

PRIVATE LIBRARY  
OF WILLIAM L. PETERS

8

4

# Miscellaneous Publications

OF THE  
Entomological Society of America



VOLUME 3

NUMBER 5

NOVEMBER, 1962

(Number 5 completes Volume 3)

Published by the  
ENTOMOLOGICAL SOCIETY OF AMERICA

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

RICHARD K. ALLEN AND GEORGE F. EDMUNDS, JR.

CONTENTS

|  |     |  |     |
|--|-----|--|-----|
| Abstract . . . . .                           | 147 | E. <i>conestee</i> Traver . . . . .                | 162 |
| Introduction . . . . .                       | 147 | E. <i>wayah</i> Traver . . . . .                   | 162 |
| Taxonomy . . . . .                           | 147 | E. <i>walkeri</i> Eaton . . . . .                  | 162 |
| Subgenus <i>Drunella</i> Needham . . . . .   | 147 | E. <i>doddsi</i> Needham . . . . .                 | 163 |
| Keys to the species and subspecies . . . . . | 149 | E. <i>pelosa</i> Mayo . . . . .                    | 164 |
| E. <i>lata</i> Morgan . . . . .              | 153 | E. <i>grandis</i> Eaton . . . . .                  | 166 |
| E. <i>cornuta</i> Morgan . . . . .           | 155 | E. <i>grandis grandis</i> Eaton . . . . .          | 171 |
| E. <i>cornutella</i> McDunnough . . . . .    | 156 | E. <i>grandis ingens</i> McDunnough . . . . .      | 175 |
| E. <i>longicornis</i> Traver . . . . .       | 157 | E. <i>grandis flavitincta</i> McDunnough . . . . . | 176 |
| E. <i>coloradensis</i> Dodds . . . . .       | 157 | E. <i>spinifera</i> Needham . . . . .              | 176 |
| E. <i>flavilinea</i> McDunnough . . . . .    | 159 | Acknowledgments . . . . .                          | 178 |
| E. <i>alleghehiensis</i> Traver . . . . .    | 160 | References Cited . . . . .                         | 178 |
| E. <i>tuberculata</i> Morgan . . . . .       | 161 |  |     |



# A Revision of the Genus *Ephemerella* (Ephemeroptera, Ephemerellidae)

## V. The Subgenus *Drunella* in North America

RICHARD K. ALLEN AND GEORGE F. EDMUNDS, JR.<sup>1</sup>

University of Utah, Salt Lake City

### ABSTRACT

The relationships and taxonomy of the known North American species of the subgenus are discussed. Of the 23 specific names heretofore recognized, the number is reduced to 15 valid species by new synonymies and the reduction of two to subspecific rank. *Ephemerella grandis* Eaton is polytypic, with subspecies *E. g. grandis* Eaton, new status (= *glacialis carsona* Day, new synonymy), *E. g. ingens* McDunnough, new status (= *glacialis* Traver, *proserpina* Traver, new synonymies), and *E. g. flavitincta* McDunnough, new status. Additional

new synonymies are as follows: *Ephemerella cornuta* Morgan (= *depressa* Ide), *E. tuberculata* Morgan (= *cherokee* Traver), *E. flavilinea* McDunnough (= *lapidula* McDunnough), *E. coloradensis* Dodds (= *wilsoni* Mayo) and *E. spinifera* Needham (= *autumnalis* McDunnough, *sierra* Mayo). Geographical or age variation, or both, are described, especially for the nymphs, of most species of the subgenus. Illustrated keys are given to the nymphs, and to the adults as far as known; and complete synonymies and distributions are included.

### 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, and Part IV (Allen and Edmunds 1962) with the subgenus *Dannella* Edmunds.

In the accounts that follow dealing with the species of the subgenus *Drunella*, collections made by the authors are indicated by initials, GFE and/or RKA. Abbreviations for collections in which specimens are deposited are as follows: AMNH, American Museum of Natural History; CAS, California Academy of Sciences; CNC, Canadian National Collection; CU, Cornell University; INHS, Illinois State Natural History Survey; BLL, B. L. Lambuth Collection; VKM, V. K. Mayo Collection; OSC, Oregon State University; SC, Sheridan College; JRT, J. R. Traver Collection; UCLA, University of California, Los Angeles; UCS, University of California, Sagehen Creek Station; UM, University of Massachusetts; and UN, University of Nebraska. Specimens without designation are deposited in the collection of the University of Utah.

### AGE AND GEOGRAPHICAL VARIATION

The nymphal forms of the 15 North American species of the subgenus *Drunella* are widely distributed, and are adapted to a variety of stream conditions. The nymphs of most species in the subgenus have tubercles on the dorsal surface of the body. In some of these species, the position, length, and sharpness of the tubercles are quite constant, while in others they are extremely variable. The variability in these nymphal structures is usually not of taxonomic importance, as it is observed among nymphs collected from the same stream; however, an interesting phenomenon has been noted in populations

of many species inhabiting the streams of the Coast Ranges and Cascade-Sierra Nevada Ranges of Western North America. These populations have longer and sharper head, thoracic, and abdominal tubercles than nymphs occurring in the inland mountain streams. *Ephemerella doddsi* Needham, *E. coloradensis* Dodds, and *E. flavilinea* McDunnough are three of the species which exhibit this interesting morphological variation.

Three eastern North American species, *E. cornuta* Morgan, *E. cornutella* McDunnough, and *E. tuberculata* Morgan also vary geographically.

Age differences have been noted in the nymphal stage of many species of the western North American *Ephemerella*, especially in those nymphs which possess dorsal tubercles. The comparative size of these tubercles has been found to be dependent upon allometric growth. Two general patterns have been observed: (1) In early instar nymphs any pair of the dorsal tubercles may be relatively small or absent, and they grow more rapidly than the rest of the body and become comparatively longer with each successive molt. (2) In early instar nymphs any pair of the dorsal tubercles may be long, in some species more than twice their relative length in mature nymphs, and the tubercles become proportionately smaller with each exuviation. In general, age variation is such a common phenomenon in the nymphs of all species of *Drunella* that identification of immature nymphs should be made with caution, and immature nymphs should never be named as new species.

### Subgenus *Drunella* Needham

*Drunella* Needham 1905, 42 (as genus); type by original designation *grandis* Eaton; Clemens 1913, 337; Clemens 1915, 124; Dodds 1923, 95; Needham 1927b, 108 (as subgenus); Seemann 1927, 45; McDunnough 1931c, 210 (= *Eatonella*); Ulmer 1932, 205; Spieth 1933, 353; Edmunds and Traver 1954, 238; Demoulin 1958, 10; Edmunds 1959, 546.

*Eatonella* Needham 1927b, 108 (as subgenus).

(*Ephemerella*) *cornuta* group McDunnough 1931a, 31.

(*Ephemerella*) Section IV McDunnough 1931c, 210.

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

(*Ephemerella*) *fuscata* group Traver 1932, 144; Traver 1935, 564.

(*Ephemerella*) *walkeri* group Burks 1953, 64.

Needham (1905) erected *Drunella* for the species *Ephemerella grandis* Eaton. In 1927, he reduced it from generic to subgeneric rank, and erected the subgenus *Eatonella* for the species *E. doddsi* Needham. McDunnough (1931c) placed *E. grandis* and *E. doddsi* in his section IV and declared *Eatonella* to be a synonym of *Drunella*. Traver (1932, 1935) followed McDunnough's sections, but referred to them as species groups and thus called section IV the *fuscata* group. Following Spieth's (1940) placement

of *E. fuscata* (Walker) as a junior synonym of *E. walkeri* Eaton, Burks (1953) applied the term *walkeri* group for the species in this subgenus. Edmunds and Traver (1954), in listing the Holarctic Ephemerellidae, included *Drunella* as a subgenus. Demoulin (1958) and Edmunds (1959) followed this arrangement.

The subgenus *Drunella* may be characterized in the adult male stage by: (1) the terminal segment of the genital forceps being two to three times as long as broad (figs. 5-10), (2) the long second segment of the genital forceps being more or less distinctly bowed (figs. 5-10), and (3) the penes being without

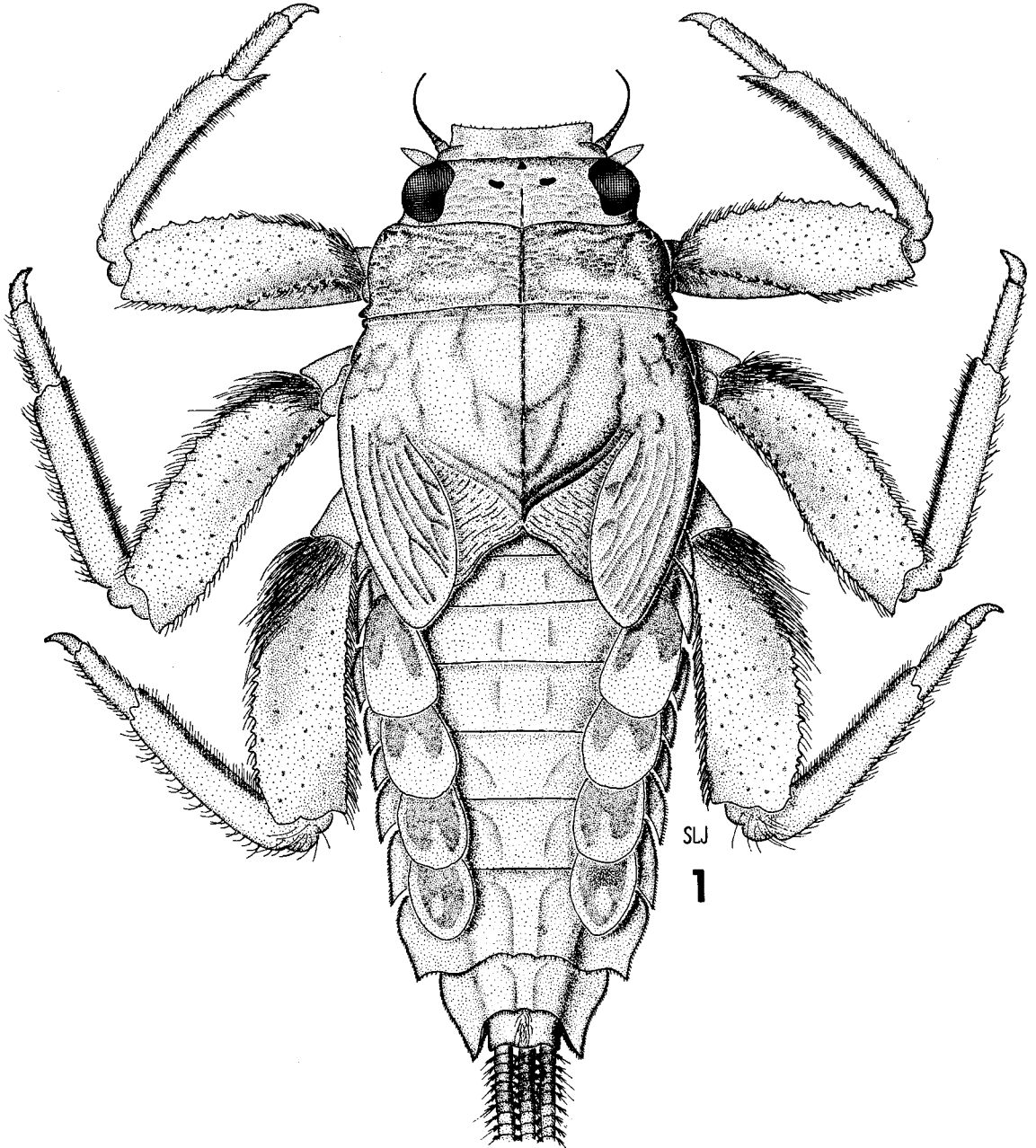


FIG. 1.—*Ephemerella doddsi*, mature female nymph, dorsal view.

lateral tubercles, lobes, or dorsal or ventral spines. The nymphal stage (fig. 1) is characterized by: (1) having gills on abdominal segments 3-7, (2) the terminal filament and lateral cerci being subequal and fringed with long hair, (3) the tarsal claws usually having only a few denticles (1-4), and (4) tubercles usually being present on the ventral margin of the forefemora (figs. 42-49); when tubercles are lacking on the forefemora (figs. 50 and 62), paired tufts of hair or well-developed tubercles are present on the occiput, thorax, and abdomen (figs. 55-57).

The subgenus *Drunella* as treated herein contains only fifteen valid North American species: *Ephemerella lata* Morgan (= *inflata* McDunnough 1926, 187), *E. cornuta* Morgan (= *depressa* Ide 1930, 212, new synonymy), *E. cornutella* McDunnough, *E. longicornis* Traver, *E. coloradensis* Dodds (= *wilsoni* Mayo 1952, 100, new synonymy), *E. flavilinea* McDunnough (= *lapidula* McDunnough 1935, 96, new synonymy), *E. tuberculata* Morgan (= *cherokee* Traver 1932, 175, new synonymy), *E. allegheniensis* Traver, *E. conestee* Traver, *E. wayah* Traver, *E. walkeri* Eaton (= *fuscata* Walker 1853, 570, nec Stephens 1835, 66; *bispina* Needham 1905, 43), *E. doddsi* Needham, *E. grandis* Eaton (= *glacialis* Traver 1934, 207, new synonymy; *proserpina* Traver 1934, 223, new synonymy; *yosemite* Traver 1934, 225), *E. spinifera* Needham (= *autumnalis* McDunnough 1934, 158, new synonymy; *sierra* Mayo 1952, 96, new synonymy), and *E. pelosa* Mayo.

The nymphal stages of the species included in the subgenus *Drunella* are diverse in structure and are adapted to a variety of stream habitats. The nymphal head is modified in various ways; some species have large occipital tubercles, others have a broad frontal shelf and genae which are broadly produced with antero-lateral projections. All except three species have broad flattened forefemora with tubercles on the ventral (leading) edge. The presence of paired dorsal body tubercles is a character common in *Ephemerella*. The development of these structures is extreme in some species of *Drunella* as they have long and sharp dorsal tubercles on all body regions; in others they are moderately developed, small, or completely lacking. Most species possess ventral abdominal hair, but in two species the hair is abundant and modified so as to form an adhesive disc.

On the basis of these and other nymphal characters groups of closely related species are easily recognized. The male imago of several species is unknown, but where known the male genitalia appear to reflect the same groupings suggested by the nymphs.

*Ephemerella lata*, *E. cornutella*, *E. cornuta*, and *E. longicornis* form a compact species-group. They all possess lateral frontoclypeal projections on the head (figs. 21-24) and are without dorsal body tubercles, although they have small paired submedian ridges on the abdominal terga.

*Ephemerella coloradensis* and *E. flavilinea* are cognate species which are difficult to distinguish from each other in both the nymphal and adult stages.

These species are characterized by having small paired abdominal tubercles on terga 1-9, by lacking thoracic tubercles, and by being without head projections except that they may have small occipital tubercles (figs. 38-41).

*Ephemerella allegheniensis* and *E. tuberculata* are closely related species characterized by having well-developed occipital tubercles (figs. 34-35), a large median tubercle on the metanotum, and small paired abdominal tubercles on terga 2-7 or 2-8.

*Ephemerella wayah* and *E. walkeri* are closely related as they have heads with a broad round frontal shelf, expanded genae with moderately developed antero-lateral projections (figs. 26-27), and suboccipital, prothoracic, and small abdominal tubercles. *Ephemerella conestee* appears to be allied to the above-mentioned species as it possesses a round frontal shelf and expanded genae (fig. 25). It differs, however, from *E. walkeri* and *E. wayah* in that its genae are only narrowly expanded and the head has well-developed occipital tubercles and moderately developed lateral frontoclypeal tubercles. The nymph of *E. doddsi* is very distinctive and the most easily recognized species in the subgenus. The head has a broad square frontal shelf and genae which are produced into long antero-lateral projections. It is a robust nymph with broad flattened femora all margined with tubercles on the anterior edge and with ventral abdominal hair which is modified into an adhesive disc (fig. 1).

*Ephemerella pelosa* is the most aberrant species in *Drunella*. This species lacks body tubercles, but has paired submedian tufts of hair on the head, thorax, and abdomen. Its femora are without tubercles, but margined with thick hair (fig. 50), and it has a partial adhesive disc analogous to that of *E. doddsi*. The inclusion of *E. pelosa* in this subgenus is only tentative; it is placed here because its features are most similar to those found in *Drunella*. When the adult is known its systematic position can be determined with more confidence.

Nymphs of *E. grandis* and *E. spinifera* are distinguished as a species-group as they possess well-developed occipital, thoracic, and abdominal tubercles (figs. 56 and 68); lack tubercles on the ventral (leading) edge of the forefemora (fig. 62); and usually have a moderate number of denticles (4-8) on the tarsal claws.

The following keys will serve to distinguish the species and subspecies of the subgenus *Drunella*.

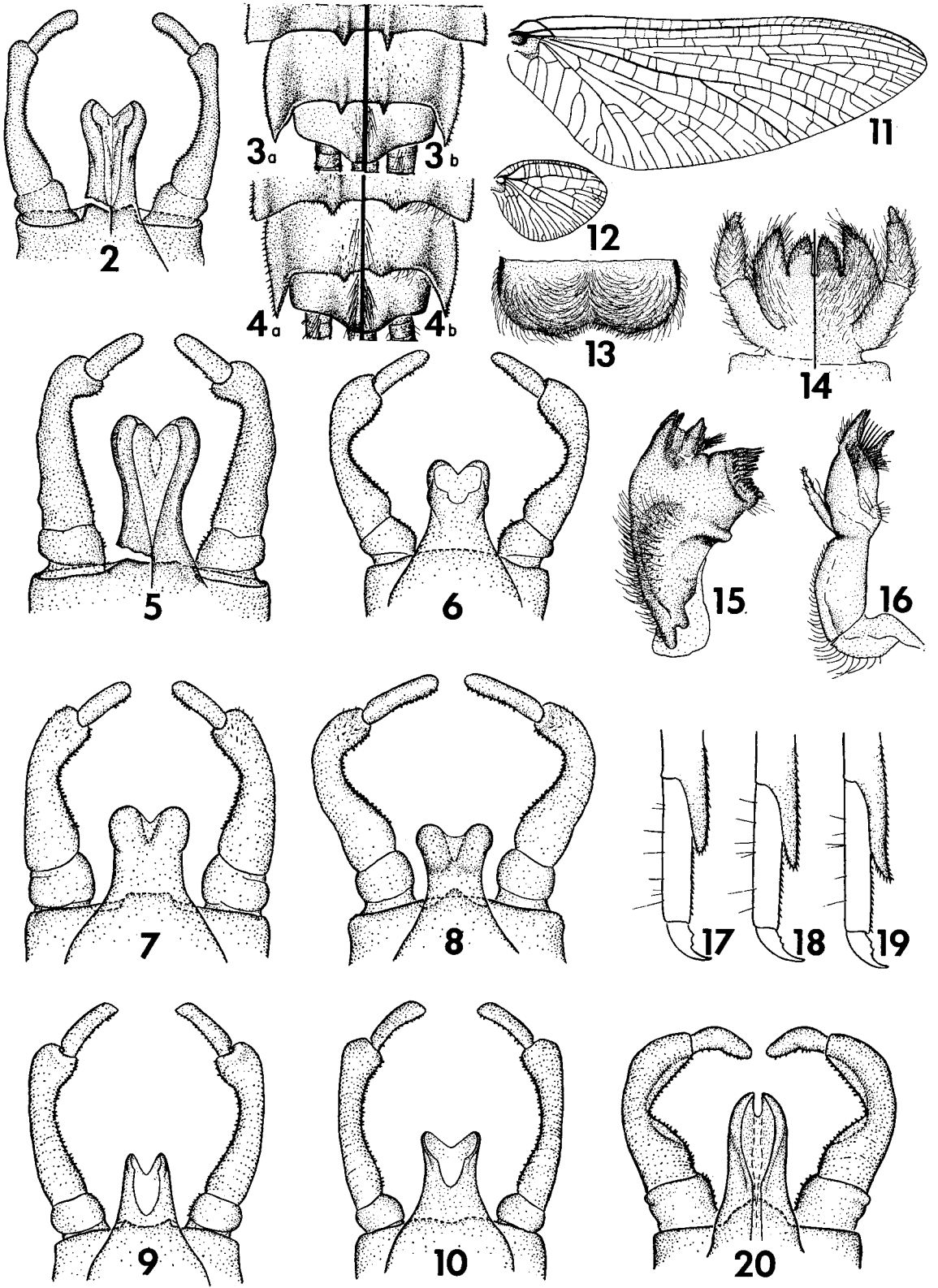
#### MALE IMAGOS<sup>2</sup>

1. Western North American species, eastern limits in New Mexico, Colorado, Wyoming, Montana, and Alberta..... 2
- Eastern North American species, western limits in Michigan, Illinois, and Ontario..... 8
- 2(1). Second segment of genital forceps strongly bowed, with a deep constriction near the middle; lobes of penes constricted apically (fig. 20) ..... **doddsi**

<sup>2</sup> The male imagoes of *E. longicornis* Traver, *E. conestee* Traver, *E. wayah* Traver and *E. allegheniensis* Traver are unknown.

