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An Annotated Key to the Nymphs of the Families and Subfamilies of Mayflies (Ephemeroptera)

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INTRODUCTION

Attempts to provide keys to the families and subfamilies of Ephemeroptera nymphs in general entomology textbooks (i.e. Essig (1942), Chu (1949), and Brues, Melander and Carpenter (1954)) have been far from satisfactory. This difficulty exists largely because of the failure of specialists of the Ephemeroptera to provide keys of world-wide application that are sufficiently illustrated to be of value to non-specialists. In the last few decades, however, there have been many figures published that will aid any person attempting to construct such keys. Excellent figures of a variety of families are found in such works as those of Barnard (1932), Spieth (1933), Needham, Traver and Hsu (1935), Ulmer (1940), Crass (1947), Berner (1950), Tshernova (1952), and Burks (1953). Despite the increasing knowledge of the immature stages, mayfly specialists have not attempted to provide keys to families and subfamilies of nymphal Ephemeroptera except on a regional basis. Although such keys are destined to be imperfect as new discoveries are made, it appears to us that this is a propitious time to construct and publish a key. There is now a considerable degree of agreement among specialists on the families to be recognized in the Ephemeroptera, although the relationships between families are highly controversial (see Edmunds, 1962, for a discussion).

Separation of families is dependent upon the existence of distinct gaps in the continuity of characters. Since only about three-fourths of the genera have one or more species known in the nymphal stages, the gaps between families or subfamilies and the key characters chosen to separate families or subfamilies could be readily invalidated by the discovery of new forms. Examples where new discoveries are most likely to fill in some of the gaps are found in the present separation of the Siphlaenigmatidae and Baetidae from the Nesameletus-complex of the Siphlonuridae, and the separation of the Tricorythidae from the *Ephemerellina*-complex of the Ephemerellidae. The keys and figures presented herein should, however, provide better information for use in entomological textbooks and will undoubtedly be of considerable service to mayfly workers who lack a familiarity with the world fauna.

The present key is presented with the hope that it will stimulate the description of additional genera in the immature stages. It is presented also with the realization that it can, by employing the remarks on distribution, be modified to form less complex, more utilitarian keys for limited geographic regions. For example, the involved couplets necessary to characterize the Leptophlebiidae, or to separate the nymphal Baetidae and Siphlonuridae are necessary largely because of a few genera in the southern hemisphere. Also the separation of nymphs of Ephemerellidae and Tricorythidae is difficult only in the Ethiopian and Oriental regions.

Regional keys to the nymphal stages of the genera are available for many parts of the world. For a few groups world-wide keys are available or else one of the regional keys includes all genera in the subfamily; in these cases, we have noted such keys in the notes on the family.

For Europe the most useful publications are those of Macan (1961), Grandi (1960), Ujheliyi (1959), Schoenemund (1930), Ulmer (1929) and Lestage (1917, 1919). For the Palearctic region of Asia the most useful keys are given by Tshernova (1952), Imanishi (1940) and Ueno (1928). For the Oriental region of Asia the only keys to the nymphs are those by Ulmer (1940). For the Australasian region the most comprehensive keys are those of Phillips (1930) for New Zealand and Riek (1955), Harker (1954, 1950) and Tillyard (1936, 1933) for Australia and Tasmania. For South America the only extensive and utilitarian key is that of Traver (1944). Traver (1938) has also provided keys to the nymphs for Puerto Rico. For the North American fauna the most useful keys to the nymphs are those of Edmunds (1959), Burks (1953) and Needham, Traver and Hsu (1935).

ACKNOWLEDGMENTS

The research on which this paper is based necessitated not only a review of the literature, but an extensive study of mayfly genera from all parts of the world, some of them as yet undescribed. This paper would have been impossible without the generous cooperation of many persons who have enabled us to study specimens, especially from areas outside North America. All of the following persons have given us such specimens, or made loans of specimens in their personal or institutional collections. We express our sincere thanks to each of them as follows: J. D. Agnew and A. D. Harrison, National Institute for Water Research, Pretoria, South Africa; C. P. Alexander and Marion Smith, University of Massachusetts; Lewis Berner, University of Florida; Edward I. Coher, Worcester, Massachusetts; R. S. Crass, Natal Parks, Game and Fish Preservation Board, South Africa; P. J. Darlington, Jr., Museum of Comparative Zoology Cambridge, Massachusetts; Georges Demoulin, Musee Royal des Sciences Naturelles, Bruxelles, Belgium; Gordon Field, U.S. Army Medical Command, Japan; M. T. Gillies, East African Malaria Unit, Amani, Tanganyika; M. Grandi, Bologna, Italy; Alan Hirsch, Division of Water Supply and Pollution Control, U.S. Public Health Service; J. Illies, Hydrobiologische Anstalt, Max-Planck-Gesellshaft, Plön, Germany; Carlo Jensen, Tarm, Denmark; M. Keffermüller, Universitet Adama Mickiewicza, Poznan, Poland; D. E. Kimmins, British Museum (Natural History), London; V. Landa, Institute of Entomology, Prague, Czechoslovakia; H. G. McFarlane, Christchurch, New Zealand; P. L. Miller, Makerere College, Kampala, Uganda; Guy G. Musser, University of Michigan; J. G. Penniket, Dobson, New Zealand; E. F. Riek, Commonwealth Scientific and Industrial Research Organization, Canberra; E. S. Ross, Hugh B. Leech and A. Don MacNiell, California Academy of Sciences, San Francisco; Herbert H. Ross and Leonora K. Gloyd, Illinois Natural History Survey, Urbana; J. G. Rozen, Jr., American Museum of Natural History, New York; Ing. S. Schachovskoy, Intendencia de Parques Nacionales, San Martin des Los Andes, Neuquen, Argentina; R. B. Selander, University of Illinois, Urbana; A. Dean Stock, University of Utah; Thomas Thew, Chicago, Illinois; Belindo Torres, Museo de La Plata, Argentina; J. R. Traver, Amherst, Massachusetts; Masuzo Uéno, Otsu Hydrobiological Station, Otsu-Shi, Shiga-Ken, Japan; Georg Ulmer, Hamburg, Germany; and, Rupert L. Wenzel, Chicago Natural History Museum.

The published references to the described nymphs in each genus were assembled in multilithed copy and distributed to several colleagues who kindly corrected errors and made useful suggestions. We are grateful to D. E. Kimmins, J. R. Traver, M. Uéno, M. T. Gillies, J. D. Agnew, Georges Demoulin and Lewis Berner for critical comments on this preliminary list.

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KEY

1 — The thoracic notum enlarged to form a shield extending to the sixth abdominal segment; the gills enclosed beneath the shield (figs. 77–78) 2

— The thoracic notum not enlarged as above; at least some of the abdominal gills exposed (figs. 63 and 65–76) or rarely absent (fig. 64)[1] 3

2 (1) — The head and thorax forming a single, oval outline (fig. 78) .... Prosopistomatidae

— The head clearly separated in outline from the thorax (fig. 77) .... Baetiscidae

3 (1) — Gills on abdominal segments 2–7 forked and with the margins fringed (figs. 46, 73, 74), gills on segment one variable or absent; mandibular tusks *usually* present and projecting in front of head (figs. 73–74), if tusks are absent, the anterolateral angles of the head and pronotum with a dense crown of spines (fig. 41) 4

— Gills on abdominal segments variable, not as above (figs. 63, 65–72, 75–76); mandibular tusks *rarely* present, if so, the gill margins are not fringed 11

4 (3) — Gills ventral; antero-lateral angles of head and pronotum with a dense crown of spines and without mandibular tusks (fig. 41) .... Behningiidae

— Gills lateral or dorsal; head without such a crown of spines, mandibular tusks present and projecting in front of the head (figs. 42, 48–51, 73, 74) 5

5 (4) — Gills lateral; the forelegs not adapted for digging, tibia cylindrical (fig. 73) 6

— Gills dorsal; the forelegs fossorial, tibia flattened (figs. 47a, 74) 7

6 (5) — The mandibular tusks with numerous long hairs (fig. 42); the maxillary palpi more than twice as long as the galea-lacinia (both measured from base of palpifer) .... Euthyplociidae

— The mandibular tusks with short hairs (fig. 73); the maxillary palpi less than twice as long as the galea-lacinia .... Potamanthidae

7 (5) — The ventral edge of apex of the tibiae of the hind legs projected into a distinct acute point (fig. 47); a row of spines usually present on the apical margin; the labial palpi in the same plane as the labium .... Ephemeridae

— The apex of the tibiae of the hind legs variable, not as above; the labial palpi nearly at right angles to the labium, so as to meet or nearly meet beneath the labium 8

8 (7) — The mandibular tusks broad with crenulate or serrate outer margins (figs. 51, 52), frontal process (fp) wider at apex than at base (fig. 51) .... Palingeniidae

— The mandibular tusks not as above, either slender (figs. 48, 49) or without serrate or crenulate outer margins (fig. 50) frontal process absent (figs. 49, 50) or wider at base than at apex (fig. 48) .... Polymitarcidae, 9

9 (8) — Mandibular tusks short, broad and robust (fig. 50) .... Asthenopodinae

— Mandibular tusks relatively elongate and slender (figs. 48, 49) 10

10 (9) — Mandibular tusks with numerous tubercles on the upper and outer surfaces (fig. 48) .... Polymitarcinae

— Mandibular tusks without such tubercles, inner surface with one or more distinct tubercles or serrations (fig. 49) .... Campsurinae

11 (3) — Gills on segment 2 operculate, quadrate, meeting or nearly meeting at the midline of the abdomen (figs. 75, 76); gills on segment one vestigial; gills on segments 3–7 with fringed margins (figs. 54, 60) 12

— Gills variable, if those on segment 2 operculate, not quadrate and not meeting at midline (fig. 71) 13

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[1] The genus *Murphyella* known from Chile and Argentina lacks abdominal gills. The very distinctive nymph (fig. 64) is clearly an aberrant member of the subfamily Coloburiscinae (family Siphlonuridae) (see couplet 30).

12 (11) — With developing metathoracic wing pads; mature nymphs medium to large (body length, 8–14 mm.); a median carina may be present on abdominal segments 6 to 8; pronotum may have a distinct carina terminating at the antero-lateral angles (fig. 75) .... Neoephemeridae

— Without developing metathoracic wing pads; mature nymphs small to medium (body length, 3–7 mm.); no thoracic or abdominal carinae as described above (fig. 76) .... Caenidae

13 (11) — Gills absent or vestigial and thread-like on abdominal segment one (fig. 70), may be absent from segment 2, or 2 and 3 (fig. 69); lamellate gills present on abdominal segments 2–4, 2–5, 2–6, 3–7 or 4–7 (figs. 32, 69–72) 14

— Gills present on abdominal segments 1–5, 1–6, or 1–7 (figs. 63, 65–68) 19

14 (13) — Lamellate gills present on abdominal terga 2–5 or 2–6 and without postero-median tubercles on abdominal terga 3–7 (figs. 70 to 72)[2] .... Tricorythidae, 15

— Lamellate gills present on abdominal terga 2–4, 2–5 or 2–6 (fig. 32), 3–7 or 4–7 (fig. 69) (vestigial thread-like gills may be present on segment one), when gills are present on tergum 2 postero-median single (fig. 32) or double (fig. 33) tubercles on abdominal terga 3–7 .... Ephemerellidae

15 (14) — Compound eyes narrowly separated and elevated above the vertex (fig. 35); gills enclosed in a receptacle elevated above the terga (fig. 36) .... Machadorythinae

— Compound eyes usually widely separated and not elevated above the vertex; gills not enclosed, lying on the surface of the terga (figs. 71, 72) or extended somewhat laterally (fig. 70) 16

16 (15) — Abdominal gills a single lamella, with fringed margins (fig. 40); with two caudal filaments only; venter of thorax with an adhesive disc .... Dicercomyzinae

— Abdominal gills bilamellate, the upper lamella entire, without fringed margins (fig. 70); with three caudal filaments; without an adhesive disc on the venter of the thorax 17

17 (16) — Gills imbricate, extending somewhat laterally (fig. 70); glossae and paraglossae of labium fused (fig. 34); lateral margin of mandibles with a row of long hair (fig. 70) .... Tricorythinae

— Gills on segment 2 operculate or semioperculate (figs. 71 and 72); glossae (gl) and paraglossae (pgl) of labium only partly fused (figs. 38, 39); lateral margin of mandibles without a row of long hair 18

18 (17) — Antero-lateral angles of pronotum projecting distinctly anteriorly (fig. 37); second segment of labial palpi nearly as broad and long as basal segment (fig. 38) .... Ephemerythinae

— Antero-lateral angles of pronotum not projecting anteriorly (figs. 71, 72); second segment of labial palpi much shorter and narrower than basal segment (fig. 39) .... Leptohyphinae

19 (13) — Abdominal gills on middle segments either forked (fig. 23), divided at apex (fig. 25), in clusters of filaments (fig. 24), lanceolate (fig. 26), or with double lamellae with fringes (fig. 27) or projections (figs. 28–30), but never with spines; in some southern hemisphere forms each gill of one lamella with margins entire, if so, the head flattened and the mandibles form part of the upper surface and outline of the head (fig. 31) .... Leptophlebiidae

— Abdominal gills on middle segments variable but not as above, if gills forked they are heavily spined (fig. 6); if gill lamellae double they are without fringes or projections; if gill lamellae single and head is flattened, the mandibles do *not* form part of the upper surface or outline of the head (figs. 18, 19, 66, 67) 20

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[2] The genus *Machadorythus* of the Tricorythidae known from tropical Africa has postero-median tubercles on terga 2, 8 and 9. The nymph is distinguished by an elevated dorsal abdominal gill receptacle on terga 3–7 (fig. 36) and by narrowly separated eyes which are elevated above the vertex (fig. 35) (see couplet 15).

20 (19) — A densely-branched tuft of gills present on each maxillary palpus, but none on the base of each forecoxa (fig. 16); gills usually ventral on segment one; gills on abdominal segments 2–7 lanceolate and simple (fig. 17) or with a fibrilliform ventral portion and an oval lamella less than half as long as the segment from which each arises (fig. 15) .... Oligoneuriidae, 21

— Gills not as above; if a tuft of gills is present on each maxillary palpus, a similar tuft occurs at the base of each forecoxa........ 22

21 (20) — Gills on abdominal segment one ventral (fig. 16)........ Oligoneuriinae

— Gills on abdominal segment one dorsal........ Chromarcyinae

22 (20) — Body flattened (figs. 66, 67); head capsule flattened and with a marginal rim (fig. 18); gills with a lamella and fibrilliform portion (the fibrilliform portion rarely reduced or wanting)........ Heptageniidae, 23

— Body and head variable in shape, not flattened as above, gills variable.. 26

23 (22) — Maxillary palpi very long, forming sweeping organs with long setae visible from above at the sides and front of the head (fig. 19) .... Arthropleinae

— Maxillary palpi shorter, not adapted as above........ 24

24 (23) — Tarsal claws elongate, longer than the tibiae (fig. 67); gills narrow with a lanceolate branch arising near the middle........ Pseudironinae

— Tarsal claws much shorter than the tibiae (fig. 66); gills variable, not as above........ 25

25 (24) — Gills ventral on abdominal segments, the lamellae narrow and about the same length as the fibrilliform portion (fig. 20)........ Anepeorinae

— Gills dorsal or lateral in position, the first and last pair sometimes largely ventral (fig. 66)........ Heptageniinae

26 (22) — Claws on the forelegs differ in structure from the elongate claws on the middle and hind legs (figs. 21–22)........ Ametropodidae, 27

— Claws on the forelegs similar in structure to those on the middle and hind legs (figs. 63–65) although they may be shorter (fig. 4)........ 28

27 (26) — Claws on the forelegs bifid (fig. 22a)........ Metretopodinae

— Claws on the forelegs single, with a comb of long slender denticles (fig. 21a)........ Ametropodinae

28 (26) — Glossae (gl) and paraglossae (pgl) of the labium long and narrow (fig. 11); mandibular incisors separate, not compacted into a single lobe (fig. 10); antennae *usually* at least twice as long as width of head; gills on abdominal segments, 1–5, 1–6 or 1–7; gills oval (fig. 9) or elongate oval (fig. 7), sometimes with ventral or dorsal recurved flap (fig. 12, 13) or sometimes with double lamellae (fig. 14); if gills are oval they are without a sclerotized brace; head hypognathous, short and high (fig. 8)........ 34

— Glossae and paraglossae *usually* shorter and broader, long and slender in some southern hemisphere forms, if so, the mandibular canines compacted into a single lobe (fig. 3) and the gills with a sclerotized brace (fig. 2); antennae often shorter than width of head; gills variable on abdominal segments; head variable........ Siphlonuridae, 29

29 (28) — The femora and tibiae of the forelegs with a dense row of hair on the ventral (leading) edge (fig. 64)........ 30

— The forelegs without such a row of hair (figs. 63, 65)........ 31

30 (29) — The femora of the middle pair of legs with rows of hair similar to those on the forelegs; abdominal gills *absent* (fig. 64) or bifid and clothed with spines (fig. 6)........ Coloburiscinae, subfam. nov.

