

Revision of the Stonefly
Family Nemouridae (Plecoptera):
A Study of the World Fauna
at the Generic Level

RICHARD W. BAUMANN

SMITHSONIAN CONTRIBUTIONS TO ZOOLOGY • NUMBER 211

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SMITHSONIAN INSTITUTION PRESS

City of Washington

1975

ABSTRACT

Baumann, Richard W. Revision of the Stonefly Family Nemouridae (Plecoptera): A Study of the World Fauna at the Generic Level. *Smithsonian Contributions to Zoology*, number 211, 74 pages, 186 figures, 1 table, 1975.—The Northern Hemisphere family Nemouridae is revised and divided into two subfamilies: Amphinemurinae, new subfamily, and Nemourinae. Of the 17 recognized genera in the Nemouridae, 14 are described and figured and 3 are described as new: *Illiesonemoura*, *Indonemoura*, and *Mesonemoura*; 373 species are assigned to genera or listed as incertae sedis. Keys to subfamilies and genera are given for males, females, and nymphs. Structures of male and female terminalia are described and the terminology defined. A phylogeny is constructed showing the relationships of the genera. Distributions are given for all species, the zoogeography of the family is discussed, and a composite map of the distribution of all genera in Nemouridae is provided.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SI PRESS NUMBER 6007. SERIES COVER DESIGN: The coral *Montastrea cavernosa* (Linnaeus).

Library of Congress Cataloging in Publication Data

Baumann, Richard W.

A revision of the stonefly family Nemouridae (Plecoptera)
(Smithsonian contributions to zoology, no. 211)

Bibliography: p.

1. Nemouridae. 2. Insects—Classification. I. Title. II. Series: Smithsonian Institution. Smithsonian contributions to zoology; no. 211.

QL1.S54 no. 211 [QL 505.3.N4] 591'.08s [595.7'35] 75-619077

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Revision of the Stonefly Family Nemouridae (Plecoptera): A Study of the World Fauna at the Generic Level

Richard W. Baumann

Introduction

The family Nemouridae is the largest in the order Plecoptera, comprising 373 species in 17 genera. The family was erected by Newman in 1853, and he included most of the present Euholognatha in a large diverse grouping. Klapálek (1905) divided the family into four families: Capniidae, Leuctridae, Nemouridae, and Taeniopterygidae. These four families and the Southern Hemisphere family Notonemouridae were recently defined as the superfamily Nemouroidea by Zwick (1973a).

This study deals with the Nemouridae as proposed by Kimmins (1961) and adopted by the International Commission on Zoological Nomenclature (1963). Kempny (1898) divided the European species into subgenera; Kimmins (1940), Illies (1955), Winkler (1957), Hynes (1958), and Aubert (1959b) recognized four full genera: *Amphinemura*, *Nemoura*, *Nemurella*, and *Protone-mura*. The North American subgenus *Paranemoura* was described by Needham and Claassen (1925), and Ricker (1952) revised the North American Nemouridae fauna and divided the species into 12 subgenera, including *Paranemoura* and also *Nemoura* and *Amphinemura* from Europe. These subgenera were then raised to generic

status by Illies (1966). I describe three new genera: *Indonemoura*, *Mesonemoura*, and *Illiesonemoura* and one new subfamily, Amphinemurinae, in this study.

The Asian Nemouridae have always been placed in one of the European genera even though they often did not belong: Aubert (1959a, 1967), Jewett (1958), Kimmins (1947, 1950 a and b), Kawai (1967). My study shows that, although many Asian species do belong in European genera, some belong in North American genera and others represent genera and species groups that are endemic to the Asian portion of the Palearctic region.

The nymphs of the genera occurring in Europe are quite well known and have been treated by Hynes (1941), Brinck (1949), Despax (1951), and Raušer (1956, 1963a). The Asian and North American genera have, however, been studied very little. I have studied all available nymphal material, written generic descriptions, constructed nymphal keys, and used the characters found to help understand the phylogeny.

The Nemouridae are usually the dominant Plecoptera in mountain-river ecosystems, both in terms of total biomass and in numbers of species present. They are primary consumers and feed mostly on detritus. They are distributed throughout the Northern Hemisphere and a few species do just cross the equator in the Sunda Archipelago.

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MATERIALS AND METHODS.—During this study I examined all of the North American species and most of the European and Asian species. China is the only large area from which I was unable to study many specimens. Those species not examined are marked with an asterisk (*) where they appear in the "Distribution and Species Lists" at the end of each genus. This means that they were

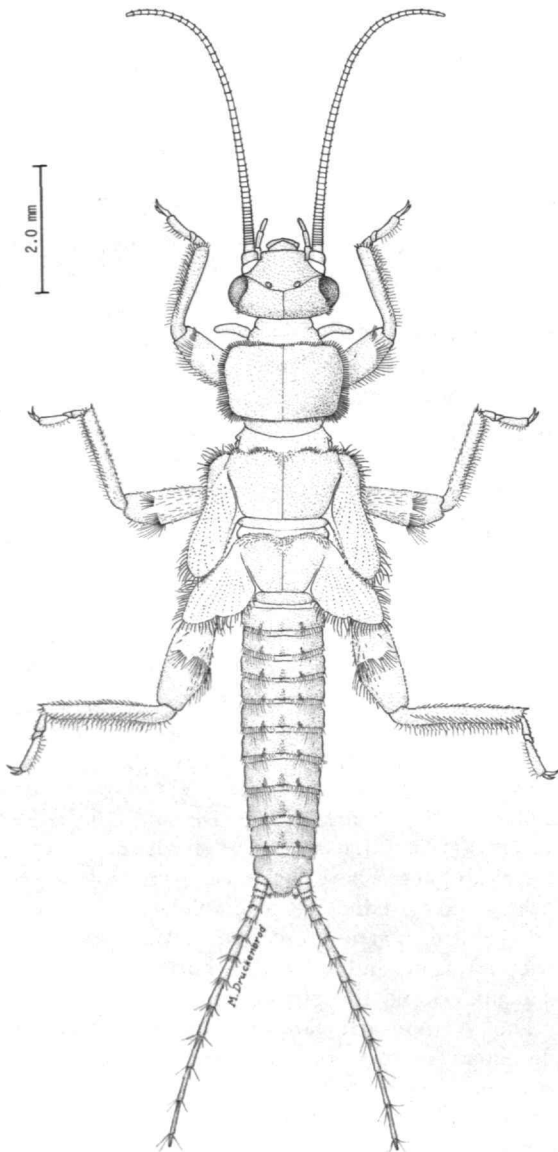


FIGURE 1.—Habitus of *Zapada haysi* (Ricker), mature female nymph.

placed in a genus based on figures or descriptions in the literature.

Studies were carried out with a Wild M-5 stereoscopic microscope, which for most of the study was illuminated with a dark field base illumination system. This made it possible to study the especially fine hairs and spines on the small structures of the epiproct and paraprocts.

For detailed examination all small parts were removed from the specimens using tiny dental files or micro dissecting knives. These parts were examined in small watch glasses containing a thin layer of beeswax and then stored in micro vials with a cotton plug at both ends. The white-cotton background made it much easier to see the tiny parts.

TERMINOLOGY.—Since there are many terms in existence for both male and female terminalia as listed in Brinck (1955), I am defining those most useful for the Nemouridae. I followed the work by Crampton (1918) because it contained most of the terms now in use.

Although some authors had recognized the different lobes of the paraprocts, the parts of the epiproct had been essentially unstudied except for Zwick (1973a) where the letters "a" and "b" are used for the dorsal and basal sclerites respectively.

The following list of definitions and abbreviations includes those from Crampton (1918) and those coined in this study.

Basal cushion (bc): rounded membranous area of the epiproct, above the base of the dorsal sclerite, between the lateral arms; found in *Nemoura* and closely related Nemourinae (Figures 45, 61, 118, 133).

Basal sclerite (bs): angular sclerites located on both sides at the base of the epiproct, between the tenth tergum and paraprocts, small and triangular or rectangular (Figures 9, 17, 25, 49, 57, 105, 137).

Dorsal sclerite (ds): sclerotized dorsal portion of the epiproct, with broad base and paired anterolateral extensions, covering all or part of the dorsal and lateral surfaces.

Epiproct (ep): unpaired process in the tergal region of the eleventh abdominal segment, composed of dorsal, ventral, and basal sclerites; also called supra-anal process.

Epiproctal flagellum (ef): long thin sclerotized process extending forward from ventral sclerite, at tip of epiproct; as in *Mesonemoura* (Figures 28–30).

Hypoproct (hp): produced portion of the male ninth sternum, containing the gonopore; also called hypandrium or subgenital plate.

Inner lobe (il): paraproctal lobes located nearest midline, usually small and inconspicuous, often hidden by hypoproct, lacking spines.

Lateral arms (la): thin darkly sclerotized anterolateral extensions of dorsal sclerite, usually connected to dorsal sclerite throughout length.

Lateral cervical sclerite (lcs): long, thin sclerotized bars located near lateral margins of cervical region (Figures 140–147).

Lateral knobs (lk): rounded hingelike structures located at basal corners of epiproct, formed from base of ventral sclerite; found in *Nemoura* and closely related Nemourinae (Figures 45, 61, 117, 133).

Outer lobe (ol): outer lobe of paraprocts, located nearest cerci, long thin and darkly sclerotized in Amphinemurinae, broad, round and with a membranous portion in Nemourinae; also called cercal lobe.

Median lobe (ml): middle lobe of paraprocts in Amphinemurinae, large and usually both sclerotized and membranous, often bearing spines.

Paraproct (pp): platelike structures situated behind the tenth tergum, located in the regions homologous with the lateral portions of the eleventh abdominal segment, may have one, two, or three lobes; also called subanal lobe.

Pregenital plate (pgp): produced portion of seventh abdominal sternum of female (Figures 51, 67, 75, 123, 131, 139).

Subgenital plate (sgp): modified area of eighth abdominal sternum of female, located near gonopore; often as broadly rounded lobe or as one or more sclerotized plates.

Ventral sclerite (vs): ventral sclerotized portion of epiproct, large, flat or keel-shaped and usually bearing spines, often extending upward dorsally and modified into single or paired structures.

Vesicle (v): lobed structure arising from anterior margin of ninth sternum or hypoproct.

ACKNOWLEDGMENTS.—I heartily thank the following people for helping me with this study by providing specimens or sharing their time and ideas: Dr. J. Aubert, Musée Zoologique, Lausanne, Switzerland; Dr. P. Brinck and Dr. C. H. Lindroth, Lund University, Lund, Sweden; Dr. P. Berthélemy, Université de Toulouse, Toulouse, France; Dr. A. R. Gaufin, University of Utah, Salt Lake City, Utah, USA; Dr. D. C. Geijskes, Rijksmuseum van Natuurlijke Historie, Leiden, Holland; Dr. J. Illies, Max-Planck-Institut für Limnologie, Schlitz, Germany; Mr. S. G. Jewett, Jr., West Linn, Oregon, USA; Dr. T. Kawai, Nara Women's University, Nara, Japan; Dr. D. E. Kimmins and Mr. P. Ward, British Museum (Natural History), London, England; Dr. M. Kohno, Aizu-Wakamatsu, Japan; Dr. A. Lillehammar, Zoological Museum, University of Oslo, Oslo, Norway; Dr. M. Meinander, Zoological Museum, University of Helsinki, Helsinki, Finland; Dr. W. E. Ricker, Fisheries Research Board of Canada, Biological Station, Nanaimo, British Columbia, Canada; Dr. B. P. Stark,

Irving, Texas, USA; Dr. K. W. Stewart, North Texas State University, Denton, Texas, USA; Dr. L. A. Zhiltzova, Zoological Institute, Academy of Sciences, Leningrad, USSR; Dr. P. Zwick, Max-Planck-Institut für Limnologie, Schlitz, Germany.

I am very grateful to Dr. Joachim Illies, who made it possible for me to spend a year of post-doctoral study at his institute in Schlitz, Germany, and I am grateful especially to Dr. P. Zwick for his friendship, help, and continued encouragement.

The drawings were made by Ms. Elizabeth K. Meyers, Mr. Michael L. Druckenbrod, Ms. Debra R. Horner, and Ms. Rebecca F. Surdick. Ms. Hollis B. Williams provided valuable support in organizing the plates and in the preparation of the phylogenetic diagram. Special thanks are given to Mrs. Joan B. Miles for typing the manuscript.

This study was supported in part by a Sigma Xi Grant-in-Aid of Research and a research fellowship from the Max-Planck Society.

Morphology

The characters used in this study are best considered by examining body sections and systems as separate entities. My study was supplemented by the works of Crampton (1918), Wu (1923), Ricker (1952), Moulins (1968), and Zwick (1973a).

HEAD.—The head region is very similar in all nemourid genera. The modification of the last segment of the labial palpi into a large, flat, rounded structure is very distinctive, especially in the adults. Since the adults feed on algae, lichens, and other plant material, it is possible that the palpi aid in locating food. It is also possible that the enlarged palpal segments are sensory in function, because adult nemourids are very active and drop immediately if the substrate upon which they are resting is disturbed.

The mandibles and maxillae are broad and modified for chewing plant material and do not vary enough from one genus to another to be useful for taxonomic analysis.

Branched gills that originate between the labium and submentum are present in *Visoka*. These gills are considered apomorphic because of their placement and because they are well developed with five definite branches. They are called submental gills in this study but should not be con-

fused with the submental gills of the Perlodidae, which originate at the base of the submentum.

NECK OR CERVIX.—The cervical region is mostly membranous but has long, thin, cervical or jugular sclerites along the lateral margins. These lateral cervical sclerites are lightly sclerotized and fairly distinct. They are excellent points of orientation because cervical gills, when present, are located just inside or outside of the sclerites.

Cervical gills are simple extensions of the ventral tracheae leading to the head. They do not have any muscles attached but do have osmoregulatory structures at the base, "Sensilla discoidea" (Zwick, 1973a, and Wichard and Komnick, 1974). Gills are present in all of the primitive Plecoptera families and are considered plesiomorphic in the simple unbranched condition. Modifications such as branching are considered apomorphic as is the partial or complete loss of gills. Thus a single, simple gill on each side of the lateral cervical sclerites, as exhibited by most *Zapada*, is considered to be the most primitive condition in Nemouridae.