Second segment of genital forceps may be strongly bowed but without a deep constriction; lobes of penes expanded apically..... 3

3(2). Sub-genital plate between bases of forceps produced and with a broad V-shaped emargination (figs. 2 and 65)..... 4

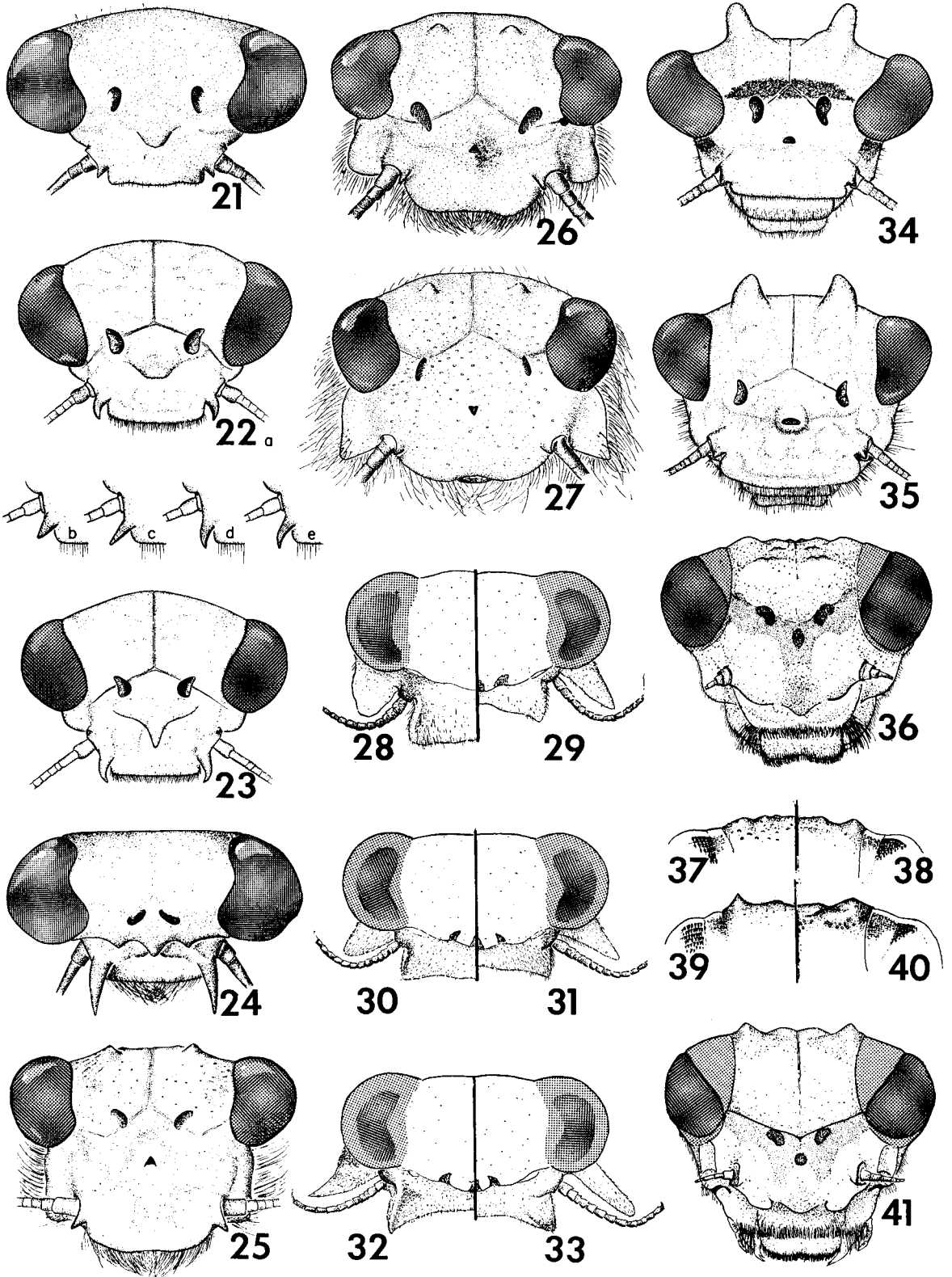


- Sub-genital plate between bases of forceps not produced and with only a shallow emargination (figs. 5 and 61)..... 5
- 4(3). Penes with a V-shaped apical median cleft (fig. 2) ..... **coloradensis**  
 Penes with a U-shaped apical median cleft (fig. 65) ..... **spinifera**
- 5(3). Apical lateral margin of penes expanded, apical portion of second segment of forceps strongly bowed (fig. 5); foreleg 11-13 mm. in length ..... **flavilinea**  
 Apical lateral margin of penes not expanded, sides nearly parallel, second segment of forceps not apically bowed (fig. 61); foreleg 15-17 mm. long ..... **grandis**..... 6
- 6(5). Forewings deep amber, apical portion hyaline ..... **grandis flavitincta**  
 Forewings hyaline or with suffusion of light amber in basal portion..... 7
- 7(6). Forewings with suffusion of light amber in basal portion..... **grandis ingens**  
 Forewings hyaline..... **grandis grandis**
- 8(1). Second segment of genital forceps strongly bowed (figs. 6 and 8)..... 9  
 Second segment of genital forceps only moderately bowed (figs. 2, 7, 9, and 10)..... 10
- 9(8). Second segment of genital forceps with a deep constriction midway of its length; sub-genital plate gently arched; and penes as in fig. 6..... **lata**  
 Second segment of genital forceps without a deep constriction; sub-genital plate with a blunt, median projection; and penes as in fig. 8 ..... **cornuta**
- 10(8). Hind femora with numerous small black dots ..... 11  
 Hind femora without numerous small black dots; genitalia as in fig. 7..... **cornutella**
- 11(10). Abdominal sterna with two submedian black dots and two sublateral oblique dashes; genitalia as in fig. 9..... **tuberculata**  
 Abdominal sterna without maculae; genitalia as in fig. 10..... **walkeri**
- MATURE NYMPHS<sup>a</sup>
1. Ventral (leading) edge of forefemora without tubercles (figs. 50 and 62)..... 2  
 Ventral (leading) edge of forefemora with tubercles (figs. 42-49)..... 6
- 2(1). Margins of forefemora with a dense row of long hair (fig. 50); abdominal sterna 3-8 with an adhesive disc of long hair..... **pelosa**  
 Margins of forefemora with only scattered hair, not arranged in a marginal row (fig. 62); abdominal sterna without an adhesive disc ..... 3
- 3(2). Paired dorsal abdominal tubercles on segments 8 and 9 more than twice as long as those on the preceding segments (fig. 67); mesonotum with three pairs of sharp tubercles, and a single median posterior tubercle (fig. 68)..... **spinifera**  
 Paired dorsal abdominal tubercles on segments 8 and 9 subequal to or slightly longer than those on the preceding segments (fig. 63); mesonotum with one or two pairs of blunt to sharp tubercles and a single median posterior tubercle (figs. 55-57).....  
 ..... **grandis**..... 4
- 4(3). Mesonotum with a submedian pair of low ridges (fig. 55); occipital tubercles short and blunt (fig. 60)..... **grandis grandis**  
 Mesonotum with a submedian pair of tubercles (figs. 56-57); occipital tubercles longer than above (figs. 58-59)..... 5
- 5(4). Head and body tubercles long, thin, and acute (figs. 57-58)..... **grandis flavitincta**  
 Head and body tubercles shorter and blunter than above (figs. 56 and 59)..... **grandis ingens**
- 6(1). Abdominal sterna with a mass of hair forming a complete adhesive disc; ventral (leading) edge of all femora with tubercles (fig. 1)..... **doddsi**  
 Abdominal sterna may have sparse hair, but never forming an adhesive disc; ventral (leading) edge of femora of second and third legs without tubercles..... 7
- 7(6). Abdomen without paired dorsal tubercles, but may have paired ridges as in fig. 1; head smooth, without paired occipital tubercles (figs. 21-24) ..... 8  
 Abdomen with paired dorsal tubercles, always well-developed on segments 5-7; head roughened (figs. 36-37), with paired sub-occipital tubercles (figs. 26-27), or with small (figs. 25, 38-41) to large (figs. 34-35) paired occipital tubercles..... 11
- 8(7). Head with short lateral frontoclypeal projections, never longer than broad (fig. 21)..... **lata**  
 Head with long lateral frontoclypeal projections, always longer than broad (figs. 22-24) ..... 9

<sup>a</sup> Mature nymphs may be recognized by the presence of black wing pads or by folded wings inside the wing pads. The key is designed to be usable, in most cases, whenever the nymphs have moderately developed wing pads.

FIGS. 2-3.—*Ephemerella coloradensis*: fig. 2, dorsal view male genitalia, cut away; fig. 3a, left side abdominal terga 8-10 (from Yellowstone Natl. Pk., Wyoming); fig. 3b, right side abdominal terga 8-10 (from southeast Alaska). FIGS. 4-5.—*E. flavilinea*: fig. 4a, left side abdominal terga 8-10 (from Yosemite Natl. Pk., California); fig. 4b, right side abdominal terga 8-10 (from Yellowstone Natl. Pk., Wyoming); fig. 5, dorsal view male genitalia, cut away. FIGS. 6-10.—Subgenus *Drunella*, dorsal view male genitalia: fig. 6, *E. lata*; fig. 7, *E. cornutella*; fig. 8, *E. cornuta*; fig. 9, *E. tuberculata*; fig. 10, *E. walkeri*. FIGS. 11-16.—*E. g. grandis*: fig. 11, forewing male imago; fig. 12, hindwing male imago; fig. 13, labrum; fig. 14, labium, dorsal and ventral; fig. 15, left mandible; fig. 16, maxilla. FIGS. 17-19.—Subgenus *Drunella*, apical portion of left nymphal forelegs: fig. 17, *E. cornutella*; fig. 18, *E. cornuta*; fig. 19, *E. longicornis*. FIG. 20.—*E. doddsi*, dorsal view male genitalia.





- 9(8). Lateral frontoclypeal projection long, more than half as long as interval between them (fig. 24); apex of tibial projection sharp and curved (fig. 19).....**longicornis**  
Lateral frontoclypeal projections moderate in length, less than half as long as interval between them (figs. 22-23); apex of tibial projection blunt to moderately sharp and straight (figs. 17-18).....10
- 10(9). Mature nymph 9-11 mm. in length; median ocellar tubercle sharp, lateral frontoclypeal projections usually semilunar (fig. 23).....**cornuta**  
Mature nymph 6-8 mm. in length; median ocellar tubercle blunt to moderately sharp, lateral frontoclypeal projections moderately curved to straight (figs. 22a-e).....**cornutella**
- 11(7). Head with long occipital tubercles (figs. 34-35); mesothorax with a long median posterior tubercle .....12  
Head roughened (fig. 36), with suboccipital tubercles (figs. 26-27), or with only small occipital tubercles (figs. 25, 41); mesothorax with only a very short median posterior tubercle .....13
- 12(11). Occipital tubercles diverge apically, frons with a dark horizontal band (fig. 34); mesothorax with a very long median posterior tubercle; forefemora as in fig. 44.....**alleggheniensis**  
Occipital tubercles not divergent apically, frons without a dark horizontal band (fig. 35); mesothorax with a moderately long median posterior tubercle; forefemora as in fig. 43.....**tuberculata**
- 13(11). Head with a broad frontal shelf, covering mouthparts anteriorly, genae produced into wide flanges (figs. 25-26) or antero-lateral projections (fig. 27); abdomen with paired dorsal tubercles on segments 3-7 or 4-7.....14  
Head without a broad frontal shelf, mouthparts visible anteriorly, genae not produced into flanges or projections (figs. 36, 41); abdomen with paired dorsal tubercles on segments 1-9 .....16
- 14(13). Head with small occipital tubercles and moderate lateral frontoclypeal projections (fig. 25); forefemora as in fig. 45.....**conestee**  
Head with only small suboccipital bumps and with barely discernible lateral frontoclypeal projections (figs. 26-27); forefemora as in figs. 46-47 .....15
- 15(14). Genae produced into sharp antero-lateral projections, frontal shelf as in fig. 27; prothorax with small paired tubercles near the middle of the segments on the lateral margin; forefemora with long hair and as in fig. 47 .....**walkeri**  
Genae produced into blunt antero-lateral projections, frontal shelf as in fig. 26; prothorax without tubercles; forefemora without long hair, as in fig. 46.....**wayah**
- 16(13). Head with paired occipital tubercles usually small and blunt (fig. 41) and paired abdominal tubercles on tergum 9 usually short and blunt (fig. 4b), if tubercles on tergum 9 are sharp (fig. 4a) the occipital tubercles are moderately long and sharp (fig. 39); ventral (leading) edge of forefemora as in fig. 48 .....**flavilinea**  
Head usually roughened only on occiput (fig. 36) and paired abdominal tubercles on tergum 9 moderately long and sharp (fig. 3a), if small blunt occipital tubercles are present (fig. 38) abdominal tubercles on tergum 9 are more acute (fig. 3b); ventral (leading) edge of forefemora as in fig. 49.....**coloradensis**

***Ephemerella lata* Morgan**

(Figures 6, 21, 42, and 53)

*Ephemerella lata* Morgan 1911, 112, 2 figs.; Morgan 1913, pls. 47 and 50; Ulmer 1920, 119; McDunnough 1931c, 211, 2 figs. (=inflata); Traver 1932, 176, 1 fig.; Traver 1935, 607, 1 fig.; Traver 1937, 71; Leonard 1950, 19; Burks 1953, 64, 2 figs.

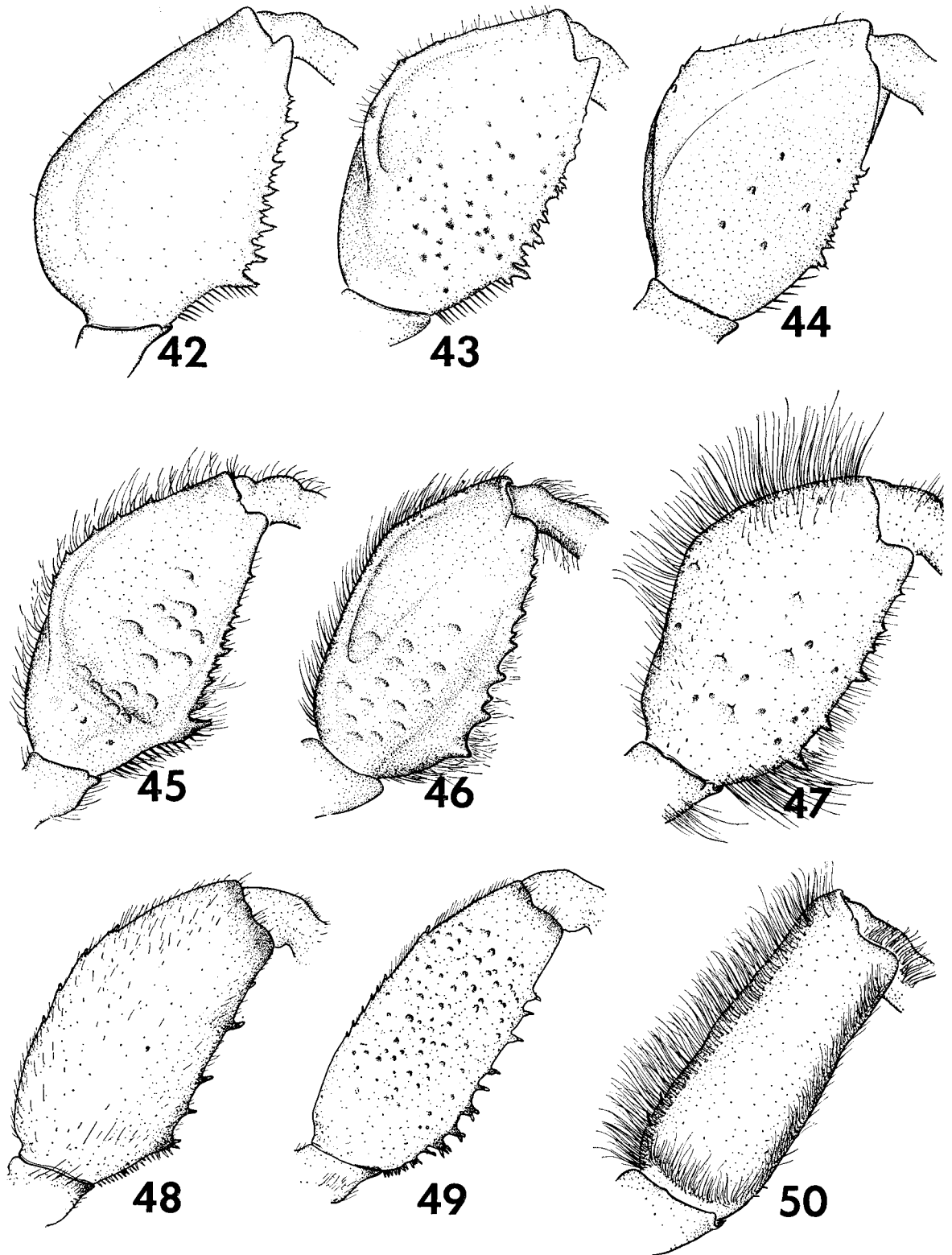
*Ephemerella inflata* McDunnough 1926, 187.

Morgan (1911) described this species from nymphs collected in Maine and New York. In 1926 McDunnough collected male and female imagoes in Quebec, Canada, and named them *Ephemerella inflata*. In 1931, after rearing nymphs of *E. lata*, he declared the name *E. inflata* to be a synonym of *E. lata*.

*Male Imago* (dry).—Length: body 6-7; forewing 6-7 mm. General color brown. Head and thorax chocolate brown; legs brown; wings hyaline, longitudinal veins brown at wing base and pale distally, crossveins pale. Abdominal terga brown, terga 6-9 with sublateral darker brown maculae; sterna light brown and without markings. Male genitalia as in fig. 6. Caudal filaments pale.

*Female Imago*.—Length: body 6-7; forewing 6-7 mm. Thorax lighter brown and abdomen darker than in male. Other characters as in male except for usual sexual differences.

FIGS. 21-41.—Subgenus *Drunella*, nymphal heads and head structures. FIG. 21, *E. lata*, dorsal view. FIG. 22a-e, *E. cornutella*: a, dorsal view; b-e, dorsal view, lateral frontoclypeal projections. FIG. 23, *E. cornuta*, dorsal view. FIG. 24, *E. longicornis*, dorsal view. FIG. 25, *E. conestee*, front view. FIG. 26, *E. wayah*, front view. FIG. 27, *E. walkeri*, front view. FIGS. 28-33, *E. doddsi*: fig. 28 (from Yukon Territory, Canada); fig. 29 (from John Day, Oregon); fig. 30 (from Glacier Natl. Pk., Montana); fig. 31 (from Yellowstone Natl. Pk., Wyoming); fig. 32 (from Santa Ana River, California); fig. 33 (from Yellowstone Natl. Pk., Wyoming). FIG. 34, *E. alleggheniensis*, front view. FIG. 35, *E. tuberculata*, front view. FIGS. 36-38, *E. coloradensis*: fig. 36, front view; figs. 37-38, vertex of head, left or right; fig. 37 (from Logan River, Utah); fig. 38 (from Lassen Natl. Pk., California). FIGS. 39-41, *E. flavilinea*: figs. 39-40, vertex of head, left or right; fig. 39 (from Yosemite Natl. Pk., California); fig. 40 (from Humboldt Co., California); fig. 41, front view.



FIGS. 42-50.—Subgenus *Drunella*, left nymphal forefemora: fig. 42, *E. lata*; fig. 43, *E. tuberculata*; fig. 44, *E. allegheniensis*; fig. 45, *E. conestee*; fig. 46, *E. wayah*; fig. 47, *E. walkeri*; fig. 48, *E. flavilinea*; fig. 49, *E. coloradensis*; fig. 50, *E. pelosa*.

*Mature Nymph*.—Length: body 6-7; caudal filaments 4.5-5.5 mm. General color light brown. Head with very short lateral frontoclypeal tubercles, and with a blunt median ocellar tubercle (fig. 21); without occipital tubercles, vertex of head nearly smooth. Without thoracic tubercles; legs light brown, ventral (leading) edge of forefemora with tubercles (fig. 42); apical tibial projection straight and blunt as in fig. 17; tarsal claws with one to three denticles. Abdomen with small paired dorsal ridges on segments 2-8. Caudal filaments light brown.

*Type Locality*.—Fall Creek, Ithaca, New York.

*Type*.—No. 3016, Cornell University Collection, Ithaca, New York.

#### DISTRIBUTION

*Ephemerella lata* is an eastern North American boreal species and is known from Nova Scotia, New Brunswick, and Michigan austrad to North Carolina (fig. 53). The authors have examined specimens of this species from the following localities:

MAINE: Phillips, 13-VII-09, A. H. Morgan (CU); Sandy River, VII-09, A. H. Morgan (CU). MICHIGAN: Sturgeon River nr. Rondo, 4-VII-48, GFE; Sturgeon River on U. S. Highway 27, 4-VII-48, GFE; Little Manistee River nr. Irons, 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). NEW BRUNSWICK: nr. St. Paul, Kent, 17-VII-50, E. L. Bousfield; NW. Mirimichi River, 13-VIII-51, E. L. Bousfield. NEW YORK: Batten Kill River, Salem, 2-VII-52, E. I. Coher; Cedar River nr. Indian Lake, Adirondack State Pk., 20-VI-41, T. H. Frison and H. H. Ross (INHS); Fall Creek (Holotype), 20-VI-09, A. H. Morgan (CU). NORTH CAROLINA: Valle Crucis, 28-V-36, J. R. Traver (CU); Davidson River, 20-IV-30, 19-VII-30, J. R. Traver (JRT). NOVA SCOTIA: Baddeck, Victoria, 7-VII-41, J. McDunnough (CNC); Annapolis River, 25-VI-50, E. L. Bousefield; nr. Brooklyn, Hants, 22-VI-50, E. L. Bousefield; nr. Albany, Annapolis, 25-VI-50, E. L. Bousefield; nr. Salem, Cumberland, 9-VII-50, E. L. Bousefield. PENNSYLVANIA: Bedford, summer 1928, Herman Wright (AMNH). QUEBEC: Fulford, 15/31-VII-30, 20-VIII-30, 21-IX-30, L. J. Milne (CNC); Mid Yamaska River, Fulford, 28-VII-29, L. J. Milne (CNC); Wakefield, 13-VI-25, F. P. Ide (CNC); Wakefield, 28-VIII-26, G. S. Walley (CNC); Wakefield, 8-VIII-31, L. J. Milne (CNC); Diable River, Mont Tremblant, 17-VII-59, B. V. Peterson.

#### *Ephemerella cornuta* Morgan

(Figures 8, 18, 23, and 53)

*Ephemerella cornuta* Morgan 1911, 114 (nymph  *nec*  adult); Morgan 1913, pl. 50, 2 figs.; Britton 1920, 28; Ulmer 1920, 119; McDunnough 1925, 212 (misidentification, *dorothea*); McDunnough 1928b, 238; Steger 1931, 28, 2 figs. (adult redescription); McDunnough 1931c, 211, 2 figs. (adult redescription); Traver 1935, 589, 1 fig.; Traver 1937, 70; Burks 1953, 65, 2 figs.

*Ephemerella depressa* Ide 1930, 212, 5 figs.; McDunnough 1931c, 212; Traver 1935, 591; Ide 1935, 44. NEW SYNONYMY.