— The middle pair of legs without such rows of long hair; gills with an oval lamella and a fibrilliform portion........ Isonychiinae

31 (29) — Claws long and thin, much longer than tarsi on the hind pair of legs; tibiae and tarsi bowed (fig. 4)........ Acanthametropodinae, subfam. nov.

— Claws shorter than tarsi on all legs (fig. 63)........ 32

32 (31) — Abdomen with a median row of projections on the anterior terga; the gills imbricate, semi-operculate or operculate, appressed to the terga (fig. 65) .... Oniscigastrinae

— Abdomen without such projections; the gills lateral or dorsal but not appressed to the terga 33

33 (32) — Maxillary and labial palpi thread-like and multi-segmented; the mandibles and maxillae with predatory fangs (fig. 5) .... Ameletopsinae

— Maxillary and labial palpi more robust and three-segmented; the mandibles and maxillae without predatory fangs (fig. 1) .... Siphlonurinae

34 (28) — Gills slender and elongate on segments 1–7 (fig. 7), New Zealand .... Siphlaenigmatidae

— Gills oval, sometimes with recurved dorsal or ventral flap or with two lamellae (figs. 9–14) .... Baetidae

FAMILIES AND SUBFAMILIES

In the following accounts we have included for each family a brief statement concerning affinities with other families and, where necessary, we have added some information concerning certain rather involved or difficult couplets in the keys.

Under each subfamly we have stated the general range of habitats in which the nymphs are likely to be encountered, the geographic range of the subfamily and in many cases the relative abundance of the subfamily. Other pertinent data are added where appropriate. Following this is a list of all genera and subgenera with reference to the description of the nymph of the genus when it is known or a statement that it is unknown. The references have been selected on the basis of availability of literature, presence of adequate figures, and the geographic origin of the species described. In some genera, many species are known in the nymphal stage and we have usually cited one or two descriptions. It was suggested to us during the preparation of this paper that we include information as to whether or not the type species is known in the nymphal stage, and that we give the geographic ranges of the genera. Both of these suggestions were given serious consideration but each one would have entailed consideration of many problems that will be solved only gradually as new data are accumulated. All persons doing critical systematic research on mayflies must concern themselves with the matter of the degree to which present nymphal associations and generic assignments are valid. In many cases nymphal and adult associations have been established on inadequate evidence and are therefore questionable. It is also certainly true that many species are still assigned to the wrong genus. These incorrect generic assignments would result in our assigning ranges which we know are incorrect; yet, it would be premature to transfer all such species to other genera where they may not belong. Critical studies will eventually result in the correct assignment of many of these poorly known species.

Two new subfamilies are proposed herein for groups of the family Siphlonuridae. These categories are proposed as a result of an extensive study of the Siphlonuridae in progress by the senior author who assumes sole responsibility for proposing the new groups. The Acanthametropodinae consist of two genera, *Acanthametropus* and a more primitive undescribed genus from Utah. They are characterized by having nymphs with modified legs with bowed tibiae and tarsi with long, thin tarsal claws, and by having carnivorous-type maxillae and mandibles and three-segmented labial palpi. The gills are formed of a single lamella, with the inner margin finely dissected in the genus *Acanthametropus*. The adults are unknown but the venation in nymphal wing pads of specimens of *Acanthametropus* from Georgia-South Carolina and the undescribed genus from Utah is of the Siphlonurid type. The second subfamily, Coloburiscinae, is proposed for the three genera of paleantarctic distribution formerly assigned with *Isonychia* as the Isonychiinae. Although *Isonychia* is the closest relative of the Coloburiscinae, it is very distinct in both adult and nymphal characters. The nymphs of Coloburiscinae are readily recognized by their robust body, the rows of stout spines on the legs and the presence of a row of hair on the mesothoracic femora. The adults are in need of additional study but are apparently recognizable as a group on the basis of the male forelegs and several minor features of the wing venation.

SUPERFAMILY HEPTAGENIOIDEA

FAMILY SIPHLONURIDAE

The nymphs of this family show extreme diversity. The family is probably an ancient one and a number of the genera retain very primitive traits. In the nymphal stage the family is divisible into very distinct subfamilies and generic groups; several of the subfamilies are so distinct that if nymphal evidences alone were considered, these would be readily recognized as families. Several difficulties in keying arise because of the apparent close affinity of the *Nesameletus*-complex of the Siphlonurinae to the Siphlaenigmatidae and Baetidae, the similarities between *Isonychia* and the Oligoneuriidae, and the apparently superficial resemblance of some genera to the Ametropodidae. *Acanthametropus* has been placed in the Ametropodidae (See Demoulin, 1958), but the wing pads of the nymph which we have studied show a Siphlonurid-type cubital area.

SUBFAMILY SIPHLONURINAE

The nymphs live in a variety of ponds, lakes, streams and rivers. They are widely distributed in the Holarctic region, and the *Metamonius*-complex of genera is distributed in southern South America, southeast Australia and New Zealand.

Ameletoides Tillyard, Tillyard (1933)
Ameletus Eaton, Eaton (1883–88, as Chirotonetes)
Dipteromimus McLachlan, Ueno (1931)
Edmundsius Day, Day (1953)
Metamonius Eaton, Demoulin (1955c)
Metreletus Demoulin, Demoulin (1951)
Nesameletus Tillyard, Phillips (1930, as Ameletus)
Parameletus Bengtsson, Bengtsson (1909, as Potameis), Traver (1935)
Siphlonisca Needham, Clemens (1915)
Siphlonurus Eaton, Eaton (1883–88, as Siphlurus)
Siphluriscus Ulmer, Nymph unknown

SUBFAMILY ACANTHAMETROPODINAE EDMUNDS, *new subfamily*

These rare forms have been found on sandy river bottoms in a few widely scattered localities in the Holarctic Realm (*Acanthametropus* in the Amur basin of Siberia and in Georgia, South Carolina and Illinois, and an undescribed genus in Utah).

Acanthametropus Tshernova, Tshernova (1948), Burks (1953, as Metreturus)

SUBFAMILY ONISCIGASTRINAE

The subfamily is known from streams and lakes in southern South America, southeast Australia, Tasmania and New Zealand.

Oniscigaster McLachlan, Eaton (1883–88)
Siphlonella Needham & Murphy, Needham & Murphy (1924)
Tasmanophlebia Tillyard, Tillyard (1933)

SUBFAMILY AMELETOPSINAE

The nymphs are known from streams in southern South America, southeast Australia and New Zealand.

Ameletopsis Phillips, Phillips (1930)
Chaquihua Demoulin, Edmunds in MS.
Chiloporter Lestage, Eaton (1883–88, nameless, plate 53)
Mirawara Harker, Riek (1955)

SUBFAMILY ISONYCHIINAE

The nymphs inhabit a wide variety of streams and rivers in the Holarctic and Oriental regions, and occur as far south as Veracruz Province in Mexico.

Isonychia Eaton, Eaton (1883–88, as Jolia), Burks, 1953

SUBFAMILY COLOBURISCINAE EDMUNDS, *new subfamily*

The nymphs occur in streams and rivers in southern South America, southeast Australia and New Zealand.

Coloburiscoides Lestage, Tillyard (1933, as Coloburiscus)
Coloburiscus Eaton, Phillips (1930)
Murphyella Lestage, Needham & Murphy (1924, as Metamonius)

FAMILY SIPHLAENIGMATIDAE

The single genus and species placed in this newly described family combines an interesting array of characters of the Baetidae and of the *Nesameletus*-complex of the Siphlonuridae. We have also examined some larvae of Baetidae that show some characters otherwise found only in the *Nesameletus*-complex. Additional studies, especially of reared material, are needed to clarify the relationships in this complex.

SUBFAMILY SIPHLAENIGMATINAE

The nymphs occur in small, slowly-moving, brush-covered streams in New Zealand.

Siphlaenigma Penniket, Penniket (1963)

FAMILY BAETIDAE

The nymphs of the Baetidae are very characteristic in their entire structural pattern. As noted above, the Siphlaenigmatidae and the *Nesameletus*-complex (and to a lesser extent *Ameletus*) are rather similar to the Baetidae. On the basis of nymphal evidence alone, the above-mentioned genera might be regarded as largely filling the gap between two supposed families. On the totality of characters in both stages it seems best to retain Baetidae, Siphlonuridae and Siphlaenigmatidae as families, even though the Siphlaenigmatidae are also somewhat intermediate in the adult stage.

SUBFAMILY BAETINAE

The nymphs are abundant and nearly Cosmopolitan in a wide variety of rivers, streams, lakes, ponds, and even in small temporary pools. The genus *Cloeon* extends onto the true oceanic islands of the Pacific.

Apobaetis Day, Day (1955)
Baetiella Ueno, Ueno (1931), Ueno (1955)
Baetis Leach, Eaton (1883–88)
Baetodes Needham & Murphy, Needham & Murphy (1924), Demoulin (1955a)
Baetopus Keffermüller, Keffermüller (1960)
Bungona Harker, Harker (1957)
Callibaetis Eaton, Eaton (1883–88)
Centroptiloides Lestage, Crass (1947)
Centroptilum Eaton, Eaton (1883–88)

Cloeodes Traver, Traver (1938)
Cloeon Leach, Eaton (1883–88)
Neobaetis Navas, Nymph unknown
Neocloeon Traver, Traver (1935)
Paracloeodes Day, Day (1955)
Procloeon Bengtsson, Macon (1961)
Pseudocentroptilum Bogoescu, Nymph unknown
Pseudocloeon Klapalek, Ulmer (1940)

FAMILY OLIGONEURIIDAE

The mouthparts of the nymph are similar throughout the family. The gills of all genera except *Homoeoneuria* resemble those of *Isonychia* except that they are usually smaller. Demoulin (1958) places *Chromarcys* (and 3 fossil genera) in a family separate from, but allied to, the Oligoneuriidae. The nymphs of *Chromarcys* appear to be typical of the family except that the first gill is dorsal. It is likely that the ancestors of the Oligoneuriidae were *Isonychia*-like; if so, the Chromarcyinae can be regarded as Oligoneuriidae that retained some *Isonychia*-like characters.

SUBFAMILY CHROMARCYINAE

The single genus *Chromarcys* (=*Pseudoligoneuria*) is of rare occurrence in Sumatra and China. Because Demoulin (1953) used the name Chromarcyinae before 1960 and the subfamily name Pseudoligoneuriinae has not had general acceptance, the proper name of this subfamily should be Chromarcyinae under the present International Rules of Zoological Nomenclature.

Chromarcys Navas, Ulmer (1940, as Pseudoligoneuria)

SUBFAMILY OLIGONEURIINAE

The nymphs live in a variety of warm rivers, especially large ones, in the Holarctic, Ethiopian and Neotropical Realms, but they reach their greatest diversity in the tropics. A key to the genera of known nymphs is provided by Edmunds (1961).

Elassoneuria Eaton, Lestage (1916), Berner (1954)
Homoeoneuria Eaton, Edmunds, Berner & Traver (1958)
Lachlania Hagen, Needham and Murphy (1924) and Edmunds, Berner & Traver (1958)
Oligoneuria Pictet, Nymph unknown
Oligoneuriella Ulmer, Eaton (1883–88, as Oligoneuria)
Oligoneurioides Demoulin, Nymph unknown
Oligoneuriopsis Crass, Crass (1947)
Oligoneurisca Lestage, Tshernova (1937, as Oligoneuriella), Adult unknown
Spaniophlebia Eaton, Spieth (1943, as Oligoneuria) and Demoulin (1955a)

FAMILY HEPTAGENIIDAE

The Heptageniidae are very distinctive in both the adult and nymphal stage. The group is one that has apparently undergone a great deal of minor radiation but the basic structural pattern is retained, even in the highly modified genera that are now placed as subfamilies separate from the Heptageniinae. The phyletic relationships of the genus *Pseudiron* are the most problematical, and the relationships of the genus *Arthroplea* and *Anepeorus* to the more primitive Heptageniinae are uncertain.

SUBFAMILY HEPTAGENIINAE

The nymphs are inhabitants of a wide variety of streams and rivers and the wave-washed shores of lakes. They are abundant and diverse in the Holarctic and Oriental regions, but are also known from the Ethiopian region. In the New World at least three genera extend to Central America (Costa Rica) and a single specimen has been reported from Brazil.

Afronurus Lestage, Barnard (1932)
Atopopus Eaton, Nymph unknown
Bleptus Eaton, Ueno (1931)
Cinygma Eaton, McDunnough (1933)
Cinygmina Kimmins, Nymph unknown
Cinygmula McDunnough, McDunnough (1933)
Compsoneuria Eaton, Ulmer (1940)
Compsoneuriella Ulmer, Ulmer (1940)
Ecdyonurus Eaton, Eaton (1883–88, pl. 62, figs. 1–23)
Epeorella Ulmer, Nymph unknown
Epeorus Eaton
  Sg. Epeorus s.s, Eaton (1883–88)
  Sg. Iron Eaton, Eaton (1883–88)
  Sg. Ironopsis Traver, Traver (1935)
  Sg. Ironodes Traver, Traver (1935)
Heptagenia Walsh, Eaton (1883–88)
Notonurus Crass, Nymph unknown
Ororotsia Traver, Nymph unknown
Paegniodes Eaton, Nymph unknown
Rhithrogena Eaton, Eaton (1883–88)
Rhithrogeniella Ulmer, Nymph unknown
Stenonema Traver, Eaton (1883–88, nameless, pls. 57 and 58)
Thalerosphyrus Eaton, Ulmer (1940)

SUBFAMILY ARTHROPLEINAE

The single known genus *Arthroplea* occurs in bog ponds and on lake shores in the northern Holarctic region with southern limits in England, Czechoslovakia, Ontario and Massachusetts.

Arthroplea Bengtsson, Ide (1930, as Cinygma), Burks (1953)

SUBFAMILY PSEUDIRONINAE

Nymphs are known only from large sandy rivers in southeastern, central, and western North America. The nymphs have not been reared, but the nymphal form keyed and figured here (fig. 67) has been associated in Utah with an adult by matching color markings on the nymph and adult legs of specimens from nearby localities.

Pseudiron McDunnough, ? Spieth (1938, as new carnivorous heptagenid)

SUBFAMILY ANEPEORINAE

The nymph keyed here is only tentatively identified as *Anepeorus* but there is good evidence to suggest that the association is correct. The habitat and distribution is very similar to that of *Pseudiron.*

Anepeorus McDunnough, ? Burks (1953)

FAMILY AMETROPODIDAE

The relationship of the two subfamilies of this family to one another and to the rest of the Heptagenioidea is problematical. A study of the internal anatomy (see Landa, 1959) should clarify these questions if adequate material of these genera can be obtained for study.

SUBFAMILY AMETROPODINAE

The single genus here included, *Ametropus*, is found buried in firm, slightly silty, sand on the bottoms of larger rivers at widely scattered places in the Holarctic Realm.

Ametropus Albarda, Traver (1935)

SUBFAMILY METRETOPODINAE

The subfamily is distributed primarily in the northern Holarctic region with some species extending south into central Europe and the United States. The nymphs are found in streams, rivers and lakes. The nymphs of the two genera are keyed by Edmunds (1959), but we have recently discovered that the characters used are not adequate. Reared material of several species of *Siphloplecton* are needed to clarify the characters that will separate the nymphs of what appear to be two genera on the basis of adult characters.