Cervical gills are technically called cervical gill remnants in the adult stage, but because the gills in Nemouridae are still well preserved in the adult stage, I am simply calling them gills in all cases.

THORAX (Nymphs).—The pronotum is always square or rectangular in shape and very stout. The lateral margins and much of the dorsal surface are covered with stiff spines. The mesonotum and metanotum are similar in shape but are slightly more rounded and contain large wing pads in mature specimens. The wing pads diverge outward in a wide angle from the longitudinal body axis. Spines are usually present along the lateral margins of the mesonotum and metanotum and also on the dorsal surface, especially along the anterior margins.

Presence of spines is considered an apomorphic character state, and they are found on most of the Nemouridae. Modification into specialized rows or patterns is a further apomorphic condition.

WINGS.—The wings of Nemouridae are highly uniform throughout the family. They are very simple when compared to those of most Plecoptera families and have very few crossveins. The most distinctive character is the so-called nemourid "X" that is formed in the forewings at the cord (Figures 148–157). The "X" is formed primarily by the

terminal portion of vein Sc, which slopes abruptly to the cord, and by the presence of a costal crossvein running between C and R at or slightly beyond the cord. In *Paranemoura* the crossvein joins Sc instead of R, and I consider this a derived character. Zwick (1973a) noted that the "X" in the forewings was also found in some Capniidae and Taeniopterygidae. Although it is plesiomorphic, the "X" is found in all genera of Nemouridae and is an excellent character for general field and curatorial separation. The "X" can be skewed as noted by Lillehammer (1974) but is always present. Veins A₁ and A₂ are fused near the outer margin of the forewings in *Soyedina*. This is an apomorphic state which is sometimes variable in a single population. Wing color is not a valid criterion for separation at the generic level because of the extreme variation possible. It is, however, useful for separating species complexes as noted by Baumann and Gaufin (1972).

LEGS.—The legs are generally very uniform throughout the family. The femur and tibia are of approximately equal length and tarsal segment two is much smaller than segment one.

The nymphs can often be distinguished at the generic level by the kind and pattern of spines on the legs. All genera have some spines, but they become useful as taxonomic characters when they are arranged in definite patterns. *Zapada*, for example, has very specialized whorls of large spines on all femora.

ABDOMEN (nymphs).—All genera have fringes of spines along the posterior margins of the abdominal terga. Some species have specialized stout or long spines arranged in narrow longitudinal rows, but these arrangements of spines do not help in separating genera.

ABDOMEN (adults).—The anterior abdominal segments are seldom modified. *Soyedina* does, however, contain two species with modified tergites in the male sex: *S. vallicularia* Wu has tergites six to eight elevated, and *S. producta* Claassen has knobs on numbers two to four. The males of many species in the *Nemoura* species complexes *Cercispinosa* and *Ovocercia* exhibit modifications of tergites eight and nine. Some *Amphinemura* and *Mesonemoura* species have greatly modified ninth terga, such as *A. mirabilis* Martynov and *A. zimmermani* Joost, which are also asymmetrical. *Protonemura* contains many species that have

produced areas covered with spines on terga seven, eight, and nine.

In most genera tergum ten is sclerotized and formed into a flat or concave base under the epiproct. It also bears large spines or prongs in some species of *Ostrocerca* and the *Cercispinosa* and *Ovocercia* complexes. Thin paired sclerotized bars present in *Nemurella*, *Ostrocerca*, *Podmosta*, and *Shipsa* run laterally and attach to the bases of the cerci instead of the usual single, wide, median bar. In *Podmosta*, *Paranemoura*, and *Lednia* the lateral margins are enlarged and modified into specialized structures that are covered with spines or hairs. *Shipsa* has even larger lateral projections which extend backward beyond the tips of the cerci.

TERMINALIA OF MALES

HYPOPROCT.—The hypoproct is usually formed into a broad, flat plate which is wide at the base and tapers to a narrow tip. It is greatly enlarged and very elongate in *Soyedina*, *Nemurella*, and some species of *Ostrocerca*. The apex is enlarged and terminates in a truncate tip in other species of *Ostrocerca*. The tip bears the genital opening, and the length of the apex is dependent on the structure of the paraprocts and epiproct because they usually function together to transport sperm during mating (Zwick, 1973a).

A vesicle is present at the anterior margin of the hypoproct or ninth sternum in all genera except *Paranemoura* and *Lednia*. The vesicle is a sensory organ as noted by Rupprecht and Gnatzy (1974). I consider the absence of a vesicle to be apomorphic.

EPIPROCT.—The epiproct is actually composed of four sclerotized structures: dorsal sclerite, ventral sclerite, and two basal sclerites.

The basal sclerites are paired angular sclerotized plates located at the basolateral corners. Zwick (1973a) calls these the "b" sclerites. They are present in all genera and vary in shape from small and triangular to large and rectangular or ovoid.

The dorsal sclerite is composed of a large darkly sclerotized horseshoe-shaped base, lateral sclerotized arms, and a large lightly sclerotized dorso-lateral area made up of many tiny scales or plates. Zwick refers to the horseshoe-shaped base and the lateral arms as part of sclerite "a." *Nemoura* and

closely allied species of *Nemourinae* have a large membranous dorsal area located directly ahead of the horseshoe-shaped base of the dorsal sclerite. I call this area the basal cushion.

The ventral sclerite is the flat, convex or keel-shaped ventral portion of the epiproct. It is connected to the tenth tergum by a single or paired sclerotized bars. The ventral sclerite usually bears spines or prongs somewhere along the ventral margin. It is often highly modified dorsally and extends upward inside the lateral folds of the dorsal sclerite. The dorsal portion can be single but is usually paired. It is often visible on the dorsal surface of the epiproct and extends forward as a flagellum in *Mesonemoura* and rarely in other genera of *Amphinemurinae*. In *Nemoura*, *Illiesonemoura*, *Zapada*, and *Soyedina* the lateral basal corners are formed into distinct lateral knobs resembling ball and socket hinges. This derived character often obscures the lateral arms of the dorsal sclerite as they extend forward from the horseshoe-shaped base.

I consider the plesiomorphic state of the epiproct as being similar to some species of *Amphinemura* where the dorsal and ventral sclerites are similar in size but are little modified. They bear spines somewhere ventrally and are connected to the tenth tergum by a single wide sclerotized bar.

PARAPROCTS.—These structures are very stable and provide excellent taxonomic characters. They are located ventrally in the region of the eleventh tergum. They are paired and separated by the midline into bilateral structures. They can be one-, two-, or three-lobed.

The subfamily *Amphinemurinae* has paraprocts with three lobes, and the subfamily *Nemourinae* has paraprocts with one or two lobes. Those with three lobes have small sclerotized inner lobes which are naked of spines. The inner lobe has a muscle connected along the inner margin. The median lobes are large, well developed, and have a sclerotized base and membranous apex which often bears a few spines or prongs. There is a muscle that connects to the lobes near the apex and extends throughout the length. The outer or cercal lobes are usually small, thin and are located near the base of the cerci. They are darkly sclerotized and sometimes bear spines or prongs. These lobes have a muscle attached at the base.

In the *Nemourinae*, where only two lobes are

present, the inner lobes are narrow and often difficult to see because they are located on the inner margins under the apex of the hypoproct. Some genera like *Nemurella*, *Ostrocerca*, *Visoka*, and *Lednia* have well-developed inner lobes which extend to the base of the epiproct and possibly aid in sperm transport as noted by Zwick (1973a). The outer lobes are usually broad and membranous but sometimes have a sclerotized base. Where a single lobe is present, the inner lobe has been lost and the outer lobes cover the complete ventral region.

The primitive Plecoptera families like Austroperlidae, Pteronarcyidae, and Scopuridae have single large paraproctal lobes. The apomorphic condition is a divided paraproct, but in the Nemouridae the condition of a large outer lobe and tiny inner lobe like in *Nemoura* is plesiomorphic and the three-lobed condition is derived.

TERMINALIA OF FEMALES

PREGENITAL PLATE.—The seventh sternum is often enlarged and modified into a pregenital plate. The median posterior margin is produced and lightly sclerotized and extends onto sternum eight. Many species in the Nemourinae have a highly developed pregenital plate which covers the genital opening and much of the eighth sternum. Modification of sternum eight is the usual condition in Plecoptera, so formation of a pregenital plate is taken to be apomorphic.

SUBGENITAL PLATE.—The eighth sternum is usually modified into some sort of subgenital plate. The Amphinemurinae are characterized by having paired vaginal lobes on the posterior margin. *Protonemura*, *Indonemoura*, and *Mesonemoura* also have a large median plate, and *Malenka* and *Amphinemura* usually have a distinct median notch.

The Nemourinae show less development of sternum eight. It is usually narrow and covered by sternum seven. It is developed laterally in *Nemurella* and also in some *Ostrocerca* species. *Lednia* and *Shipsa* have small platelike areas medially and *Podmosta* exhibits distinctive sclerotized patterns. In *Prostoia*, segments seven and eight are essentially unmodified.

CERCI.—*Nymphs:* The cerci of the nymphs are quite long and covered with spines. They are approximately the length of the complete abdomen. Whorls of spines are found at the distal margins of all segments. The length of the spines varies even between species and sometimes the ventral spines or bristles are slightly longer as shown by Harper and Hynes (1971). Intermediate spines are often present on the segments between the joints. No good generic characters have been found using the cerci, but they are useful at the specific level in small genera and when considering species in limited geographical areas.

Adults: The adult cerci are reduced to single segments. They are usually simple, membranous, and covered by short hairs. The only departures from this plesiomorphic state in the Amphinemurinae are the lengthening of the segments as in *Indonemoura* and the development of a mesobasal sclerotized lobe by the males of *Malenka*. The mesobasal lobe is located at the base of the cerci on the dorsolateral margin.

Most of the Nemourinae also have simple cerci, but *Nemoura* males have a distinctive lateral sclerotized portion which usually ends in a multi-forked tip at the apex. In the *Cercispinosa* complex large spines may occur anywhere throughout the length of the cerci. The *Ovocercia* complex has enlarged cerci that are lightly sclerotized and modified in shape but do not bear spines. *Visoka* also has sclerotized cerci that end in single projections.

Nemurella and *Ostrocerca* males have greatly enlarged sclerotized cerci. They are elongate and globose in *Nemurella* and naked of projections but they have a greatly enlarged base. In *Ostrocerca* they are thin, elongate, and terminate in sharp points. They are bent in an S-shape in lateral aspect in some *Ostrocerca* species.

The females of most genera have simple, unsclerotized cerci, but those of *Nemoura*, *Nemurella*, and *Visoka* are lightly sclerotized laterally and slightly modified in shape.

I submit that the occurrence of sclerotized, modified cerci in scattered genera of Nemourinae is the result of convergence.

Key to the Subfamilies and Genera of Nemouridae

MALES

1. Paraprocts divided into three lobes; with spines or prongs on middle or outer lobes (Figures 7, 15, 23, 31, 39) (Amphinemurinae, new subfamily) 2
Paraprocts single or divided into two lobes; lacking spines on outer lobes (Figures 63, 71, 95, 119, 127) (Nemourinae) 6
2. (1) Cervical gills as two highly branched structures on each side of midline, one inside and one outside of lateral cervical sclerites (Figures 140, 141) 3
Cervical gills simple, reduced or partially absent, those outside of lateral cervical sclerites may be forked (Figures 142, 143) 4
3. (2) Mesobasal lobe present at base of cerci in dorsal aspect (Figure 24); gill branches not all extending to gill base (Figure 141) (Nearctic) *Malenka*
Mesobasal lobe absent (Figure 8); gill branches all extending to gill base (Figure 140) (Holarctic, Oriental) *Amphinemura*
4. (3) Cervical gills simple inside of lateral cervical sclerites and forked outside (Figure 143) (Palearctic) *Protonemura*
Cervical gills absent inside of lateral cervical sclerites and reduced to short stubby knobs outside (Figure 142) 5
5. (4) Paraprocts with three well-defined lobes, median lobes greatly enlarged with large apical prongs (Figure 15); epiproct without epiproctal flagellum or only very small process present (Figure 13) (Oriental) *Indonemoura*, new genus
Paraprocts with lobes generally fused near base, median lobes relatively small, with hairs or spines apically (Figure 31); epiproct with terminal flagellum present (Figure 29) (Oriental, Palearctic) *Mesonemoura*, new genus
6. (1) Lateral knobs present at basal corners of epiproct; basal cushion present at dorsal base of epiproct (Figures 45, 61, 117, 133) 7
Lateral knobs absent from basal corners of epiproct; basal cushion absent from dorsal base of epiproct (Figures 69, 77, 93, 101, 125) 10
7. (6) Cervical gills present 8
Cervical gills absent 9
8. (7) Simple cervical gills present both inside and outside of lateral cervical sclerites (Figure 147); paraprocts large but without inward directed projection near apex (Figure 135) (Nearctic) *Zapada*
Simple cervical gills only present outside of lateral cervical sclerites (Figure 144); paraprocts large and with an inward directed process near apex (Figure 47) (Palearctic, Oriental) *Illiesonemoura*, new genus
9. (7) Paraprocts elongate and greatly enlarged (Figure 119); epiproct bilaterally asymmetrical (Figures 116-118); cerci small, unsclerotized and unmodified (Figure 120); veins A₁ and A₂ joined near margin of forewings (Figure 152) (Nearctic) *Soyedina*
Paraprocts large and rectangular (Figure 63); epiproct bilaterally symmetrical (Figures 60-62); cerci large, mostly sclerotized, with large hooks or spines or bulbous at base (Figure 64); veins A₁ and A₂ not joined in forewings (Figure 154) (Holarctic, Oriental) *Nemoura*
10. (6) Dorsal sclerite of epiproct large and lateral arms well developed (Figures 68, 78, 92, 108) 11
Dorsal sclerite of epiproct reduced in size and lateral arms poorly developed (Figures 52, 84, 100, 124) 14
11. (10) Cerci greatly enlarged and modified (Figures 72, 80); paraprocts bilobed, inner lobe large and heavily sclerotized and outer lobe mostly membranous (Figures 71, 79) 12
Cerci small and unmodified; paraprocts with single large lightly sclerotized lobe (Figures 95, 111) 13
12. (11) Cerci long, narrow throughout length and pointed at apex (Figures 80-82) (Nearctic) *Ostrocerca*
Cerci stout, enlarged at base and with broadly rounded apex (Figures 72-74) (Palearctic) *Nemurella*