Morgan named this species from a nymph and a male subimago. In 1931 McDunnough examined the male subimago and stated that it might be the male subimago of *Ephemerella dorothea* Needham. In this same paper he presented a redescription of the male adult. Steger (1931) also published a description of the male adult. The synonymous *Ephemerella depressa* was described from a nymph and female subimagoes collected in the Georgian Bay drainage in Ontario.

The senior author has examined an adult female paratype and mature nymphs of *E. depressa* Ide. These specimens were compared with adults and nymphs of *E. cornuta* and found to be morphologically indistinguishable. We, therefore, place *E. depressa* Ide as a synonym of *E. cornuta*.

*Male Imago* (dry).—Length: body 10-11; forewing 10-11 mm. General color dark brown. Head and thorax deep ruddy brown; legs dark brown; wings hyaline, longitudinal veins brown, crossveins pale. Abdominal terga ruddy brown; sterna light brown and without markings. Male genitalia as in fig. 8. Caudal filaments brown with dark brown bands.

*Female Imago*.—Length: body 10-11; forewing 11-12 mm. Thorax lighter brown and abdomen darker brown than in male. Other characters as in male except for usual sexual differences.

*Mature Nymph*.—Length: body 9-11; caudal filaments 7-9 mm. General color brown. Head with moderately long, usually curved, lateral frontoclypeal tubercles, and with a sharp median ocellar tubercle (fig. 23); without occipital tubercles, vertex of head roughened. Without thoracic tubercles; legs brown, ventral (leading) edge of forefemora with tubercles; apical tibial projection usually straight and moderately sharp (fig. 18); tarsal claws with two to four denticles. Abdomen with small paired dorsal ridges on segments 2-8. Caudal filaments brown.

*Type Locality*.—Salisbury, Connecticut.

*Type*.—Destroyed.

#### DISTRIBUTION

*Ephemerella cornuta* is a boreal eastern North American species and is distributed from Ontario, Quebec, and Nova Scotia austrad to North Carolina and Tennessee (fig. 53). We have examined specimens from the following localities:

CONNECTICUT: Salisbury (labeled type lot, no other data) (CU). KENTUCKY: Quicksand, 8-V-47, P. O. Ritcher and M. W. Sanderson (INHS); Jackson, 8-V-47, P. O. Ritcher and M. W. Sanderson (INHS). NEW HAMPSHIRE: Thompson Falls, Gorham, 20-VII-29, J. McDunnough and G. S. Walley (CNC); Imp Creek, Pinkham Notch nr. Mt. Washington, 23-VI-41, T. H. Frison and H. H. Ross (INHS); Warren, 21-VI-41, T. H. Frison and H. H. Ross (INHS). NEW YORK:

North of Spencer, 23-V-30, A. L. Steger (CU); Beaverkill, 2-VI-35, H. T. Spieth (AMNH). NORTH CAROLINA: North Toe River, Minneapolis, 8-VI-26, J. R. Traver (CU); Catawba River, 19-VI-29, J. R. Traver (JRT); Valle Crucis, 10-VI-36, J. R. Traver (JRT); Black Mountain, 29-VI-30, J. R. Traver (JRT); Flat Creek, tributary of Swannanoa River, 11-VI-30, J. R. Traver (JRT); North Fork Swannanoa River, 14-VI-29, J. R. Traver (JRT); Hazelwood, 24-IV-38, H. H. Ross and B. D. Burks (INHS). NOVA SCOTIA: Cape Breton Is., Baddeck, 2-VIII-36, T. N. Freeman (CNC); Hunters Creek, Baddeck, 27-VI-36, T. N. Freeman (CNC); Baddeck Forks, 30/31-VII-36, J. McDunnough (CNC); West of Middle River, 24-VI-36, J. McDunnough (CNC); Cr. I, Route 5, 20-VI-36, J. McDunnough (CNC); Cape George, Antigonish, 19-VI-36, J. McDunnough (CNC); Mohrod Stream, 6-VII-50, E. L. Bousefield. MAINE: Sheffield, 29-VI-10 (CU); Aroostook Co., Mud Lake on Fish River, 27-VII-39 (INHS); Soldiers Pond, 22-VII-39 (INHS). ONTARIO: Hornings Mills, 6-VII-28, F. P. Ide (Paratype, *E. depressa*) (CNC). PENNSYLVANIA: Middle Creek, Beavertown, VI-39, C. M. Wetzel (INHS). QUEBEC: Mont Tremblant, 14/16-VII-59, B. V. Peterson; West Bolton Creek, Knowlton, 24-VII-29, J. McDunnough (CNC); Knowlton, 27-VI/13-VII-29, L. J. Milne and J. McDunnough (CNC); Pasture Creek, Knowlton, 22-VII-29, J. McDunnough (CNC); Sutton Mountain Creek, Sutton, 11-VII-29, J. McDunnough (CNC). VERMONT: Downer State Forest, 16-VI-51, E. I. Coher; Averys Gore, 15-VII-52, E. I. Coher; Battell State Park, 19-VI-52, E. I. Coher. VIRGINIA: Shenandoah River, Berryville, 12-V-38, E. Surber (JRT).

#### TAXONOMY

*Ephemerella cornuta* nymphs from southeastern Canada and northeastern United States are large (10-11 mm.), robust, and have prominent sharp lateral frontoclypeal projections and a median ocellar tubercle. However, nymphs from the southeastern United States (Kentucky, North Carolina, and Virginia) are generally smaller (9 mm.) and have less prominent and blunter head tubercles.

*Ephemerella cornuta* is a cognate species of *E. cornutella* McDunnough and the nymphs are difficult to distinguish morphologically. The most reliable character for recognizing *E. cornuta* is its large size, specimens more than 9 mm. long being confidently referred to *E. cornuta*. Specimens shorter than 8.5 mm. with visible folds of the developing wing or black wing pads are referable to *E. cornutella*. The greater development and sharper apex of the median ocellar tubercle is a dependable character which will separate *E. cornuta* from *E. cornutella* except for some specimens from the southern part of the range of these species. The frontoclypeal projections are also generally more curved in *E. cornuta* than in *E. cornutella*.

Geographical variation has not been observed in the small number of imagoes examined.

#### *Ephemerella cornutella* McDunnough

(Figures 7, 17, 22, and 53)

*Ephemerella cornutella* McDunnough 1931b, 82; McDunnough 1931c, 211, 2 figs. (nymph); Traver 1932, 163; Traver 1935, 589, 1 fig.; Traver 1937, 70; Wright and Berner 1949, 295; Burks 1953, 65, 1 fig.; Pugh 1956, 26.

McDunnough (1931b) described this species from all stages collected in southern Quebec. Later the same year he published a more detailed, but still incomplete, description of the nymphal stage.

*Male Imago* (dry).—Length: body 6-7; forewing 7-8 mm. General color dark brown. Head and thorax deep chocolate brown; legs dark brown; wings hyaline, veins pale. Abdominal terga brown with dark brown sublateral patches; sterna light brown, posterior segments darker brown. Male genitalia as in fig. 7. Caudal filaments pale with dark brown bands at segmental joinings.

*Female Imago*.—Length: body 6-7; forewing 7-8 mm. General color lighter brown than male. Other characters as in male except for usual sexual differences.

*Mature Nymph*.—Length: body 6-8; caudal filaments 5-6 mm. General color brown. Head with moderately long, nearly straight (fig. 22b-c) to gently curved (fig. 22a, d-e), lateral frontoclypeal tubercles, and a blunt median ocellar tubercle (fig. 22a); without occipital tubercles, vertex of head roughened. Without thoracic tubercles; legs light brown, ventral (leading) edge of forefemora with tubercles, apical tibial projection straight and moderately sharp (fig. 17); tarsal claws with one to three denticles. Abdomen with small paired dorsal ridges on segments 2-8. Caudal filaments light brown.

*Type Locality*.—Knowlton, Quebec.

*Type*.—No. 3273, Canadian National Collection, Ottawa, Ontario.

#### DISTRIBUTION

This species is known from Quebec, New Brunswick, and Nova Scotia austrad to Georgia (fig. 53). Specimens examined by the authors are from the following localities:

KENTUCKY: Jackson, 8-V-47, P. O. Ritcher and M. W. Sanderson (INHS); Slade, 8-V-47, P. O. Ritcher and M. W. Sanderson (INHS). NEW BRUNSWICK: Boiestown, 10-VII-28, W. J. Brown (CNC); SW. Mirimichi River, 6-VI-51, E. L. Bousefield; Mirimichi River, 18-VII-50, E. L. Bousefield; Charlo River, 2-VIII-50, E. L. Bousefield; Cocagne River nr. Notre Dame, 17-VII-50, E. L. Bousefield. NEW HAMPSHIRE: Peabody River, Gorham, 18-VII-29, G. S. Walley and J. McDunnough (CNC). NEW YORK: Salmon Creek nr. Lansing, 7-VII-32, J. R. Traver (CU). NORTH CAROLINA: Tributary of Laurel River, 5 mi. E.

Hot Springs, 8-VII-30, J. R. Traver (JRT); Flat Creek, Tributary of Swannanoa River, 8-VII-30, J. R. Traver (JRT); Allens Creek, tributary of Pigeon River, 26-VII-29, J. R. Traver (JRT); Smokemont, 3-VIII-30, H. T. Spieth (AMNH); Wayah Creek (Franklin), 1-VIII-30, J. R. Traver (JRT). NOVA SCOTIA: Annapolis Royal, 21-VII-28, W. J. Brown (CNC); Cape Breton Island, Cr. I, Route 5, 20-VI-36, J. McDunnough (CNC); nr. Margaree Harbor, 6-VII-50, E. L. Bousefield; Hunters Creek, 22-VI-26, J. McDunnough (CNC); nr. Salem, 19-VII-50, E. L. Bousefield; Cape George, Antigonish, 19-VI-36, J. McDunnough (CNC); Dr. Brook, Antigonish, 19-VI-36, J. McDunnough (CNC); Tory Creek, 3-IX-36, T. N. Freeman (CNC); Guysburo, 6-VIII-36, J. McDunnough (CNC). MICHIGAN: Cheboygan Co., Indian River, VII-48, GFE. PENNSYLVANIA: Scranton, summer 1945, H. K. Townes (JRT). QUEBEC: Knowlton (Holotype), 2-VIII-29, G. S. Walley (CNC); Covey Hill, 1-VII-27, G. S. Walley (CNC); West Bolton Creek, Knowlton, 1-VII-29, J. McDunnough (CNC); Mississiquoi River, 13-VII-29, G. S. Walley (CNC); Sutton Mt. Creek, Sutton, 11-VII-29, G. S. Walley and L. J. Milne (CNC). TENNESSEE: Elkmont, 11-VIII-30, H. T. Spieth (AMNH); LeConte Creek, Gatlinburg, 14-V-39, T. H. Frison and H. H. Ross (INHS); Little River, Townsend, 15-V-39, T. H. Frison and H. H. Ross (INHS).

#### TAXONOMY

The nymphs of *E. cornutella* from North Carolina, Kentucky, and Tennessee are variable in the character of the frontal head tubercles. Nymphs from Ontario and Quebec have a blunt median ocellar tubercle and gently curved, moderately sharp lateral frontoclypeal projections (fig. 22a), while populations from the southeastern states have, on the average, a sharper median ocellar tubercle and straighter sharper lateral frontoclypeal projections (figs. 22b-d). Although these frontal head protuberances in the southeastern populations are on the average sharper than those in the north, the degree of development of these structures grades imperceptibly through intermediate populations with the characteristics of nymphs from Quebec and Ontario.

*Ephemerella cornutella* is a cognate species of *E. cornuta* Morgan and occurs geographically with this species and the related *E. longicornis* Traver. It may be distinguished from these above-named species by its small size at maturity (6-8 mm.), and by the genitalic structures in the male imago.

#### *Ephemerella longicornis* Traver

(Figures 19, 24, and 54)

*Ephemerella longicornis* Traver 1932, 164; Traver 1935, 608, 3 figs.; Traver 1937, 70; Howell 1941a, 314; Howell 1941b, 407.

*Ephemerella cornuta* (Variety A) Traver 1932, 164.

*Ephemerella longicornis* was named from a series of nymphs, a female imago, and two male subimagos. These adult specimens were examined by the senior

author but, since they do not have characters which are useful in distinguishing this species from all other known species in the genus, diagnoses are not included in this report.

*Male Imago*.—Unknown (subimago only).

*Mature Nymph*.—Length: body 9-11; caudal filaments 7-8 mm. General color light reddish brown. Head with long lateral frontoclypeal tubercles, and a sharp median ocellar tubercle (fig. 24); without occipital tubercles, vertex of head roughened. Without thoracic tubercles; legs light brown, ventral (leading) edge of forefemora with tubercles, apical tibial projection sharp and curved (fig. 19); tarsal claws with one to three denticles. Abdomen with small paired dorsal ridges on segments 2-8. Caudal filaments brown.

*Type Locality*.—Cedar Creek near Glenville, North Carolina.

*Type*.—No. 1095.1, Cornell University Collection, Ithaca, New York.

#### DISTRIBUTION

*Ephemerella longicornis* is an eastern North American species known from North Carolina and Tennessee and from a single record from New York (fig. 54). The authors have examined specimens of this species from the following localities:

NEW YORK: Green Lake, 16-V-31, J. R. Traver (JRT). NORTH CAROLINA: Allens Creek, tributary of Pigeon River, 26-VII-29, J. R. Traver (JRT); Flat Creek, tributary of Swannanoa River, VI-29, J. R. Traver (JRT); tributary of Tuckaseegee River, 28-VI-29, J. R. Traver (JRT); tributary of Pigeon River, 17-VII-29, J. R. Traver (JRT); Macon Co., Big Creek, 3-VI-38, T. Howell (JRT); nr. Banners Elk, 3-VI-36, J. R. Traver (JRT); Glenville, 15-VI-36, J. R. Traver (JRT); Valle Crucis, 30-V-36, J. R. Traver (JRT); Heaton, 3-VI-36, J. R. Traver (JRT); Andrews Geysers, Catawba River, 16/17-VI-29, J. R. Traver (JRT); Balsam, 24-IV-38, H. H. Ross and B. D. Burks (INHS); Pisgah Natl. For., Hot Springs, 15-VI-34, H. H. Ross (INHS); Flag Creek, 21-VI-30, J. R. Traver (CU); Selicia, 13-VI-30, J. R. Traver (CU); Collins Creek, Smokehurst, VI-30, J. R. Traver (CU); Cedar Creek (Holotype), 14-VII-30, J. R. Traver (CU). TENNESSEE: LaConte Creek, Gatlinburg, 14-VI-40, T. H. Frison and H. H. Ross (INHS).

#### *Ephemerella coloradensis* Dodds

(Figures 2-3, 36-38, 49, and 51)

*Ephemerella coloradensis* Dodds 1923, 97, 2 figs.; Dodds and Hisaw 1924, 146, 1 fig.; Lestage 1925, 234, 275, 277; Needham and Christensen 1927, 9, 1 fig.; McDunnough 1929, 170, 1 fig.; Walley 1930, 19, 3 figs.; Traver 1935, 586; Day 1954, 28; Edmunds 1954, 66; Allen and Edmunds 1956, 87; Day 1956, 96, 2 figs.

*Ephemerella wilsoni* Mayo 1952, 100, 2 figs. NEW SYNONYMY.

Dodds (1923) described *E. coloradensis* from all stages, collected in Tolland, Colorado.

Mayo (1952) distinguished *E. wilsoni* Mayo from *E. coloradensis* by color characters and by the degree of development of the occipital and abdominal tubercles. The authors examined topotypes of *E. wilsoni* and find that the differences proposed by Mayo fit within the limits of morphological variability of *E. coloradensis*. We therefore place *E. wilsoni* as a synonym of *E. coloradensis*.

*Male Imago*.—Length: body 11-12; forewing 11-13 mm. General color variable. Head and thorax dark brown, anterolateral area on mesonotum yellowish brown, pleura pale; forelegs dark brown, other legs yellowish brown; wings subhyaline, longitudinal veins brown, crossveins pale. Abdominal terga brown, dark brown near pleural margins, posterior and pleural margins pale; sterna purplish brown, posterior margins pale. Male genitalia as in fig. 2. Caudal filaments dark brown at base, pale distally.

*Female Imago*.—Length: body 11-12; forewing 11-13 mm. General color yellowish brown. Head and thorax yellowish brown, abdomen lighter in color than male. Other characters as in male except for usual sexual differences.

*Mature Nymph*.—Length: body 10-11; caudal filaments 7-8 mm. General color variable, from unicolorous dark brown to light brown with variable dark brown markings. Vertex of head roughened (fig. 36), often with small blunt (fig. 37) to moderately sharp (fig. 38) occipital tubercles. Without thoracic tubercles; legs brown, often light brown with dark brown transverse bands, forefemora as in fig. 49; tarsal claws with two to four denticles. Abdomen with sharp paired dorsal submedian tubercles on segments 1-9 (figs. 3a-b). Caudal filaments pale with a single broad transverse dark band near the middle, often dark at apex and base.

*Type Locality*.—Tolland, Colorado.

*Type*.—Academy of Natural Sciences of Philadelphia, Pennsylvania.

#### DISTRIBUTION

*Ephemerella coloradensis* is a boreal western North American species with a long latitudinal distribution. This species is known from southeastern Alaska and the Yukon Territory of Canada austrad to northern California, central Nevada, southern New Mexico, and southern Arizona (fig. 51). Day (1956) reported *E. coloradensis* nymphs as being widespread in the mountain streams of California; however, our records are restricted to the streams in the Sierra Nevada Mountains of northern California. The authors have examined specimens from 209 localities, of which the following are marginal and representative.

ALASKA: Unidentified stream nr. Juneau (elev. 800'), 21-VI-58, Grant Miller; Admiralty Island, SE. Alaska (elev. 50-75'), 13-VII-58, Grant Miller; Stream 0.5 mi. N. Cape Farshaw, SE. Alaska, 9-VII-58, Grant Miller; Stream, base of Kapho Mountains (elev. 2'), 19-V-58, Grant Miller. ALBERTA:

Pass Creek, Waterton Lakes Pk., 5-VII-37, "Rawson" (INHS). ARIZONA: Gila Co., Horton Creek, Tonto Natl. For., 20-VII-36, C. M. Tarzwell. BRITISH COLUMBIA: Capilano River, W. Vancouver, 3-VII-40, H. H. Ross (INHS); Wilson Creek nr. New Denver, 12-VIII-40, V. K. Mayo (VKM); Brexton, 14-VII-40, V. K. Mayo (VKM); Trepanage Creek, Peachland, 28-VII-58, GFE. CALIFORNIA: Shasta Co., Kings Creek, Lassen Natl. Pk., 3-VII-59, RKA. COLORADO: Grand Co., Swift Creek, Berthoud Pass (elev. 10,000'), 24-VII-38, H. H. and J. A. Ross (INHS); El Paso Co., Green Mountain Falls, 22-VI-38, H. H. Ross (INHS). IDAHO: Blaine Co., Big Wood River, 5-IX-44, GFE; Teton Co., Moose Creek, Victor, T. H. Frison and T. H. Frison, Jr. (INHS). MONTANA: Glacier Natl. Pk., Roes Creek, 12-VII-40, H. H. and J. A. Ross (INHS); Lake Co., Lolo Creek, Flathead Lake, 25-VI-49, L. T. Nielsen; Jefferson Co., Toll Creek Camp, 20 mi. SE. Butte, 22-VI-49, S. Preece. NEVADA: Elko Co., inlet of Angel Lake, Ruby Mts., 23-IX-57, GFE and RKA; Washoe Co., Galena Creek on Nevada Highway 27, 21-IX-57, GFE and RKA. NEW MEXICO: San Miguel Co., Cow Creek, Santa Fe Natl. For., 9-IX-37, C. M. Tarzwell; Taos Co., Santa Barbara River, Carson Natl. For., 22-VII-37, C. M. Tarzwell; San Doval Co., Rock Creek, Santa Fe Natl. For., 16-VII-37, C. M. Tarzwell. OREGON: Jefferson Co., Metolius River at Sherman Camp, 23-VIII-54, GFE and RKA; Mt. Hood, White River, 27-VIII-54, GFE and RKA. UTAH: Salt Lake Co., Big Cottonwood Canyon 24-VII-50, GFE; San Juan Co., Miller Creek, LaSal Mountains, 14-VI-45, S. and D. Mulaik; Daggett Co., 8 mi. SE. Fishlake Pass, Uinta Mountains, 5-VIII-46, S. and D. Mulaik. WASHINGTON: Jefferson Co., Quinalt River nr. Eena Creek, Olympic Natl. Pk., 3-IX-58, GFE and RKA; Skamania Co., Lewis River, Mt. Adams Area, 31-VIII-58, GFE and RKA; Spokane Co., Little Spokane River, 3-VII-55, RKA. WYOMING: Big Horn Mountains, 30-VII-40, T. H. Frison and T. H. Frison, Jr. (INHS); Grand Teton Natl. Pk., Cascade Canyon, 9-VIII-40, T. H. Frison and T. H. Frison, Jr. (INHS). YUKON TERRITORY: Yukon Highway milepost 632, Watson Lake, 24-VI-52, C. P. Alexander (UM).

#### TAXONOMY

*Ephemerella coloradensis* and *E. flavilinea* McDunnough are cognate species; however, they are distinguishable in both the nymphal and male adult stages. The nymphs of *E. coloradensis* have much sharper abdominal tubercles than do those of *E. flavilinea*, and the male adults differ from *E. flavilinea* in genitalic structures.

The nymphs of *E. coloradensis* exhibit marked color and morphological variation. Most nymphs of this species are a unicolorous dark brown color, but quite often the nymphs have a variable color pattern.

The color varies from white through various shades of brown and red; and the darker markings, which have no set pattern, vary from light brown to black. The one constant color feature is the black band near the middle of the caudal filaments. These color variations have been observed among nymphs collected throughout the known range of this species and several of them may occur in a single population.