Metretopus Eaton, Traver (1935)

Siphloplecton Clemens, Clemens (1915)

SUPERFAMILY LEPTOPHLEBIOIDEA

FAMILY LEPTOPHLEBIIDAE

The family Leptophlebiidae is a very distinct one that appears to be of ancient origin. In the northern hemisphere the nymphs show only moderate diversity. In the southern hemisphere some of the genera are so highly modified that the inclusion of them in the key has necessitated a complex couplet. Even in the highly modified forms, most of the nymphs of this family have very characteristic legs and mouthparts. The gills show an extreme range of modification.

SUBFAMILY LEPTOPHLEBIINAE

The nymphs occupy an extremely diverse variety of standing and running waters. They are virtually cosmopilitan except that they do not occur on many smaller oceanic islands. In the southern hemisphere they have undergone considerable adaptive radiation, with a number of remarkable types convergently approximating the forms characteristic of other families not represented in the southern land masses.

Adenophlebia Eaton, Barnard (1932)

Adenophlebiodes Ulmer

  Sg. Adenophlebiodes s.s., Crass (1947, as *Euphlebia*)

  Sg. Hyalophlebia Demoulin, Agnew (1962)

Aprionyx Barnard, Barnard (1932)

Atalomicria Harker, Harker (1957)
Atalonella Needham & Murphy, ? Needham & Murphy (1924)
Atalophlebia Eaton, Tillyard (1933)
Atalophlebioides Phillips, Phillips (1930)
Borinquena Traver, Traver (1938)
Calliarcys Eaton, Nymph unknown
Castanophlebia Barnard, Barnard (1932)
Choroterpes Eaton, Eaton (1883–88)
Choroterpides Ulmer, Ulmer (1940)
Cryptopenella Gillies, Nymph unknown
Deleatidium Eaton, Phillips (1930)
Dipterophlebiodes Demoulin, Nymph unknown
Euthraulus Barnard, Barnard (1932)
Fulleta Navas, Nymph unknown
Fulletomimus Demoulin, Nymph unknown
Habrophlebia Eaton
    Sg. Habrophlebia s.s., Eaton (1883–88)
    Sg. Habroleptoides Schoenemund, Ujhelyi (1959)
Habrophlebiodes Ulmer, Burks (1953)
Hagenulodes Ulmer, Nymph unknown
Hagenulopsis Ulmer, ? Traver (1944)
Hagenulus Eaton, ? Morrison (1919)
Hermanella Needham & Murphy
    Sg. Hermanella s.s., Needham & Murphy (1924)
    Sg. Hermanellopsis Demoulin, Demoulin (1955a)
Homothraulus Demoulin, ? Demoulin (1955a) or ? Traver (1960)
Isca Gillies, Nymph unknown
Jappa Harker, Harker (1954)
Kirrara Harker, Nymph unknown
Leptophlebia Westwood
    Sg. Leptophlebia s.s., Grandi (1960)
    Sg. Blasturus Eaton, Eaton (1883–88)
Massartella Demoulin, ? Demoulin (1955a)
Massartellopsis Demoulin, Nymph unknown
Miroculis Edmunds, Nymph unknown
Nathanella Demoulin, Nymph unknown
Neohagenulus Traver, Traver (1938)
Nousia Navas, Nymph unknown
Paraleptophlebia Lestage, Eaton (1883–88, as Leptophlebia)
Simothraulus Ulmer, Nymph unknown
Thraulodes Ulmer, Traver (1944)
Thraulophlebia Demoulin, Nymph unknown
Thraulus Eaton, Eaton (1883–88)
Traverella Edmunds, Edmunds (1948)
Ulmeritus Traver
    Sg. Ulmeritus s.s., Traver (1956)

- Sg. Pseudulmeritus Traver, Nymph unknown
- Sg. Ulmeritoides Traver, Nymph unknown

Ulmerophlebia Demoulin, Nymph unknown

Zephlebia Penniket

- Sg. Zephlebia s.s., Phillips (1930, as *Atalophlebia versicolor*)
- Sg. Neozephlebia Penniket, Phillips (1930, as *Atalophlebia nodularis*)

FAMILY EPHEMERELLIDAE

The Holarctic Ephemerellidae show a great diversity of nymphal types all assigned to various subgenera of the genus *Ephemerella* and are readily distinguished as a group. The African, Oriental and Australian forms are apparently more primitive. They approach the more primitive Tricorythidae very closely and, in the nymphal stage, it is difficult to separate readily the primitive Tricorythidae from the primitive Ephemerellidae. It would be premature to lump the two families together on the basis of the present evidence. They are currently recognized as separate families and their relationship will be determined only by a thorough study of all genera of both families. The nymph of *Melanemerella* is unknown but the adult structures suggest to us that *Melanemerella* is a member of the Ephemerellidae rather than the Tricorythidae as suggested by Demoulin (1955b).

SUBFAMILY EPHEMERELLINAE

The nymphs are found in a wide variety of streams, rivers, lakes and ponds, especially in fast flowing cold or cool waters. They are abundantly represented in the Holarctic but are also found in the Oriental and Ethiopian Realms and in Australia.

Ephemerella Walsh

- Sg. Ephemerella s.s., Burks (1953, as invaria-group), Edmunds (1959)
- Sg. Serratella Edmunds, Traver (1935, as serrata-group), Burks (1953, as serrata-group)
- Sg. Crinitella Allen and Edmunds, Allen and Edmunds (1963), Adult unknown
- Sg. Torleya Lestage, Lestage (1917, as genus)
- Sg. Caudatella Edmunds, Allen and Edmunds (1961a)
- Sg. Drunella Needham, Traver (1935, as fuscata-group), Allen and Edmunds (1962b)
- Sg. Attenuatella Edmunds, Allen and Edmunds (1961b)
- Sg. Dannella Edmunds, Allen and Edmunds (1962a)
- Sg. Eurylophella Tiensuu, Traver (1935, bicolor-group)
- Sg. Timpanoga Needham, Traver (1935, hecuba-group), Allen and Edmunds (1959)

Ephemerellina Lestage, Barnard (1932)

Teloganella Ulmer, Nymph unknown

Teloganodes Eaton, Ulmer (1940)

Teloganopsis Ulmer, Ulmer (1940)

SUBFAMILY MELANEMERELLINAE

The only genus in the subfamily occurs in Brazil.

Melanemerella Ulmer, Nymph unknown

FAMILY TRICORYTHIDAE

The Tricorythidae are very diverse in the nymphal stage. As noted above, the more primitive members are very closely allied to the Ephemerellidae, but some of the nymphal forms are so distinctive, that, if nymphal structures were the only ones considered, such remarkable forms as *Dicercomyzon* and *Machadorythus* would probably be placed in separate families.

SUBFAMILY TRICORYTHINAE

The nymphs occur in a wide variety of streams and rivers in the tropics and subtropics in the Ethiopian and Oriental regions.

Tricorythus Eaton, Demoulin (1957), Corbet (1960)

Neurocaenis Navas, Ulmer (1940, as Tricorythus)

SUBFAMILY MACHADORYTHINAE

The remarkable nymphs are almost certainly inhabitants of sand in rivers or streams. The genus is known from two localities in tropical Africa, the type locality and from one mature nymph from Belgian Congo, 13 mi. E. Kenge, 4-VIII-1957, E. S. Ross and R. E. Leech, California Academy of Sciences Collection.

Machadorythus Demoulin, Demoulin (1959), Adult unknown

SUBFAMILY EPHEMERYTHINAE

The nymphs occur in a wide variety of streams and rivers in East Africa.

Ephemerythus Gillies, Kimmins (1955)

SUBFAMILY LEPTOHYPHINAE

The nymphs are known from streams and rivers in the Neotropical and Nearctic regions and adults of the subfamily are also known from tropical Africa. The genus *Bruchella* is based on an error of observation of the form of the hind wing. Its type species, *B. nigra* Navas, is a typical *Leptohyphes.*

Tricorythopsis Traver, Nymph unknown

Leptohyphes Eaton, Needham and Murphy (1924) (=Bruchella Navas, 1920, *new synonymy*)

Leptohyphodes Ulmer, Traver (1944)

Tricorythafer Lestage, Nymph unknown

Tricorythodes Ulmer, Traver (1935), Burks (1953)

SUBFAMILY DICERCOMYZINAE

The very unusual nymphs of the only genus, *Dicercomyzon,* are known from streams and rivers in wooded areas. They are widespread in equatorial Africa.

Dicercomyzon Demoulin, Demoulin (1954)

SUPERFAMILY EPHEMEROIDEA

FAMILY BEHNINGIIDAE

The Behningiidae are so unique that they are readily recognizable by any of a large number of characters. The phylogenetic relationship to the other families is questionable, but on the basis of present evidence it appears best to continue to recognize the family as an atypical member of the Ephemeroidea.

SUBFAMILY BEHNINGIINAE

The three genera are known from warm rivers. The nymphs burrow in sand. The subfamily is known from a small number of collections in widely scattered localities of the Holarctic realm. Tshernova and Baikova (1960) give a key to the nymphs of the genera, and Edmunds and Traver (1959) review the species of *Behningia* and *Dolania.*

Behningia Lestage, Edmunds & Traver (1959)
Dolania Edmunds & Traver, Edmunds & Traver (1959), Adult unknown
Protobehningia Tshernova, Tshernova and Baikova (1960), Adult unknown

FAMILY POTAMANTHIDAE

The members of this family are very distinctive. Although the key characters used to separate this family from the Euthyplociidae are rather trivial, the mouthparts, gills, etc. of the two families are strikingly different.

SUBFAMILY POTAMANTHINAE

The known nymphs are sprawlers on sandy or silty stream bottoms. The subfamily is widely distributed in the Holarctic and Oriental Realms.

Neopotamanthodes Hsu, Nymph unknown
Potamanthindus Lestage, Nymph unknown
Potamanthodes Ulmer, ? Imanishi (1940, as Potamanthus (Potamanthodes) formosus)
Potamanthus Pictet, Eaton (1883–88)
Rhoenanthopsis Ulmer, Nymph unknown
Rhoenanthus Eaton, Ulmer (1940)

FAMILY EUTHYPLOCIIDAE

The nymphs of Euthyplociidae are readily distinguished from all other families. The mandibular tusks of the Euthyploiidae are very long and sickle-shaped; this is also true of "*Potamanthus nb*" (Imanishi, 1940) from Manchuria, but the characters given in the key should readily separate the two families.

SUBFAMILY EUTHYPLOCIINAE

The nymphs appear to be sprawlers on sandy bottoms of rivers and streams primarily in the tropics and subtropics of the world.

Afroplocia Lestage, Barnard (1940, as Exeuthyplocia)
Campylocia Needham & Murphy, Eaton (1883–88, as Euthyplocia)
Euthyplocia Eaton, Ulmer (1920)
Exeuthyplocia Lestage, Nymph unknown
Mesoplocia Demoulin, Nymph unknown
Polyplocia Lestage, Nymph unknown

FAMILY EPHEMERIDAE

The Ephemeridae form a readily recognizable family with similarities in nymphal mouthparts, gills, legs, etc. The genus *Pentagenia* is a rather distinctive member of the family, differing from the others, especially in the mouthparts, and the nymph of *Ichthybotus* is also rather distinctive.

We find inadequate differences between *Ichthybotus* and other Ephemeridae to remove the former from the family. Demoulin (1957) states that the nymphs of *Ichthybotus* have the general aspect of Ephemeridae, but with mandibles similar to the Polymitarcidae. The mandibles of *Ephoron* of the Polymitarcidae are armed with tubercles that are immovable outgrowths of the body wall (fig. 43); in the Ephemeridae, the armature of the mandibles is set in movable sockets (fig. 44). Examination of *Ichthybotus* nymphs show that the mandibular armature is also set in movable sockets (fig. 45). Thus, although superficially resembling the Polymitarcide, the armature is homologous with that of the Ephemeridae. The characteristics of the adults of *Ichthybotus* also seem to fit well within those of the Ephemeridae. The first anal vein of the Ephemeridae is attached to the hind margin of the wing by three to many cross veins. In *Ichthybotus*, the first anal vein is said to be irregularly forked. The variable "fork" is actually formed by two cross-veins attaching the first anal vein to the hind margin, and many specimens we have examined have three such cross veins, although the third may be incomplete. The anal vein, therefore, is attached in *Ichthybotus* in a manner very similar to that seen in *Pentagenia* or *Eatonica*. The genital forceps of males of *Ichthybotus* are not unusual for the Ephemeridae being much like those of *Pentagenia* or *Ephemera* except that the basal segment is partly fused to the second segment as is figured by Kimmins (1960). The form of the penes is not unlike that of *Pentagenia* or *Eatonica,* except that the lobes are shorter. Thus, examination of our material reveals that *Ichthybotus* is a member of the Ephemeridae and that its rather peculiar characters are paralleled in other members of the family. If Demoulin (*op. cit.*) examined only the literature available in 1957, he could easily have been misled by the figures then available. In totality of characters *Ichthybotus* is a more typical member of the Ephemeridae than is *Pentagenia*.

SUBFAMILY EPHEMERINAE

The nymphs are burrowers in sand, silt, or mud in streams, rivers and lakes. They are nearly Cosmopolitan in distribution, being absent only in Australia, Madagascar and the Oceanic Islands.

- Afromera Demoulin, Nymph unknown
- Eatonica Navas, Crass (1947)
- Eatonigenia Ulmer, Nymph unknown
- Ephemera Linnaeus, Eaton (1883–88)
- Hexagenia Walsh
    - Sg. Hexagenia s.s., Eaton (1883–88)
    - Sg. Pseudeatonica Spieth, Nymph unknown
- Ichthybotus Eaton, Phillips (1930)
- Pentagenia Walsh, Needham (1920)

FAMILY POLYMITARCIDAE

This family and the Palingeniidae appear to be the most specialized of the burrowing forms. The three subfamilies of the Polymitarcidae appear to be similar in structure, habitat and behavior. Each subfamily is readily distinguished from the others by the form of the head, particularly the mandibular tusks.

SUBFAMILY POLYMITARCINAE

The nymphs of the single genus *Ephoron* (=*Polymitarcys, Eopolymitarcys*) burrow in firm clay or mud or clay-filled sand in the bottoms and banks of rivers and lakes. They occur in the Holarctic and Oriental Realms and in southern Africa.

- Ephoron Williamson, Eaton (1883–88, as Polymitarcys)

SUBFAMILY CAMPSURINAE

The nymphs are burrowers in the bottoms and banks of streams and rivers, especially the large rivers, in the Neotropical and Nearctic regions. A key to the two genera is provided by Edmunds (1959).

Campsurus Eaton, Ulmer (1920)
Tortopus Needham & Murphy, Scott, Berner & Hirsch (1959)

SUBFAMILY ASTHENOPODINAE

The known nymphs burrow in silt, in wood, or in freshwater sponges in lakes and rivers in the tropics of the Ethiopian, Oriental and Neotropical Realms.

Asthenopodes Ulmer, Nymph unknown
Asthenopus Eaton, ? Eaton (1883–88, as Palingenia, Brazil)
Povilla Navas, Ulmer (1940)

FAMILY PALINGENIIDAE

The Palingeniidae appear to be rather closely allied to the Polymitarcidae. The nymphs of the two families are similar in many characters, but the adults of the two families show much less similarity.

SUBFAMILY PALINGENIINAE

The nymphs burrow in silt and mud in the bottom and banks of larger rivers and lakes. They are found principally in the Palearctic and Oriental regions but they are also known from New Guinea and Madagascar.