13. (11) Tenth tergum enlarged at lateral proximal corners into long sclerotized projections (Figure 113) (Nearctic) *Shipsa*
 Tenth tergum with only stout lateral produced areas (Figure 97) (Holarctic) ... *Podmosta*
14. (10) Epiproct composed almost completely of ventral sclerite; dorsal sclerite reduced to small projections, connected at base (Figures 100-102) (Nearctic) *Prostoia*
 Epiproct composed of both dorsal and ventral sclerites, with dorsal sclerite slightly reduced in size (Figures 53, 85, 125) 15
15. (14) Paraprocts with long thin inner and mostly membranous outer lobe (Figures 55, 127); terminal costal crossvein of forewing joining R (Figure 154) 16
 Paraprocts with single large lightly sclerotized lobe (Figure 87); terminal costal crossvein of forewing joining Sc (Figure 153) (Nearctic) *Paranemoura*
16. (15) Submental gills present and highly branched (Figure 146); vesicle present on ninth sternum (Figure 130) (Nearctic) *Visoka*
 Submental gills absent; vesicle absent from ninth sternum (Figure 58) (Nearctic) *Lednia*

FEMALES

1. Cervical gills highly branched (Figures 140, 141), outer gills forked (Figure 143) or outer gills short and stubby with inner gills absent (Figure 142); submental gills absent; seventh sternum usually poorly developed; eighth sternum well developed, sclerotized and often notched (Figures 11, 19, 27, 35, 43) (Amphinemurinae, new subfamily) 2
 Cervical gills usually simple or absent (Figures 144, 145, 147) (if branched, seventh sternum well developed and completely covering poorly developed eighth sternum) or submental gills present (Figure 146); seventh sternum usually more well developed than eighth sternum (Figures 51, 67, 75, 83, 91, 123, 131, 139) or neither segment well developed (Figures 59, 99, 107, 115) (Nemourinae) 6
2. (1) Cervical gills highly branched both outside and inside of lateral cervical sclerites; eighth sternum without large median lobe, with sclerotized vaginal lobes or sclerotization restricted to margins of narrow median notch (Figures 11, 27) 3
 Cervical gills simple inside and forked outside of lateral cervical sclerites or simple outside and absent inside of sclerites; eighth sternum well developed into large median lobe or subgenital plate, sclerotized vaginal lobes present (Figures 19, 35, 43) 4
3. (2) Gill branches not all extending to gill base (Figure 141); eighth sternum sclerotized only along median notch (Figure 27) (Nearctic) *Malenka*
 Gill branches all extending to gill base (Figure 140); eighth sternum with sclerotized vaginal lobes (Figure 11) (Holarctic, Oriental) *Amphinemura*
4. (2) Cervical gills simple inside of lateral cervical sclerites and forked outside (Figure 143) (Palearctic) *Protonemura*
 Cervical gills absent inside of lateral cervical sclerites and reduced to short stubby projections outside (Figure 142) 5
5. (4) Subgenital plate large and extending onto ninth sternum, usually darkly sclerotized (Figure 19) (Oriental) *Indonemoura*, new genus
 Subgenital plate small and not extending onto ninth sternum, usually only lightly sclerotized (Figure 35) (Oriental, Palearctic) *Mesonemoura*, new genus
6. (1) Seventh sternum enlarged into pregenital plate which covers poorly developed eighth sternum (Figure 51); with cervical gills or veins A₁ and A₂ joined in forewings near margin (Figure 152) or cerci enlarged, lightly sclerotized and truncate at apex (Figure 67); submental gills absent 7
 Seventh sternum enlarged or reduced; without cervical gills, without veins A₁ and A₂ joined in forewings, without cerci elongate and sclerotized (except in *Nemurella* which has large sclerotized patches on eighth sternum) or with submental gills present 10
7. (6) Cervical gills present 8
 Cervical gills absent 9
8. (7) Cervical gills present both inside and outside of lateral cervical sclerites (Figure 147) (Nearctic) *Zapada*

- Cervical gills present only on outside of lateral cervical sclerites (Figure 144) (Palearctic, Oriental) *Illiesonemoura*, new genus
9. (7) Veins A_1 and A_2 joined near margin of forewings (Figure 152); cerci small, membranous and round at apex (Figure 120) (Nearctic) *Soyedina*
 Veins A_1 and A_2 not joined in forewings (Figure 154); cerci enlarged, lightly sclerotized and truncate at apex (Figure 67) (Holarctic, Oriental) *Nemoura*
10. (6) Submental gills present (Figure 146) (Nearctic) *Visoka*
 Submental gills absent 11
11. (10) Terminal costal crossvein of forewings joining Sc (Figure 153) or with seventh sternum not modified but eighth sternum developed into a distinctive median platelike patch bordered by lateral sclerotized patches (Figure 59) 12
 Terminal costal crossvein joining R (Figure 149); with both seventh and eighth sterna enlarged and modified (Figure 75) or both simple and only slightly modified (Figures 99, 107) 13
12. (11) Terminal costal crossveins joining Sc (Figure 153); seventh sternum enlarged and eighth sternum small and unmodified (Figure 91) (Nearctic) *Paranemoura*
 Terminal costal crossveins joining R (Figure 154); seventh sternum not enlarged but sternum modified into median platelike and lateral sclerotized patches (Figure 59) (Nearctic) *Lednia*
13. (10) Eighth sternum enlarged and modified; seventh sternum usually enlarged and modified (Figures 75, 83) 14
 Eighth sternum not enlarged but sometimes with distinct sclerotized pattern or small median lobe; seventh sternum sometimes slightly produced (Figures 99, 107, 115) ... 15
14. (13) Seventh sternum enlarged into pregenital plate which extends over most of eighth; eighth sternum with enlarged, sclerotized vaginal lobes (Figure 75) (Palearctic) *Nemurella*
 Seventh sternum sometimes enlarged and formed into median nipplelike projection; eighth sternum enlarged and modified into subgenital plate (Figure 83) (Nearctic) *Ostrocerca*
15. (13) Eighth sternum with small median subgenital plate (Figure 115) (Nearctic) *Shipsa*
 Eighth sternum sclerotized medially but not formed as subgenital plate (Figures 99, 107) 16
16. (15) Eighth sternum with distinct median sclerotized pattern (Figure 99); forewings mostly clear with small dark area near veins at cord (Holarctic) *Podmosta*
 Eighth sternum with indistinct, median sclerotized area near posterior margin (Figure 107); forewings mostly fumose with narrow light band running across outer field (Figure 148) (Nearctic) *Prostoia*

MATURE NYMPHS

(Lednia unknown)

1. Cervical gills present (Figures 140–143); submental gills absent; whorls of spines absent from forelegs (Figures 158–161) (Amphinemurinae, new subfamily) 2
 Cervical gills usually absent (Figure 145), if present whorls of spines present on forelegs (Figures 169, 172) or submental gills present (Figure 146) (Nemourinae) 5
2. (1) Cervical gills as two highly branched gills on each side of midline, one inside and one outside of lateral cervical sclerites (Figures 140, 141) 3
 Cervical gills simple, reduced or partially absent, gills outside of lateral cervical sclerites may be forked (Figures 142, 143) 4
3. (2) Gill branches not all extending to gill base (Figure 141) (Nearctic) *Malenka*
 Gill branches all extending to gill base (Figure 140) (Holarctic, Oriental) *Amphinemura*
4. (3) Cervical gills simple inside of lateral cervical sclerites and forked outside (Figure 143) (Palearctic) *Protonemura*
 Cervical gills absent inside of lateral cervical sclerites and reduced to short stubby projections outside (Figure 142) (Oriental, Palearctic) *Mesonemoura*, new genus, and (Oriental) *Indonemoura*, new genus
5. (1) Pronotum with a definite fringe of spines on lateral margins, spines in single row and of equal length or with gradual shift in length toward corners (Figure 1); mesonotum and metanotum with fringes of spines along lateral margins (Figure 1) 6

- Pronotum without a fringe of spines, or if present not arranged in a single row or of unequal lengths (Figure 146); mesonotum and metanotum without fringes of spines or with very sparse fringes mostly visible near posterolateral margins9
6. (5) Cervical gills present (Figures 144, 147); whorls of spines present on forelegs (Figures 169, 172)7
 Cervical gills absent (Figure 145); whorls of spines usually absent from forelegs (Figures 170, 171)8
7. (6) Two cervical gills present on each side of midline one inside and one outside of lateral cervical sclerites (Figure 147); whorls of femoral spines present on all leg pairs (Figure 1) (Nearctic) *Zapada*
 One cervical gill present on each side of midline, located outside of lateral cervical sclerites (Figure 144); whorls of femoral spines present only on forelegs (Figure 169) (Palearctic, Oriental) *Illiesonemoura*
8. (6) Pronotum rounded at corners and without a definite notch on lateral margins (Holarctic, Oriental) *Nemoura*
 Pronotum angular at corners and with a definite notch on lateral margins (Nearctic) *Soyedina*
9. (5) Foreleg with numerous large spines on femur and tibia, outer margin of tibia with row of large spines and often with fringe of long hairs (Figures 162, 163, 164, 166, 167); submental gills absent10
 Foreleg with few large spines on femur and tibia, outer margin of tibia with spines of similar length to those on surface and without fringe of long hairs (Figure 165) or foreleg with many spines and submental gills present (Figure 168)14
10. (9) Pronotum with irregular fringe of moderate to large spines11
 Pronotum without fringe of moderate to large spines12
11. (10) Pronotum wider than long, with irregular fringe of large spines; tibiae with only scattered large spines along outer margins (Figure 167) (Palearctic) *Nemurella*
 Pronotum as long as wide, with irregular fringe of moderate spines; tibiae with two definite rows of large spines along outer margins (Figure 162) (Nearctic) ... *Ostrocerca*
12. (10) Foretibiae with fringe of long hairs along outer margin (Figures 164, 166)13
 Foretibiae without fringe of long hairs along outer margin but sometimes with a few scattered long hairs (Figure 163) (Holarctic) *Podmosta*
13. (12) Tibiae with two rows of stout spines along outer margins (Figure 164) (Nearctic) *Protoia*
 Tibiae without rows of stout spines along outer margins (Figure 166) (Nearctic) ... *Shipsa*
14. (9) Submental gills present (Figure 146); foreleg with numerous large spines and long hairs (Figure 168) (Nearctic) *Visoka*
 Submental gills absent; foreleg with few large spines or long hairs (Figure 165) (Nearctic) *Paranemoura*

AMPHINEMURINAE, new subfamily

Amphinemura is the type-genus for this subfamily, which also includes the genera *Indonemoura*, *Malenka*, *Mesonemoura*, and *Protonemura*. The subfamily is recognized by the following characters:

1. Paraprocts divided into three lobes.
2. Middle and outer lobes of paraprocts usually bearing spines or prongs.
3. Epiproct elongate, generally laterally compressed and with ventral sclerite forming a rounded or triangular keel.
4. Cervical gills present.

5. Subgenital plate well developed in females but pregenital plate usually poorly developed.

The Amphinemurinae are well represented in the Palearctic and Nearctic regions and also extend south into the Oriental region. *Amphinemura* is found in the Nearctic, Palearctic, and Oriental regions (Figure 173); *Mesonemoura* occurs in the Oriental and Palearctic regions (Figure 175); *Protonemura* (Figure 176) and *Indonemoura* (Figure 174) are found only in the Palearctic and Oriental regions respectively; and *Malenka* is restricted to the western part of the Nearctic region (Figure 174).

Amphinemura Ris

FIGURES 4-11, 140, 155, 159, 173

Nemura (*Amphinemura*) Ris, 1902:384. [Type-species: *Nemoura cinerea* Olivier = *Amphinemura sulcicollis* Stephens.]

Amphinemura.—Claassen, 1940:47.

ADULT.—Length: small to medium (5-10 mm). Wings (Figure 155): macropterous, venation typical for family, clear or fumose to dark and mottled, veins dark and distinct, sometimes with light spots in cells or light bands on dark background. Gills (Figure 140): 2 branched cervical gills on each side of midline, 1 arising inside and 1 outside of lateral cervical sclerites, minimum branches 5, maximum observed 16, all branches extending to gill base.

MALE TERMINALIA.—Hypoproct (Figure 10): broad at base, tapering to narrow apex, extending distally over inner lobes of paraprocts, tip extending to base of epiproct and sometimes recurved dorsally; vesicle present. Paraprocts (Figure 7): divided into 3 lobes; inner lobes lightly sclerotized, naked, short and closely applied at midline, often completely hidden by hypoproct; median lobes mostly sclerotized but with membranous inner portion, bearing few to many hairs or spines, lobes large and elongate, lying alongside hypoproct and recurved dorsally parallel to epiproct; outer lobes mostly sclerotized, sometimes with small membranous portion, shape variable, often recurved dorsally alongside cerci, usually with a few hairs or spines. Cerci (Figures 8-10): membranous, short and unmodified. Epiproct (Figures 4-6): short and usually fairly broad in dorsal aspect and narrow with ventral projections in lateral aspect, completely recurved, bilaterally symmetrical; dorsal sclerite, large and broad at base of epiproct, extending dorsolaterally toward apex, darkly sclerotized lateral arms on lateral margins, variously modified, apical portion large and extending laterally over ventral sclerite, bearing small spines or sclerotized scales; basal sclerites, as 2 broad triangular patches located at basolateral margins of epiproct; ventral sclerite, heavily sclerotized, broad at base and becoming narrower toward apex, forming median keel-shaped ridge, apical portion inserted between folds of dorsal sclerite and variously modified, often extending to dorsal margin, sclerite bearing few to many spines which are often

very large. Tenth tergum (Figure 8) all or mostly sclerotized, forming a large flat area anterior to base of epiproct, usually bare but sometimes with spines or projections. Ninth tergum sclerotized and usually produced along distal margin, produced portion bearing spines or hairs, produced area sometimes large and bizarre and can even be asymmetrical.