We have noted before that, in some *Drunella* nymphs from the mountains of the Pacific Coast, the occipital, thoracic, and abdominal tubercles are larger and sharper. This is true of the occipital (fig. 38) and abdominal (fig. 3b) tubercles of the nymphs of *E. coloradensis*. The degree of development of the occipital tubercles is a character which has been used to distinguish nymphs of *E. flavilinea* McDunnough from *E. coloradensis*. The occipital tubercles of *E. coloradensis* nymphs collected from southeastern Alaska austrad to northern California (fig. 38) are nearly as well developed as those of typical *E. flavilinea* nymphs (fig. 41). Since the character of these head projections are so similar in the nymphs of both of these species, the degree of development and the sharpness of the abdominal tubercles (fig. 3a-b) and the character of the forefemora (fig. 49) must be used, in combination with the occipital tubercles, to distinguish these species in the nymphal stage.

#### BIOLOGY

The nymphs of *E. coloradensis* have been collected in a wide variety of streams. They are commonly found in medium to large rapidly flowing streams, but have also been collected in streams only a few inches wide. They occur rather freely in many different bottom types, but are most commonly found among rocks, gravel, debris, and on vegetation. *Ephemerella coloradensis* nymphs usually occur in colder waters, with summer temperatures near 40°F., but have been collected in streams with summer temperatures near 60°F.

Adults of this species have been collected from early July to early October.

#### *Ephemerella flavilinea* McDunnough

(Figures 4-5, 39-41, 48, and 51)

Allied to *Ephemerella*, Nymph No. 1 Eaton 1884, 131, pl. 38.

*Ephemerella* sp. Lestage 1925, 287.

*Ephemerella flavilinea* McDunnough 1926, 188; McDunnough 1929, 169, 1 fig.; Walley 1930, 18, 5 figs.; Traver 1935, 586, 2 figs.; McDunnough 1935, 95; Mayo 1952, 94; Day 1956, 96, 2 figs.; Allen and Edmunds 1956, 87.

*Ephemerella lapidula* McDunnough 1935, 96; Traver 1935, 628. NEW SYNONYMY.

This species was first reported by Eaton (1884) as "Nameless ally to *Ephemerella* No. 1," from Wenas and Klikitat Valleys, Washington Territory (Klikitat Co., Washington?). It was named by McDunnough in 1926 from a male imago collected

at Waterton Lakes, Alberta, Canada. In 1930 Walley described the nymphal stage of this species; but, subsequent examination of this material by McDunnough (1935) led him to create the name *Ephemerella lapidula*, which he distinguished from *E. flavilinea* by some minor morphological characters. He stated, "Nymph.....Very close to that of *flavilinea*, differing principally in the shape of the dorsal abdominal tubercles; . . ." "Male.....Scarcely separable from *flavilinea* . . ." "Topotype nymphs and reared male and female imagoes of *E. lapidula* from the Canadian National Collection were compared with *E. flavilinea* nymphs and adults. The minor differences distinguishing *E. lapidula* nymphs and male imagoes fall within the normal variation of *E. flavilinea*; *E. lapidula* is a synonym of *E. flavilinea*."

*Male Imago*.—Length: body 12-13; forewing 12-13 mm. General color reddish brown. Head and thorax reddish brown; femora reddish, tibiae and tarsi pale; wings subhyaline, longitudinal veins pale to brown, crossveins pale. Abdominal terga reddish brown; sterna reddish. Male genitalia as in fig. 5. Caudal filaments pale, brown at base.

*Mature Nymph*.—Length: body 10-11; caudal filaments 8-9 mm. General color brown, often light brown with variable dark brown markings. Head with small blunt (fig. 40) to sharp (fig. 39) paired occipital tubercles. Without thoracic tubercles; legs unicolorous brown, often with brown femoral, tibial, and tarsal transverse bands, forefemora as in fig. 48; tarsal claws with two to three denticles. Abdomen with blunt (fig. 4b) to rather sharp (fig. 4a) paired dorsal submedian tubercles on segments 1-9, tubercles small on segment 1, blunt on segment 9. Caudal filaments pale with a single broad dark transverse band near middle, often dark at apex and base.

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

*Type*.—No. 1945, Canadian National Collection, Ottawa, Ontario.

#### DISTRIBUTION

*Ephemerella flavilinea* is a boreal western North American species known from southern British Columbia austrad to west-central Wyoming, central Idaho and Baja California (fig. 51). We have examined specimens of this species from the following localities:

BAJA CALIFORNIA: Rancho San Antonio, Ste. Domingo Rio, 17-V-36, P. R. Needham (JRT). BRITISH COLUMBIA: Steelhead Creek, Slave Falls, 6-VII-40, H. H. and J. A. Ross (INHS). CALIFORNIA: Napa Co., Sage Creek, 5-VII-50, W. C. Day; Amador Co., Dry Creek nr. Dry Town, 11-V-38, V. K. Mayo (VKM); Jackson Creek nr. Jackson, 25-V-38, V. K. Mayo (VKM); Tehama Co., Mill Creek, 5 mi. N. Childs Meadows, 3-VII-59, RKA; Humboldt Co., Stream, 5 mi. N. Willow Creek, 2-VII-59, RKA; Bluff Creek, Six Rivers Natl. For., 2-VII-59, RKA; Mad River at Blue Lake



Public Camp, 2-VII-59, RKA; Trinity River (Bridge 4-139), Hoopa Valley, 2-VII-59, RKA; Stream, 7 mi. S. Orleans, 2-VII-59, RKA; Madera Co., Chilacoot Creek above Bass Lake, 19-VI-59, RKA; Tulare Co., Yosemite Natl. Pk., Merced River, 19-VI-59, RKA; Kaweah River, 4 mi. S. Three Rivers, 18-VI-59, RKA; Los Angeles Co., East Fork San Gabriel River at Camp Bonita, 16-VI-59, RKA and E. E. Ruzicka; Riverside Co., North Fork San Jacinto River, Idyllwild, 13-V-59, GFE; San Bernardino Co., Barton Flats, 30-VI-50, J. N. Belkin (UCLA); Siskiyou Co., Thompson Creek, 7.7 mi. W. Seiad Valley, 2-VII-59, RKA; Stream at Cottage Grove, 2-VII-59, RKA; Beaver Creek, 1 mi. E. Klamath River, 3-VII-59, RKA; Klamath River at jct. with Beaver Creek, 3-VII-59, RKA; Trinity Co., Stream on Hoopa Valley Indian Reservation (Bridge 4-138), 2-VII-59, RKA; Shasta Co., Shasta River, 3 mi. W. Weed, 3-VII-59, RKA; Hat Creek at Sandy Public Camps, 2 mi. N. Old Station, 3-VII-59, RKA; Burney Creek, below McArthur, nr. Clayton, 17-IV-46, H. G. Nelson; Plumas Co., Stream, 3 mi. N. Spring Garden, 3-VII-59, RKA; North Fork Deer Creek, 5 mi. N. Fire Mountain, 3-VII-59, RKA; Mendicino Co., Bridges Creek nr. Reynolds, 2-VII-59, RKA; Nevada Co., Sagehen Creek nr. Univ. of Calif. Station, 6-VIII-59, RKA. IDAHO: Custer Co., Big Lost River, Mackay, VII-48, G. F. Edmunds, Sr.; Warm River N. Ste. Anthony, 13-VI-46, GFE. MONTANA: Flathead Co., Whitefish River below Whitefish, 6-VI-52, T. N. Wilson; Ravalli Co., Rye Creek, 6 mi. S. Darby, U. S. Highway 93, 30-VI-59, GFE; Mineral Co., Clark Fork, 12 mi. W. Ste. Regis, 3-VI-59, GFE; Glacier Natl. Pk., Quartz Creek, 7-VII-49. OREGON: Benton Co., Woods Creek, vicinity Corvallis, 24-IV-48, E. P. Hughes; Greasy Creek, 5 mi. W. Philomath, 5-III-39, "Brantner" (OSC); Woods Creek, 2 mi. W. Philomath, 13-V-37, Kebbe (OSC); Oak Creek, Corvallis, 20-IV-34, E. E. Ball; Lane Co., Rat Creek, 1.6 mi. above Dorene Dam, 14-VI-58, M. L. Johnson; Smith Creek, 6 mi. above Dorene Dam, 14-VI-58, M. L. Johnson; Middle Fork Willamette River, Shady Dell For. Camp, 17-VI-58, M. L. Johnson; McKenzie River, 1.2 mi. from H. J. Morton For. Camp, 15-VI-58, M. L. Johnson; Crescent Creek, 1 mi. down from Crescent Lake, 17-VI-58, M. L. Johnson; Odell Creek, 8 mi. from Highway 50, 7-VI-58, M. L. Johnson; Jefferson Co., Lake Creek, Sherman Camp, 20-VI-54, GFE; Grant Co., John Day River, John Day, 13-VI-54, GFE; Deschutes Co., Deschutes River, Cline Falls State Pk., 18-VI-54, GFE; Deschutes River, Tumalo State Pk., 25-VI-54, GFE. WASHINGTON: King Co., Green River, 21-IV-41, B. L. Lambuth (BLL); Stevens Co., Springdale Creek, 19-VI-55, GFE and RKA; Spokane Co., Little Spokane River, Dartford, 13-VI-55, RKA. WYOMING: Grand Teton Natl. Pk., Cottonwood Creek, 5-VIII-40, T. H. Frison and T. H. Frison, Jr. (INHS); Yellowstone Natl. Pk., Firehole River, Biscuit Basin, 21-VI-49, GFE; Nez Perce Creek, 10-VI-46, GFE; Yellowstone River, Hayden Valley, 10-VI-46, GFE; Crawfish Creek, 5-VI-46, GFE;

Firehole River, Old Faithful, 6-VI-42, GFE; Firehole River (below station), 22-VII-28, J. McDunnough (CNC); Firehole River (above observation bridge), 22-VII-28, J. McDunnough (CNC); Fremont Co., Hornecker Creek, 2 mi. SW. Lander, 11-VI-61, GFE and W. L. Peters; Popo Agie River at bridge 0.5 mi. below Sinks, 11-VI-61, GFE and W. L. Peters.

#### TAXONOMY

*Ephemerella flavilinea* is a cognate species of *E. coloradensis* Dodds. The nymphs of *E. flavilinea* are readily distinguishable from those of *E. coloradensis* throughout most of the range occupied by both species; however, the California populations of these two species have a convergence of characters which makes determination often difficult. This difficulty arises as the paired dorsal abdominal tubercles of the nymphs of *E. flavilinea* (fig. 4a) occurring in central California approach the size and sharpness of the paired dorsal abdominal tubercles so characteristic of the nymphs of *E. coloradensis* (fig. 3a). Such nymphs, however, have larger and more acute occipital tubercles than most nymphs of *E. flavilinea*. In this character they are more markedly different from *E. coloradensis* than usual. Also we are not certain that *E. coloradensis* occurs in central and southern California.

#### BIOLOGY

*Ephemerella flavilinea* and *E. coloradensis* nymphs are found inhabiting the same streams in many areas where the ranges of these two species coincide, although *E. flavilinea* seems to extend into warmer streams than does *E. coloradensis* and is also unable to occupy colder streams where *E. coloradensis* is found. McDunnough (1929) stated that the nymphs of this species mature in June and July, a month earlier than *E. coloradensis*. We have examined mature nymphs of *E. flavilinea* collected only as late as the first week of August, whereas mature *E. coloradensis* nymphs may be found as late as early October.

#### *Ephemerella allegheniensis* Traver

(Figures 34, 44, and 54)

*Ephemerella allegheniensis* Traver 1934, 221; Traver 1935, 580, 1 fig.

This species was described from nymphs collected from the southeastern United States. The male and female imagoes are still unknown.

*Mature Nymph*.—Length: body 8-9; caudal filaments 4-5 mm. General color brown. Well-developed occipital tubercles (fig. 34). Two pairs of prothoracic tubercles, one pair of submedian tubercles, and a small pair of lateral marginal tubercles; three mesothoracic tubercles, a pair of anterior sublateral tubercles, and a well-developed single median tubercle; legs brown, forefemur as in fig. 44; tarsal claws with three to four denticles. Paired dorsal abdominal tubercles on segments 2-8, usually small on segments 2 and 8. Caudal filaments brown.

*Type Locality*.—Cacapon River, West Virginia.

*Type*.—No. 1288.1, Cornell University Collection, Ithaca, New York.

#### DISTRIBUTION

*Ephemerella allegheniensis* is known from North Carolina, West Virginia, and Maryland (fig. 54). We have examined specimens from the following localities:

MARYLAND: Potomac River nr. Harpers Ferry, 16-VI-26, V. Argo (CU). NORTH CAROLINA: Murphy, 27-VII-30, H. T. Spieth (AMNH); Almond, 4-VIII-30, H. T. Spieth (AMNH). WEST VIRGINIA: Cacapon River, 13-VIII-30, J. R. Traver (Holotype) (CU); Cacapon River, 13-VIII-30, J. G. Needham (CU); Elk Garden, 21-VIII-30, J. G. Needham (CU).

#### *Ephemerella tuberculata* Morgan

(Figures 9, 35, 43, and 54)

*Ephemerella tuberculata* Morgan 1911, 112, 3 figs.; Morgan 1913, fig. 43; Ulmer 1920, 119; McDunnough 1931c, 213, 2 figs. (adult); Traver 1932, 175, 1 fig.; Traver 1935, 625, 2 figs.; Burks 1953, 65, 1 fig.; Pugh 1956, 26.

*Ephemerella cherokee* Traver 1937, 71; Howell 1941a, 313. NEW SYNONYMY.

*Ephemerella tuberculata* was described from a single nymph collected in New York. McDunnough (1931c) reported and described the male and female adults from Ontario and Quebec.

Traver (1937) named *Ephemerella cherokee* from nymphs and imagoes from North Carolina which she had previously (1932) considered to be *E. tuberculata*. The type of *E. tuberculata*, a single mature nymph, had been destroyed so she based her earlier determination on Morgan's (1911) figures and description. These same nymphs and imagoes were later compared with reared material of *E. tuberculata* from the Canadian National Collection, and some minor morphological and color differences were noted between the two samples. The senior author examined the types of *E. cherokee* and found that this nominal species fits within the variability of *E. tuberculata*, and is a synonym of it.

*Male Imago* (in alcohol).—Length: body 9-11; forewing 9-11 mm. General color brown. Head and thorax brown; legs brown, femora with numerous small black dots; wings hyaline, longitudinal veins brown, crossveins pale. Abdominal terga light brown with a dark brown median stripe, and dark brown submedian and sublateral maculae; sterna pale with submedian light brown oblique marks and sublateral dark brown dashes. Male genitalia as in fig. 9. Caudal filaments brown basally, paler distally.

*Female Imago*.—Length: body 9-11; forewing 9-11 mm. General color lighter than male, abdominal sterna without brown maculae. Other characters similar to male except for usual sexual differences.

*Mature Nymph*.—Length: body 7-9; caudal fila-

ments 4-5 mm. General color light brown with pale and dark brown markings. Head with well-developed occipital tubercles (fig. 35). Prothorax with a small pair of submarginal tubercles and a posterior pair of submedian tubercles; mesothorax with small anterior submarginal projections, two anterior submedian ridges, and a blunt posterior median tubercle; legs brown, dark brown warts on femora as in fig. 43; tarsal claws with two to four denticles. Abdomen with paired dorsal tubercles on segments 2-7, very small on segment 2. Caudal filaments brown.

*Type Locality*.—Fall Creek, Ithaca, New York.

*Type*.—Destroyed.

#### DISTRIBUTION

*Ephemerella tuberculata* is a boreal eastern North American species known from Quebec and Ontario austrad to North Carolina and Tennessee (fig. 54). The authors have examined specimens of this species from the following localities:

NEW YORK: Route 11D, Mount Champlain, 17-VI-52, E. I. Coher. NORTH CAROLINA: Cedar Creek nr. Glenville, 25-VII-30 (Holotype, *cherokee*), 30-VI-29, J. R. Traver (CU); Conestee Creek nr. Cedar Mountain, 11-VII-30 (JRT), 19-VII-30, J. R. Traver (CU); Ocona Lufly River nr. Cherokee, 28-VI-30, J. R. Traver (CU); Ocona Lufly River, 6-VII-30, J. R. Traver (JRT); Allens Creek, Hazelwood, 12-VII-30, J. R. Traver (CU). MARYLAND: Paint Branch Creek, Beltsville, 4-VI-30, A. Rutledge (INHS). ONTARIO: Westboro, 5-VI-37, G. S. Walley (CNC). PENNSYLVANIA: Bedford, summer 1928, Herman Wright (AMNH). QUEBEC: Knowlton, 7-VII-29, J. McDunnough, 9-VII-29, G. S. Walley (CNC); Ottawa Golf Club, 27-VII-27, G. S. Walley (CNC); Foster Power Plant, Mid Yamaska River, VII-29, G. S. Walley, 5-VII-29, L. J. Milne (CNC); Wakefield, 23-VII-30, G. S. Walley (CNC); Fulford, 9-VII-30, L. J. Milne (CNC); Vaudreuil, 25-VI-30, G. S. Walley (CNC); Diable River at Biological Station, Mont Tremblant, 17-VII-59, B. V. Peterson. TENNESSEE: Little River, Elkmont, 12-VI-38, 17-VI-38, T. H. Frison and T. H. Frison, Jr., 14-V-39, T. H. Frison and H. H. Ross (INHS). VIRGINIA: Shenandoah River, Berryville, 12-V-38, E. Surber (JRT).

#### TAXONOMY

The nymphal stage of *E. tuberculata* exhibits clinal variation from north to south in several characters. Specimens collected in North Carolina are more slender and elongate than those taken from streams in southern Quebec. The southern population also has fewer tubercles on the ventral (leading) edge of the forefemora, and shorter more-rounded occipital and thoracic tubercles. Traver (1937) also reported that adults of *E. tuberculata* (reported as *E. cherokee*) from North Carolina have darker wing venation than adults from southern Canada. These morphological differences are clinal with intermediate characteristics in populations from intervening localities; they are

not sufficient to warrant recognizing these North Carolina specimens as a separate race.

***Ephemerella conestee* Traver**

(Figures 25, 45, and 54)

*Ephemerella conestee* Traver 1932, 168, 5 figs.; Traver 1935, 587, 1 fig.; Howell 1941a, 313; Howell 1941b, 407.

*Ephemerella conestee* was described from a series of nymphs, a female imago, and a male subimago collected in North Carolina. Since the male subimago and the female imago do not have characters that are useful in distinguishing this species from all other known species of the genus, diagnoses are not included for these stages.

*Male Imago*.—Unknown (subimago only).

*Mature Nymph*.—Length: body 8-9; caudal filaments 4-5 mm. General color brown. Head with short lateral frontoclypeal tubercles, blunt lateral genal projections, a broad round frontal shelf, and small conical occipital tubercles (fig. 25). Thoracic tubercles absent; legs brown, forefemora as in fig. 45; tarsal claws with two to three denticles. Abdomen with paired dorsal submedian tubercles on segments 3-7, posterior margins of segments 8-10 with long hair. Caudal filaments brown.

*Type Locality*.—Tributary of Pigeon River near Hazelwood, North Carolina.

*Type*.—No. 1096.1, Cornell University Collection, Ithaca, New York.

DISTRIBUTION

This species is known only from the Appalachian Mountains of North Carolina and Tennessee (fig. 54). We have examined specimens from the following localities:

NORTH CAROLINA: Tributary of Pigeon River nr. Hazelwood, 2-VIII-30, J. R. Traver (Holotype) (CU); Allens Creek, Hazelwood, 12-VII-30, J. R. Traver (CU); tributary of Pigeon River, Waynesville, 20/26-VII-30, J. R. Traver (CU); Ocona Lufty River, 28-VII-30, J. R. Traver (CNC); Macon Co., Overflow Creek, 25-VIII-38, T. Howell (JRT); Forneys Creek, Great Smoky Mountains, 26-VIII-31, J. G. Needham (JRT); Dry Creek, Great Smoky Mountains, 25-VIII-31, J. G. Needham (JRT); 0.9 mi. from Headquarters Coweeta Expt. For., 30-VII-57, S. and D. Mulaik; 1.1 mi. SW. Nantahala, on Route 19, 20-VII-57, S. and D. Mulaik; Edwards Creek, 5.6 mi. from Highlands Biol. Sta., 3-VII-57, S. and D. Mulaik; Bryson City, 6-VIII-30, H. T. Spieth (AMNH). TENNESSEE: Elkmont, 11-VIII-30, H. T. Spieth (AMNH).

***Ephemerella wayah* Traver**

(Figures 26, 46, and 54)

*Ephemerella wayah* Traver 1932, 172, 9 figs.; Traver 1935, 627, 2 figs.; Howell 1941a, 314; Pugh 1956, 26. *Ephemerella* sp. Day 1956, fig. 18b.

Traver (1932) described this species from nymphs

and male and female subimagoes, collected in North Carolina.

*Male Imago*.—Unknown.

*Female Imago*.—Unknown.

*Mature Nymph*.—Length: body 6-7; caudal filaments 2-4 mm. General color light brown with variable dark brown markings. Head with very short lateral frontoclypeal projections, blunt lateral genal projections, a broad round frontal shelf, and paired suboccipital tubercles (fig. 26). Thorax without tubercles; legs light brown with dark brown femoral, tibial, and tarsal bands, forefemora as in fig. 46; tarsal claws with one to three denticles. Abdomen with small paired dorsal tubercles on segments 3-7, long hair on segments 8 and 9; sterna with numerous fine hairs on segment 9 and on lateral margins of 2-8. Caudal filaments light brown with dark brown bands.

*Type Locality*.—Wayah Creek near Franklin, North Carolina.

*Type*.—No. 1097.1, Cornell University Collection, Ithaca, New York.

DISTRIBUTION

*Ephemerella wayah* is known only from North Carolina (fig. 54). We have examined specimens of this species from the following localities:

NORTH CAROLINA: Wayah Creek nr. Franklin, 1-VII-29, J. R. Traver (Holotype) (CU); Allens Creek, 1-VII-29, J. R. Traver (CU).

***Ephemerella walkeri* Eaton**

(Figures 10, 27, 47, and 54)

*Baetis fuscata* Walker 1853, 570 (in part), *nec Baetis fuscata* Stephens 1835, 66; Hagen 1861, 47.

*Ephemerella walkeri* Eaton 1884, 129, new name for *Baetis fuscata* Walker *nec* Stephens; Clemens 1915, 114; Ulmer 1920, 119; Spieth 1940, 334 (rejection of *fuscata* reaffirmed); Leonard 1950, 19; Burks 1953, 65, 2 figs.