Anagenesia Eaton, Ulmer (1920)
Chankagenesia Buldovskii, Tshernova (1952, as Anagenesia (subgenus Chankagenesia))
Cheirogenesia Demoulin, Nymph unknown
Mortogenesia Lestage, Nymph unknown
Palingenia Burmeister, Schoenemund (1930)
Plethogenesia Ulmer, Ulmer (1940)

SUPERFAMILY CAENOIDEA

FAMILY NEOEPHEMERIDAE

The systematic position of the family Neoephemeridae has been a matter of continual dispute ever since the first species was described from the nymph in 1870. These disputes have arisen because the nymphs of the family resemble those of the Caenidae, while the adult wing venation is very similar to that found in the Potamanthidae. The similarities of the known nymphs of Neoephemeridae to the nymphs of the Caenidae (except for the specialized genus *Brachycercus*) are not superficial. The general body form is similar. The gills are also much alike in the two families. The anterior gill pairs beneath the operculate gills are branched pectinately in some Neoephemeridae (fig. 60) and have a small fringed plate or filament attached near the base, while those of *Caenis* (fig. 54) are dichotamously branched and have no additional structure near the base; however, the posterior pairs of gills of the Neoephemeridae are similar to the entire gill series in the Caenidae. The legs in the two families are also smilar (see figs. 56 and 59). All of the mouthparts are much alike in the two groups (see figs. 53, 55, 57 of *Caenis* and 58, 61, 62 of *Neoephemera*). There are even similarities in minute structures such as the detail of the median excavation of the labrum. A thorough study of a great variety of adult and nymphal structures in several species of each genus is needed for a full evaluation of this problem.

It is our opinion that the Neoephemeridae are closely related to the Caenidae, but that since the divergence of the two groups the nymphs have evolved very slowly. In contrast, the adults of the Caenidae have become highly modified since the two stocks separated. It is interesting to speculate that most of the modification of the adult Caenidae may have resulted from new natural selection factors associated with reduction in size. This is strongly suggested by the fact that most of the modifications of the Caenidae are paralleled by similar structural modifications in adults of the equally small *Tricorythodes* (Tricorythidae) and *Prosopistoma* (Prosopistomatidae), but the function of the structures involved is so poorly known that interpretation of the adaptive significance is obscure.

We are of the opinion that the similarities of the nymphal Neoephemeridae and Caenidae are a result of common ancestry; convergent evolution is improbable because the similarities are too numerous and are concerned with too many functions of the exoskeleton. In view of the obvious similarities in the nymphs and the striking differences between the adults of the two groups, we believe that it is best to recognize the Neoephemeridae as a family and place them in the same superfamily as the Caenidae. Tshernova (1962) would place the Neoephemeridae in a superfamily by themselves and Landa (1959) would combine the Caenoidea (*sensu* Edmunds and Traver, 1954) with the Prosopistomatoidea (*sensu* Edmunds and Traver, 1954). Landa (*op. cit.*) suggests this grouping on the basis of internal anatomy of the nymphs. Landa's findings were of great importance in clarifying the relationships of the genera *Prosopistoma* and *Baetisca* to the other families of Ephemeroptera. The Neoephemeridae and Caenidae are apparently more closely allied to one another than they are to the Baetiscidae and Prosopistomatoidea, which also show many features in common. Therefore, the question of whether to recognize one or two superfamilies is rather unimportant as both classifications are, in our opinion and Landa's (*op. cit.*), consistent with phylogeny. We continue to recognize two superfamilies largely on the basis of convenience and historical stability of the classification systems.

SUBFAMILY NEOEPHEMERINAE

The nymphs occur usually in small numbers in a variety of streams and rivers. The known distribution is Holarctic and Oriental. *Neoephemera* is known from eastern North America, France, Lithuania and Macedonia, and *Neoephemeropsis* from Java and *Potamanthellus* from Asia.

Neoephemera McDunnough
  Sg. Neoephemera s.s., Berner (1956, *N. bicolor*)
  Sg. Oreianthus Traver, Traver (1935, *O. purpureus*)
  Sg. Leucorhoenanthus Ulmer, Ikonomov (1961, as Oreianthus)
Neoephemeropsis Ulmer, Ulmer (1940)
Potamanthellus Lestage, Nymph unknown

FAMILY CAENIDAE

The Caenidae, as noted above, appear to be closely allied to the Neoephemeridae and were probably derived from a Neoephemerid-like ancestor. The difference between the two families is noted in the key and in the discussion of the Neoephemeridae.

SUBFAMILY CAENINAE

The nymphs are common in a great variety of ponds, lakes, streams and rivers over most of the earth. They are not known from New Zealand or Madagascar but they are widely scattered over the continents and a number of islands. Keys and diagnoses of the genera are given by Thew (1960).

Austrocaenis Barnard, Barnard (1932)
Brachycercus Curtis, Schoenemund (1930)
Caenis Stephens, Eaton (1883–88)
Caenodes Ulmer, Thew (1960)
Caenomedea Thew ,Thew (1960)
Tasmanocoenis Lestage, Thew (1960)

SUPERFAMILY PROSOPISTOMATOIDEA

FAMILY BAETISCIDAE

The genus *Baetisca* occupies an isolated position in the Ephemeroptera but is apparently most closely allied to *Prosopistoma* (Prosopistomatidae). Both have a mesonotal shield over the gills and the gills have fringed margins. The mouthparts of *Baetisca* are quite unlike those of *Prosopistoma*.

SUBFAMILY BAETISCINAE

The family includes only the genus *Baetisca* which is rather widespread and diverse in eastern North America, but also extends west to Wyoming and Washington. The nymphs are sand inhabitants in lakes and rivers.

Baetisca Walsh, Eaton (1883–88)

FAMILY PROSOPISTOMATIDAE

The genus *Prosopistoma* is unique but appears to be most closely allied to *Baetisca* as noted above and to a lesser degree to the Caenoidea as noted under that family.

SUBFAMILY PROSOPISTOMATINAE

The single known genus is widely distributed in the Old World. It is most diverse in Africa but is found also in Madagascar, Europe (France, Czechoslovakia, Hungary) and the Oriental Realm (Ceylon, Philippine Islands, Java). The correct name of the genus is in question, but the failure to apply the generic name *Binoculus* Geoffroy to this genus between its use by Dumeril in 1816 and its use by Demoulin in 1954 and the continuous use of the name *Prosopistoma* from 1882 to 1954 seemingly validates *Prosopistoma* for the genus.

Prosopistoma Latreille, Eaton (1883–88)

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APPENDIX

COLLECTION DATA ON SPECIMENS FIGURED

Fig. 1. *Ameletus* sp., Yellowstone River at Canyon, Yellowstone National Park, Wyoming.

Fig. 2. *Metamonious anceps* (Eaton), Rio Golgol, Chile, L. Peña.

Fig. 3. *Nesameletus* sp., Kaupokonui River, Taranaki Prov., New Zealand, A. Hirsch.

Fig. 4. *Acanthametropus* sp., Savannah River, Georgia-South Carolina, T. Dolan IV.

Fig. 5. *Mirawara megaloprepia* Riek, Coomera River, Lanington National Park, Queensland, Australia, E. F. Riek.

Fig. 6. *Coloburiscus* sp., Otakiha, Taranaki Prov., New Zealand, A. Hirsch.

Fig. 7. *Siphlaenigma janae* Penniket, Baxter's Stream, New Zealand, J. G. Penniket.

Figs. 8–9. *Baetis tricaudatus* Dodds, South Willow Canyon, Tooele Co., Utah.

Figs. 10–11. *Cloeon dipterum* (Linnaeus), Chertal, Belgique, G. Demoulin.

Figs. 12–13. *Callibaetis coloradensis* Banks, East of Castilla, Utah.

Fig. 14. *Cloeon dipterum* (Linnaeus), Chertal, Belgique, G. Demoulin.

Figs. 15–16. *Lachlania powelli* Edmunds, Green River, Hideout Canyon, Daggett Co., Utah.

Fig. 17. *Homoeoneuria* sp., Escalante River, Kane Co., Utah. G. Musser and G. Smith.

Fig. 18. *Heptagenia* sp., Willamette River, nr. Walker, Lane Co., Oregon.

Fig. 19. *Arthroplea bipunctatum* (McDunnough), Cushman, Mass.

Fig. 20. ? *Anepeorus,* Mt. Carmel, Ill., C. O. Mohr and B. D. Burks.

Fig. 21. *Ametropus albrighti* Traver, Green River, Hideout Canyon, Daggett Co., Utah.

Fig. 22. *Siphloplecton basale* (Walker), Amherst, Mass., L. Bartlett.

Fig. 23. *Paraleptophlebia* sp., John Day River, Oregon.

Fig. 24. *Habrophlebia fusca* (Curtis), Yernce, Ombre, Belgique, G. Demoulin.

Fig. 25. *Adenophlebiodes* sp., Dayi River, Kpandu, Gold Coast, L. Berner.

Fig. 26. *Borinquena carmencita* Traver, Hicaco River, Rio Blanco, Puerto Rico, J. García-Díaz.

Fig. 27. *Traverella albertana* (McDunnough), Green River, Hideout Canyon, Daggett Co., Utah.

Fig. 28. *Choroterpes nigrescens* Barnard, Groot Drakenstein, Great Berg River, W. Cape Prov., South Africa, A. D. Harrison.

Fig. 34. *Tricorythus* sp., Shiro River, Nyasaland, L. Berner.

Fig. 35. *Machadorythus palanquim* Demoulin, 13 mi. E. Kenge, Belgium Congo, E. S. Ross and R. E. Leech.

Figs. 37–38. *Ephemerythus* sp., 13½ mi. E. Ft. Johnston, Nyasaland, L. Berner.

Fig. 39. *Leptohyphes* sp., Lago Carangeira, Cachimbo, Brazil, 27° 12′ B. 51° 46′ L., F. Plaumann.

Fig. 40. *Dicercomyzon* sp., Namwera, Nyasaland, L. Berner.

Fig. 41. *Dolania americana* Edmunds and Traver, Upper Three Runs, S. of Atkin, South Carolina, T. Dolan IV and S. Roback.

Fig. 42. *Campyplocia anceps* (Eaton), Bartica District, British Guiana.

Fig. 43. *Ephoron leukon* Williamson, Smoke Hole, Pendleton Co., West Virginia.

Fig. 44. *Ephemera danica* Muller, Berounka River, Middle Bohemia, V. Landa.

Fig. 45. *Icthybotus hudsoni* McLachlan, Wainue-a-mata, New Zealand.

Fig. 46. *Pentagenia vittigera* (Walsh), Rock River, McConnell, Ill., D. H. Thompson.

Fig. 47. *Ephemera danica* Muller, Brook Uneticky, Middle Bohemia, V. Landa.

Fig. 48. *Ephoron leukon* Williamson, Smoke Hole, Pendleton Co., West Virginia.

Fig. 49. *Campsurus* sp., Ariranha River, Nova Teutonia, Brazil, F. Plaumann.

Fig. 50. *Asthenopus* sp., "Amazon River, above Teffe, Brazil, Coary."

Fig. 51. *Palingenia longicauda* Oliver, Vardar, Bulgaria, V. Landa.

Fig. 52. *Anagenesia robusta* (Eaton), redrawn from Gravely, 1920, Records Indian Mus., 18: fig. 7, pl. 18.

Figs. 53–57. *Caenis* sp., Olentangy River, Columbus, Ohio, T. A. Woolley.

Figs. 58–62. *Neoephemera youngi* Berner, Sweetwater Branch, Liberty Co., Florida, J. G. Needham.

Fig. 63. *Siphlonisca aerodromia* Needham, Fish House, New York, C. P. Alexander.

Fig. 64. *Murphyella needhami* Lestage, Crest of Sierra Nahuelbuta, W. of Angol, Chile, E. S. Ross and A. E. Michelbacher.

Fig. 65. *Siphlonella* sp., 20 km. E. Temuco, Chile, E. S. Ross and A. E. Michelbacher.

Fig. 66. *Epeorus longimanus* (Eaton), Soda Butte Creek, 1 mi. E. Soda Butte, Yellowstone National Park, Wyoming.

Fig. 67. *Pseudiron* sp., Green River, Sweetwater Co., Wyoming, G. Musser and G. Smith.

Fig. 68. *Thraulodes* sp., Lago Caranegeira, Cachimbo, Brazil, 27° 12′ B. 51° 46′ L., F. Plaumann.

Fig. 69. *Ephemerella attennata* McDunnough, New Brunswick, E. L. Bousefield.

Fig. 70. *Neurocaenis* sp., Porac, Pampanga Prov., Luzon, H. Hoogstraal.

Fig. 71. *Tricorythodes* or allied genus, Red River, Carson National Forest, Taos Co., New Mexico, C. M. Tarzwell.

Fig. 72. *Leptohyphes* sp., Lago Carangeira, Cachimbo, Brazil, 27° 12′ B. 51° 46′ L., F. Plaumann.

Fig. 73. *Potamanthus* sp., Rock Riv., Cleaveland, Ill., T. Thew.

Fig. 74. *Pentagenia vittigera* (Walsh)?, Guadalupe River, South Victoria, Texas, T. Dolan IV.

Fig. 75. *Neoephemera purpurea* Traver, Davidson River, Pisgah National Forest, North Carolina, J. R. Traver.

Fig. 76. *Brachycercus* sp., Green River, Sweetwater Co., Wyoming, G. Smith and G. Musser.

Fig. 77. *Baetisca columbiana* Edmunds, Columbia River, Pasco, Franklin Co., Washington, J. J. Davis.

Fig. 78. *Prosopistoma wouterae* Lieftinck, E. slope Mt. McKinley, Davao, Mindanao, Philippine Islands, F. Werner.

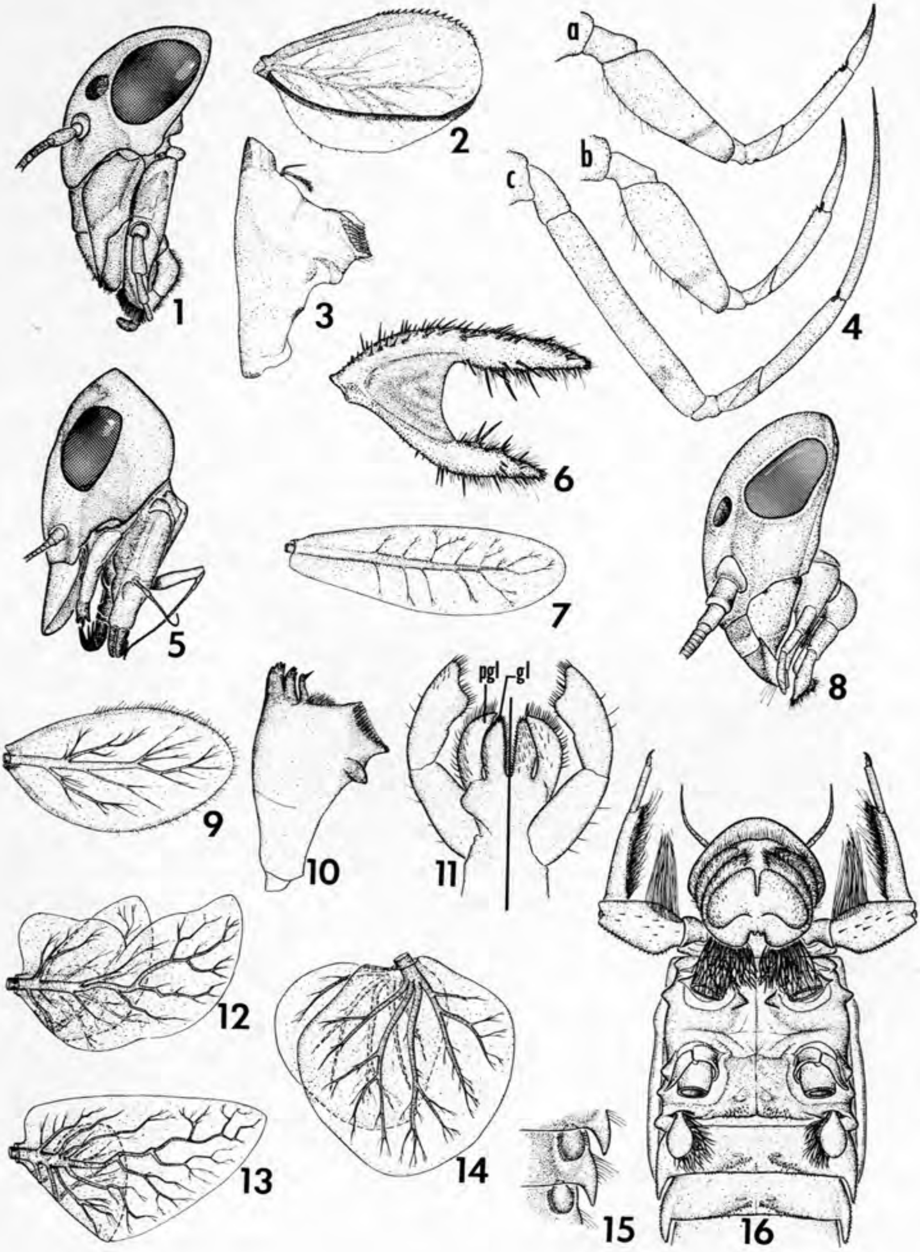

PLATE I. 1. *Ameletus* sp., lateral view of head. 2. *Metamonius*, gill segment four. 3. *Nesameletus*, mandible. 4. *Acanthametropus* sp., legs. 5. *Mirawara*, lateral view of head. 6. *Coloburiscus*, gill, segment four. 7. *Siphlaenigma*, gill, segment four. 8. *Baetis*, lateral view of head. 9. *Baetis*, gill, segment four. 10. *Cloeon*, mandible. 11. *Cloeon*, labium. 12. *Callibaetis*, gill, segment one. 13. *Callibaetis*, gill, segment four. 14. *Cloeon*, gill, segment four. 15. *Lachlania*, gills on segments five and six. 16. *Lachlania*, ventral view of head, thorax, and abdominal segments one to three.