FEMALE TERMINALIA (Figure 11).—Seventh sternum produced and extended at distal margin forming small pregenital plate, covering part of sternum eight, produced area lightly sclerotized. Eighth sternum forming subgenital plate, size of plate variable but usually quite small and bifid, divided at genital opening into symmetrical sclerotized vaginal lobes which are often quite distinctive, lobes usually restricted to eighth sternum but occasionally extend over anterior margin of ninth sternum.

NYMPH.—Gills (Figure 140): 2 branched cervical gills on each side of midline, 1 arising inside and 1 outside of lateral cervical sclerites, minimum branches 5, maximum observed 16, all branches originating at same place near base. Forelegs (Figure 159): femur and tibia of approximately equal length, whole leg covered with fine short hairs; femur with row of long spines along posterior margin and often with a few long hairs intermingled, dorsal surface with few to numerous long spines on distal half; tibia with rows of medium-sized spines along anterior and posterior surfaces, few to numerous long hairs intermingled with spines on posterior margin. Pronotum with fringe of spines along lateral margins. Abdominal terga with fringes of spines along distal margins. Cerci with whorls of large spines at distal margins of segments, segments covered randomly with numerous small intermediate spines.

DISCUSSION.—*Amphinemura* is the most widespread genus in the family Nemouridae, ranging from the Arctic in the north to North Africa, the Sunda Archipelago and southern Mexico respectively in the south. It contains 90 known species and surely many more that are unstudied. Members of the genus are easily recognized in both the nymphal and adult stages by their highly branched cervical gills (Figure 140).

It is found in a wide variety of freshwater habitats but is most common in cold, clear mountain streams that run throughout the year.

DISTRIBUTION AND SPECIES LIST.—Holarctic and Oriental (Europe, Asia, North Africa, North America, Orient).

- amatulai* Aubert 1967, Assam
apache Baumann & Gaufin 1972, Arizona
arcadia (Aubert) 1956a, Greece
banksi Baumann & Gaufin 1972, Rocky Mountains
bilolai Aubert 1967, Assam
bomdilai Aubert 1967, Assam
borealis (Morton) 1894, Europe, northern Asia, Mongolia
chiffensis (Aubert) 1956c, Morocco
**chui* (Wu) 1935, China
**claassenia* (Wu) 1935, China
**claviloba* (Wu) 1973, n. comb., China
coreana Zwick 1973c, Korea
**cornuloba* (Wu) 1973, n. comb., China
**cryptocercia* (Wu) 1938, n. comb., China
**curvispina* (Wu) 1973, n. comb., China
**decemseta* Okamoto 1922, Japan
delosa (Ricker) 1952, eastern United States
**dentiloba* (Wu) 1973, n. comb., China
dichotoma (Kawai) 1954, Japan
**falciloba* (Wu) 1973, n. comb., China
**fililoba* (Wu) 1973, n. comb., China
**flavicollis* Klapálek 1912b, Taiwan
**flavostigma* Okamoto 1922, Japan
**fleurdelia* (Wu) 1949, n. comb., China
**forcipiloba* (Wu) 1962, n. comb., China
**furcospinata* (Wu) 1949, n. comb., China
**furcostyla* (Wu) 1973, n. comb., China
gressitti Kawai 1969, Viet Nam
gritsayae Zhiltzova 1971, central Asia
handschini (Geijskes) 1937, Java, Sumatra, Viet Nam
**hastata* (Wu) 1973, n. comb., China
**kiangsiensis* (Wu) 1935, China
**lagnucula* Harper 1975, Nepal
**licenti* (Wu) 1938, China
linda (Ricker) 1952, eastern and northern North America
lithami Aubert 1967, Assam
**longispina* (Okamoto) 1922, Japan
luteipes Kimmins 1947, Himalaya, Assam
**macrolamellata* (Wu) 1935, n. comb., China
manipurensis Aubert 1967, Assam
**maoi* (Wu) 1938, China
maracandica (McLachlan) 1875, central Asia
megaloba (Kawai) 1960, Japan
mexicana Baumann 1972, Mexico
minuta Kawai 1969, Borneo
mirabilis (Martynov) 1928, western Asia
mockfordi (Ricker) 1952, Tennessee
mogollonica Baumann and Gaufin 1972, southwestern United States
**mokanshenensis* (Wu) 1938, China
monotuberculata (Kawai) 1956, Japan
moshingi Aubert 1967, Assam
**multispina* (Wu) 1973, n. comb., China
**nepalensis* Harper 1975, Nepal
nigritta (Provancher) 1876, eastern North America
**nigritula* Navás 1932, Formosa
nongrimi Aubert 1967, Assam
norvegica Tobias 1973, Norway
nubila Kimmins 1950a, southern India
okinawaensis Kawai 1968a, Okinawa
paraluteipes Aubert 1967, Assam, Nepal
**pentagona* (Okamoto) 1922, Japan
**pieli* (Wu) 1938, n. comb., China
pseudoluteipes Aubert 1967, Assam
puebla Baumann 1972, Mexico
rahungi Aubert 1967, Assam
reinerti Baumann 1976, Mexico
renata Kimmins 1950b, Assam
**rostromba* Wu 1962, n. comb., China
**sagittata* (Okamoto) 1922, Japan
schmidi (Aubert) 1959a, Pakistan
**sinensis* (Wu) 1926, China
sperchiana Berthélemy 1971, Greece
**spinata* (Wu) 1949, n. comb., China
standfussi (Ris) 1902, Europe
steinmanni Zwick 1973c, Korea
sulcicollis (Stephens) 1835, Europe
talungdzongi Aubert 1967, Assam
tetraspinosa (Kawai) 1960, Japan
thienemanni (Geijskes) 1952, Java
tragula Kimmins 1950a, Turkestan, Tadzhikistan
**trassaerti* (Wu) 1938, China
trialetica Zhiltzova 1957, Caucasus, Asiatic Turkey
triangularis Ris 1902, Europe
tricantha (Jewett) 1958, Himalaya
**tiramia* (Wu) 1962, n. comb., China
**unihamata* (Wu) 1973, n. comb., China
varshava (Ricker) 1952, eastern United States
venusta (Banks) 1911, Arizona, Mexico
verrucosa Zwick 1973c, Korea
wui (Claassen) 1936, eastern North America
zimmermanni Joost 1970b, Tien Shan
**zonata* Okamoto 1922, Japan

Indonemoura, new genus

FIGURES 12–19, 174

TYPE-SPECIES.—*Protonemoura indica* Kimmins, 1947:727, herein designated.

ADULT.—Length: medium to large (7–15 mm). Wings: macropterous, venation typical for family, clear or fumose, veins dark and distinct. Gills: single short oval gills on each side of midline, located on outside of lateral cervical sclerites.

MALE TERMINALIA.—Hypoproct (Figure 18): broad at base, tapering to narrow apex, extending to base of epiproct, often covering inner lobes of paraprocts; vesicle present. Paraprocts (Figure 15): divided into 3 lobes; inner lobes small and lightly sclerotized, often closely affixed to large

median lobes; median lobes mostly sclerotized, broad at base, basal half lightly sclerotized and covered with hairs, apical half darkly sclerotized, long narrow and formed into one or more long prongs or projections, usually with a small inner membranous portion; outer lobes well developed, darkly sclerotized, long narrow and almost completely encircling cerci, tip often terminating in one or more sharp prongs. Cerci (Figures 16–18): membranous, very long and thin, extending beyond tip of abdomen, covered with thin hairs. Epiproct (Figures 12–14): usually long and narrow in dorsal aspect, lateral aspect narrow near base but expanded near apex, completely recurved, bilaterally symmetrical; dorsal sclerite, large and fairly broad at base of epiproct, extending dorso-laterally toward apex, sometimes enlarged at bend, apical portion usually greatly enlarged, especially near tip; basal sclerites as 2 broad triangular patches at basolateral margins of epiproct; ventral sclerite, heavily sclerotized, broad at base and becoming narrower toward apex, forming median keel-shaped ridge, usually with few to many spines in small rounded area near apex, tip inserted in membranous folds of dorsal sclerite and rarely with tubelike structure extending from tip. Tenth tergum (Figure 16) all or mostly sclerotized but with large membranous area under apex of epiproct, usually forming a flat or concave plate but sometimes with 1 or 2 large upwardly directed protuberances. Ninth tergum sclerotized and produced along distal margin, produced portion bearing spines or hairs, and sometimes large and bizarre in shape.

FEMALE TERMINALIA (Figure 19).—Seventh sternum somewhat produced at distal margin, extending slightly onto eighth sternum medially, produced area lightly sclerotized. Eighth sternum forming subgenital plate, median area enlarged and heavily sclerotized, forming distinctive plate which covers genital opening and extends over part of vaginal lobes, shape of plate highly angular and darkly sclerotized. Cerci long, thin, membranous, and unmodified.

NYMPH.—Unknown (included in nymphal key using adult gill characters).

DISCUSSION.—*Indonemoura* includes the Indica group of Aubert (1967) and two large species from the Sunda Archipelago. It probably occurs in other parts of Asia, especially Burma and Thailand. It

is similar to *Mesonemoura*, regarding the type of cervical gills present, but can be separated in the male by the large, highly developed and ornamented paraprocts (Figure 15) and in the female by the large darkly sclerotized subgenital plate (Figure 19) which nearly covers the very small vaginal lobes.

The generic name *Indonemoura* is taken from the stem "Indo-" referring to India or the East Indies, where the genus occurs.

DISTRIBUTION AND SPECIES LIST.—Oriental (south central Asia). The following species are assigned to the genus *Indonemoura*:

- assami* (Aubert) 1967, n. comb.
- dirangdzongi* (Aubert) 1967, n. comb., Assam
- gigaoni* (Aubert) 1967, n. comb., Assam
- indica* (Kimmins) 1947, n. comb., Assam, India
- jacobsoni* (Klapálek) 1912a, n. comb., Bali, Java, Malaya, Sumatra
- javanica* (Banks) 1920, n. comb., Java
- kamengi* (Aubert) 1967, n. comb., Assam
- maclachlani* (Kimmins) 1950b, n. comb., Assam
- manipuri* (Aubert) 1967, n. comb., Assam
- nahkui* (Aubert) 1967, n. comb., Assam
- nyukmadongi* (Aubert) 1967, n. comb., Assam
- quadridentata* (Kimmins) 1950b, n. comb., Assam
- sangtii* (Aubert) 1967, new comb., Assam
- shergaoni* (Aubert) 1967, n. comb., Assam

Malenka Ricker

FIGURES 20–27, 141, 151, 158, 174

Nemoura (*Malenka*) Ricker, 1952:29. [Type-species: *Nemoura cornuta* Claasen.]

Malenka.—Illies, 1966:190.

ADULT.—Length: small to medium (5–10 mm). Wings (Figure 151): macropterous, venation typical for family, clear or slightly fumose at veins which are dark and distinct. Gills (Figure 141): 2 branched cervical gills on each side of midline, 1 arising inside and 1 outside of lateral cervical sclerites, minimum branches 5, maximum observed 8, some branches arising above gill base.

MALE TERMINALIA.—Hypoproct (Figure 26): broad at base, tapering to narrow apex, extending distally over inner lobes of paraprocts, tip extending nearly to base of epiproct; vesicle present. Paraprocts (Figure 23): divided into 3 lobes; inner lobes lightly sclerotized, naked, short and closely applied to midline, often completely hidden by hypoproct; median lobes lightly sclerotized api-

cally, naked or with small hairs, base broad and membranous, apical half tapering to a narrow tip that terminates in a sclerotized point or prongs, lying alongside hypoproct and extending to or beyond tips of cerci; outer lobes sclerotized, shape variable, recurved alongside cerci, often curving in front of median lobes dorsally, nearly fused to median lobes throughout length, naked except in *M. marionae* (Hitchcock) which has numerous short dark spines at apex. Cerci (Figures 24–26: with distinctive mesobasal lobes which may be membranous or heavily sclerotized, with single or bifurcate apex, main lobe of cerci membranous and unmodified. Epiproct (Figures 20–22): usually short and broad in dorsal aspect and narrow in lateral aspect, completely recurved, lightly sclerotized, bilaterally symmetrical; dorsal sclerite, fairly large and broad at base of epiproct, extending dorsolaterally toward apex, apical portion modified in structure, usually enlarged and extending over ventral sclerite laterally, covered with many tiny spines or scales; basal sclerites, as 2 broad triangular plates located at basolateral margins of epiproct; ventral sclerite, heavily sclerotized, broadest at base, narrower toward apex, forming median keel-shaped ridge which is naked of spines, apical portion inverted between lateral folds of dorsal sclerite, extending to apex where it forms a small rounded tip. Tenth tergum (Figure 24) all or mostly sclerotized, forming a large flat sclerotized area anterior to base of epiproct, mostly bare but often with a few spines along the anterior median margin. Ninth tergum sclerotized and usually slightly produced along distal margin, produced portion bearing spines or hairs.

FEMALE TERMINALIA (Figure 27).—Seventh sternum produced at mesoposterior margin, lightly sclerotized, bearing a nipplelike projection best seen in lateral view. Eighth sternum forming subgenital plate which is divided at genital opening by a median notch into 2 equal sternites or vaginal lobes, notch often lined by heavy sclerotization, lobes often swollen or produced but do not overlap ninth sternum.

NYMPH.—Gills (Figure 141): 2 branched cervical gills on each side of midline, 1 arising inside and 1 outside of lateral cervical sclerites, minimum branches 5, maximum observed 8, some branches originating some distance from base toward apex. Forelegs (Figure 158): femur and tibia of approxi-

mately equal length, most of leg covered with small fine hairs; femur with long hairs along posterior margin and bunched near distal end of dorsal surface; tibia with rows of long spines along posterior margin, with many long hairs intermingled with spines, anterior margin with row of short spines. Pronotum with fringe of spines along lateral margins. Abdominal terga with spines along distal margins. Cerci with whorls of large spines at distal margins of segments, intermediate areas with randomly arranged small spines.

DISCUSSION.—*Malenka* is the sister genus of *Amphinemura* and is restricted to western North America. It is found in small streams and creeks and is also common in small springs. It usually emerges in the late summer or fall, while most other nemourid species emerge in the early spring.