*Ephemerella bispina* Needham 1905, 43, 1 fig. (in part, adult *nec* nymph); Banks 1907, 17 (in part, adult *nec* nymph).

*Ephemerella fuscata* McDunnough 1931, 214 (= *bispina*); Ide 1935, 44; Traver 1935, 600, 2 figs.; Britton 1938, 12.

Walker (1853) based this species upon two specimens, a male imago and a male subimago, and gave a brief and inadequate description of each. Eaton (1884) stated that the male subimago is probably a *Rhithrogena*, and the name *Baetis fuscata* Walker is preoccupied by *Baetis fuscata* Stephens, 1835, and renamed the male imago *Ephemerella walkeri*.

Needham (1905) named *Ephemerella bispina* from single male and female imagoes, a male subimago, and three nymphs. McDunnough (1931c) established the identity of *E. walkeri* by sending newly collected specimens from Canada to the British Museum for comparison with the type. He also compared these

identified specimens with part of the type lot of *E. bispina* and showed that the adults were synonymous with *E. walkeri*, but he did not assure the stability of his actions by designating a lectotype. To preserve the present application of these names in this genus we herein designate the adult male of *E. bispina* as the lectotype, thus formalizing the accepted synonymy.

*Male Imago* (dry).—Length: body 8-9; forewing 9-10 mm. General color brown. Head and thorax brown; legs brown, femora with numerous small black dots; wings hyaline, longitudinal veins light brown, crossveins pale. Abdominal terga ruddy brown; sterna light brown posteriorly and ruddy brown anteriorly, segment 9 ruddy brown. Male genitalia as in fig. 10. Caudal filaments light brown.

*Female Imago*.—Length: body 7-8; forewing 9-10 mm. Similar to male except for usual sexual differences.

*Mature Nymph*.—Length: body 8-10; caudal filaments 3-5 mm. General color brown. Head with very short lateral frontoclypeal tubercles, sharp hairy lateral genal projections, a broad round frontal shelf, and paired suboccipital tubercles (fig. 27). Prothorax with small paired submarginal tubercles; legs light brown with dark brown femoral, tibial, and tarsal bands, forefemora as in fig. 47; tarsal claws with one to three denticles. Abdomen with very small paired dorsal tubercles on segments 3-7, long hair on segments 8 and 9; abdominal sterna sparsely clothed with fine hair on lateral margins of segments 2-9. Caudal filaments light brown.

*Type Locality*.—Saint Martins Falls, Albany River, Hudson Bay.

*Type*.—British Museum, London, England.

#### DISTRIBUTION

*Ephemerella walkeri* is a boreal eastern North American species known from Nova Scotia to Ontario and Michigan and austrad to Indiana (fig. 54). The authors have examined specimens from the following localities:

CONNECTICUT: Redding, 1-V-33, H. T. Spieth (AMNH). MASSACHUSETTS: Bachelor Brook, S. Hadley, 14-V-49, T. Dolan and J. R. Traver (JRT). MICHIGAN: Platte River, Honor, 27-V-39, T. H. Frison and H. H. Ross (INHS). NEW BRUNSWICK: Boiestown, 13-VII-28, W. J. Brown (CNC); NW. Mirimichi River, 6-VI-51, 13-VII-51, E. L. Bousefield. NEW YORK: Cedar River near Indian Lake Adirondack Park, 20-VI-41, T. H. Frison and H. H. Ross (INHS). NOVA SCOTIA: Annapolis River, 25-VI-50, E. L. Bousefield. ONTARIO: Cardinal, 18-VI-31, L. J. Milne (CNC). QUEBEC: Vaudreuil, 24-VI-30, G. S. Walley (CNC); Fulford, 20-VI-30, 4-VII-30, G. S. Walley (CNC); Cascades Point, 4-VII-30, G. S. Walley (CNC); Knowlton, 28-VII-30, L. J. Milne (CNC); Ste. Annes, 24-VI-25, F. P. Ide (CNC); Ste. Lambert, 4-VII-27, G. S. Walley (CNC); LaPrairie, 7-VII-25, F. P. Ide (CNC); Broadbie, 13-VII-23, R. Ozburn (CNC).

#### *Ephemerella doddsi* Needham

(Figures 1, 20, 28-33, and 52)

Allied to *Ephemerella*, Nymph No. 3 Eaton 1884, 132, pl. 39.

(*Ephemerella*) *Drunella grandis* Dodds 1923, 95, 2 figs. nec Eaton 1884, 128; Dodds and Hisaw 1924, 145, 1 fig. (*Ephemerella*) *Drunella* sp. Lestage 1925, 294.

*Ephemerella doddsi* Needham 1927, 111; Needham 1927, 133; Needham and Christensen 1927, 7, 1 fig.; McDunnough 1928, 8; Walley 1930, 14, 2 figs.; McDunnough 1931, 210; Traver 1935, 591, 1 fig.; Linduska 1942, 27; Edmunds 1954, 66; Day 1956, 96, 2 figs.; Allen and Edmunds 1956, 87.

*Ephemerella doddsi* was first reported in the literature by Eaton (1884) as "Nameless ally to *Ephemerella*, No. 3," from Idaho (Idaho Springs?), Colorado. Dodds (1923) reared this nymph in Colorado and identified it as *Ephemerella grandis* Eaton. Needham (1927b) reared Eaton's nymph No. 3 in Utah and found Dodds' identification to be incorrect; he named the species *Ephemerella doddsi*.

*Male Imago*.—Length: body 13; forewing 14 mm. Head and thorax dark brown; pleural sutures and antero-lateral margin of mesonotum pale; forefemora dark purplish brown, tibiae and tarsi yellowish brown; wing hyaline, venation dark brown, stigmatic area cloudy. Abdominal terga 2-6 semi-hyaline, 8-10 opaque, each tergum with a broad purplish brown transverse band; sterna marked similar to terga. Male genitalia as in fig. 20. Caudal filaments purplish brown at base, paler distally.

*Female Imago*.—Length: body 10-12; forewing 14-16 mm. Much paler in color than male. Head and thorax light yellowish brown; legs and wings colored as in male. Abdominal terga light yellowish brown, each tergum with a broad purplish brown transverse band as in male; sterna marked similarly to those of male. Caudal filaments colored as in male.

*Mature Nymph*.—Length: body 10-12; caudal filaments 5-6 mm. General color uniformly brown. Head with a broad square frontal shelf and long lateral genal projections (figs. 1, 28-33); without occipital tubercles. Thoracic tubercles absent; legs brown, femora as in fig. 1; tarsal claws with one to three denticles. Abdomen without paired dorsal submedian tubercles, terga with paired submedian ridges as in fig. 1; sterna with abundant fine hair, forming a distinctive adhesive disc on segments 1-9. Caudal filaments pale.

*Type Locality*.—Logan River, Utah.

*Type*.—Cornell University Collection, Ithaca, New York.

#### DISTRIBUTION

*Ephemerella doddsi* is a boreal western North American species with an extreme latitudinal distribution. It occurs from southeastern Alaska austrad to central New Mexico, Arizona, and southern California (fig. 52). The authors have examined specimens from 226 localities of which the following are marginal and representative.

ALASKA: Campbell Creek, Anchorage, 21-IV-48, "Lienk." (INHS). ALBERTA: Lower Pipestone Creek, 27-VII-38, "Rawson." BRITISH COLUMBIA: Capilano River, North Vancouver, 3-VII-40, H. H. Ross (INHS). CALIFORNIA: San Bernardino Co., Barton Flats, 27-VI-50; Nevada Co., Eure Valley, 4-VII-48, W. C. Day. COLORADO: Boulder Co., Como Creek, Boulder, 24-VII-39, "Lanham" (INHS); El Paso Co., Green Mountain Falls Canyon, 19-VII-48, H. H. and J. A. Ross (INHS). IDAHO: Blaine Co., Big Wood River, 3-IX-44, GFE. MONTANA: Park Co., Soda Butte Creek, Silver Gate, 2-VIII-40, T. H. Frison and T. H. Frison, Jr. (INHS); Flathead Co., Dutch Creek, Glacier Natl. Pk., 11-VII-43, H. H. and J. A. Ross (INHS). NEVADA: Elko Co., Lamoille Creek (elev. 6,268'), 19-IX-57, GFE and RKA; Washoe Co., Galena Creek on Nevada Highway 27, 21-IX-57, GFE and RKA. NEW MEXICO: San Miguel Co., Terrero, 2-VII-43 (JRT). OREGON: Wallawa Co., Shady Camp, Lostine River, 18-VIII-52, GFE; Benton Co., Oak Creek, Corvallis, 12-IV-38, "Seghetti" (OSC). UTAH: Salt Lake Co., Big Cottonwood Canyon, 24-VII-50, GFE; San Juan Co., Miller Creek, LaSal Mountains, 14-VI-46, S. Mulaik. WASHINGTON: King Co., Tolt River, 29-V-41, J. J. Davis (BLL); Whatcom Co., Bagley Creek, Shucksan, 24-VII-36, H. H. Ross (INHS). WYOMING: Park Co., North Fork Shoshone River, Pahaska Tepee, 29-VII-40, T. H. Frison and T. H. Frison, Jr. (INHS); Albany Co., North Fork Little Laramie River, Centennial, 11-VI-61, GFE and W. L. Peters. YUKON TERRITORY: Alaska Highway mile post 632, Watson Lake, 15-VI-52, C. P. Alexander (UM).

#### TAXONOMY

The nymphs of *E. doddsi* are among the most distinctive in the genus and are readily distinguished from all other species by the broad frontal shelf on the head and the unique ventral adhesive disc on the abdomen. The morphological variability within the nymphs of this species is minimal. The only structures that show extreme variation are the lateral genal projections and the frontal shelf of the head (figs. 28-33); these differ in shape, sharpness, and degree of development. This variation is so striking that it would appear to be a racial character. This is not so, however, as there may be as much variation in the nymphs within a given stream as there is between the nymphs collected at extreme limits of its range. The nymph illustrated in figure 28 was collected from the Yukon Territory, Canada, while those illustrated in figures 29 to 33 were collected respectively, in central Oregon, northern Montana, northern Wyoming, southern California, and northern Wyoming. A comparison of these nymphal heads indicates the range of variation in the shape of these projections; however, nymphal series collected from any given stream have head projections which may include several of these types. Figures 31 and 33 were drawn from specimens collected in the same stream in Yellowstone National Park, Wyoming.

Series of nymphs of *E. doddsi* collected from the coastal streams of California, Oregon, and Washington are readily distinguished from other nymphs of this species by the sharpness of the frontal projections (fig. 32).

#### BIOLOGY

The nymphs of *E. doddsi* are found in streams at elevations from 6,000 to 11,000 feet. The size of the stream seems to be of little importance as long as the flow is rapid, the water cold, and the bottom is clean of silt and has large stones or coarse gravel present. This species has never been collected among leaves, debris, or silt. *Ephemerella doddsi* is well equipped for swift currents with its flattened appendages, frontal shelf, contoured body, and ventral adhesive disc with which it is able to cling to stones in the water. This nymph, however, is often found on the undersides of large stones where current-resistant devices would not seem necessary for survival. It is possible that they use the suction cups when they feed or move around on exposed surfaces. Nymphs have been observed on the surface of large rocks in the face of the current, but they never seem to move directly into it. They have a rather peculiar sideways movement.

Young nymphs have been collected throughout the range of this species from September 19 to June 2, while nearly mature to mature nymphs have been found from February 17 to September 22. Adults have been reared and collected from June 19 to August 18.

#### *Ephemerella pelosa* Mayo

(Figures 50 and 51)

*Ephemerella pelosa* Mayo 1951, 121, 2 figs.; Allen and Edmunds 1956, 87; Day 1956, 98.

This species, apparently one of the rarest in the genus, was described from a single nymph collected in California. Allen and Edmunds (1956) reported *E. pelosa* from Oregon, also from a single nymph.

*Male Imago*.—Unknown.

*Female Imago*.—Unknown.

*Mature Nymph*.—Length: body 8; caudal filaments 8 mm. General color dark brown with yellow markings. Head with a long fringe of olive hair on genae from eyes to mouthparts; paired submedian tufts of hair on the occiput; thorax with submedian rows of hair; forefemora as in fig. 50, all legs with heavy fringe on anterior surface of all segments; tarsal claws with three denticles. Abdominal terga with paired submedian tufts of hair on segments 1-9; hair along median line on segment 10; abdominal sterna with an adhesive disc formed of hairs on segments 3-8. Caudal filaments yellow with a brown transverse band near the base.

*Type Locality*.—North Fork Creek, above Bass Lake, California.

*Type*.—California Academy of Sciences, San Francisco, California.

## DISTRIBUTION

*Ephemerella pelosa* is presumably a boreal species. It is known from scattered localities from Washington austrad to southern California (fig. 51). The authors have examined specimens from the following localities:

CALIFORNIA: Los Angeles Co., Elizabeth Lake, 16-V-51, J. N. Belkin (UCLA). OREGON: Benton Co., Rock Creek, 5 mi. W. Philomath, 2-V-52, V. Roth. WASHINGTON: King Co., Green River, 21-IV-41, B. L. Lambuth (BLL).

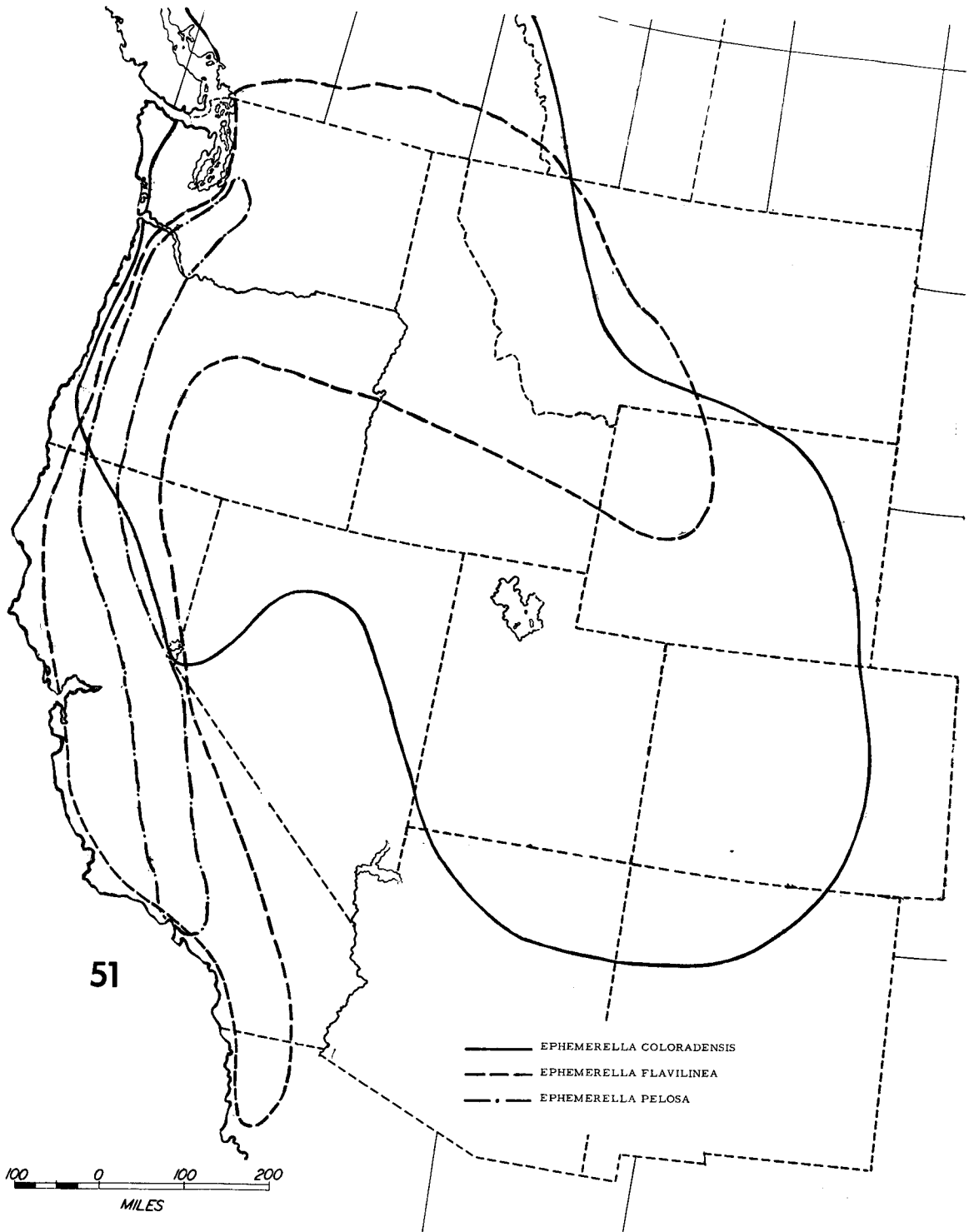


FIG. 51.—Distribution map of *Ephemerella coloradensis*, *E. flavilinea*, and *E. pelosa*.

**Ephemerella grandis** Eaton

*Ephemerella grandis* was originally described from a male subimago and a female imago by Eaton (1884). In this same publication, Eaton described the nymph of the species as "*Ephemerella, sedis incertae, Nymph No. II.*" Needham (1905) correctly recog-

nized this nymph as *E. grandis* by comparing the venation of the developing wing of a mature nymph with Eaton's (*op. cit.*) figures. Needham (1927b) later affirmed this association by rearing the species.

*Male Imago*.—Length: body 17-19; forewing 17-19 mm. Head yellowish brown to reddish brown; upper portion of eyes yellow to brown, lower portion black.

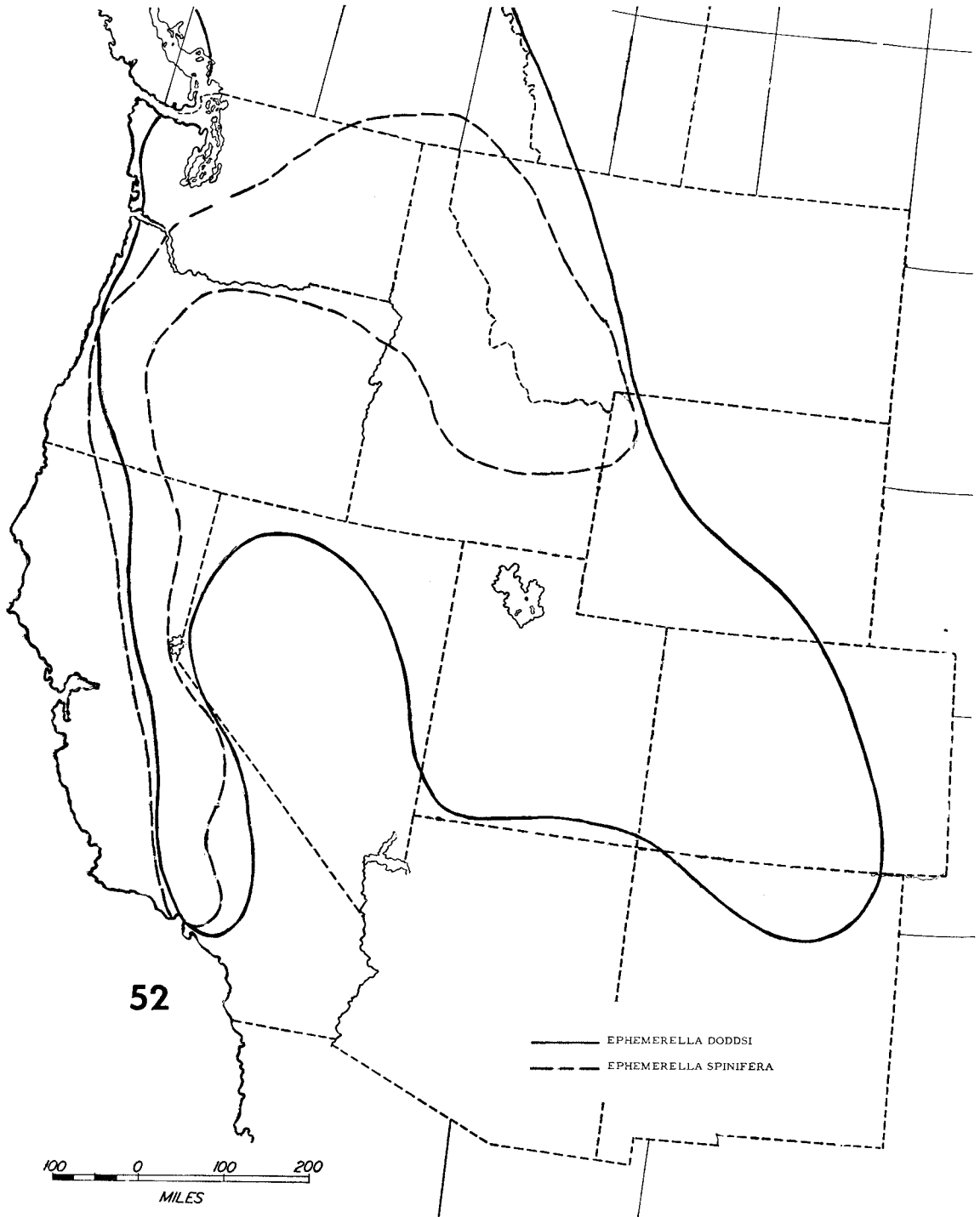


FIG. 52.—Distribution map of *Ephemerella doddsi* and *E. spinifera*.