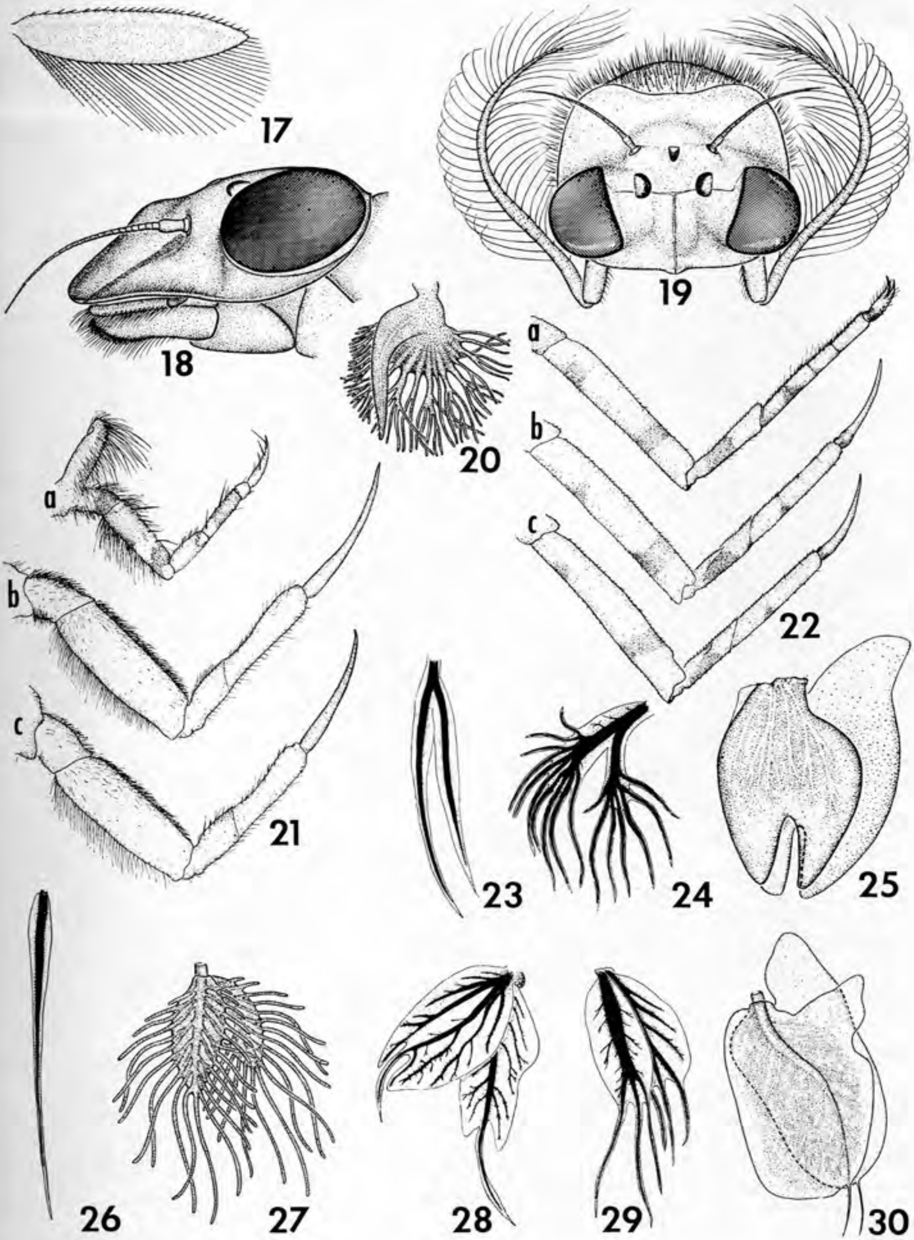

PLATE II. 17. *Homoeoneuria*, gill, segment four. 18.*Heptagenia*, lateral view of head. 19. *Arthroplea*, dorsal view of head. 20. ? *Anepeorus*, gill, segment four. 21. *Ametropus*, legs. 22. *Siphloplecton*, legs. 23. *Paraleptophelebia*, gill, segment four. 24. *Habrophlebia*, gill, segment four. 25. *Adenophlebiodes*, gill, segment four. 26. *Borinquena*, gill, segment four. 27. *Traverella*, gill, segment four. 28. *Choroterpes*, gill, segment four. 29. *Euthraulus*, gill, segment four. 30. Leptophlebiidae, *genus incertus* (Brazil), gill, segment four.

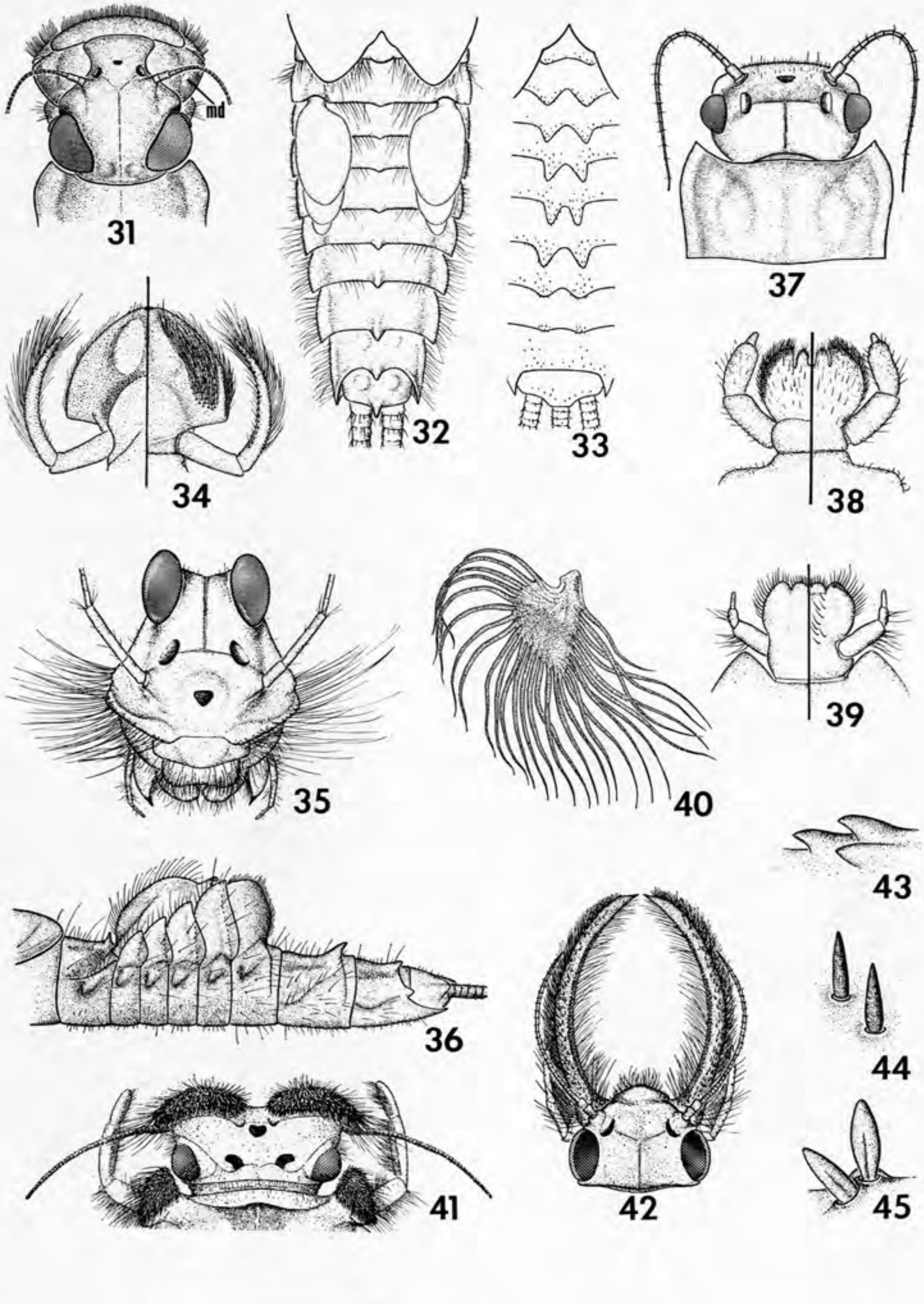

PLATE III. 31. Leptophlebiidae, *genus incertus* (New Caledonia), dorsal view of head. 32. *Teloganodes*, abdominal terga. 33. *Ephemerellina*, median area of abdominal terga. 34. *Tricorythus*, labium. 35. *Machadorythus*, frontal view of head. 36. *Machadorythus*, lateral view of abdomen. 37. *Ephemerythus*, dorsal view of head and prothorax. 38. *Ephemerythus*, labium. 39. *Leptohyphes*, labium. 40. *Dicercomyzon*, gill, segment four. 41. *Dolania*, dorsal view of head and part of prothorax. 42. *Campylocia*, dorsal view of head. 43. *Ephoron*, detail of mandibular armature. 44. *Ephemera*, detail of mandibular armature. 45. *Ichthybotus*, detail of mandibular armature.

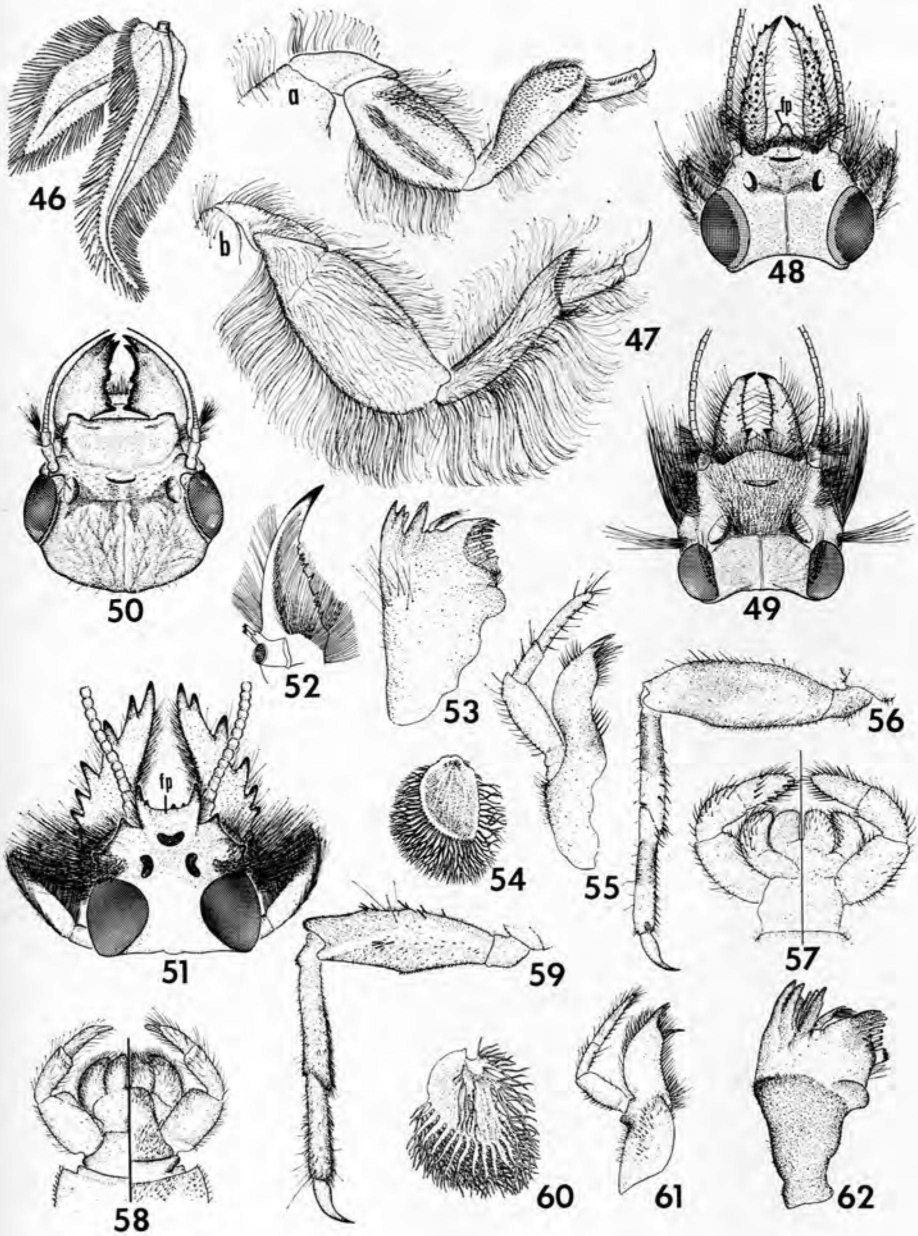

PLATE IV. 46. *Pentagenia*, gill, segment four. 47. *Ephemera*, fore and hind legs. 48. *Ephoron*, dorsal view of head. 49. *Campsurus*, dorsal view of head. 50. ? *Asthenopus*, dorsal view of head. 51. *Palingenia*, dorsal view of head. 52. *Anagenesia*, mandible (redrawn from Gravely). 53. *Caenis*, mandible. 54. *Caenis*, gill, segment three. 55. *Caenis*, maxilla. 56. *Caenis*, foreleg. 57. *Caenis*, labium. 58. *Neoephemera*, labium. 59. *Neoephemera*, foreleg. 60. *Neoephemera*, gill, segment three. 61. *Neoephemera*, maxilla. 62. *Neoephemera*, mandible.

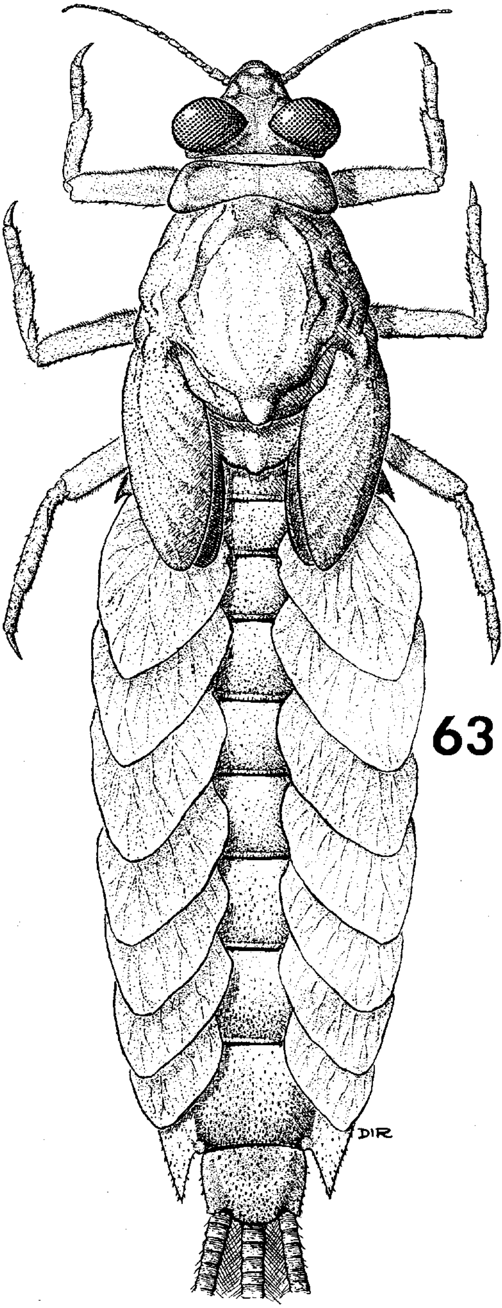

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PLATE V. 63. *Siphlonisca aerodromia* Needham, nymph.