It can be distinguished in the nymphal stage by its highly branched cervical gills which have some branches that do not extend to the gill base (Figure 141). The male can be recognized by the presence of mesobasal lobes on the cerci (Figure 24), and the females have a nipplelike ventral projection on the seventh sternum and a distinctive notch on the median posterior margin of the eighth sternum (Figure 27).

DISTRIBUTION AND SPECIES LIST.—Nearctic (western North America). The genus *Malenka* contains the following known species:

bifurcata (Claassen) 1923, northwestern United States
biloba (Claassen) 1923, California
californica (Claassen) 1923, western North America
coloradensis (Banks) 1897, Rocky Mountains
cornuta (Claassen) 1923, northwestern North America
depressa (Banks) 1898, northwestern United States
flexura (Claassen) 1923, western North America
marionae (Hitchcock) 1958, California
perplexa (Frison) 1936, northwestern United States
tina (Ricker) 1952, western United States
wenatchee (Ricker) 1965, Washington

Mesonemoura, new genus

FIGURES 28–35, 142, 161, 175

TYPE-SPECIES.—*Nemoura vaillanti* Navás 1922:9, herein designated.

ADULT.—Length: medium to large (7–12 mm). Wings: macropterous, venation typical for family, clear or fumose, veins dark and distinct. Gills (Figure 142): single short oval gills on each side of

midline, located outside of lateral cervical sclerites.

MALE TERMINALIA.—Hypoproct (Figure 34): broad at base, tapering to narrow apex, extending to and covering part of inner lobes of paraprocts; vesicle present. Paraprocts (Figure 31): divided into 3 lobes; inner lobes lightly sclerotized but sometimes with darkly sclerotized projections, lobes well developed and fairly broad; median lobes partially sclerotized, with large membranous inner and apical portions, sclerotized area often bearing spines, membranous area with many hairs, lobes quite large and recurved toward base of epiproct; outer lobes mostly sclerotized, long thin and curved around cerci, often bearing a few small spines. Cerci (Figures 32–34): membranous, long, narrow and thin near apex, usually longer than paraprocts. Epiproct (Figures 28–30): usually short and broad in dorsal aspect and narrow in lateral aspect, completely recurved, mostly sclerotized, usually bilaterally symmetrical except for ventral apical tube-like structure which varies in shape from long and thin to short and stout; dorsal sclerite, large and broad at base of epiproct, extending dorso-laterally toward apex, apical portion enlarged and extending over onto ventral sclerite; basal sclerites as 2 broad triangular patches at basolateral margins of epiproct; ventral sclerite heavily sclerotized, broad at base and becoming narrower toward apex, forming median keel-shaped ridge, tubelike sclerotized structure extending from tip, apical portion inserted between folds of dorsal sclerite, ventral sclerite usually bearing few to many spines along keel-shaped ridge. Tenth tergum (Figure 32) all or mostly sclerotized forming a large flat area anterior to base of epiproct, usually bare but sometimes with a few spines or hairs. Ninth tergum sclerotized and produced along distal margin, bearing spines or hairs, produced area sometimes large and bizarre and can even be asymmetrical.

FEMALE TERMINALIA (Figure 35).—Seventh sternum somewhat produced at distal margin, extending slightly onto eighth sternum at midline, produced area lightly sclerotized. Eighth sternum forming subgenital plate, median area enlarged and sclerotized, forming plate that covers most of segment and genital opening, lateral posterior margins of segment enlarged and lightly sclerotized, forming small vaginal lobes.

NYMPH.—Gills (Figure 142): single short oval gills on each side of midline, arising outside of

lateral cervical sclerites, gills shaped like small rounded knob slightly longer than wide. Forelegs (Figure 161): femur and tibia of approximately equal length, whole leg covered with fine short hairs; femur with a row of very small spines along posterior margin, with a few large long spines on basal half on posterior margin and dorsal surface; tibia with row of small spines near anterior margin, posterior margins with fringes of long hairs. Pronotum with fringe of spines along lateral margins. Abdominal terga with fringes of spines along distal margins, often also with two longitudinal rows of single large spines. Cerci with whorls of large spines at distal margins of segments, areas between joints covered randomly with numerous intermediate spines.

DISCUSSION.—*Mesonemoura* contains species that were once assigned to *Amphinemura*, *Protonemura*, and *Nemoura*. It is similar to *Amphinemura* in many respects but is most similar to *Indonemoura*. It differs from *Amphinemura* in only having single, simple cervical gills on the outside of the lateral cervical sclerites (Figure 142). The nymph labeled *Nemoura* sp. (no. 102) in Kawai (1963) seems to belong in *Mesonemoura*. It can be separated from *Indonemoura* by the smaller less developed paraprocts (Figure 31) and by the presence of a long thin epiproctal flagellum (Figures 28–30). Females of *Mesonemoura* have a small median subgenital plate and two small vaginal lobes (Figure 35), while *Indonemoura* females have a single large, darkly sclerotized subgenital plate, which nearly obscures the vaginal lobes (Figure 19).

Most of the species presently assigned to this genus occur in the high mountains of Central Asia.

DISTRIBUTION AND SPECIES LIST.—Oriental and Palearctic (south central Eurasia).

- brachyfiligera* (Aubert) 1967, n. comb., Assam
- falcata* (Kimmins) 1950b, n. comb., Assam
- filigera* (Kimmins) 1947, n. comb., Himalaya, Nepal
- **flagellata* (Wu) 1935, n. comb., China
- **hamistyla* (Wu) 1962, n. comb., China
- **longicercia* (Okamoto) 1922, n. comb., Japan
- metafiligera* (Aubert) 1967, n. comb., Assam
- mishmica* (Kimmins) 1950b, n. comb., Assam
- **multispira* (Wu) 1973, n. comb., China
- paraflagigera* (Aubert) 1967, n. comb., Assam
- paraproctalis* (Aubert) 1967, n. comb., Assam
- pseudofiligera* (Aubert) 1967, n. comb., Assam
- skardui* (Aubert) 1959a, n. comb., Pakistan, Afghanistan

**spiroflagellata* (Wu) 1973, n. comb., China
tianschanica (Zhiltzova) 1971, n. comb., central Asia
vaillantii (Navás) 1922, n. comb., China, Afghanistan, Pakistan

Protonemura Kempny

FIGURES 36-43, 143, 157, 160, 176

Nemura (*Protonemura*) Kempny, 1898:51. [Type-species: *Nemoura meyeri* Pictet = *Protonemura meyeri* (Pictet).]
Protonemura.—Claassen, 1940:68.

ADULT.—Length: medium to large (7-15 mm). Wings (Figure 157): macropterous, venation typical for family, clear, fumose or mottled, veins dark and distinct. Gills (Figure 143): 2 cervical gills, 1 on each side of lateral cervical sclerites, outer gills with single branch at base forming 2 long thin nearly equal parts, inner gills long, thin and single.

MALE TERMINALIA.—Hypoproct (Figure 42): broad at base, tapering to narrow apex, extending distally over inner lobes of paraprocts, tip extending to base of epiproct; vesicle present. Paraprocts (Figure 39): divided into 3 lobes; inner lobes lightly sclerotized, naked, short, and closely applied to midline, often completely hidden by hypoproct; median lobes heavily sclerotized but with large membranous apical portion, sclerotized portion broad at base, tapering to apex, which is often branched, inner branch darkly sclerotized and bearing one or more prongs or spines near apex, membranous portion bulbous and covered with small hairs; outer lobes mostly sclerotized, elongate and recurved dorsally alongside cerci, usually with one or more spines at apex. Cerci (Figures 40-42: membranous, short and unmodified. Epiproct (Figures 36-38): usually long and thin in dorsal aspect and thin but enlarged apically in lateral aspect, completely recurved, mostly sclerotized, bilaterally symmetrical, occasionally with an apical tubelike projection arising from the ventral sclerite; dorsal sclerite, large and broad at base of epiproct, extending dorsolaterally to apex, apical portion enlarged covering dorsolateral margins, heavily sclerotized lateral arms variously modified, apex of sclerite round, covered with small spines or scales; basal sclerites shaped like broadly rounded triangles, located at basolateral margins of epiproct; ventral sclerite, broadest at base, becoming narrower toward apex, apical por-

tion inserted between folds of dorsal sclerite, often extending to dorsal margin, ventral margin of sclerite bearing spines along complete length or in a tuft near apex. Tenth tergum (Figure 40) all or mostly sclerotized, forming a large flat area anterior to base of epiproct, usually bearing small spines or hairs. Ninth tergum sclerotized and usually produced, especially along distal margin, bearing spines and hairs and often distinctly shaped. Eighth tergum usually enlarged, bearing spines and hairs. Seventh tergum usually normal and bare but sometimes with a few spines and hairs.

FEMALE TERMINALIA (Figure 43).—Seventh sternum slightly produced at distal margin, seldom extending over segment eight, produced area lightly sclerotized. Eighth sternum forming subgenital plate, central area enlarged and sclerotized forming plate that covers most of segment and genital opening, lateral posterior margins of segment produced and sclerotized, forming vaginal lobes.

NYMPH.—Gills (Figure 143): 2 cervical gills on each side of midline, 1 arising inside and 1 outside of lateral cervical sclerites, outer gills forked at base into 2 nearly equal branches, inner gills single, gills long thin and often constricted one or more times. Forelegs (Figure 160): femur and tibia of approximately equal length, femur with spines along posterior margin, extending to dorsal surface on distal half; tibia with rows of spines along posterior margins, intermingled with scattered small spines and hairs, anterior half covered with random spines that become most dense at distal end covering entire surface. Pronotum with fringe of spines along lateral margins. Abdominal terga with fringes of spines along lateral margins, often with 2 longitudinal rows of single large spines. Cerci with whorls of large spines at distal margins of segments, areas between joints covered randomly with small intermediate spines.

DISCUSSION.—*Protonemura* is very common in southern Europe and seems to fill the niche occupied by *Amphinemura* in North America and most of Asia. It is a large genus containing over 80 species.

The distinctive features of the genus are the cervical gills and the well developed female subgenital plate. The outer cervical gills have a single deep fork and the inner gills are long and simple (Figure 143). The female eighth sternum is well

developed into a large median subgenital plate and large sclerotized vaginal lobes (Figure 43).

DISTRIBUTION.—Palearctic (Europe, Asia, North Africa).

abchasica Zhiltzova 1964, Caucasus
aestiva Kis 1965a, Balkans, Carpathians
albanica Raušer 1963b, Albania
alcazaba (Aubert) 1954b, Spain
algerica (Aubert) 1956c, Algeria, Morocco
algovia Mendl 1968a, Alps
allicola Zhiltzova 1958, Caucasus
angelieri Berthélemy 1963, Pyrenees
auberti Illies 1954, central Europe
ausonia (Consiglio) 1955, Italy
autumnalis Raušer 1956, Balkans, Carpathians
bacuriana Zhiltzova 1957, Caucasus, Asia Minor
beatensis (Despax) 1929, Pyrenees, Italy
beaumonti (Aubert) 1956a, Balkans
besucheti Zwick 1971, Turkey
bifida Martynov 1928, Caucasus, Iran
bipartita Consiglio 1962, Italy
bithynica Aubert 1964b, Turkey
**brevilobata* Klapálek 1912b, Taiwan
brevistyla (Ris) 1902, Alps, Carpathians
bucolica (Consiglio) 1957b, Corsica
capitata Martynov 1928, Caucasus, Armenia
caprai (Aubert) 1954c, Italy
consiglioi (Aubert) 1953b, Italy
corsicana (Morton) 1930, Corsica
costai (Aubert) 1953a, Italy
dilatata Martynov 1928, Caucasus
elbourzi Aubert 1964a, Iran
eumontana Zhiltzova 1957, Caucasus, Asia Minor
gladifera Balinsky 1950, Caucasus
hassankifi Aubert 1964a, Iran
hiberiaca Aubert 1963a, Spain
hirpina (Consiglio) 1958, Italy
hispanica (Aubert) 1956b, Spain
**hotakana* Uéno 1931, Japan
hrabei Raušer 1956, central Europe
ichnusae (Consiglio) 1957a, Sardinia
illiesi Kis 1963, Balkans, Carpathians
intricata (Ris) 1902, Europe
italica (Aubert) 1954a, Italy
**jezoensis* Okamoto 1922, Japan
lagrecai (Aubert) 1954a, Italy
lateralis (Pictet) 1836, Europe
libanica Aubert 1964b, Lebanon
macrura (Aubert) 1953b, Italy
mattheyi (Aubert) 1956a, Greece
meyeri (Pictet) 1841, Europe
microstyla Martynov 1928, Caucasus, Armenia
montana Kimmins 1941, Europe
navacerrada (Aubert) 1954b, Spain
nimborella Mosely 1930, Alps
nimborum (Ris) 1902, central Europe
nitida (Pictet) 1835, Europe

**nohirae* Okamoto 1922, Japan
oitica Aubert 1963c, Greece
orcas Martynov 1928, Caucasus
praecox (Morton) 1894, Europe
pseudonimborum Kis 1965, Carpathians
pyrenaica Mosely 1930, Pyrenees
ressli Zwick 1971, Asia Minor
risi (Jacobson & Bianchi) 1902, central Europe
ruffoi Consiglio 1961, Italy
salfii (Aubert) 1954a, Italy
sicula Consiglio 1961, Sicily
spinulata Martynov 1928, Caucasus
strandschaensis Braasch & Joost 1972, Bulgaria
talboti (Navas) 1929, North Africa
taygetiana (Aubert) 1956a, Greece
teberdensis Zhiltzova 1958, Caucasus, Asia Minor
**towadensis* Kawai 1954, Japan
**triangulata* Martynov 1928, Caucasus
tuberculata (Despax) 1929, Pyrenees
tyrrhena (Festa) 1938, Italy, Morocco
vandeli Berthélemy 1963, Pyrenees
vercingetorix Aubert 1963a, France
vernalis Zhiltzova 1958, Caucasus, Armenia
viridis Balinsky 1950, Caucasus
waliabadi Aubert 1964a, Iran
zernyi Aubert 1964b, Lebanon, Israel

NEMOURINAE Newman, 1853

Nemoura is the type-genus for this large subfamily, which also contains the following genera: *Illiesonemoura*, *Lednia*, *Nemurella*, *Ostrocerca*, *Paranemoura*, *Podmosta*, *Prostoia*, *Shipsa*, *Soyedina*, *Visoka*, and *Zapada*.

