (5) brown bands on the caudal filaments. We take pleasure in naming this species in honor of Dr. Herbert H. Ross, Head of Section, Section of Faunistic Surveys and Insect Identification, Illinois State Natural History Survey, Urbana.

Ephemerella hispida, new species
(Fig. 45, 79)

Ephemerella sp. no. 4 Traver 1937, 69.

Mature Nymph.—Length: body 8–12 (mature male nymph 8–9 mm; mature female nymph 10–12 mm); caudal filaments 6–8 mm. General color light brown, with slightly darker brown markings. Head brown, with light brown vermiculate markings; without occipital tubercles. Thoracic notum brown with irregular dark brown maculae; thoracic notum very irregular and furrowed, but without tubercles; thorax with a complex pattern of fine spicules; legs unicolorous brown except apex of tibiae darker, with spines and setae; forefemora with a subapical band of spines; tarsal claws with 8–10 denticles. Abdomen brown, progressively darker toward segment 10; terga with paired submedian tubercles on segments 1–9, tubercles small to barely discernible on segment 1, increasing in size on segments 2–7, and decreasing in size on segments 8–9 (Fig. 45); all tubercles covered with small spicules; distinct postero-lateral projections on segments 4–9; each abdominal sternum with paired sublateral maculae. Caudal filaments brown with whorls of apical segmental spines on segments in basal ⅔ and sparse setae on distal segments; filaments brown, progressively darker distally.

Holotype.—Mature male nymph, Twenty Mile Creek, Great Smoky Natl. Park, N. C., 3-IV-34, J. G. Needham, in collection of J. R. Traver, Amherst, Mass. Allotype: Mature female nymph, Twenty Mile Creek, Great Smoky Natl. Park, N. C., 4-IV-34, J. G. Needham in collection of J. R. Traver, Amherst, Mass. Paratopotypes: 23 ♀ and 5 ♂ nymphs, 2 ♂ and 4 ♀ nymphs in collection of University of Utah, Salt Lake City; 6 ♀ nymphs and 1 ♂ nymph in collection of Cornell University, Ithaca, N. Y., others in collection of J. R. Traver. Paratypes: 1 ♀ and 1 ♂ nymphs, Hazel Creek, Great Smoky Natl. Park, N. C., 4-IV-34, J. G. Needham, in collection of Cornell University; 1 ♂ nymph, Tributary Little River, Elkmont, Tenn., 14-V-39, T. H. Frison and H. H. Ross, in collection of Illinois State Natural History Survey, Urbana, Ill.

Remarks.—*E. hispida* is known from only the nymphal stage and superficially appears closely related to either *E. aurivillii* (Bengtsson) or *E. needhami* McDunnough. The paired dorsal abdominal tubercles are reminiscent of both species, and they are large, especially on female nymphs, as is the case with *E. aurivillii.* This species may be distinguished from all known *Ephemerella,* s. s., by the combination of size, general color, and the arrangement, shape, and number of paired dorsal abdominal tubercles (Fig. 45).

Ephemerella berneri Allen and Edmunds
(Fig. 42, 53, 81)

Ephemerella berneri Allen and Edmunds 1958, 222, 7 Fig.

This species is known in the nymphal stage only.

Mature Nymph.—Length: body 11–13; caudal filaments 8–9 mm. General color brown with black markings. Head without occipital tubercles. Thoracic notum with small paired submedian pronotal and mesonotal tubercles and a larger median tubercle between wing pads; legs short and thick; legs pale, without distinct markings and without femoral spines (Fig. 53); tarsal claws with 8–10 denticles. Abdominal terga with paired submedian tubercles on segments 1–10; tubercles on segments 1 and 10 small, long on segments 2–9 (Fig. 42); abdominal terga pale, paired dorsal abdominal tubercles and postero-lateral projections black; distinct postero-lateral projections on segments 3–9; abdominal sterna pale, without conspicuous markings. Caudal filaments without whorls of spines on apex of basal segments and only sparsely setaceous on distal segments; filaments light brown.

Type-Locality.—Flat Shoals, Flint River, 5.6 mi. W Concord, Pike Co., Ga.

Type.—Illinois State Natural History Survey, Urbana, Ill.