Thorax yellowish brown to reddish brown; pleural sutures pale, with purplish brown markings; scutellum bordered with blackish brown; forelegs brown, tarsi paler, middle and hind legs yellowish brown, all femora with a broad purplish subapical trans-

verse band on the distal half; wings amber to hyaline, venation dark brown (figs. 11-12). Terga largely purplish brown with pale pleural and posterior margins, giving a distinct ringed appearance to the abdomen; paired pale paramedian stripes dividing the

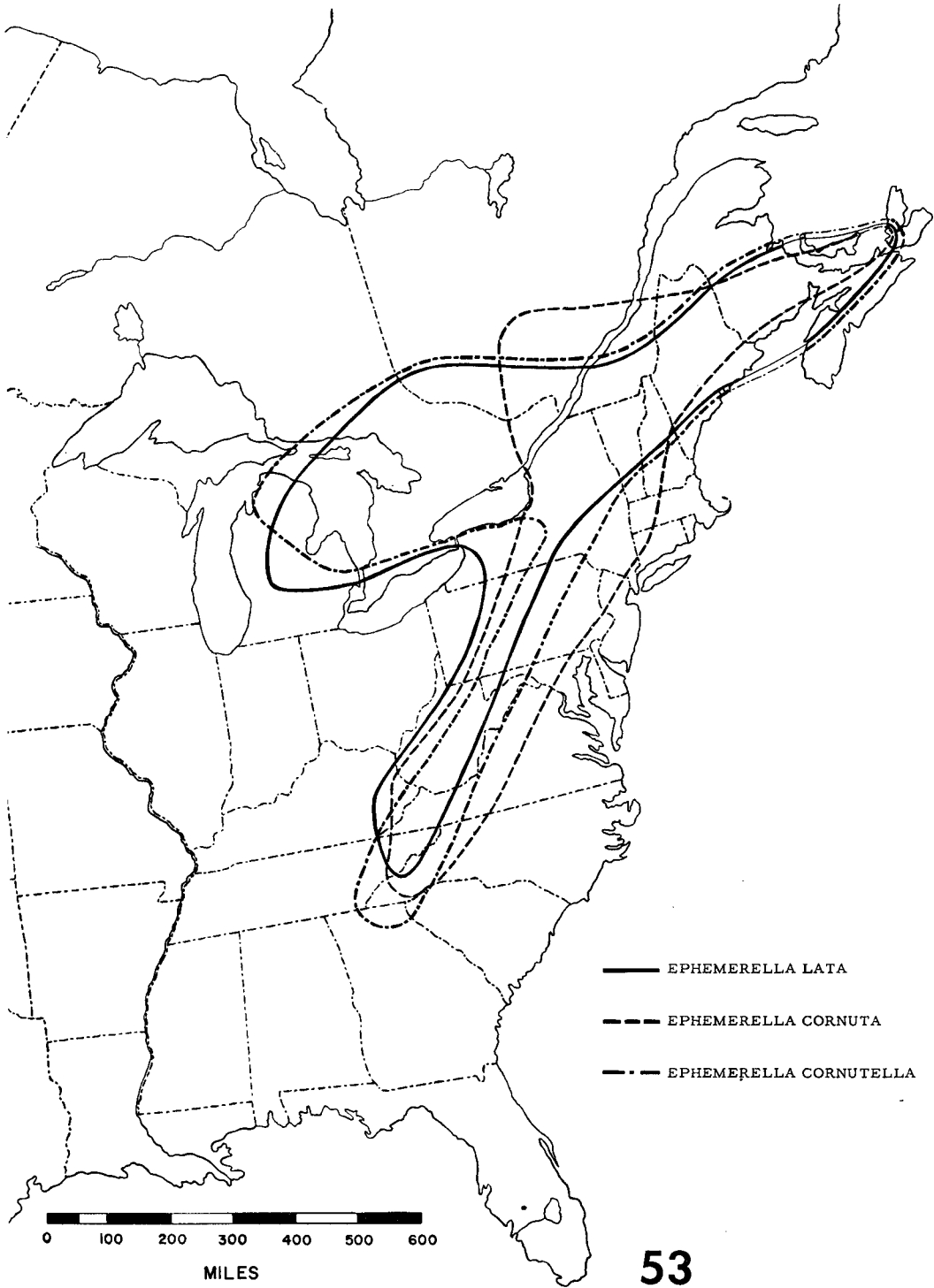


FIG. 53.—Distribution map of *Ephemerella lata*, *E. cornuta*, and *E. cornutella*.



purplish brown section of the terga into three parts; sterna similar in color to terga, but without submedian pale stripes. Genitalia as in fig. 61. Caudal filaments deep purplish brown at base, paler distally.

*Female Imago*.—Length: body 17-19; forewing 17-19 mm. Head pale, purplish brown along posterior margin. Thorax much paler in color than in male; legs and wings colored and marked as in male. Ab-

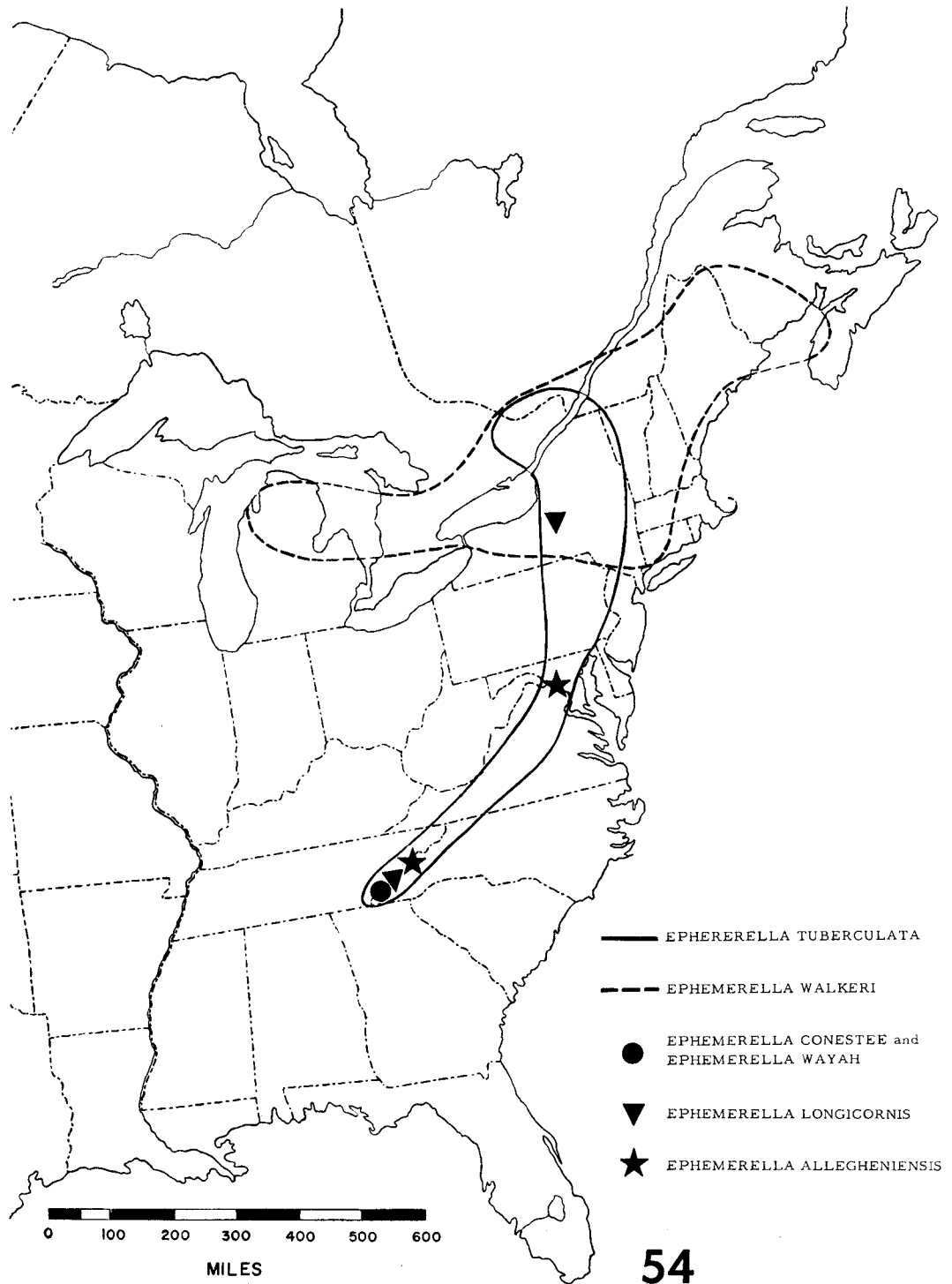


FIG. 54.—Distribution map of *Ephemera tuberculata*, *E. walkeri*, *E. allegheniensis*, *E. conestee*, *E. wayah*, and *E. longicornis*.

domen purplish brown, divided by a pale median line. Caudal filaments colored as in male.

*Mature Nymph*.—Length: body 12-15; caudal filaments 8-9 mm. General color brown. Head with occipital tubercles (figs. 55-60); mouthparts as in figs. 13-16. Pronotum with a variable pair of antero-lateral submarginal tubercles and a group of two or three paired submedian tubercles, the anterior pair usually longer than the posterior pair, median pair, when present, smallest; mesonotum with paired submedian tubercles on the anterior margin, paired submedian ridges or blunt to sharp tubercles near middle of mesonotum and a single posterior tubercle between bases of wing pads (figs. 55-57); legs brown, tarsi often with dark proximal and distal transverse bands, forefemora without tubercles (fig. 62); tarsal claws with three to six denticles. Abdominal terga with prominent paired dorsal submedian tubercles on segments 2-9; sterna usually reddish brown with pale posterior and lateral margins on segments 1-9. Caudal filaments pale with several irregular dark-brown bands.

#### DISTRIBUTION

*Ephemerella grandis* is a boreal western North American species and is one of the most widely distributed western *Ephemerella*. This species is known from southeastern Alaska austrad to southern California, Arizona, and New Mexico. The eastern limits of this species appear to be along the east slope of the Rocky Mountains in New Mexico, Colorado, and Wyoming (fig. 70).

#### TAXONOMY

*Ephemerella grandis* has been known in the literature by a total of seven different names, six of which were heretofore recognized as valid. This taxonomic confusion has resulted mainly from the failure of mayfly specialists to appreciate the fact that the nymphs of this species exhibit both age and geographic variation to a greater degree than any other species in the genus.

In the very young nymphs of *E. grandis* the paired occipital, thoracic, and abdominal tubercles on segments 2-7 are small, relative to the over-all size of the nymph. However, the paired dorsal abdominal tubercles on segments 8-9 are often more than twice as long as the abdominal tubercles of segments 2-7 (fig. 64). As the nymph matures these last two pairs of abdominal tubercles develop at a slower rate than the tubercles on segments 2-7, until the tubercles form a nearly regular series in most fully mature nymphs (fig. 63). The length of the abdominal tubercles on segments 8-9 may remain slightly larger than those on segments 2-7 in fully mature nymphs. Similar disproportionate growth also occurs on the tubercles of the head and thorax. The relative proportion of one pair of tubercles to another is thus so variable as to be useless as a diagnostic character.

As a result of the study of long series of nymphs and of all available adults from most of the geographic range of the species, we have arrived at what

we believe to be a sound interpretation of the nature of this species. *Ephemerella grandis* is polytypic and consists of three subspecies, *E. g. grandis* Eaton, *E. g. ingens* McDunnough, and *E. g. flavitincta* McDunnough.

The paired dorsal tubercles of *E. g. grandis* nymphs are short and blunt, and the subspecies is easily recognized by the lack of well-developed tubercles on the mesonotum (fig. 55). The nymphs of *E. g. ingens* have moderately developed thin occipital, thoracic, and abdominal tubercles (fig. 56), while the nymphs of *E. g. flavitincta* have very long thin acute tubercles (fig. 57). The antero-lateral prothoracic tubercles of *E. g. flavitincta* are long and thin (fig. 57), while those of *E. g. ingens* are only moderately developed (fig. 56) and those of *E. g. grandis* are barely discernible (fig. 55). However, an occasional nymph of *E. g. ingens* has these tubercles so well developed that it is not separable from *E. g. flavitincta* by this character alone.

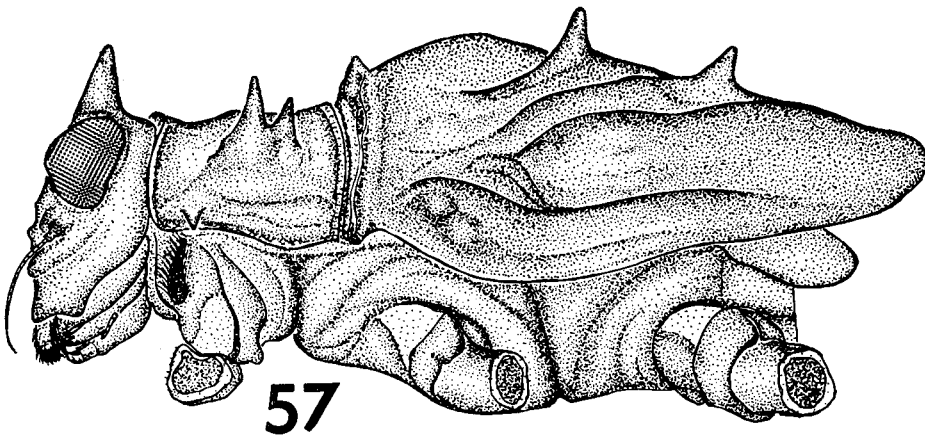
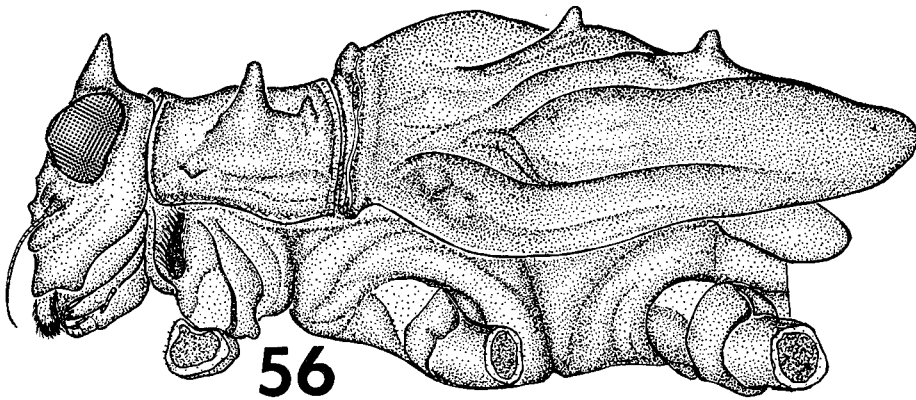
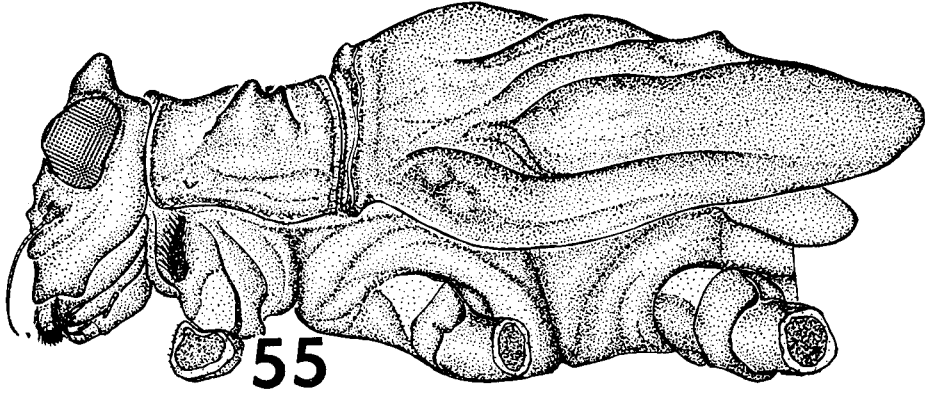
The adult stages of the genus *Ephemerella* are rare in collections, and long series of *E. grandis* have not been available for study. Only three adults of *E. g. flavitincta* are known at the present time, and only a few adults of the other two subspecies have been reared or collected. The forewings of *E. g. flavitincta* are colored with deep amber, while the forewings of *E. g. ingens* have only an amber suffusion in the basal portion, and those of *E. g. grandis* are hyaline. The known adults of *E. g. flavitincta* are larger in size than those of *E. g. grandis* or *E. g. ingens*, while *E. g. ingens* adults average slightly larger than those of *E. g. grandis*. Size, however, is a variable character and dependent upon too many environmental factors to be of racial significance in the small samples now known. The male genitalia of *E. g. grandis*, *E. g. ingens*, and *E. g. flavitincta* have been compared and no structural differences have been observed.

*Ephemerella g. grandis* intergrades with *E. g. ingens* in two disjunct areas where their ranges are known to meet. Populations of nymphs from streams on the east slope of the Sierra Nevada Mountains and from a broad zone in Wyoming, Montana, and Idaho show intergradation of both subspecies; whereas, all samples collected outside these zones of intergradation have only the characters of their respective subspecies. Nymphs of *E. g. flavitincta* from central Oregon indicate intergradation of this subspecies with *E. g. ingens*, but more material from this critical area must be studied in order to clarify these relationships.

A collection of 15 nymphs from Cottonweed Creek near Oasis Ranch, Mono County, California, 11-VI-39, V. K. Mayo (VKM) (reported as *Ephemerella* Species Number 1 by Mayo 1951: 124) have occipital and mesothoracic tubercles typical of *E. g. grandis*, but the abdominal tubercles of these specimens resemble those of *E. g. ingens*. These nymphs are considered to be intergrades of these subspecies. Two mature nymphs from the Walker River in California have been examined. One nymph from near Bridgeport, 3-VII-38, V. K. Mayo (VKM), has charac-

ters typical of *E. g. ingens*, while the other nymph from near Coleville (elev. 6,600'), 5-VII-39, V. K. Mayo (VKM), has characters typical of *E. g. grandis*. These nymphs are probably extremes of an intergrading population, but since they are from separate localities and collections they have been assigned to their respective subspecies. Four mature nymphs from the Consumnes River, Pi Pi Valley,

California, 5-VI-38, V. K. Mayo (VKM), are clearly intergrades of these two subspecies. All of these specimens have a high mesonotal ridge with a small tubercle, and long thin occipital and abdominal tubercles. Three mature nymphs from Martis Creek near Truckee, California, have characters typical of *E. g. ingens*, but this small sample does not preclude the possibility that these races intergrade in this



FIGS. 55-57.—*Ephemerella grandis*, lateral view of head and thorax of each subspecies: fig. 55, *E. g. grandis* (from Green Mountain Falls, Colorado); fig. 56, *E. g. ingens* (from Glacier Natl. Pk., Montana); fig. 57, *E. g. flavitincta* (from Yaquina River nr. Nashville, Oregon).

area. Long series of very young nymphs have been collected from the West Fork of the Carson River, 2 miles northeast of Woodfords, California; the West Fork of the Carson River, 3 miles east of the California State Line, Nevada; and two localities from the Truckee River near Reno, Nevada. All of these nymphs possess mesonotal tubercles; however, very young nymphs of *E. g. grandis* also possess mesonotal tubercles. The subspecific affinities of these nymphs from this known area of intergradation cannot be determined and the records have therefore been omitted from the distribution map (fig. 70).

The other area in which these subspecies intergrade occurs in northern Wyoming, western Montana, and southern Idaho. Of 88 mature nymphs collected in Vale Creek, Sheridan County, Wyoming, 4-VI-59, A. G. Dumont (SC), 61 specimens have a high mesonotal ridge, thin sharp abdominal tubercles, and short blunt occipital tubercles. All of these specimens are clearly intergrades of these two subspecies. Sixteen specimens have characters typical of *E. g. grandis*, while 11 specimens have characters typical of *E. g. ingens*. A collection of six mature nymphs from Canyon Creek, Poudre River Pass, Big Horn Mountains, Wyoming, 21-VI-40, H. H. and J. A. Ross (INHS), have the same general characters as the intergrades from Vale Creek. A single mature nymph from the Big Lost River, Mackay, Idaho, VII-48, G. F. Edmunds, Sr., has a small tubercle on a high mesonotal ridge, occipital tubercles intermediate between *E. g. grandis* and *E. g. ingens*, and thin sharp abdominal tubercles. Since this specimen has characters of both subspecies it has been placed as an intergrade. A collection of five mature nymphs from the Bitterroot River, U. S. Highway 93, 30-VI-59, GFE, have well-developed occipital and abdominal tubercles typical of *E. g. ingens*, but low mesonotal ridges typical of *E. g. grandis*. A larger series of 31 mature nymphs collected from Clark Fork, 12 miles west of St. Regis, Montana, 30-VI-59, GFE, show intergradation. Twenty-five of the nymphs have a mesonotal tubercle, but the development of the occipital tubercles varies from that typical of *E. g. grandis* to that typical of *E. g. ingens*. Five nymphs have only a low mesonotal ridge, but well-developed occipital tubercles.

A long series of mature nymphs from Yellowstone National Park and a smaller series from the Blue Mountains of Oregon are typical *E. g. grandis*. The records from the Madison River in Montana and the Salmon River, Idaho, are of single mature nymphs, while the sample from Phillipsburg, Montana, is a series of rather young nymphs. All of these specimens are, however, typical of *E. g. ingens*. A single young nymph from near Bozeman, Montana, and a series of very young nymphs from the Payette River near Crouch, Slate Creek near Lucile, and the Salmon River near Whitebird in western Idaho are too young to be placed to subspecies.

Nymphs which agree with McDunnough's (*op. cit.*) characterization of *E. flavitincta* have been collected from the coast of Oregon, Washington, Yukon

Territory, and Alaska. However, nymphs collected just a few miles inland in Oregon show a reduction in the acuteness of these tubercles and are difficult to distinguish from nymphs of *E. g. ingens*. A collection of 53 half-grown nymphs from the Metolius River (elev. 2,940'), Oregon have characters which are intermediate between *E. g. ingens* and *E. g. flavitincta*. Two fully mature nymphs from the McKenzie River in Oregon are both intermediate in characters; however, in another collection of two fully mature nymphs from the McKenzie River, one nymph possesses characters of *E. g. ingens* while the other has characters of *E. g. flavitincta*. Four nymphs in two collections from the Willamette River in Oregon have characters of *E. g. ingens* and have been placed as this subspecies, while three mature nymphs collected farther inland, from the Calapooya River in Oregon, are typical *E. g. flavitincta*. The intermediate forms may represent one step of a cline or intergrades of two interbreeding populations. We do not have adequate series of mature nymphs to determine whether *E. flavitincta* is best recognized as a separate race or merely as a clinal extreme of *E. g. ingens*. Since the name *E. flavitincta* has been proposed and both the nymphal and adult stages are apparently distinguishable morphologically, we are herein considering *flavitincta* to be a subspecies of *E. grandis*. This conclusion should be reconsidered when series of mature nymphs, or preferably reared specimens, become available from the critical areas.