The subfamily can be distinguished by the following characters:

1. Paraprocts with a thin inner lobe and a broad outer lobe or just a single broad lobe.
2. Paraprocts lacking spines or prongs.
3. Epiproct usually short and dorsoventrally compressed, with the ventral sclerite enlarged, especially at base.
4. Cervical gills usually absent.
5. Pregenital plate well developed in females or neither pregenital plate nor subgenital plate especially well developed.

Nemourinae is a very diverse grouping that contains one large genus, *Nemoura*, and many small genera, four of which are monotypic. *Nemoura* is found throughout the Holarctic and also extends to the Oriental region (Figure 178). *Illiesonemoura* is Palearctic and Oriental, and *Nemurella* is Palearctic (Figures 177, 179). *Podmosta* extends

from the Nearctic into the eastern part of the Palearctic (Figure 181); *Lednia*, *Ostrocerca*, *Paranemoura*, *Prostoia*, *Shipsa*, *Soyedina*, *Visoka*, and *Zapada* have been found only in the Nearctic region (Figures 177, 179–186).

This subfamily may prove to be a polyphyletic lineage, but it is treated in this study as a monophyletic lineage based on the shape and structure of the ventral sclerite of the epiproct.

Illiesonemoura, new genus

FIGURES 44–51, 144, 156, 169, 177

TYPE-SPECIES.—*Nemoura punctata* Jewett, 1958: 324, herein designated.

ADULT.—Length: small to large (5–12 mm). Wings (Figure 156): macropterous, venation typical for family, fumose, mottled or with light spots in cells on dark background, veins dark and distinct. Gills (Figure 144): 1 unbranched cervical gill on each side of midline, arising on outside of lateral cervical sclerites, gills triangular-shaped and of medium length, small gill-like nubs on inside of lateral cervical sclerites.

MALE TERMINALIA.—Hypoproct (Figure 50): broad at base, tapering to narrow apex, extending distally over base of paraprocts, often covering inner lobes of paraprocts; vesicle present. Paraprocts (Figure 47): consisting of 2 lobes; inner lobes sclerotized, short and narrow, closely applied to midline and often turned inward, sometimes completely hidden by hypoproct; outer lobes sclerotized ventrally and membranous dorsally, very large and generally triangular in shape, with inward directed sclerotized projection from outer margin near cerci. Cerci (Figures 48–50): mostly membranous, long thin and often bent. Epiproct (Figures 44–46): short and broad in dorsal aspect, short and varying from broad to rather thin in lateral aspect, apex rounded, completely recurved, bilaterally symmetrical; dorsal sclerite large and broad at base of epiproct, extending dorsolaterally, becoming narrow around lateral knobs and then very large and triangular, often completely covering lateral aspects of epiproct and much of ventral aspect, most darkly sclerotized areas at base and near posterior end immediately ahead of basal cushion, anterior area lightly sclerotized; basal sclerites as 2 broad triangular or rectangular patches located near basolateral corners of epi-

proct; ventral sclerite heavily sclerotized, broad at base and with lateral knobs at basolateral corners, becoming narrower toward apex, forming parallel ridges, one on each side of midline, each bearing a row of spines, usually covered by dorsal sclerite near tip of epiproct, extending inward and upward to dorsal surface, extended portion paired and highly variable in shape, usually visible dorsally and can even extend out of epiproct near apex. Tenth tergum (Figure 48) mostly sclerotized, forming a large flat or concave area anterior to base of epiproct, sometimes produced at lateral basal margins, usually bearing thin hairs. Ninth tergum sclerotized but not produced, most heavily sclerotized along distal margin, bearing thin hairs.

FEMALE TERMINALIA (Figure 51).—Seventh sternum enlarged and extended distally forming pregenital plate, covering most or all of eighth sternum, produced area lightly sclerotized. Eighth sternum narrow, with sclerotized patch over genital opening. Cerci medium sized, membranous and simple.

NYMPH.—Gills (Figure 144): 1 cervical gill on each side of midline, arising outside of lateral cervical sclerites, gills short and triangular, small gill-like nubs on inside of lateral cervical sclerites. Forelegs (Figure 169): femur and tibia of approximately equal length; femur with a whorl of long spines near distal end, spines in loosely arranged row, scattered spines along dorsal posterior margin; tibia with a row of long spines along dorsal posterior margin and with occasional long hairs intermingled with spines, with a row of spines near dorsoanterior margin, ventral surface with rows of spines along anterior and posterior margins. Middle and hind legs without whorls of spines on femur. Pronotum with fringe of long spines on lateral margins. Mesonotum with fringe of long spines. Abdominal terga with fringe of long spines along distal margins. Cerci with whorls of large spines at distal margins of segments, intermediate segmental spines usually absent.

DISCUSSION.—*Illiesonemoura* is made up mostly of the species of the Pakistani and *Polystigma* groups of Aubert (1959a) and a cluster of species studied by Jewett in (1958). *Nemoura* sp. (no. 102) in Kawai (1966a) appears to fit in this genus. *Illiesonemoura* is very similar to *Zapada* in most respects but can be most easily separated by the structure of the cervical gills, which in *Illieso-*

nemoura are only present outside of the lateral cervical sclerites (Figure 144). The nymph of *Illiesonemoura* can also be separated by the absence of whorls of spines on the femora of the middle and hind legs.

Illiesonemoura is named in honor of Professor Dr. Joachim Illies of Schlitz, Germany, for his many contributions to the study of Plecoptera and especially for his help with this revision.

DISTRIBUTION AND SPECIES LIST.—Palearctic and Oriental (central Asia). The following species are placed in the genus *Illiesonemoura*:

- **alabeli* (Zhiltzova) 1971, n. comb., central Asia
- ampula* (Jewett) 1958, n. comb., Himalaya
- atripes* (Aubert) 1959a, n. comb., Pakistan
- battakundi* (Aubert) 1959a, n. comb., Pakistan
- besali* (Aubert) 1959a, n. comb., Pakistan
- **bispinosa* (Kawai) 1968b, n. comb., Taiwan
- cordata* (Jewett) 1958, n. comb., Himalaya
- **falcifera* (Harper) 1975, n. comb., Nepal
- **gosainkundensis* (Harper) 1975, n. comb., Nepal
- lilami* (Aubert) 1959a, n. comb., Pakistan
- maluksari* (Aubert) 1959a, n. comb., Pakistan
- pakistani* (Aubert) 1959a, n. comb., Pakistan
- polystigma* (Aubert) 1959a, n. comb., Pakistan
- punctata* (Jewett) 1958, n. comb., Himalaya
- punjabensis* (Jewett) 1958, n. comb., Himalaya
- ornata* (McLachlan) 1875, n. comb., central Asia
- **tuberostyla* (Wu) 1962, n. comb., China
- **verrucosa* (Harper) 1975, n. comb., Nepal

Lednia Ricker

FIGURES 52–59, 177

Nemoura (*Lednia*) Ricker, 1952:27. [Type-species: *Nemoura tumana* Ricker.]

Lednia.—Illies, 1966:190.

ADULT.—Length: small (4–6 mm). Wings: macropterous, venation typical for family, hyaline but with small dark area at cord, veins dark brown and distinct. Gills: absent but with small single membranous gill-like nubs on outside of lateral cervical sclerites, base of lateral cervical sclerites very broad.

MALE TERMINALIA.—Hypoproct (Figure 58): sclerotized, elongate, broad at base, becoming gradually narrower toward pointed apex, extending over paraprocts to base of epiproct; vesicle absent. Paraprocts (Figure 55): composed of 2 lobes; inner lobes long, thin and heavily sclerotized, with base at lateral basal margin of cerci and extending to near midline, apical half extending backward

parallel to hypoproct, long thin and lancet-shaped, reaching to base of epiproct; outer lobes broad rounded and membranous, extending from cerci to midline. Cerci (Figures 56–58): medium, membranous and unmodified. Epiproct (Figures 52–54): broad, flat and mostly sclerotized, bilaterally symmetrical; dorsal sclerite with broad flat base, lateral corners broad and darkly sclerotized, extending forward near apex, replaced at apex by 2 long narrow patches of small spines or overlapping plates, very lightly sclerotized; basal sclerites as large broad triangles, located at basolateral corners of epiproct; ventral sclerite large and broad at base, thin in cross section and trough-shaped, becoming gradually narrower toward pointed apex, sclerite smooth and naked. Tenth tergum (Figure 56) highly modified, median basal area deeply concave, sclerotized and forming a large smooth surface under epiproct, posterior lateral areas greatly produced into long narrow prongs, with rounded heavily sclerotized tips, bearing many small stout spines. Ninth tergum lightly sclerotized, not produced or modified, bearing a few small spines and hairs.

FEMALE TERMINALIA (Figure 59).—Seventh sternum slightly produced and enlarged at midline, produced area lightly sclerotized. Eighth sternum mostly sclerotized, median area sclerotized and formed into broad somewhat triangular subgenital plate, apex rounded or slightly bilobed and covering genital opening, lateral posterior areas with large, slightly triangular sclerotized patches. Cerci small, membranous and unmodified. Paraprocts large, triangular and with rounded corners.

NYPH.—Unknown.

DISCUSSION.—This genus is monotypic and has only been collected from two localities in Glacier National Park (Ricker, 1952; Gaufin et al., 1972). It lacks a vesicle on the ninth sternum of the male (Figure 58) like *Paranemoura perfecta* but otherwise is most similar to *Visoka cataractae* in the details of the epiproct and paraprocts. *Visoka* is, however, very distinctive because it has submental gills and also has sclerotized, modified cerci.

Further collecting in small streams at high elevations in the Northern Rocky Mountains should add to our knowledge of this rare genus.

DISTRIBUTION.—Nearctic (western North America). The genus *Lednia* contains only one species: *tumana* (Ricker) 1952, Montana

Nemoura Latreille

FIGURES 60-67, 145, 154, 171, 178

Nemoura Latreille, 1796:101.—International Commission on Zoological Nomenclature, 1963:29-30. [Type-species: *Perlacinerea* Retzius = *Nemoura cinerea* (Retzius).]

ADULT.—Length: small to large (5-15 mm). Wings (Figure 154): macropterous, venation typical for family, hyaline, fumose or mottled, veins dark and distinct. Gills (Figure 145): absent but with single small membranous gill-like nubs outside of lateral cervical sclerites.

MALE TERMINALIA.—Hypoproct (Figure 66): broad at base, tapering to narrow apex, extending distally to base of paraprocts, often covering inner lobes; vesicle present. Paraprocts (Figure 63): consisting of 2 lobes; inner lobes sclerotized, short and narrow, closely applied to midline and usually turned inward, sometimes completely hidden by hypoproct; outer lobes sclerotized ventrally and membranous dorsally, very large and triangular or elongate in shape. Cerci (Figures 64-66): mostly sclerotized, lateral portion as sclerotized strip that usually terminates at apex into 1 to 3 spines or hooks, but spines may occur anywhere or be entirely absent, body of cercus usually elongate and of moderate width but sometimes greatly enlarged at base. Epiproct (Figures 60-62): generally short and broad in dorsal aspect, short and varying from broad to rather thin in lateral aspect, apex rounded, completely recurved, sclerotized and membranous, bilaterally symmetrical; dorsal sclerite large and broad at base of epiproct, extending dorsolaterally, becoming narrow around lateral knobs and then very large and triangular, usually completely covering lateral aspects of epiproct and part of ventral aspect, most darkly sclerotized areas at base and near dorsoposterior margin immediately ahead of basal cushion, anterior area usually lightly sclerotized but bearing spines in some species; basal sclerites as 2 large, broad, triangular or rectangular patches located near basolateral corners of epiproct; ventral sclerite darkly sclerotized, broad at base, with lateral knobs at basolateral corners, becoming narrower toward apex, forming parallel ridges, 1 on each side of midline, each bearing a row of spines, usually covered by dorsal sclerite near tip of epiproct, extending inward and upward to dorsal surface, visible portion paired and quite variable in shape, usually semicircular

near apex, often bearing spines or hooks. Tenth tergum (Figure 64) mostly sclerotized, forming a large flat or concave area anterior to base of epiproct, usually bearing only thin hairs and small spines but with large spines or projections in some exotic species. Ninth tergum sclerotized, but not produced, bearing thin hairs and spines. Eighth tergum produced and modified in some species.

FEMALE TERMINALIA (Figure 67).—Seventh sternum enlarged and extended distally, covering most or all of eighth sternum, produced area sclerotized. Eighth sternum narrow and mostly membranous, with small sclerotized area at genital opening. Cerci mostly sclerotized, quite angular and truncate at apex.

NYMPH.—Gills (Figure 145): absent but with very small nubs outside of lateral cervical sclerites on each side of midline. Forelegs (Figure 171): femur and tibia of approximately equal length, whole leg usually covered with small spines or hairs; femur with randomly scattered large spines along posterior margin and near distal end (*N. mortoni* has whorls of large spines), with a few long hairs often intermingled with spines; tibia with rows of small spines along dorsal anterior and posterior margins, ventral surface without rows of spines or with very short spines. Pronotum with fringe of short spines on lateral margins. Mesonotum and metanotum with sparse fringe of small spines along lateral margins. Abdominal terga with fringes of short spines along distal margins. Cerci with whorls of spines at distal margins of segments, intermediate segmental spines very small and sparse.

DISCUSSION.—*Nemoura*, the type-genus, received many species over the years that belonged in Nemouridae but could not be easily assigned to any of the known genera. Most of these misplaced species have been removed and placed in other genera in this paper. The genus is, however, still not a completely homogeneous unit, as evidenced by the included species groups.

As a result of this study, I feel that the typical *Nemoura* species are primarily found in more northern areas. The species figured in this paper belong to the typical concept of *Nemoura*. *Nemoura* males have distinctive sclerotized cerci with terminal hooks (Figures 64-66). The females have a large pregenital plate and lightly sclerotized truncate cerci (Figure 67).

I did, however, delineate two species complexes from exotic areas in Asia that, although they are here placed in *Nemoura*, exhibit some variation in the structure of the male terminalia. These species complexes can be distinguished by the following characteristics:

Cercispinosa Complex: Cerci enlarged and quite thick, bearing one or more spines at apex, near base or somewhere along the length. Tenth tergum with large spines or protuberances. Ninth tergum bearing large spines and somewhat produced. Aubert (1967) in his study of the Nemouridae of Assam provides excellent figures of many species in this complex.