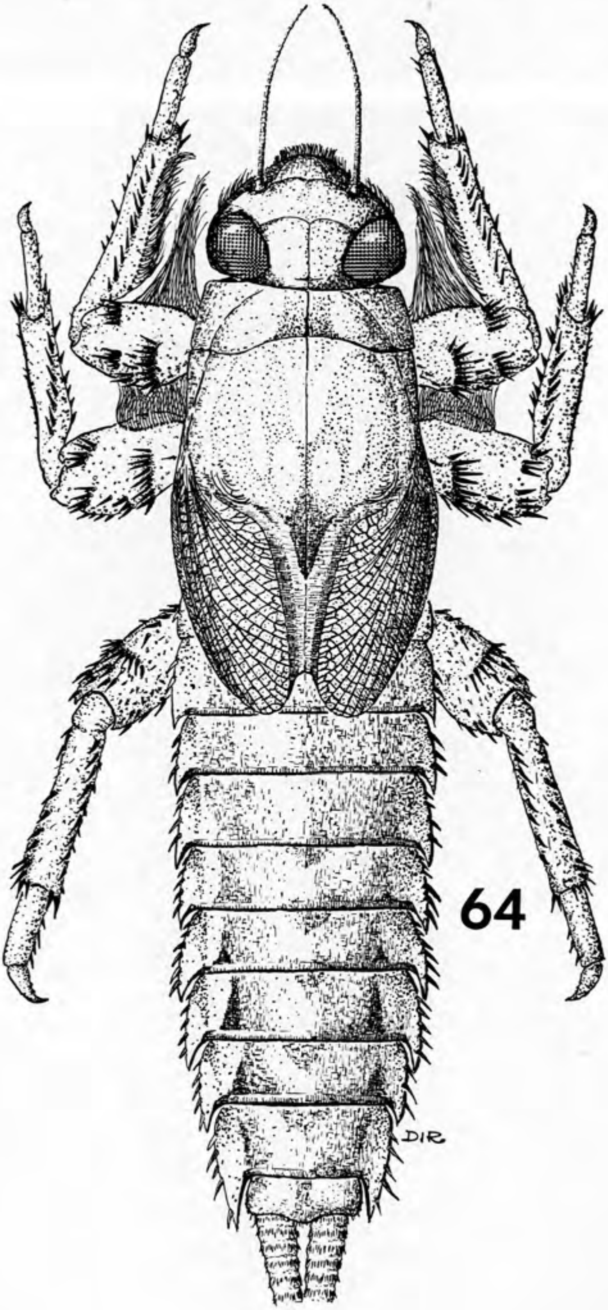

PLATE VI. **64.** *Murphyella needhami* Lestage, nymph.

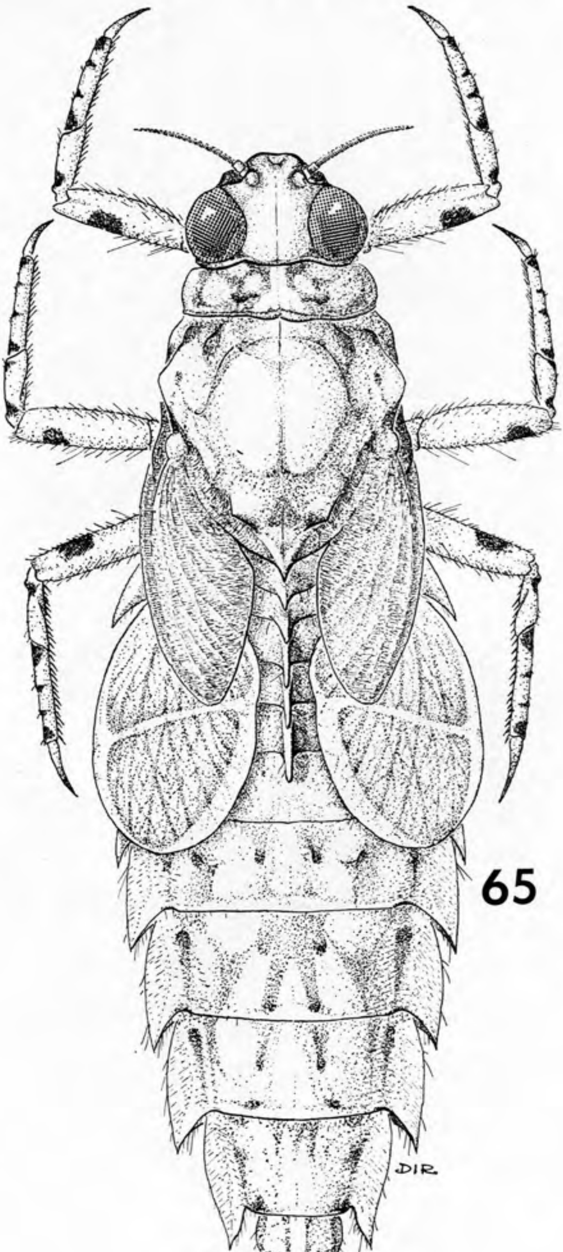

PLATE VII. **65.** *Siphlonella* sp., nymph.

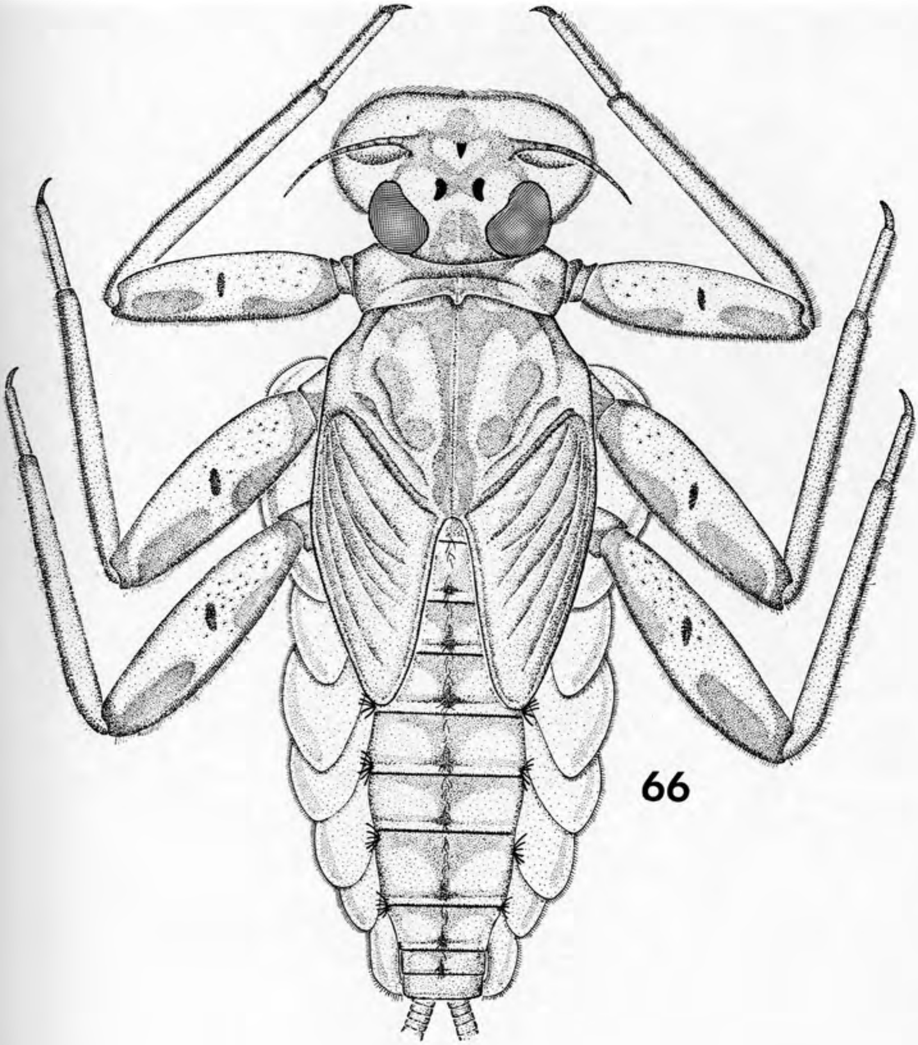

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PLATE VIII. **66.** *Epeorus longimanus* (Eaton), nymph.

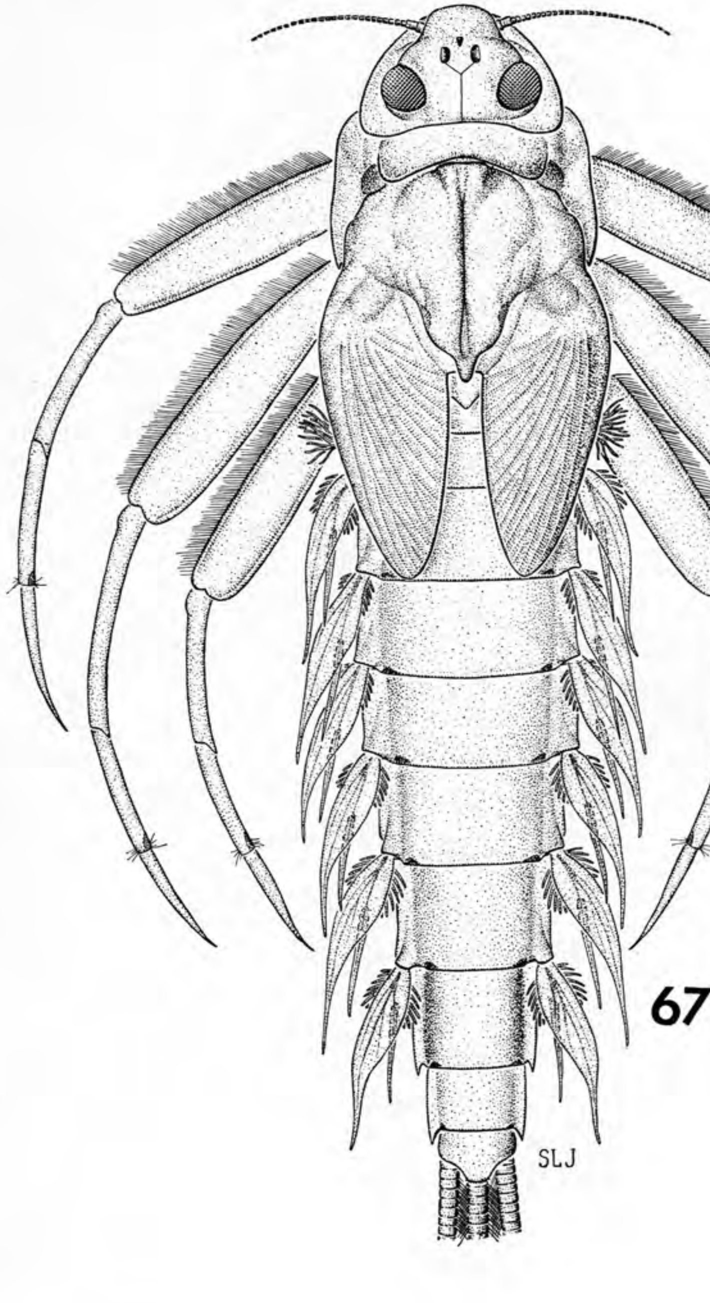

PLATE IX. 67. *Pseudiron* sp., nymph.

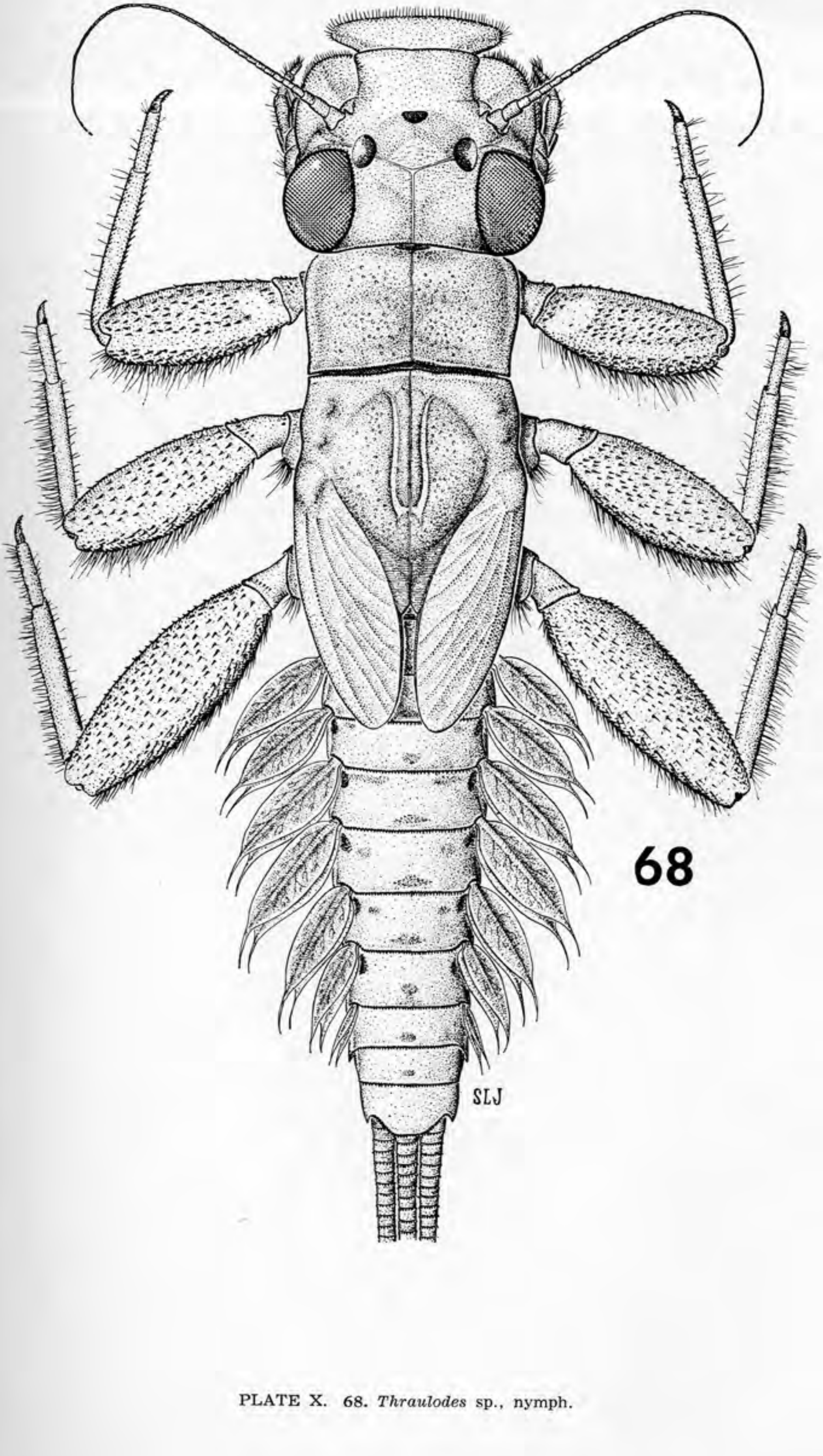

PLATE X. 68. *Thraulodes* sp., nymph.