The characters used to separate the three subspecies may suggest to some that it would be best to treat the entire species as clinal, but most of the range of the species is occupied by non-clinal series of populations with great subspecific integrity. As an example, series of nymphal *E. g. grandis* from Yellowstone National Park in northwestern Wyoming are morphologically indistinguishable from series from central New Mexico. Such subspecific integrity of coastal populations of *E. g. flavitincta* seems well established, but if study of subsequent collections reveals that the geographical zone of intergradation with *E. g. ingens* is larger than the range of the morphologically uniform coastal population, we would be inclined to recognize the coastal populations only as the end of an *E. g. ingens* cline. We also believe that the present treatment of *E. grandis* should be re-examined if future collections of series of adults reveal discordance in the geographical distribution of adult and nymphal subspecific characters.

***Ephemerella grandis grandis* Eaton, new status**  
(Figures 11-16, 55, 60, 61-64, and 70)

*Ephemerella grandis* Eaton 1884, 128, pl. 14; Banks 1892, 347; Banks 1904, 100; Banks 1907, 17; Needham 1927b, 108, line 26 of 111, 1 fig.; Needham and Christensen 1927, 8, 1 fig.; Walley 1930, 17; Traver 1935, 601, fig. 151g; Spieth 1941, 96; Edmunds 1954, 66; Day 1956, 96, 2 figs.

*Drunella grandis*, Needham 1905, 43, pl. 10.

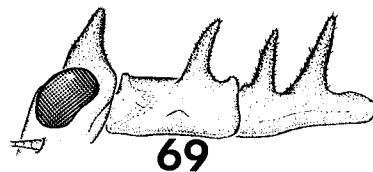
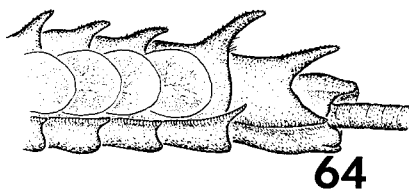
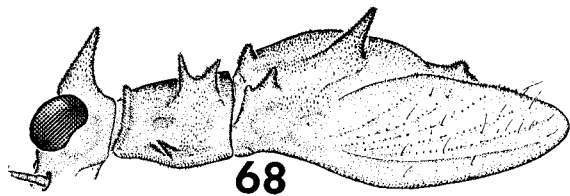
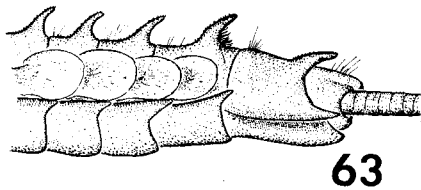
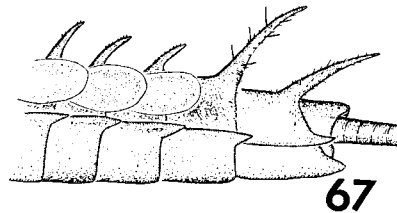
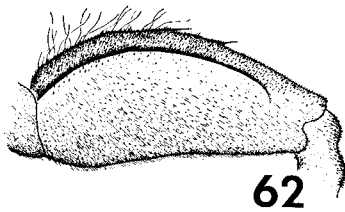
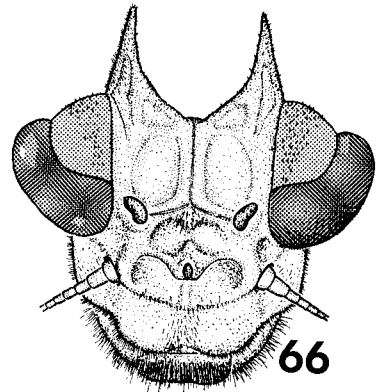
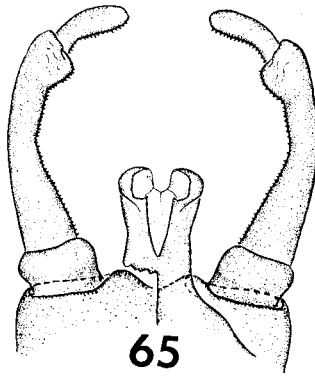
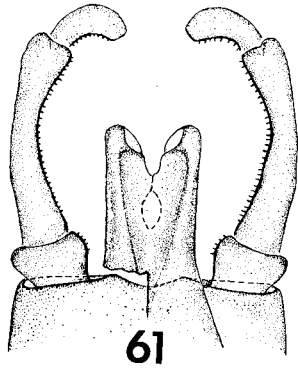
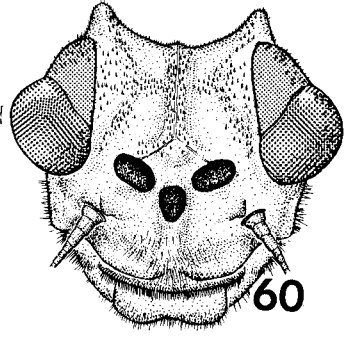
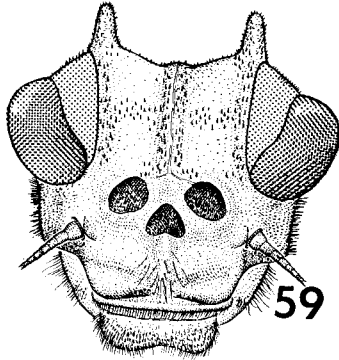
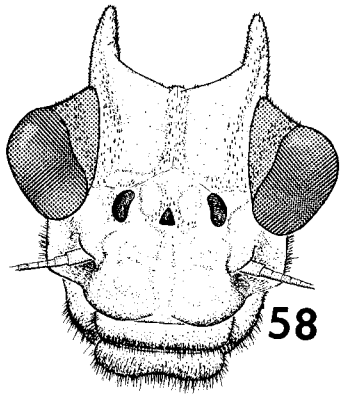
*Ephemerella* sp. No. 1, Mayo 1951, 124, 5 figs.

*Ephemerella glacialis carsona* Day 1952, 32, 5 figs., NEW SYNONYMY.

Eaton established the name of this subspecies in describing the species.

Day (1954) described *Ephemerella glacialis carsona* from the Carson River of California from a

population which our studies now prove to be intergrades between *E. grandis grandis* and *E. g. ingens*. The nymphs of this population have better developed mesonotal ridges and occipital tubercles than typical



*E. g. grandis* nymphs, and thin abdominal tubercles similar to typical *E. g. ingens*.

*Imagoes*.—The adults of this race may be distinguished by having the wings hyaline and without amber markings.

*Mature Nymph*.—The immature stage of this race may be distinguished by having short blunt occipital (fig. 60) and pronotal tubercles, and a low mesonotal ridge (fig. 55). The abdominal tubercles are usually blunt and thick.

*Type Locality*.—"Colorado."

*Type*.—McLachlan Collection, British Museum, London, England.

#### DISTRIBUTION

*Ephemerella grandis grandis* is an inland subspecies known from the Blue Mountains of eastern Oregon to northern Wyoming and austrad to Mono County, California, southern Arizona, and northern New Mexico (fig. 70). The authors have examined specimens typical of this subspecies from 92 localities of which the following selected examples are marginal and representative.

ARIZONA: Gila Co., Horton Creek, Tonto Natl. For., 1-VI-37, C. M. Tarzwell; Greenlee Co., Black River, Apache Natl. For., 21-VI-37, C. M. Tarzwell; Apache Co., Voigt River, East Fork Little Colorado River, 28-VI-37, C. M. Tarzwell. CALIFORNIA: Walker River (elev. 6,600'), 5-VII-39, V. K. Mayo (VKM). COLORADO: Grand Co., Frazier River, Granby, 24-VII-38, H. H. and J. A. Ross (INHS); El Paso Co., Fountain Creek, Manitou Springs, 27-VIII-31, D. Hamlett (AMNH); Green Mountain Falls, 19-VI-38, H. H. and J. A. Ross (INHS); Rocky Mountain Natl. Pk., Fall River, Horseshoe Park, 18-II-43, T. H. Frison (INHS); Gunnison Co., Alpine (elev. 10,000'), 20 mi. S. Gunnison, 18-IV-46, R. J. Drake. NEVADA: Elko Co., Columbia Creek, Bull Run Mountains, 20-IX-57, GFE and RKA; Secret Creek, 8 mi. NW. Authur, 19-IX-57, GFE and RKA; Franklin River, 12 mi. S.W. Authur, 19-IX-57, GFE and RKA; stream at Authur, 19-IX-57, GFE and RKA; Lander Co., stream at Youngs Ranch, Highway 8A, 22-IX-57, GFE and RKA. NEW MEXICO: San Miguel Co., Pecos River nr. Cowles, 6-VIII-41 (JRT); Pecos River 17 mi. above Pecos, 30-VII-43 (JRT). OREGON: Grant Co., Canyon Creek, John Day, 24-V-37, Carson; Silvies River, Bear Valley Rangers Station, 21-VIII-54, GFE and RKA. UTAH: Cache Co., Logan River, 9-VII-26,

J. G. Needham (CU); Juab Co., Trout Creek, 8-V-34, R. Christenson (JRT); Uintah Co., Ashley Creek nr. Vernal, 7-VI-46, D. R. Merkle; Beaver Co., Beaver River, 5 mi. E. Beaver, 28-VIII-44, GFE; Washington Co., Pine Valley, 20-IV-50, L. T. Nielsen. WYOMING: Wind River Mountains, Red Rock Pass, 29-VIII-48, "R.R.L." (UN); Uinta Co., Bear River, Wyoming State Highway 33, 16-VII-48, L. T. Nielsen; Blacks Fork Creek, Fort Bridger, 12-VI-61, GFE and W. L. Peters; Yellowstone Natl. Pk., Firehole River, Biscuit Basin, 21-VI-49, GFE; Gibbon River, 30-VIII-49, "R.R.L." (UN); Soda Butte Creek, 1 mi. E. Soda Butte, 17-VIII-59, GFE and W. L. Peters; Lamar River, Jct. with Soda Butte Creek, 17-VIII-59, GFE and W. L. Peters; Fremont Co., Little Popo Agie River, 16-VI-60, GFE; 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; Albany Co., Little Laramie River, 6 mi. E. Centennial on Wyoming State Highway 130, 7-VI-61, GFE and W. L. Peters; Johnson Co., Clear Creek, Lucusta Camp, 2 mi. W. Buffalo on U. S. Highway 16, 10-VI-61, GFE and W. L. Peters; Carbon Co., North French Creek, 1 mi. above Brush Creek Rangers Sta., 7-VI-61, GFE and W. L. Peters.

#### TAXONOMY

Mature nymphs of *E. g. grandis* exhibit a minimum of morphological variability except in regions where it interbreeds with *E. g. ingens*. Only a small sample of adults of this subspecies have been examined, but they all have rather uniform morphological characters.

#### BIOLOGY

The nuptial flight of this species has never been observed. Despite its abundance in certain streams, all adults have been taken as subimagoes as they emerged from the stream. Needham (1927b) likewise failed to see the nuptial flight of this subspecies in Logan Canyon, Utah. The females have been observed ovipositing in midmorning on a cloudy day. The subimagoes emerge throughout the day, but do so especially in the late afternoon.

*Ephemerella g. grandis* nymphs have been collected from streams at 4,000 to 10,000 feet elevation. However, these nymphs are more commonly found in warmer streams below 7,000 feet elevation, but we have several records from Colorado up to 8,400 feet and one from 10,000 feet (Alpine, Colorado). Adults have been collected from early June to early July, but at the higher altitudes mature nymphs are occasionally

FIGS. 58-60.—*Ephemerella grandis*, front view of the head of each subspecies: fig. 58, *E. g. flavitincta* (from Yaquina River nr. Nashville, Oregon); fig. 59, *E. g. ingens* (from Glacier Natl. Pk., Montana); fig. 60, *E. g. grandis* (from Green Mountain Falls, Colorado). FIGS. 61-64.—*Ephemerella grandis grandis*: fig. 61, dorsal view of male genitalia, cut-away; fig. 62, left foreleg; fig. 63, lateral view of posterior abdominal segments of fully mature nymph (from Apache Natl. For., Arizona); fig. 64, lateral view of posterior abdominal segments of very young nymph (from Tonto Natl. For., Arizona). FIGS. 65-69.—*Ephemerella spinifera*: fig. 65, dorsal view male genitalia, cut away; fig. 66, front view of head; fig. 67, lateral view of posterior abdominal segments of fully mature nymph; fig. 68, lateral view of head and thorax of fully mature nymph; fig. 69, lateral view of head and thorax of very young nymph.

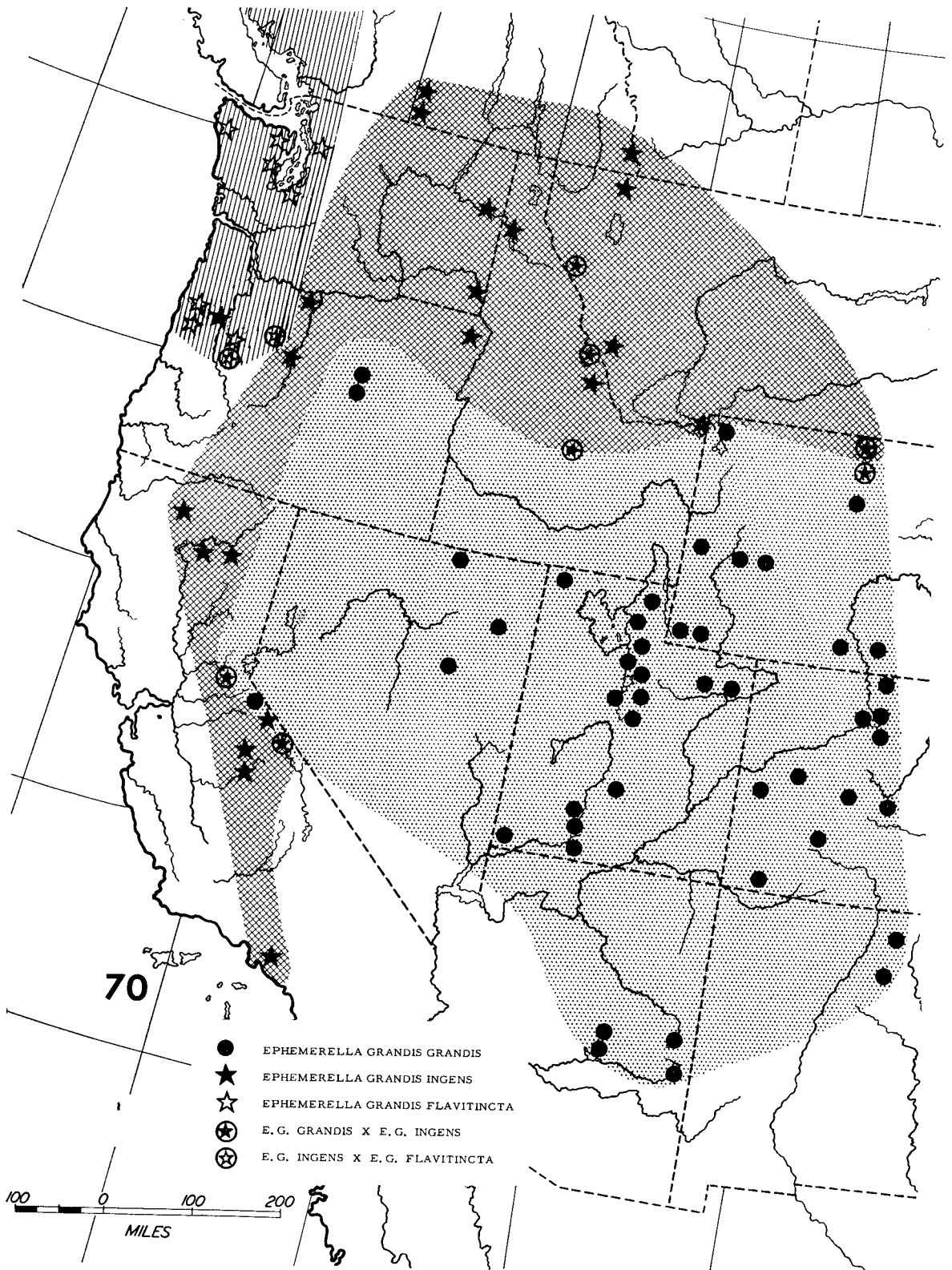


FIG. 70.—Distribution of the subspecies of *Ephemerella* (*Drunella*) *grandis*.

found until late August. The eggs usually hatch in September, and young nymphs are found throughout the winter. Growth is slow in the winter months but increases rapidly in the spring and early summer. The total nymphal life is thus 9 to 10 months.

***Ephemerella grandis ingens* McDunnough,**  
new status

(Figures 56, 59, and 70)

*Ephemerella, sedis incertae*, Nymph No. 2, Eaton 1884, 131, pl. 38.

*Ephemerella grandis*, Walley 1930, 17.

*Ephemerella ingens* McDunnough 1934, 154, 1 fig.; Traver 1935, 606.

*Ephemerella glacialis* Traver 1934, 207; Traver 1935, 601. NEW SYNONYMY.

*Ephemerella proserpina* Traver 1934, 223; Traver 1935, 615; Day 1954, 26 (=yosemite Traver, 1934); Day 1956, 97; Allen and Edmunds 1956, 87. NEW SYNONYMY.

*Ephemerella yosemite* Traver 1934, 225; Traver 1935, 627.

McDunnough (1934) described *E. ingens* from all stages collected in British Columbia and Traver (1934) described *E. glacialis* from a series of nymphs collected in Montana. Descriptions of these two species were in press at the same time and each author was apparently unaware of the other's publication. However, Traver (1935) recognized both species as valid on the basis of McDunnough's description. After a comparison of numerous specimens from Montana and British Columbia, and an examination of the holotype and paratypes of both nominal species, we conclude that these names apply to the same entity. The name *ingens* has date priority.

Traver (1934) described *E. proserpina* from a single nymph and *E. yosemite* from 10 immature nymphs collected in California. Day (1954) synonymized *E. yosemite* with *E. proserpina* after he had examined the types of these two nominal species and compared them with series of nymphs from California. After study of material from throughout western North America, we consider the above names to apply to *E. g. ingens*.

*Imagoes*.—The adults of this race have a suffusion of light amber in the basal portion of the forewings.

*Mature Nymph*.—The nymphs of this subspecies have moderately long and sharp occipital (fig. 59) and thoracic (fig. 56) tubercles. The abdominal tubercles are sharp and thin.

*Type Locality*.—Oliver, British Columbia, Canada.

*Type*.—No. 3760, Canadian National Collection, Ottawa, Ontario.

#### DISTRIBUTION

The range of *E. g. ingens* is north and west of *E. g. grandis*; the subspecies is known from southern British Columbia and Alberta austrad to southern Montana, central Idaho, and the San Bernardino Mountains in southern California (fig. 70). Specimens clearly assignable to *E. g. ingens* examined by the authors are from the following localities:

ALBERTA: Glacier Creek, Crows Nest Pass, 3-VII-30, J. H. Pepper (CNC). BRITISH COLUMBIA: Oliver, 5-VI-33, A. N. Gartrell (Holotype) (CNC); Oliver, 14-VI-33, A. N. Gartrell (CNC); Shingle Creek Road, Penticton, 2-VII-35, A. N. Gartrell (CNC); Trepanier Creek, Peachland, 5-VII-34, A. N. Gartrell (CNC); Foulder, Summerland, 5-VIII-34, A. N. Gartrell (CNC). CALIFORNIA: San Bernardino Mountains, Mill Creek Canyon, 2-IV-31, C. D. Michener (Holotype, *proserpina*) (CU); Yosemite Valley, Merced River, 3-II-33, P. R. Needham (Holotype, *yosemite*) (CU); Shasta Co., Burney Creek, nr. Cayton, 17-IX-46, H. G. Nelson (INHS); Plumas Co., Feather River, Chester, 11-XI-32, P. R. Needham (CU); Glen Co., Stoney Creek, 28-VI-51, W. C. Day; Siskiyou Co., Dunsuir, 11-VI-39, Grace H. and John L. Sperry (CNC); Madera Co., stream 0.8 mi. up road to Soquel, 19-VI-59, RKA; Sequoia Natl. For., Chilacoot Creek, 1 mi. above Bass Lake, 19-VI-59, RKA; Yosemite Natl. Pk., Goose Creek, 19-VI-59, RKA; San Bernardino Co., Warm Springs Creek, 24-IX-46, H. G. Nelson (INHS). IDAHO: Kootenai Co., Couer d'Alene River, 28-V-52 (VKM); Lemhi Co., Salmon River, 17 mi. N. Salmon, 20-VI-59, GFE. MONTANA: Glacier Natl. Pk., Midvale Creek, 8-VI-32, A. S. Hazard, et al. (Holotype, *glacialis*) (CU); Gallatin Co., Madison River, 2 mi. below Hebgen Dam, 21-VI-48, S. Preece. OREGON: Benton Co., Mary's River, Philomath, 8-V-39, "R. D." (OSC); Willamette River, Corvallis, 18-V-40, O. Lueff (OSC); Linn Co., Calapooya River, 12-V-39, F. E. Kimmey (OSC); Santiam River, 8 mi. N. Albany, 26-VIII-54, GFE and RKA; Lane Co., McKenzie River, B. and K. Doris State Pk., 15-VI-58, M. L. Johnson; Douglas Co., Little Deschutes River nr. Crescent, 23-VIII-54; GFE and RKA; Clackamas Co., Salmon River, Brightwood; Jefferson Co., Deschutes River, 13 mi. NW. Madras, 30-VIII-58, GFE and RKA; Metolius River, Sherman Camp, 23-VIII-54, GFE and RKA; Deschutes Co., Deschutes River, Cline Falls State Pk., 14-VI-54, GFE. WASHINGTON: Spokane Co., Little Spokane River, Milan, 3-VII-55, RKA; Whitman Co., Pullman, 15-VIII-05 (CNC).

#### TAXONOMY

The nymphs of *E. g. ingens* are variable in the degree of development and sharpness of the occipital, thoracic, and abdominal tubercles. *Ephemerella g. ingens* intergrades with *E. g. grandis* and nymphs collected from these regions have body tubercles which are intermediate between the two subspecies. Nymphs of *E. grandis* collected from the Willamette Valley and the west slope of the Cascade Mountains in western Oregon have body tubercles intermediate between *E. g. ingens* and *E. g. flavitincta*. These specimens have more characters of *E. g. ingens* and have been placed as this subspecies; however, they may eventually be found to be intergrades of the two subspecies. Significant morphological variability has not been observed in the adult stages, but long series



from critical localities have not been available for study.