Ovocercia Complex: Cerci enlarged laterally and very broad at base, ending in a rounded tip, body of cerci naked of spines. Tenth tergum produced and often with large humps or knobs. Ninth tergum usually produced and bearing spines. Eighth tergum sometimes produced posteriorly. Kawai (1967) and Zwick (1973b) give figures of species that belong to this complex.

The distribution lists of the species included in the above complexes are separated from the rest of the *Nemoura* species for convenience.

DISTRIBUTION AND SPECIES LIST.—Holarctic and Oriental (Europe, Asia, North Africa, North America).

arctica Esben-Petersen 1910, circumpolar
avicularis Morton 1894, Europe, Siberia
babiagorensis Sowa 1964, Poland
braaschi Joost 1970a, Bulgaria
brevipennis Martynov 1928, Caucasus, Armenia, Asia Minor
bulgarica Raušer 1962, Bulgaria
cambrica Stephens 1835, Europe
carpathica Illies 1963, Carpathians
caspiica Aubert 1964a, Iran
ceciliae Aubert 1956b, Spain
cinerea (Retzius) 1783, Europe, central Asia
confusa Zwick 1970, France
dubitans Morton 1894, central and northern Europe
elegantula Martynov 1928, Caucasus
erratica Claassen 1936, western Europe, Britain
flaviscapa Aubert 1956a, Greece
flexuosa Aubert 1949, Europe, Asia Minor
fulviceps Klapálek 1902, Europe
fusca Kis 1963, Romania
**gladiata* Uéno 1929, Japan
hamata Kis 1965b, Romania
hamulata Zhiltzova 1971, Tien Shan
hesperiae Consiglio 1958, Italy
illiesi Mendl 1968b, Austria
irani Aubert 1964a, Iran

kownackorum Sowa 1970, Bulgaria
kuwayamai Kawai 1966b, Japan
lacustris Pictet 1865, Pyrenees
lepnevae Zhiltzova 1971, Tien Shan
levanidovae Zwick 1974, Siberia
lingulata Navás 1918, Pyrenees
longicauda Kis 1964, Carpathians
marginata Pictet 1835, central Europe
martynovia Claassen 1936, Caucasus, Asia Minor
**matangshanensis* Wu 1935, China
minima Aubert 1946, Alps
monticola Raušer 1965, Czechoslovakia
mortoni Ris 1902, central Europe
moselyi Despax 1934, Pyrenees
navaiensis Kawai 1954, Japan
navasi Aubert 1953c, Spain, Sicily
normani Ricker 1952, Alaska
obtusa Ris 1902, central Europe
ovoidalis Kis 1965a, Romania
palliventris Aubert 1953b, Italy
**papilla* Okamoto 1922, Japan
peristeri Aubert 1963b, Yugoslavia
pirinensis Raušer 1962, Bulgaria
pygmaea Braasch & Joost 1972, Bulgaria
rickeri Jewett 1971, Alaska
rifensis Aubert 1960, Morocco, Spain
sachaliensis Matsumura 1911, Japan, Sachalin
sahlbergi Morton 1896, Arctic Eurasia, Mongolia, Korea
sciurus Aubert 1949, central Europe
**securigera* Klapálek 1907, China
sinuata Ris 1902, Alps
subtilis Klapálek 1895, Carpathians, Balkans, Asia Minor
taurica Zhiltzova 1967, Crimea, Asia Minor
transylvanica Kis 1963, Romania
trispinosa Claassen 1923, eastern North America
**uenoi* Kawai 1954, Japan
undulata Ris 1902, Alps
viki Lillehammer 1972, Norway

CERCISPINOSA COMPLEX

**arlingtoni* Wu 1940, China
**bispinosa* Kawai 1968b, Taiwan
bokhari Aubert 1967, Assam
**cercispinosa* Kawai 1960, Japan
chattriki Aubert 1967, Assam
chugi Aubert 1967, Assam
**fulva* Šámal 1921, Japan
**furcocauda* (Wu) 1973, China
**janeti* Wu 1938, China
khassii Aubert 1967, Assam
kuhleni Aubert 1967, Assam
**manchuriana* Uéno 1941, Manchuria
mawlangi Aubert 1967, Assam
**nankinensis* Wu 1926, China
**needhamia* Wu 1927, China
**pseudostuva* Kawai 1954, Japan
schmidi Aubert 1967, Assam
serrarimi Aubert 1967, Assam

spiniloba Jewett 1954, California
spinosa Wu 1940, China, Assam
yunnanensis Wu 1940, China

OVOCERCIA COMPLEX

**akagii* Kawai 1960, Japan
 **cochleocercia* Wu 1962, China
 **geei* Wu 1929, China
lahkipuri Aubert 1967, Assam
ovocercia Kawai 1960, Japan
redimiculum Kawai 1966c, Japan
tau Zwick 1973b, Korea

***Nemurella* Kempny**

FIGURES 68-75, 167, 179

Nemura (*Nemurella*) Kempny, 1898:59. [Type-species: *Nemura inconspicua* Kempny = *Nemurella pictetii* Klapálek.]
Nemurella.—Klapálek, 1900:30.

ADULT.—Length: medium (5–10 mm). Wings: macropterous, venation typical for family, hyaline to light brown, veins dark and distinct. Gills: absent but with single membranous gill-like nubs on outside of lateral cervical sclerites.

MALE TERMINALIA.—Hypoproct (Figure 74): sclerotized, long and drawn out, broadest near base, becoming abruptly narrower at posterior margin of ninth sternum, apical half very thin and extending to bases of outer lobes of paraprocts, apex thin, rounded and lightly colored; vesicle present. Paraprocts (Figure 71): consisting of 2 lobes; inner lobes with bases extending to outer margin near base of cerci, lobes extremely long, slender and heavily sclerotized, basal third running from point of attachment laterally to apex of hypoproct, basal portion dorsoventrally flattened, apical two-thirds twisted so that thin lateral margins are seen in ventral view, extending well beyond tip of abdomen and slightly beyond epiproct, tips narrow and pointed; outer lobes extending beyond tip of epiproct, broadest at base, tapering gradually to narrowly rounded apex, lobes quite long and thin, round in cross section, most heavily sclerotized on outer surface, bearing many long thin hairs. Cerci (Figures 72–74): very large, sclerotized and almost completely covering epiproct in lateral view, broad and bulbous at base, becoming long and parallel sided, ending in broadly rounded apex, most darkly sclerotized laterally, inner surface and apex light in color, outer surfaces bearing

many small fine hairs. Epiproct (Figures 68–70): completely sclerotized, short broad and bilaterally symmetrical, not completely recurved but directed backward slightly from base; dorsal sclerite divided into 3 darkly sclerotized parts, heavy basal part shifted forward into a dorsal position, short broad and concave, forming an open-sided funnel, ending in a narrow apex with a small rounded opening, lateral arms long thin and lying between dorsal part and ventral sclerite on lateral margins, broadest at base, apex shaped like blunt forcep which forms half of forceps as lateral pieces come together at apex; basal sclerites as 2 broad triangular shaped sclerotized patches located at basolateral corners of epiproct; ventral sclerite flat, broad and darkly sclerotized, base very broad, tapering to broadly rounded apex, sclerite slightly concave dorsally, apex bifurcate with narrow groove, lateral apical areas rounded and curled under ventrally, ventral surface of sclerite flat smooth and naked except for single rows of very small spines along lateral margins. Tenth tergum (Figure 72) mostly membranous medially, paired sclerotized lateral bars extending to base of epiproct, with enlarged sclerotized areas at bases of cerci, tergum bearing a long thin patch of hairs in a lightly sclerotized area below tip of epiproct. Ninth tergum broad, heavily sclerotized and slightly produced, bearing many small thin hairs.

FEMALE TERMINALIA (Figure 75).—Seventh sternum forming pregenital plate, greatly enlarged and expanded medially over eighth sternum, produced area darkly sclerotized, triangular in shape with rounded apex which covers genital opening. Eighth sternum narrow, membranous medially, lateral portions produced as darkly sclerotized vaginal lobes. Cerci lightly sclerotized but otherwise simple and unmodified. Paraprocts large and triangular in shape, apex narrowly pointed.

NYMPH.—Gills: absent but with single membranous gill-like nubs on outside of lateral cervical sclerites. Forelegs (Figure 167): femur slightly shorter than tibia, whole leg covered with many small spines; femur with a few large spines near distal margin, occasional long hairs along posterior margin; tibia with rows of small spines along ventral margins, with an occasional long hair intermingled. Pronotum with irregular fringe of long thin spines along lateral margins, sides somewhat rounded in dorsal view. Abdominal terga with

sparse fringes of spines along distal margins, with 2 longitudinal rows of single large spines. Cerci with whorls of spines at distal margins of segments, areas between segmental joints with a few small spines.

DISCUSSION.—Although *Nemurella* is monotypic it has been recognized as a separate subgenus since 1898. It has very distinctive bilobed paraprocts that make it possible to separate it from all of the European nemourids (Figure 71). The epiproct is also highly modified with the horseshoe-shaped base of the dorsal sclerite shifted forward into a dorsal position (Figures 68–70). The females have a well-developed pregenital plate and large vaginal lobes on sternum eight (Figure 75).

It is very common throughout Europe and is often extremely abundant in spring-fed habitats.

DISTRIBUTION AND SPECIES LIST.—Palearctic (Europe). The records from the Altai Mountains and Siberia (Zapekina-Dulkeit, 1957, 1961) are unconfirmed and highly questionable. This genus contains only one known species:

pictetii Klapálek 1900, Europe

Ostrocerca Ricker

FIGURES 76–83, 162, 179

Nemoura (*Ostrocerca*) Ricker, 1952:38. [Type-species: *Nemoura foersteri* Ricker.]

Ostrocerco.—Illies, 1966:217.

ADULT.—Length: small (4–8 mm). Wings: macropterous, venation typical for family, hyaline and sometimes slightly darkened around veins near cord, veins dark and distinct. Gills: absent but with single membranous gill-like nubs outside of lateral cervical sclerites.

MALE TERMINALIA.—Hypoproct (Figure 82): broad at base, large sclerotized and extending back over base of epiproct, with a bulbous membranous inner portion, shape varying from long and narrow to very broad and truncate or flat at apex; vesicle present. Paraprocts (Figure 79): consisting of 1 darkly sclerotized lobe and 1 membranous lobe on each side of midline; inner lobes sclerotized, with bases at lateral margins near base of cerci, lobes large and quite angular in shape, sometimes with lateral projections near bend, tip pointed and directed outward; outer lobes rounded membranous

and covered with hairs. Cerci (Figures 80–82): large, sclerotized and terminating in a pointed tip, sometimes with a second subapical point, extending laterally beyond tip of epiproct, most heavily sclerotized laterally and at apex, covered with many small hairs, sometimes distinctly bent in lateral aspect. Epiproct (Figures 76–78): mostly sclerotized, short broad and bilaterally symmetrical, not completely recurved but directed at an oblique angle upward and backward from longitudinal axis of abdomen; dorsal sclerite large and broad at base, shifted forward dorsally, extending forward on dorsal and lateral aspects, lateral arms running from near base to apex along lateral surfaces, often covered by large dorsal area which is lightly sclerotized and covered by spines or scale-like plates; basal sclerites as 2 long very thin sclerotized patches, curved around basolateral corners of epiproct; ventral sclerite heavily sclerotized, broad at base and throughout most of length, apex pointed or narrowly rounded, usually with one or more prongs directed downward from or near the tip, best seen in lateral view, margins bearing small spines or scales. Tenth tergum (Figure 80) with paired sclerotized bars leading to base of epiproct, generally broad and flat or concave but sometimes with thin paired projections, located 1 on each side of apex of epiproct, extreme lateral margins below cerci enlarged and sclerotized, tergum bearing small hairs or spines. Ninth tergum sclerotized but not produced or modified, bearing many small hairs.

FEMALE TERMINALIA (Figure 83).—Seventh sternum usually enlarged and expanded distally at midline, enlarged area sclerotized and varying in shape from large slightly rounded area to narrow elongate nipplelike process similar to male hypoproct. Eighth sternum broad and heavily sclerotized, forming subgenital plate, covering genital opening, truncate, indented or incised on distal margin at midline. Paraprocts, triangular and pointed at apex. Cerci short, membranous and unmodified.

NYMPH.—Gills: absent but with single membranous gill-like nubs outside of lateral cervical sclerites. Forelegs (Figure 162): femur and tibia of approximately equal length; femur with large spines along dorsoposterior margin, randomly placed and covering entire surface near distal margin, occasionally with one or more long hairs inter-

mingled at posterior edge; tibia with rows of small spines along dorsal margins and rows of long spines along ventral margins, often with very small spines scattered over surface between margins, usually with a few long hairs along posterodorsal margin. Pronotum with irregular fringe of small spines along lateral margins. Mesonotum and metanotum with patches of short heavy spines at anterior margin, lateral margins of wing pads with a sparse fringe of thin spines. Abdominal terga with sparse fringes of small spines along distal margins, also with spines covering distal half of abdominal segments. Cerci with whorls of small spines at distal margins of segments, areas between segmental joints elongate and naked.

DISCUSSION.—*Ostrocerca* is a very distinctive genus that is very similar to *Nemurella*. The epiproct is directed backward at an angle (Figures 80–82) and the dorsal sclerite is moved forward (Figures 77–78). The paraprocts are modified with large darkly sclerotized inner lobes (Figure 79) and the cerci are large, sclerotized and have a pointed apex (Figures 80–82).

Most of the species are extremely rare in collections, but more collecting in pristine-spring areas in extreme eastern and western North America should add to the present knowledge.

DISTRIBUTION AND SPECIES LIST.—Nearctic (North America). The following species are presently recognized in the genus *Ostrocerca*:

albidipennis (Walker) 1852, eastern North America
complexa (Claassen) 1937, eastern North America
dimicki (Frison) 1936, northwestern North America
foersteri (Ricker) 1943, northwestern North America
prolongata (Claassen) 1923, eastern North America
truncata (Claassen) 1923, eastern North America

Paranemoura Needham and Claassen

FIGURES 84–91, 153, 165, 180

Nemoura (*Paranemoura*) Needham and Claassen, 1925:288.
 [Type-species: *Nemoura perfecta* Walker.]
Paranemoura.—Claassen, 1940:50.