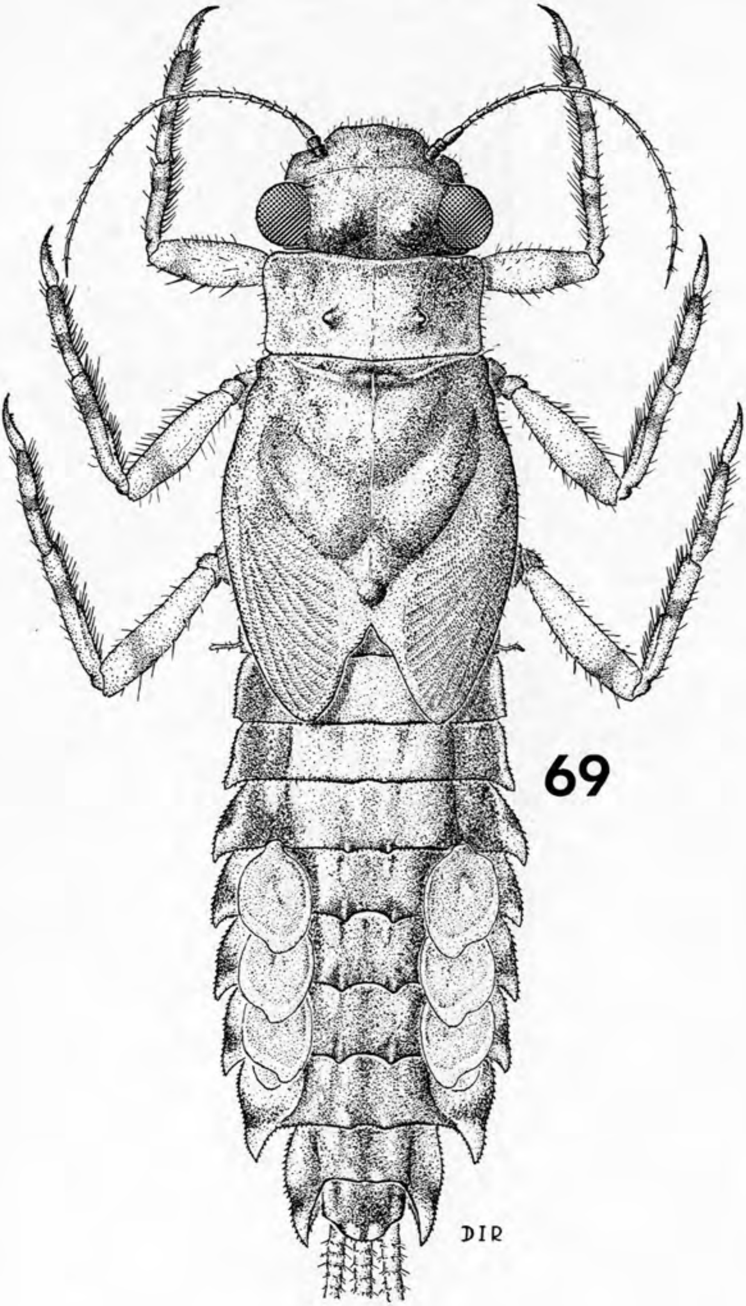

PLATE XI. **69.** *Ephemerella attenuata* McDunnough, nymph.

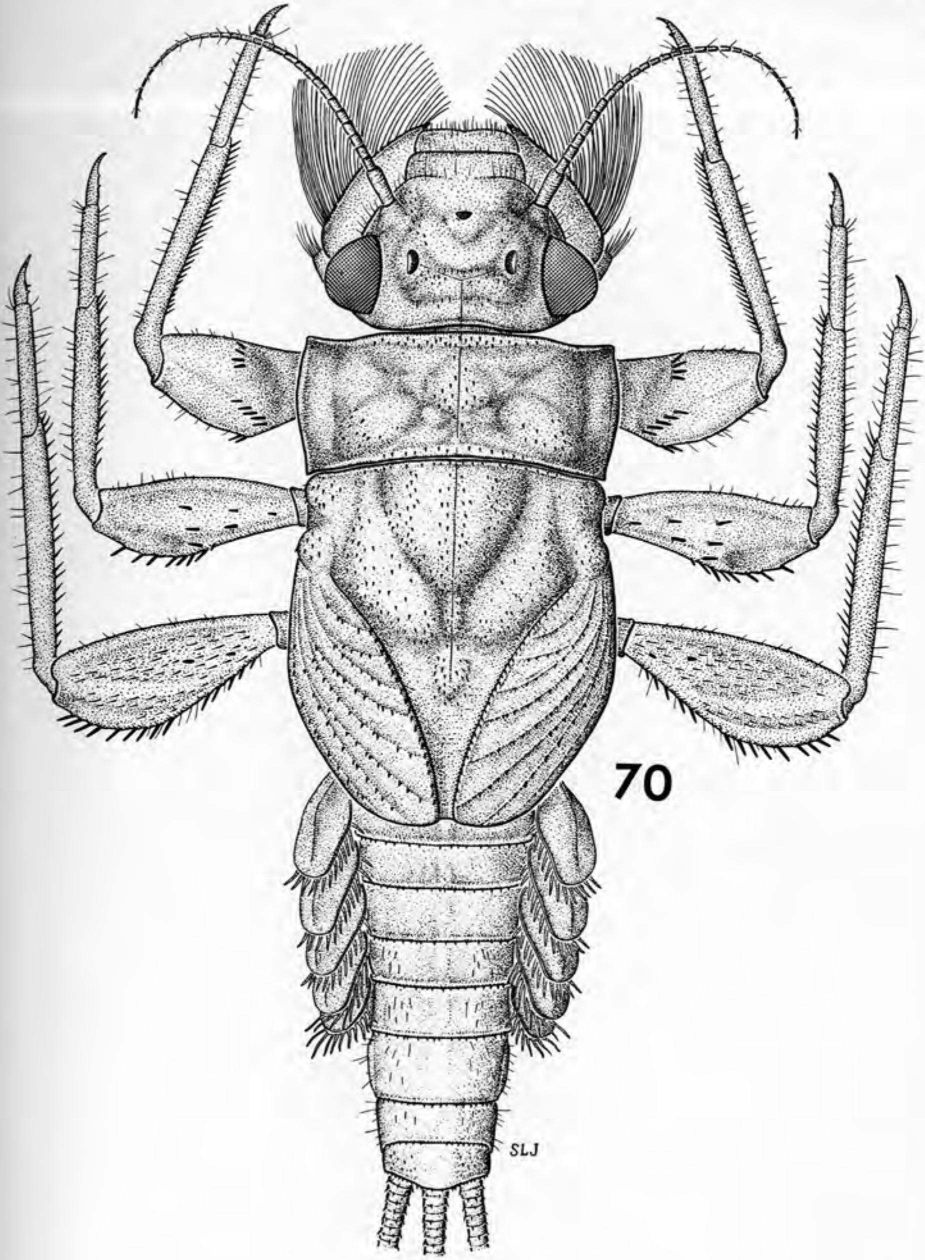

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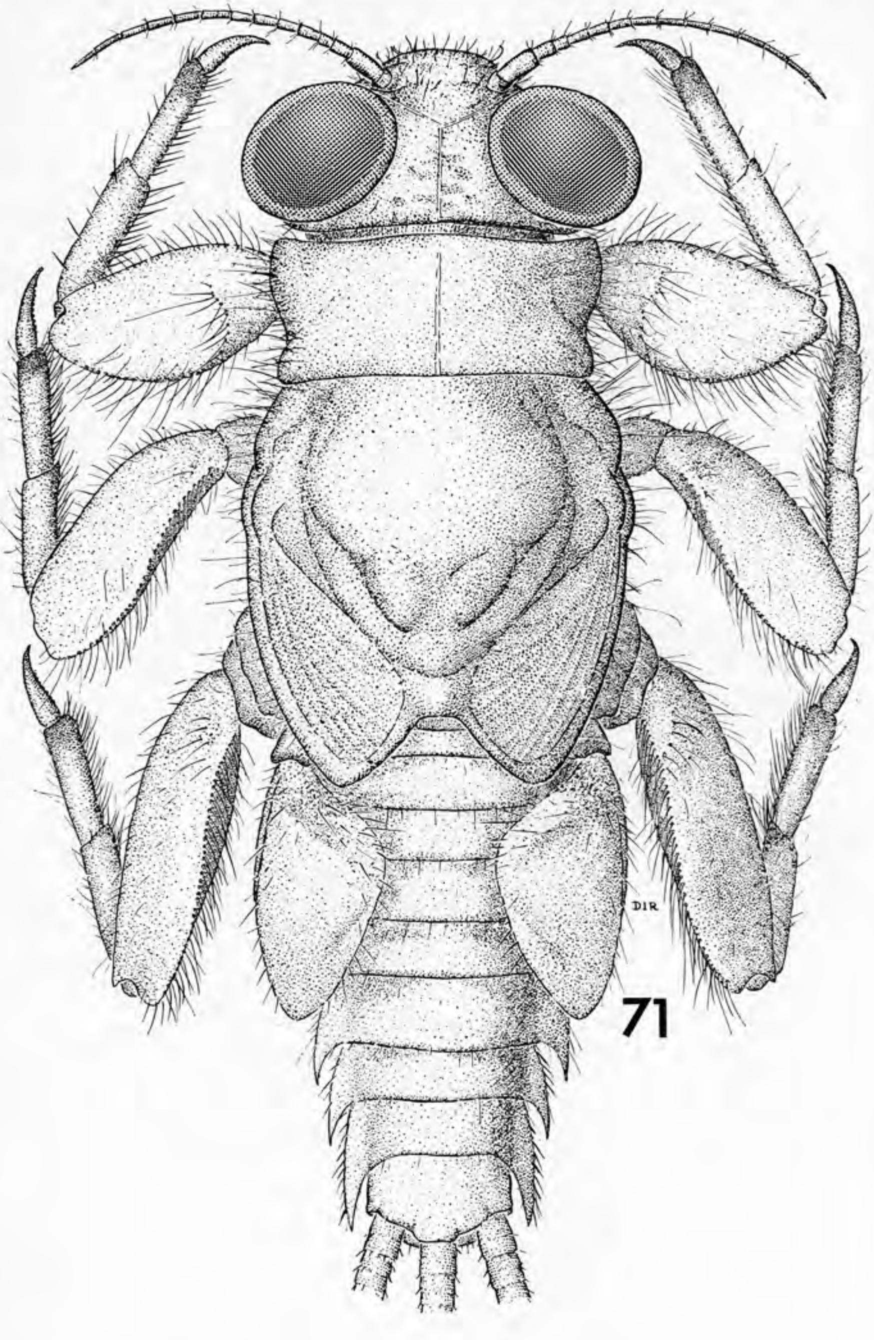
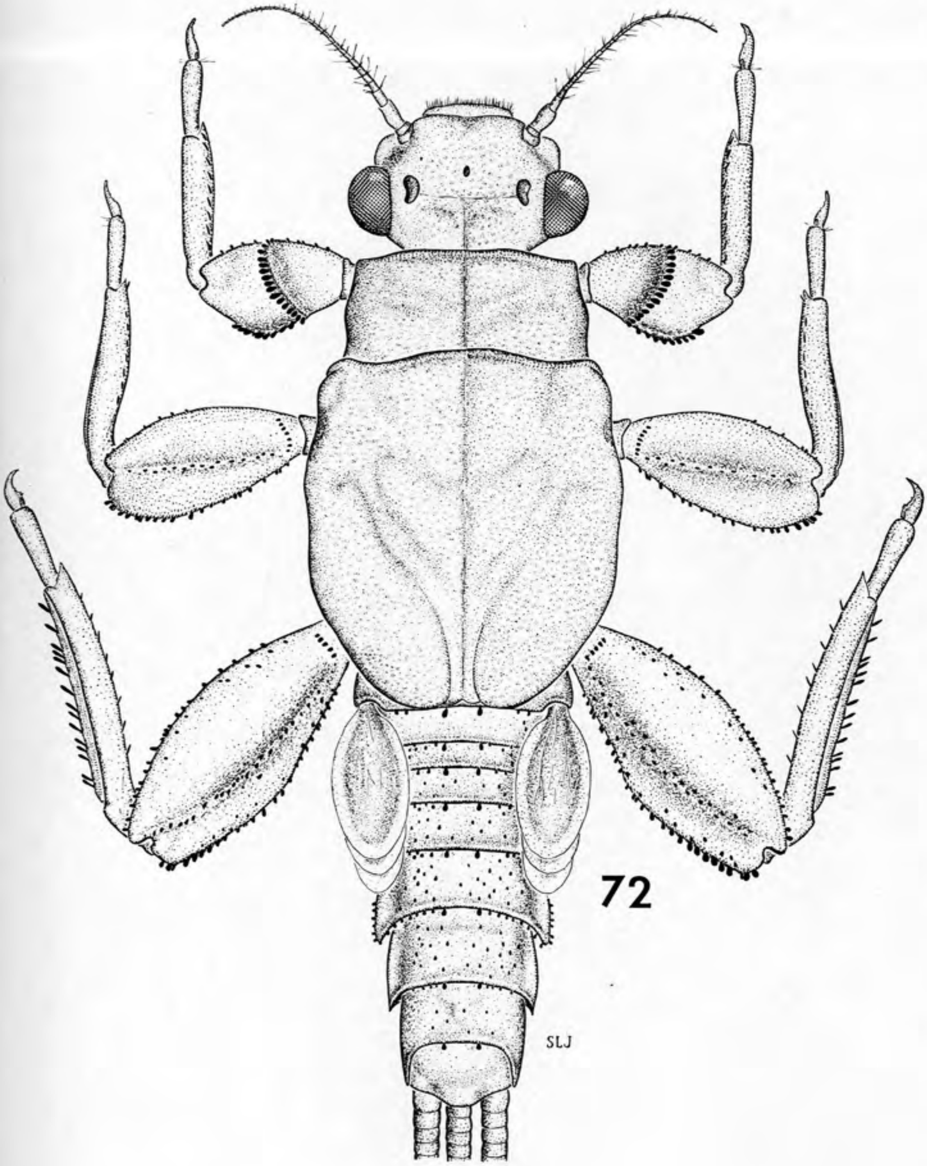
PLATE XII. 70. *Neurocaenis jacobsoni* Ulmer ?, nymph.



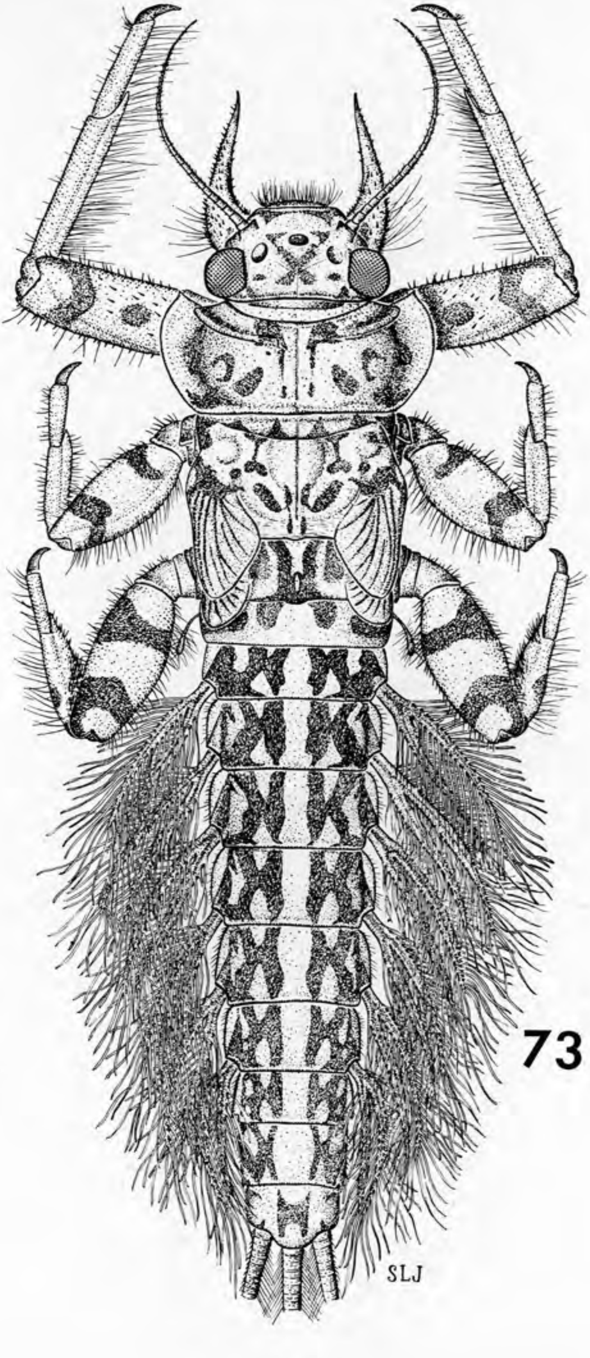
71

PLATE XIII. 71. *Tricorythodes* or allied genus, nymph.