DISTRIBUTION

E. berneri is known from only the type locality in Georgia and from Piney River, Amherst Co., Va., 24-IV-53, J. Pugh (UU, UF) (Fig. 81).

TAXONOMY

This species is one of the most distinctive in the subgenus and may be distinguished from all other known species by the great development of the paired dorsal abdominal tubercles (Fig. 42).

Ephemerella septentrionalis McDunnough

(Fig. 19, 52, 75, 81)

Ephemerella septentrionalis McDunnough 1925b, 171, 1 Fig.; McDunnough 1931b, 201, 1 Fig. (nymph); Steger 1931, 34, 5 Fig.; Traver 1932, 146; Traver 1935, 618, 1 Fig.; Traver 1937, 68.

McDunnough (1925b) described this species from a single male imago, and McDunnough (1931b) and Steger (1931) wrote descriptions for all stages.

Male Imago (dry).—Length: body 9–10; forewing 9–10 mm. Compound eyes reddish brown, lower portion grayish. Thorax yellowish brown; legs yellow; each femur with a brown subapical macula; legs long and slender; length of segments of foreleg in millimeters: femur = 2.5; tibia = 3.7; tarsus I = 0.3; tarsus II = 1.7; tarsus III = 2.1; tarsus IV = 1.4; tarsus V = 0.7; wings hyaline; venation pale. Abdominal terga 1–7 light brown and translucent, terga 6–7 darker, middle abdominal segments paler and more translucent anteriorly, terga 8–10 reddish brown and opaque; abdominal sterna yellowish, sterna 2–8 often with paired submedian spots and oblique dashes. Penes with or without spines, usually with 1–5 medial spines, position of spines usually as in Fig. 19; penes deeply emarginate with long lateral lobes; 2nd segment of genital forceps with a slight apical expansion (Fig. 19); posterior margin of subgenital plate with a distinct conical tubercle between forceps bases. Caudal filaments pale with dark annulations at apex of each segment.

Mature Nymph.—Length: body 9–10; caudal filaments 7–8 mm. General color brown with variable light brown markings, often with a pale median stripe divided at the midline by a narrow dark brown stripe on the thorax and abdomen. Head brown; without occipital tubercles, but with paired tufts of hair mediad of the compound eyes. Thoracic notum brown, mesonotum often with a dark brown transverse band; thoracic notum setaceous; mesonotum with paired low submedian ridges; legs long and slender; femora brown, often with 1 or 2 darker brown bands; forefemora without a subapical band of spines; tibiae and tarsi each with a dark band near the middle of the segment (Fig. 52); tarsal claws with 11–14 denticles (Fig. 75). Abdominal terga 2–7 with a small round median tubercle; distinct postero-lateral projections on segments 4–9; abdominal sterna light brown with paired sublateral dark maculae enclosed in pale areas. Caudal filaments with whorls of long spines at the apex of each segment and with long setae distally; filaments light brown with several brown bands.

Type-Locality.—Little Current Creek, Thunder Bay District, Ontario, Canada.

Type.—No. 1330, Canadian National Collection, Ottawa, Ontario.

DISTRIBUTION

This species is known from Ontario, Quebec, and New Brunswick austrad to North Carolina (Fig. 81). We have examined specimens from:

MASSACHUSETTS: Amherst, 1/5-VI-45, J. R. Traver (JRT); Bachelor Brook, S. Hadley, 14-V-49, J. R. Traver and T. Dolan (JRT). NEW BRUNSWICK: NW Miramichi River, 6-VI-51, E. L. Bousefield. NEW YORK: Beaverkill, 2-VI-35, H. T. Spieth (AMNH); St. Regis River, Ft. Jackson, 20-VI-32, L. Harker (JRT). NORTH CAROLINA: Valle Crucis, 27-V-36, J. R. Traver (JRT). ONTARIO: Little Current Creek, Thunder Bay District, 11-VII-03, W. J. Wilson (Holotype) (CNC). QUEBEC: Knowlton, 25-VI-29, G. S. Walley (CNC).

TAXONOMY

E. septentrionalis nymphs and male adults exhibit very little morphological variability and are readily distinguished from all other known species in the subgenus.

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