#### BIOLOGY

The biology of this subspecies is similar to that of *E. g. grandis*. Nymphs of *E. g. ingens* have been collected from 200 to nearly 7,000 feet elevation. Adults have been collected from early June to early August.

#### *Ephemerella grandis flavitincta* McDunnough, new status

(Figures 57, 58, and 70)

*Ephemerella flavitincta* McDunnough 1934, 155; Traver 1935, 598; Allen and Edmunds 1956, 87.

McDunnough (1934) described *E. flavitincta* from all stages collected in western Oregon. He distinguished it from *E. glacialis* as the nymph was larger in size than the latter species, and the occipital, thoracic, and abdominal tubercles were longer and more acute. He noted that the adults of *E. flavitincta* were distinguishable by having amber-tinted wings.

*Imagoes*.—The adults of this subspecies have deep amber forewings.

*Mature Nymph*.—The immature stage of this subspecies has long thin acute occipital (fig. 58) and thoracic (fig. 57) tubercles. The abdominal tubercles are sharp and thin.

*Type Locality*.—Luckiamute River, Hoskins, Oregon.

*Type*.—No. 3761, Canadian National Collection, Ottawa, Ontario.

#### DISTRIBUTION

*Ephemerella g. flavitincta* is a boreal Pacific Coast subspecies and is known from the Alexander Archipelago of Alaska and southern Yukon Territory austrad to west central Oregon (fig. 70). Specimens examined by the authors that are clearly assignable to this subspecies are from the following localities:

ALASKA: Anan Creek, SE. Alaska Mainland (elev. 25'), 17-VI-58, G. L. Miller; Moseman Creek, Etolin Island, SE. Alaska, 26-VI-58, G. L. Miller. OREGON: Lincoln Co., Luckiamute River, Hoskins, 6-V-33, R. Dimick (Holotype) (CNC); Elk Creek at Elk Creek Park 1 mi. W. Harlan, 9-IV-59, G. F. Kraft; Alesa River, Jensen Holes Ford Station, 2-V-34 (OSC); North Fork Alesa River, 24-IV-39, G. Bailey; Yaquina River nr. Nashville, 17-V-36, V. E. Starr (OSC). WASHINGTON: Snohomish Co., Skykomish River, 29-III-41, B. L. Lambuth (BLL); King Co., Green River, 15-IV-39, B. L. Lambuth (BLL); Tye River, 29-III-41, B. L. Lambuth (BLL); Beckler River, 14-III-41, B. L. Lambuth (BLL); Clallam Co., Dungeness River, U. S. Highway 101, 4-IX-58, GFE and RKA; Kitsap Co., Big Quilcene River, U. S. Highway 101, 4-IX-59, GFE and RKA; Pierce Co., Goat Creek, 5 mi. E. Ashford, 1-IX-59, GFE and RKA; Olympic Natl. Pk., Hoh River at Hoh River Guard Station, 3-IX-59,

GFE and RKA. YUKON TERRITORY: Watson Lake Camp, Mile Post 632, 29-VII-52, C. P. Alexander (UM).

#### TAXONOMY

McDunnough (1934) characterized *E. flavitincta* in the nymphal stage by its large size and by the development of the occipital and thoracic tubercles (fig. 57). We have found that the nymphs from near the type locality in western Oregon, in western Washington, the Yukon Territory of Canada, and western Alaska are typical populations of this subspecies.

The male holotype and the female allotype are the only known adults of this race.

#### *Ephemerella spinifera* Needham

(Figures 52 and 65-69)

*Ephemerella spinifera* Needham 1927b, 110; Walley 1930, 17, 3 figs.; McDunnough 1934, 156 (nymph); Traver 1935, 622; Day 1952, 36, 1 fig. (adult); Edmunds 1954, 66 (not in Utah); Allen and Edmunds 1956, 87; Day 1956, 97.

*Ephemerella autumnalis* McDunnough 1934, 158, 1 fig.; Traver 1935, 583. NEW SYNONYMY.

*Ephemerella sierra* Mayo 1952, 96, 3 figs.; Day 1956, 97. NEW SYNONYMY.

*Ephemerella spinifera* was described from nymphs collected from the Blackfoot River near Potomac, Montana, and from the North Fork of the Ogden River, Utah; however, Edmunds (1954) could not find this species in Utah. The single nymph from the Ogden River proved to be a young nymph of *Ephemerella grandis*. One of the nymphs from the Blackfoot River accords with Needham's description. We hereby designate this as the lectotype, and have labeled it as such in the Cornell University collection.

*Ephemerella autumnalis* McDunnough was named from imagoes and nymphs collected in British Columbia. The imagoes of *E. spinifera* were unknown at that time and unavailable for comparison. McDunnough (1934), however, compared the nymphs of *E. autumnalis* with *E. spinifera* and made the following observation: "The nymph is much the same size as that of *spinifera*, but appears considerably darker; this may, however, be merely due to the fresher condition of the material, . . . The arrangement of tubercles is essentially the same as in *spinifera*, the following differences being noted:—the twin pair on pronotum are subequal, the posterior one being larger than in *spinifera*; the lateral posterior spine-like prolongations of abdominal segments VIII and IX, . . . are shorter than in *spinifera*; the long dorsal spines of segment VIII are more strongly bent backward and downward. These differences are slight and may not always be constant, . . . the *spinifera* nymph apparently matures at high altitudes in the main chain of the Rocky Mountains in July, whereas *autumnalis* nymphs are not mature at quite low levels until fully a month later, . . ." The authors have examined mature topotypical nymphs and adults of *E. autumnalis* from the Canadian National Collection and find that they fit within the morphological varia-

bility of *E. spinifera* and they are not seasonally separated as suggested by McDunnough; therefore, the name *Ephemerella autumnalis* must be placed as a synonym of *E. spinifera* Needham.

*Ephemerella sierra* Mayo was described from nymphs collected in central California. Day (1956) stated that he could not distinguish the types of *E. spinifera* from the description of *E. sierra* published by Mayo in 1952. The authors have examined paratypes of *E. sierra* from the California Academy of Sciences and cannot distinguish this type material from specimens of *E. spinifera*. This name is based on the same variable characters as was the name *autumnalis*, and we also place this name as a synonym of *E. spinifera* Needham.

*Male Imago*.—Length: body 11-13; forewing 15 mm. Head yellow; upper portion of eyes orange, lower portion black. Thorax yellowish brown with purplish-black median and lateral lines; legs pale, femora with apical purple markings; wings hyaline, slightly opaque, especially along the costal margins. Terga purplish brown, with pale anterior margins; pleura pale; sterna colored similarly to terga. Male genitalia as in fig. 65. Caudal filaments purplish brown at base, paling apically.

*Mature Nymph*.—Length: body 9-11; caudal filaments 7-9 mm. General color brown. Head with long paired occipital tubercles (fig. 66). Pronotum with a pair of sharp anterior submarginal tubercles and two pairs of sharp, usually subequal, submedian tubercles; mesonotum with a pair of small sharp submedian tubercles on the anterior margin, a pair of small sharp sublateral tubercles, a more posterior pair of long sharp submedian tubercles, and a blunt median tubercle (fig. 68); legs brown, femora similar to fig. 62; tarsal claws with six to eight denticles. Long sharp paired dorsal tubercles on abdominal terga 2-9, tubercles on segments 8 and 9 much longer than those on segments 2-7; sterna pale with reddish markings, lateral margins brown. Caudal filaments pale with several brown bands.

*Type Locality*.—Blackfoot River near Potomac, Montana (herein restricted).

*Type*—No. 3499, Cornell University Collection, Ithaca, New York.

#### DISTRIBUTION

*Ephemerella spinifera* is a boreal western North American species known from British Columbia astricted to Yellowstone National Park and southern California (fig. 52).

The authors have examined specimens of this species from the following localities:

BRITISH COLUMBIA: Shephard Creek, Brexton, 29-VI-40, V. K. Mayo (VKM); Wilson Creek, New Denver, 10/12-VIII-year? V. K. Mayo (VKM); Shingle Creek Road, Keremeos, 23-VIII-34, 9/24-VIII-35, A. N. Gartrell (CNC). CALIFORNIA: Inyo Co., South Fork Bishop Creek (elev. 9,500'),

28-VIII-38, V. K. Mayo (Paratype, *sierra*) (CAS); North Fork Bishop Creek, 31-VII-50, V. K. Mayo (VKM); North Lake Inlet, Bishop Creek, 22-VI-34, P. R. Needham (VKM); South Fork Bishop Creek, 20-VI-34, P. R. Needham (VKM); Mono Co., Megee Creek, Tributary of Owens River, 6-VII-34, P. R. Needham (VKM); Madera Co., Stream 0.8 mi. up road to Soquel, 19-VI-59, RKA; Nevada Co., Sagehen Creek, 20-IX-54, S. Pennoyer (UCS). IDAHO: Blaine Co., Big Wood River, 2-IX-44, GFE; Leach Co., North Fork Salmon River, 17 mi. N. North Fork, 20-VI-59, GFE. MONTANA: Blackfoot River near Potomac, 20-VI-06, Frank C. Barry (Lectotype) (CU). OREGON: Lane Co., Odell Creek, 17-VI-58, M. L. Johnson; McKenzie River, 1.2 mi. from Morton State Pk., 15-VI-58, M. L. Johnson; Cape Creek nr. Sealion Point, 25-VIII-54, GFE and RKA; Hood River Co., East Fork Hood River, Mt. Hood, 27-VIII-54, GFE and RKA; Wallowa Co., Shady Camp and French Camp, Lostine River, 18-VIII-52, GFE; Wallowa River, Wallowa Lake, 18-VIII-52, GFE; Clackamas Co., Zigzag River, Mt. Hood Natl. For., 18-VI-33, R. Dimick (OSC); Benton Co., Marks Creek, Corvallis, 26-II-38, B. White (OSC); Jackson Co., Rogue River nr. McLeod, 24-VIII-54, GFE and RKA; Rogue River at highway jct. 230-62, GFE and RKA. WASHINGTON: Ferry Co., Stream 6 mi. E. Republic, Highway 3P, 29-VII-58, GFE. WYOMING: Virginia Meadows, Gibbon River, Yellowstone Natl. Pk., 30-VIII-40, T. H. Frison and T. H. Frison, Jr. (INHS).

#### TAXONOMY

The morphological variability found in the mature nymphs of *E. spinifera* is moderate. The thoracic and abdominal tubercles vary in size, relative to the other tubercles, but this variability is within narrow limits. The greatest morphological variability in this species is in the degree of development of the occipital, thoracic, and abdominal tubercles as a result of age of the individual (figs. 68-69). In early instar nymphs the occipital and submedian thoracic tubercles are well-developed, while the sublateral tubercles have not even appeared (fig. 69). As the nymph matures these submedian tubercles become proportionately reduced in length (fig. 68).

Series of adults have not been available for study, but morphological variability in the adult stages appears to be negligible.

#### BIOLOGY

*Ephemerella spinifera* nymphs inhabit cold or cool (40°-50° F. in August and early September) streams. These nymphs have been collected in association with *Ephemerella teresa*, *E. coloradensis* and *E. grandis ingens*. They are commonly found in streams with a rocky bottom type where they live under rocks and submerged debris, but have also been collected on debris in pools. Nymphs have been collected from February 26 to August 31, and adults are known to emerge from late July to early September.

## ACKNOWLEDGMENTS

We thank the following individuals for loan of specimens from the collection under their care, as indicated: G. P. Holland and J. E. H. Martin (Canadian National Collection), Herbert H. Ross and Leonora K. Gloyd (Illinois Natural History Survey), Velma K. Mayo (personal collection), P. O. Ritcher and F. F. Hasbrouck (Oregon State College), Willis J. Gertsch and Jerome G. Rozen, Jr. (American Museum of Natural History), J. R. Traver (personal collection), Harry Dietrich (Cornell University), P. R. Needham (University of California), and B. L. Lambuth (personal collection). We also thank C. P. Alexander (University of Massachusetts), E. W. Hamilton (University of Nebraska), A. G. Dumont (Sheridan College), L. T. Nielsen and Dr. and Mrs. Stanley Mulaik (University of Utah), E. L. Bousefield (National Museum of Canada), B. V. Peterson (Canada Department of Agriculture), C. M. Tarzwell (U. S. Public Health Service), J. N. Belkin (University of California at Los Angeles), and E. I. Coher, W. C. Day, G. L. Miller and M. L. Johnson (personal collections) for the loan and/or donation of specimens. Most of the illustrations included in this report were prepared by Steve L. Jensen and David I. Rasmussen under the direction of the authors.

## REFERENCES CITED

- Allen, R. K., and G. F. Edmunds, Jr.** 1956. A list of the mayflies of Oregon. *Proc. Utah Acad. Sci., Arts and Letters* 33: 85-87.
1959. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). I. The subgenus *Timpanoga*. *Canadian Entomol.* 91: 51-58.
- 1961a. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). II. The subgenus *Caudatella*. *Ann. Entomol. Soc. Amer.* 54: 603-12.
- 1961b. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). III. The subgenus *Attenuatella*. *Jour. Kansas Entomol. Soc.* 34: 161-73.
1962. A revision of the genus *Ephemerella* (Ephemeroptera: Ephemerellidae). IV. The subgenus *Dannella*. *Jour. Kansas Entomol. Soc.* (in press).
- Banks, N.** 1892. Ephemeroptera, pp. 331-332 and 345-348. *In*: A synopsis, catalogue, and bibliography of the neuropteroid insects of temperate North America. *Trans. Amer. Entomol. Soc.* 19: 327-73.
1904. Neuropteroid insects from New Mexico. *Trans. Amer. Entomol. Soc.* 30: 97-110.
1907. Catalogue of the neuropteroid insects (except Odonata) of the United States. *Trans. Amer. Entomol. Soc.* 33: 1-53.
- Britton, W. E.** 1920. Checklist of the insects of Connecticut. *Bull. Connecticut State Geol. and Nat. Hist. Surv.* 31: 5-397.
1938. Additions to the check-list of the insects of Connecticut. *Bull. Connecticut State Geol. and Nat. Hist. Surv.* 60: 9-201.
- Burks, B. D.** 1953. The mayflies or Ephemeroptera of Illinois. *Bull. Illinois Nat. Hist. Surv.* 26 (Art. 1): 1-216.
- Clemens, W. A.** 1913. New species and new life histories of Ephemeridae or mayflies. *Canadian Entomol.* 45: 246-262, 329-341.
1915. Rearing experiments and ecology of Georgian Bay Ephemeridae. *Contr. Canadian Biol., Sessional Paper* 39b: 113-28.
- Day, W. C.** 1952. New species and notes on California mayflies (Ephemeroptera). *Pan-Pacific Entomol.* 28: 17-39.
1954. New species and notes on California mayflies. II. (Ephemeroptera). *Pan-Pacific Entomol.* 30: 15-29.
1956. Ch. 3, Ephemeroptera, pp. 79-105. *In*: R. L. Usinger [ed.], *Aquatic Insects of California*. Berkeley and Los Angeles: University of California Press. 508 pp.
- Demoulin, G.** 1958. Nouveau schema de classification des Archodonates et des Ephemeropteres. *Bull. Inst. Roy. Sci. Nat. Belgium* 34(27): 1-19.
- Dodds, G. S.** 1923. Mayflies from Colorado, description of certain species and notes on others. *Trans. Amer. Entomol. Soc.* 49: 93-114.
- Dodds, G. S., and F. L. Hisaw.** 1924. Ecological studies of aquatic insects, I. Adaptations of mayfly nymphs to swift streams. *Ecol.* 5: 137-48.
- Eaton, A. E.** 1884 (1883-1888). A revisional monograph of recent Ephemeridae or mayflies. *Trans. Linn. Soc. London, Sec. Ser. Zool.*, 3: 77-152 (1-352).
- Edmunds, G. F., Jr.** 1954. The mayflies of Utah. *Proc. Utah Acad. Sci., Arts and Letters* 31: 64-66.
1959. Subgeneric groups within the mayfly genus *Ephemerella* (Ephemeroptera: Ephemerellidae). *Ann. Entomol. Soc. Amer.* 52: 543-7.
- Edmunds, G. F., Jr., and J. R. Traver.** 1954. An outline of a reclassification of the Ephemeroptera. *Proc. Entomol. Soc. Washington* 56: 236-40.
- Hagen, H. A.** 1861. Ephemeridae, pp. 38-55. *In*: Synopsis of the Neuroptera of North America, with a list of South American species. *Smithsonian Misc. Coll.* 4: xx + 347 pp.
- Howell, T.** 1941a. Notes on Ephemeroptera and aquatic Diptera of western North Carolina. *Jour. Elisha Mitchell Sci. Soc.* 57: 306-17.
- 1941b. Some aquatic insects from the Great Smoky Mountains National Park. *Jour. Tennessee Acad. Sci.* 16: 406-7.
- Ide, F. P.** 1930. Contribution to the biology of Ontario mayflies with descriptions of new species. *Canadian Entomol.* 62: 204-13, 218-31.
1935. The effect of temperature on the distribution of the mayfly fauna of a stream. *Univ. Toronto Studies, Biol. Ser.* 39, *Publ. Ontario Fish Res. Lab.* 50: 9-76.

- Leonard, J. W.** 1950. Seasonal occurrence of mayflies in a Michigan stream. Michigan Conservation 19: 18-20, 30.
- Lestage, J. A.** 1925. Contribution a l'étude des larves des Ephémères. Serie III. Le groupe Ephémérelidien. Ann. Biol. Lacustre 13: 227-302.
- Linduska, J. P.** 1942. Bottom type as a factor influencing the local distribution of mayfly nymphs. Canadian Entomol. 74: 26-30.
- McDunnough, J.** 1925. The Ephemeroptera of Covey Hill, Que. Trans. Roy. Soc. Canada. 19: 207-24.
1926. Notes on North American Ephemeroptera with descriptions of new species. Canadian Entomol. 58: 184-96.
- 1928a. The Ephemeroptera of Jasper Park, Alta. Canadian Entomol. 60: 8-10.
- 1928b. Ephemerid notes with description of a new species. Canadian Entomol. 60: 238-40.
1929. Notes on North American Ephemeroptera with descriptions of new species, II. Canadian Entomol. 61: 169-80.
- 1931a. The *bicolor* group of the genus *Ephemerella* with particular references to the nymphal stages (Ephemeroptera). Canadian Entomol. 63: 30-42, 61-68.
- 1931b. New species of North American Ephemeroptera. Canadian Entomol. 63: 82-93.
- 1931c. The eastern North American species of the genus *Ephemerella* and their nymphs (Ephemeroptera). Canadian Entomol. 63: 187-97, 201-16.
1934. New species of North American Ephemeroptera, IV. Canadian Entomol. 66: 154-64, 181-8.
1935. Notes on western species of Ephemeroptera. Canadian Entomol. 67: 95-104.
- Mayo, V. K.** 1951. New western Ephemeroptera, II. Pan-Pacific Entomol. 27: 121-5.
1952. New western Ephemeroptera, III. Pan-Pacific Entomol. 28: 93-103.
- Morgan, A. H.** 1911. Mayflies of Fall Creek. Ann. Entomol. Soc. Amer. 4: 93-119.
1913. A contribution to the biology of mayflies. Ann. Entomol. Soc. Amer. 6: 371-413.
- Needham, J. G.** 1905. Ephemeroptera, pp. 17-62. In: J. G. Needham, K. J. Morton, and O. A. Johannsen, Mayflies and midges of New York. New York Mus. Bull. 86: 1-352.
- 1927a. The life history and habits of a mayfly from Utah. Canadian Entomol. 59: 133-6.
- 1927b. The Rocky Mountain species of the mayfly genus *Ephemerella*. Ann. Entomol. Soc. Amer. 20: 107-17.
- Needham, J. G., and R. O. Christensen.** 1927. Economic insects in some streams of northern Utah. Utah Agric. Expt. Sta. Bull. 201: 1-36.
- Pugh, J. E.** 1956. Observations of the mayfly fauna of a stream in central Virginia. Virginia Jour. Sci. 7: 22-28.
- Seemann, T.** 1927. Ephemerida, pp. 40-51. In: Dragonflies, mayflies and stoneflies of Southern California. Jour. Entomol. and Zool. 19: 1-69.
- Spith, H. T.** 1933. The phylogeny of some mayfly genera. Jour. New York Entomol. Soc. 41: 55-86, 327-91.
1940. The North American Ephemeropteran species of Francis Walker. Ann. Entomol. Soc. Amer. 33: 324-38.
1941. The North American Ephemeropteran types of the Rev. A. E. Eaton. Ann. Entomol. Soc. Amer. 34: 87-98.
- Steger, A. L.** 1931. Some preliminary notes on the genus *Ephemerella*. Psyche 38: 27-35.
- Stephens, J. F.** 1835. Illustrations of British Entomology. Vol. 6. 240 pp., London.
- Traver, J. R.** 1932. Mayflies of North Carolina. Jour. Elisha Mitchell Sci. Soc. 47: 85-161, 163-236.
1934. New North American species of mayflies (Ephemera). Jour. Elisha Mitchell Sci. Soc. 50: 189-254.
1935. Part II. Systematic, pp. 237-739. In: J. G. Needham, J. R. Traver, and Yin-Chi Hsu, *The Biology of Mayflies*. Ithaca, N. Y.: Comstock Publishing Co. 759 pp.
1937. Notes on mayflies of the Southeastern States (Ephemeroptera). Jour. Elisha Mitchell Sci. Soc. 53: 27-86.
- Ulmer, G.** 1920. Übersicht über die Gattungen der Ephemeropteren nebst Bemerkungen über einzelne Arten. Stettiner Entomol. Zeit. 81: 97-144.
1932. Bemerkungen über die seit 1920 neu aufgestellten Gattungen der Ephemeropteren. Stettiner Entomol. Zeit. 93: 204-19.
- Walker, F.** 1853. Ephemeridae, pp. 533-585. In: Catalogue of the specimens of Neuropterous insects in the collection of the British Museum, Pt. III. Termitidae and Ephemeridae. London: British Museum pp. 477-585.
- Walley, G. S.** 1930. A review of the *Ephemerella* nymphs of Western North America (Ephemeroptera). Canadian Entomol. 62: 12-20.
- Wright, M., and L. Berner.** 1949. Notes on mayflies of Eastern Tennessee. Jour. Tennessee Acad. Sci. 24: 287-98.