72

PLATE XIV. **72.** *Leptohyphes* sp., nymph.



73

PLATE XV. 73. *Potamanthus* sp., nymph.

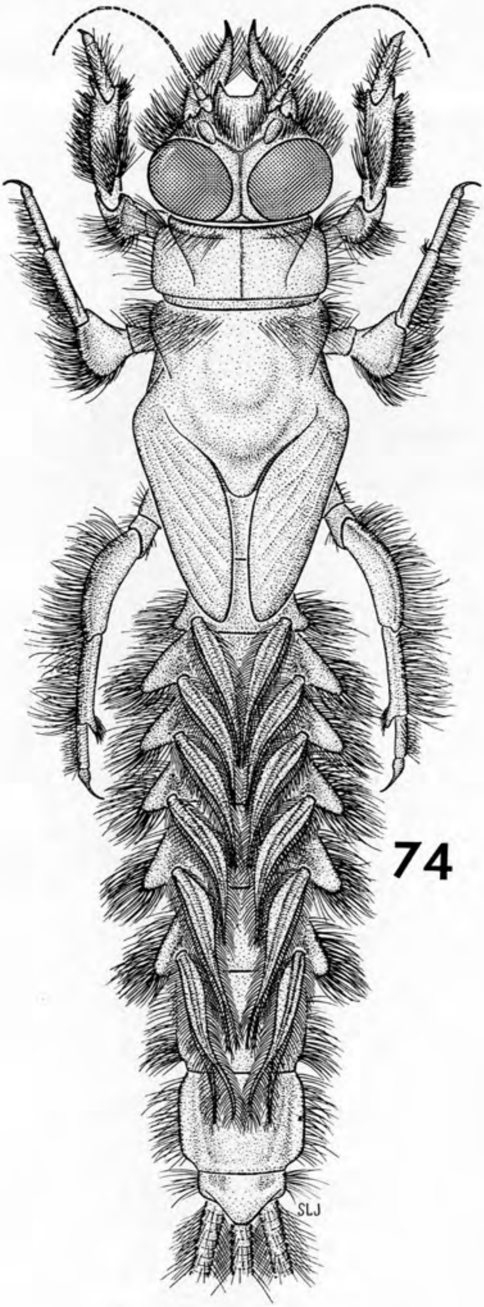


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PLATE XVI. **74.** *Pentagenia vittigera* (Walsh) ?, nymph.

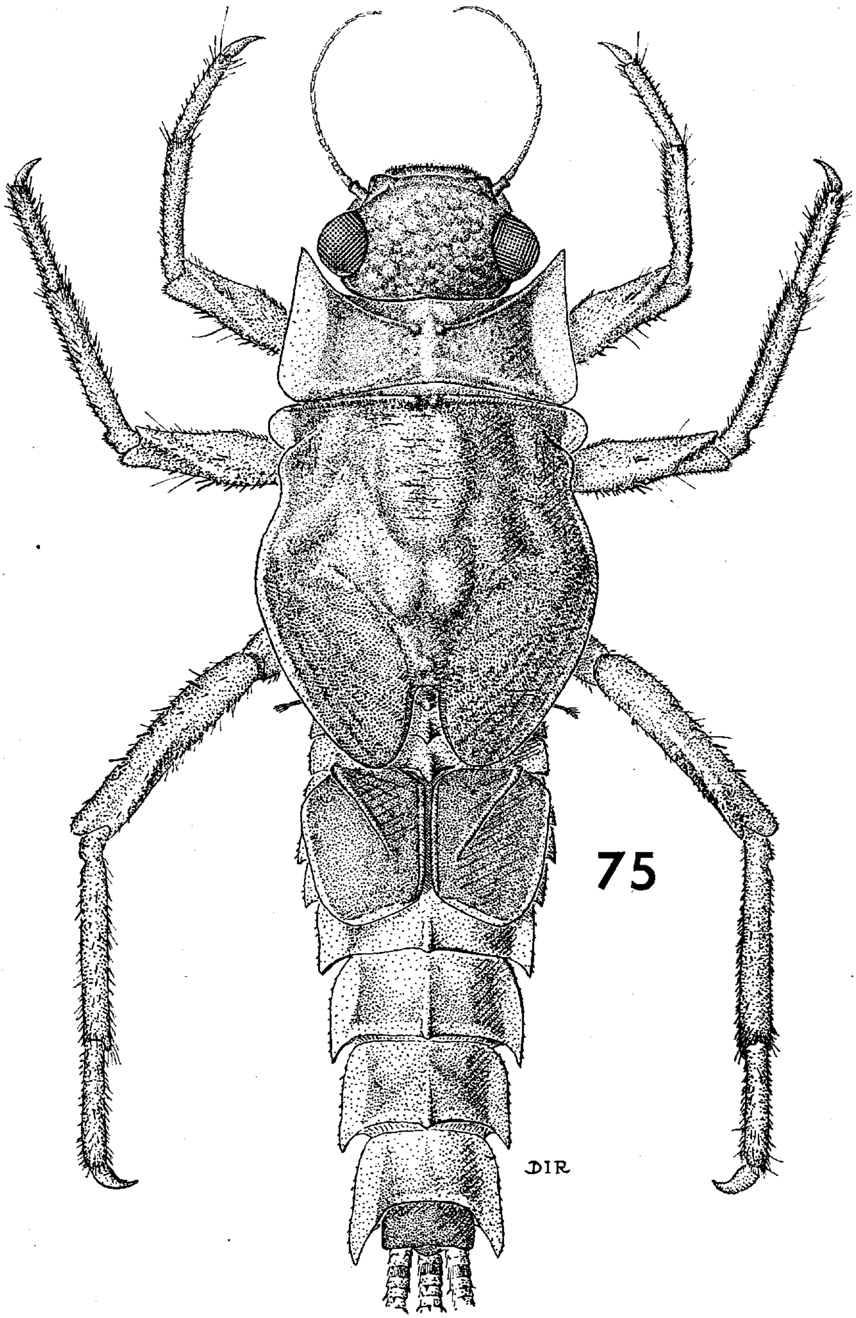

PLATE XVII. 75. *Neoephemera purpurea* Traver, nymph.

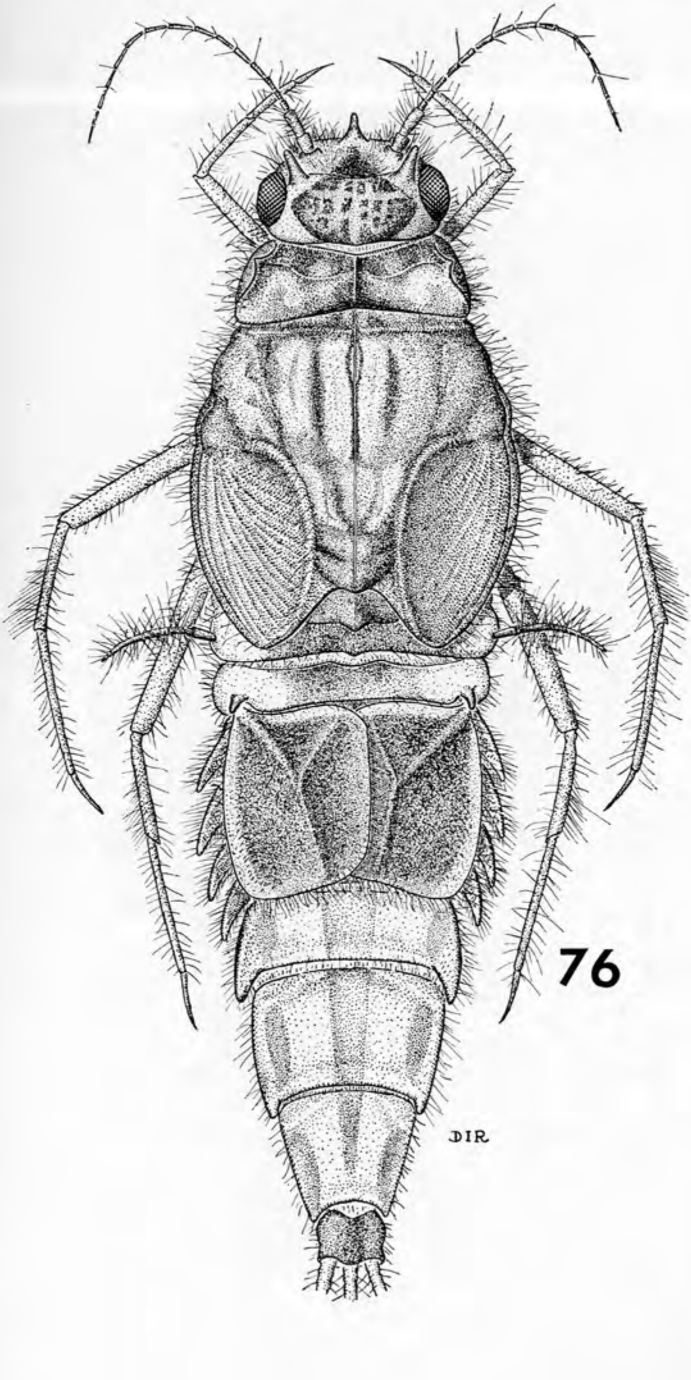

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PLATE XVIII. **76.** *Brachycercus* sp. (possibly *prudens* McDunnough), nymph.

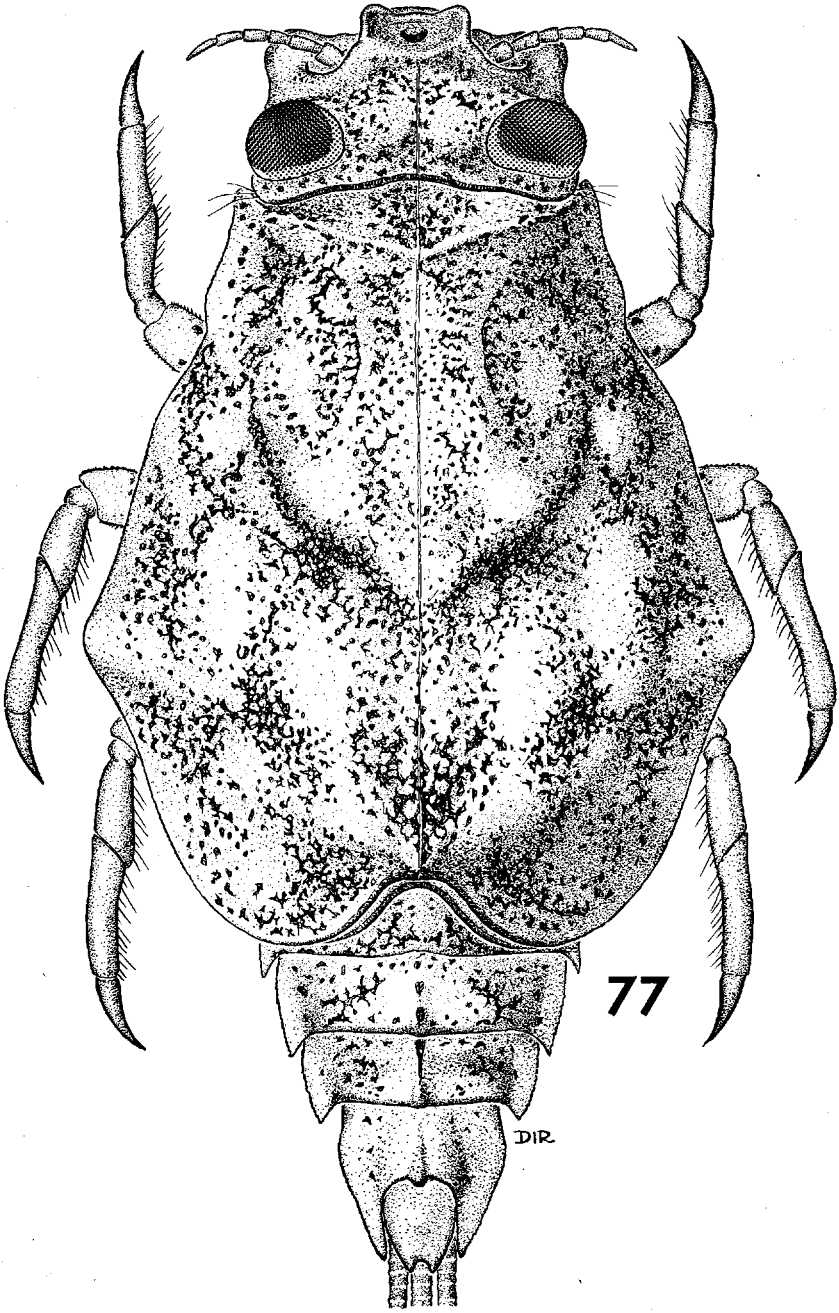

PLATE XIX. 77. *Baetisca columbiana* Edmunds, nymph.

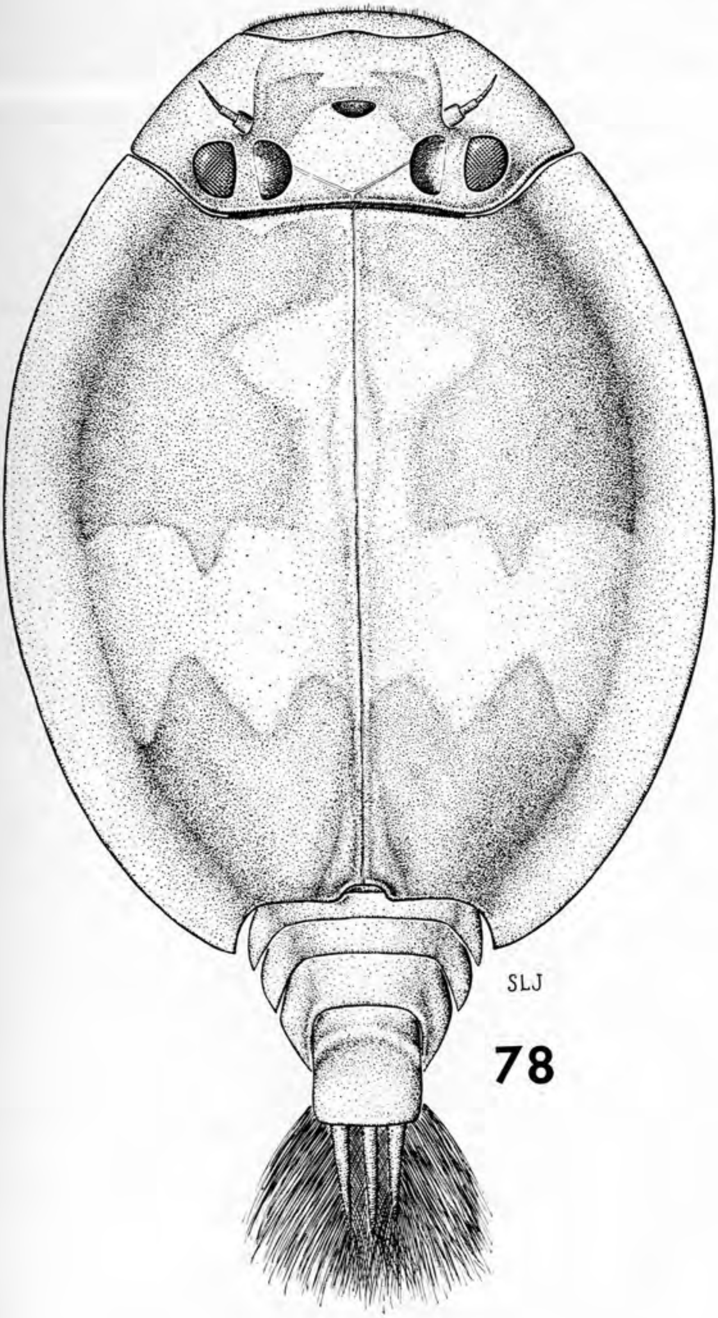

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PLATE XX. 78. *Prosopistoma wouterae* Lieftinck, nymph.

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