ADULT.—Length: medium (5–8 mm). Wings (Figure 153): macropterous, terminal costal cross-vein connected to Sc instead of R as is typical for the family, hyaline with fumose areas at and near the cord region, veins dark brown and distinct. Gills: absent but with small single membranous

gill-like nubs on outside of lateral cervical sclerites.

MALE TERMINALIA.—Hypoproct (Figure 90): sclerotized, broad at base, tapering to narrow rounded apex, extending to and between paraprocts; vesicle absent. Paraprocts (Figure 87): consisting of 1 large sclerotized lobe on each side of midline, lobes shaped like broad triangles, covered with short thin hairs. Cerci (Figures 88–90): short, membranous and unmodified. Epiproct (Figures 84–86): mostly sclerotized, composed primarily of ventral sclerite, broad at base with long thin apex, bilaterally symmetrical, completely recurved; dorsal sclerite with thin base at posterior basal end, lateral portions of sclerite extending upward and forward as thin paired arms which fit into large groove formed by ventral sclerite, apex of paired arms becoming abruptly large and sickle-shaped, pointed tips directed backward and protruding slightly from dorsoposterior margins of epiproct; basal sclerites as large broad triangles, located at basolateral corners of epiproct; ventral sclerite very large and broad at base, convex ventrally and curving upward laterally to enclose dorsal sclerite, dorsolateral margins heavily sclerotized and bearing small stout spines, apical third narrow and elongate, forming naked pointed apex. Tenth tergum (Figure 88) almost completely bisected at midline, median membranous area very broad and concave, with sclerotized areas near base of epiproct and at base of segment directly under tip of epiproct, lateral areas produced, heavily sclerotized and bearing many small spines. Ninth tergum heavily sclerotized, not produced but constricted and quite narrow at midline, bearing a few small hairs and spines.

FEMALE TERMINALIA (Figure 91).—Seventh sternum slightly produced at midline, produced area lightly sclerotized, extending over anterior margin of eighth sternum. Eighth sternum narrow, posterior median margin indented toward genital opening, dark triangular sclerotized area over genital opening. Cerci small membranous and unmodified. Paraprocts large, triangular and with rounded corners.

NYMPH.—Gills: absent but small membranous gill-like nubs on outside of lateral cervical sclerites. Forelegs (Figure 165): tibia slightly longer than femur, whole leg covered with many small spines; femur with a few long thin spines along posterior margin, and on surface near distal end, occasional

long hairs extending from posterior margin; tibia with fringes of long thin spines along anterior margins, with an occasional long hair along posterior margin. Pronotum with many small spines covering entire surface, without definite lateral fringe of spines, corners rounded, segment longer than wide. Mesonotum and metanotum with a few stout spines along anterior margins. Abdominal terga sparsely covered with small spines, fringes of spines along distal margins sparse, with longer spines near lateral margins. Cerci with whorls of spines along distal margins of segments, areas between segmental joints with a few small spines.

DISCUSSION.—*Paranemoura* is presently monotypic, but I have seen specimens of another species belonging to this genus. The wings do not exhibit a perfect "X" because the terminal costal cross-vein that usually runs from C to R runs from C to Sc at the cord (Figure 153). The vesicle is absent from the ninth sternum (Figure 90) as in *Lednia*, but the paraprocts in *Paranemoura* are single, short, and membranous (Figure 87). The epiproct is specialized with the dorsal sclerite being enclosed in groove of the ventral sclerite and located near the base of the epiproct (Figures 84–85).

This genus is uncommon and known only from isolated localities in northeastern North America.

DISTRIBUTION AND SPECIES LIST.—Nearctic (North America). *Paranemoura* contains one known species:

perfecta (Walker) 1852, eastern North America

Podmosta Ricker

FIGURES 92–99, 163, 181

Nemoura (*Podmosta*) Ricker, 1952:42. [Type-species: *Nemoura decepta* Frison.]

Podmosta.—Illies, 1966:219.

ADULT.—Length: small (3–6 mm). Wings: macropterous, venation typical for family, hyaline but with dark areas around veins in area of cord, veins dark brown and distinct. Gills: absent but with small single membranous gill-like nubs on outside of lateral cervical sclerites, base of lateral cervical sclerites very broad.

MALE TERMINALIA.—Hypoproct (Figure 98): lightly sclerotized medially, heavily sclerotized around margins and at apex, base broad, tapering abruptly to narrow pointed apex which reaches to

base of epiproct; vesicle present. Paraprocts (Figure 95): consisting of one large lightly sclerotized lobe on each side of midline, lobes shaped like short triangles, covered with many small hairs. Cerci (Figures 96–98): short membranous and unmodified. Epiproct (Figures 92–94): complex in structure, often with dorsal and ventral sclerites separated at apex and throughout length but joined at base, mostly sclerotized, short broad and bilaterally symmetrical, not completely recurved but directed upward at an angle to the body axis; dorsal sclerite with broad lightly sclerotized base, often bearing long hairs, base shifted forward to base of dorsal surface, median area very large and produced, with a lightly sclerotized dorsal band or patch, lateral arms of sclerite darkly sclerotized, long and thin, extending laterally from base to near apex of epiproct, tips modified as hooks or prongs; basal sclerites as long, broad triangles, located at basolateral corners of epiproct; ventral sclerite long, sclerotized and flat, apex often enlarged and bearing small paired sclerotized patches ventrally, dorsal surface usually with paired sclerotized bars, curved at apex. Tenth tergum (Figure 96) greatly produced laterally, usually darkly sclerotized and with many small hairs or spines, anterior median area concave and membranous, tergum often nearly completely bisected, lateral posterior corners enlarged and sclerotized, basal concave area mostly membranous but with paired sclerotized bars which attach to base of epiproct. Ninth tergum not produced or greatly modified, sometimes with small incised area along anterior margin, bearing hairs or spines.

FEMALE TERMINALIA (Figure 99).—Seventh sternum usually slightly produced and lightly sclerotized at posterior margin. Eighth sternum with sclerotized median area that terminates at genital opening, sometimes overlapping into opening, in one case formed into a small subgenital plate, sometimes with small lightly sclerotized vaginal lobes. Cerci small membranous and unmodified. Paraprocts small and triangular, with rounded corners.

NYMPH.—Gills: absent but with small single membranous gill-like nubs on outside of lateral cervical sclerites, base of cervical sclerites very broad. Forelegs (Figure 163): tibia and femur of approximately equal length; femur with very small spines and very large spines mixed along

posterior margin and on distal third; tibia with fringe of medium, stout spines along posterior margin, sparse fringe of long hairs also along posterior margin, whole segment with numerous small spines. Pronotum with sparse areas of small spines along lateral margins but without a definite lateral fringe, corners rounded producing an almost oval shape. Mesonotum and metanotum with a few stout spines at anterior margins. Abdominal terga with fringes of moderate spines along distal margins. Cerci with whorls of spines at distal margins of segments, areas between segmental joints naked near base of cerci but with occasional spines near apex.

DISCUSSION.—*Podmosta* is a small genus and is very distinctive in both the male and female. The males have an epiproct which is directed upward at an angle almost perpendicular to the body axis (Figure 97). Both the dorsal and ventral sclerites are highly developed and often nearly separate except at the base (Figures 92–94). The females have a distinct darkly sclerotized patch along the midline of the eighth sternum (Figure 99).

This genus is common in western North America in small cold streams at high elevations. It also occurs in northeastern Canada and one species has recently been collected by Dr. L. A. Zhiltzova in the Soviet Far East (pers. comm.).

DISTRIBUTION AND SPECIES LIST.—Holarctic (North America, Asia). The genus *Podmosta* contains the following species:

decepta (Frison) 1942, western North America
delicatula (Claassen) 1923, western North America
macdunnoughi (Ricker) 1947, eastern Canada
obscura (Frison) 1936, northwestern United States
weberi (Ricker) 1952, Alaska, northeastern Asia

Prostoia Ricker

FIGURES 100–107, 148, 164, 182

Nemoura (*Prostoia*) Ricker, 1952:47. [Type-species: *Nemoura completa* Walker.]

Prostoia.—Illies, 1966:220.

ADULT.—Length: small (4–7 mm). Wings (Figure 148): macropterous, venation typical for family, hyaline with scattered fumose areas, large dark areas near apex and beginning at cord and extending to posterior margin of forewing, distinctive narrow light vertical stripe formed between fumose areas, veins dark brown and distinct.

Gills: absent but with small single membranous gill-like nubs on outside of lateral cervical sclerites.

MALE TERMINALIA.—Hypoproct (Figure 106): sclerotized, broad at base and throughout most of length, apex tapering abruptly to narrow pointed tip, extending between paraprocts; vesicle present. Paraprocts (Figure 103): single lightly sclerotized lobe on each side of midline, lobes shaped like small short equilateral triangles, bearing many thin hairs. Cerci (Figures 104–106): moderately long, membranous and unmodified. Epiproct (Figures 100–102): completely sclerotized, dorsal sclerite and ventral sclerite almost completely separated, ventral sclerite comprising most of epiproct which is long, narrow and completely recurved dorsally; dorsal sclerite with long, moderately thick base, running from one basolateral corner to the other, not extending above base of epiproct, lateral arms beginning at lateral corners, fused to base of sclerite, hooking forward and outward nearly parallel to ventral sclerite, usually very small but nearly three-fourths length of epiproct in one species; basal sclerites as long broad triangles, located at basolateral corners of epiproct below base of dorsal sclerite; ventral sclerite heavily sclerotized, lateral aspect long and narrow, curving upward laterally to form dorsal surfaces, dorsal aspect long but quite broad, bilaterally symmetrical, with a definite dorsal groove, whole sclerite smooth and naked. Tenth tergum (Figure 104) little produced but extending forward and nearly dividing ninth tergum at midline, mostly sclerotized, flat and broad, almost completely bisected at midline by narrow membranous band that lies directly under ventral sclerite, sclerotized portions covered with many small hairs or spines. Ninth tergum broad laterally but very narrow and almost divided at midline, not produced but covered with many small hairs or spines.

FEMALE TERMINALIA (Figure 107).—Seventh sternum slightly produced, broadly rounded and often appearing connected to eighth sternum at midline, produced area often lightly sclerotized. Eighth sternum broad and little developed, sclerotized at posterior margin near genital opening, subgenital plate poorly developed except in one species where the posterolateral margins are extended as short flat platelike lobes. Cerci small membranous and unmodified. Paraprocts small and triangular, with rounded corners.

NYMPH.—Gills: absent but with small single membranous gill-like nubs on outside of lateral cervical sclerites. Foreleg (Figure 164): tibia and tarsus of approximately equal length, most of leg covered with many small spines; femur with few very large spines found along posterior margin on distal half; tibia with fringe of large spines along posterior margin, fringe of long hairs intermingled along posterior margin. Pronotum with sparse areas of small spines on lateral margins but without definite lateral fringe, corners rounded producing an almost oval shape. Mesonotum and metanotum with a few stout spines at anterior margins. Abdominal terga with fringes of spines along distal margins, sometimes with two longitudinal rows of single or double long spines. Cerci with whorls of spines at distal margins, areas between segmental joints naked except for occasional spines near apex of cerci.

DISCUSSION.—*Prostoia* is highly modified and is very similar in the shape of the epiproct to some species of Capniidae, especially the genus *Mesocapnia*. The males have a very small dorsal sclerite located at the basolateral margins of the epiproct. The ventral sclerite is very large and completely sclerotized both dorsally and ventrally (Figures 100–102). The females have no definite pregenital or subgenital plate but only a small sclerotized area along the posterior margin of the eighth sternum (Figure 107).

This genus can be very common in the early spring and is often collected on bridges along with species of Capniidae and Taeniopterygidae.

DISTRIBUTION AND SPECIES LIST.—Nearctic (North America). The genus *Prostoia* includes three known species:

besametsa (Ricker) 1952, western North America
completa (Walker) 1852, eastern North America
similis (Hagen) 1861, eastern North America

***Shipsa* Ricker**

FIGURES 108–115, 149, 166, 183

Nemoura (*Shipsa*) Ricker, 1952:49. [Type-species: *Nemoura rotunda* Claassen.]

Shipsa.—Illies, 1966:247.

ADULT.—Length: medium (5–8 mm). Wings (Figure 149): macropterous, venation typical for family, basically hyaline but with scattered dark areas in forewing, large dark area at apex and wide

dark stripe running downward from cord, separated by narrow light strip running the width of forewing, veins dark and distinct. Gills: absent but with small single membranous gill-like nubs on outside of lateral cervical sclerites, base of lateral cervical sclerites very broad.

MALE TERMINALIA.—Hypoproct (Figure 114): sclerotized, short and broad, broadest at base, tapering abruptly at apex to short narrow rounded tip, extending to base of epiproct; vesicle present. Paraprocts (Figure 111): consisting of 1 large heavily sclerotized lobe on each side of midline, lobes shaped like short broad triangles. Cerci (Figures 112–114): medium, membranous and unmodified. Epiproct (Figures 108–110): mostly sclerotized, short, broad and bilaterally symmetrical, not completely recurved but directed upward slightly at base; dorsal sclerite divided into 3 heavily sclerotized parts, heavy basal part shifted somewhat forward and extending onto dorsal surface at lateral margins, base broad and heavily sclerotized, apical portions broad and ending in slanted points, lateral arms arising below apices of basal part, long thin and horn-shaped, curving outward and upward at narrow apex; basal sclerites large and broad, shaped like short broad triangles, located at basolateral corners of epiproct, usually covered by paraprocts; ventral sclerite flat and very broad ventrally, naked except for single small stout spines on anterolateral margins, paired lightly sclerotized bands extending outward from apex, bands curving backward onto epiproct between dorsal sclerite and extending upward dorsally where they become very large, appearing as two thick sclerotized forceplike plates on dorsal surface. Tenth tergum (Figure 112) bisected medially, paired lateral sclerotized bars leading to base of epiproct, lateral distal portions large and produced into long inward curved processes, outer margin of processes heavily sclerotized, inner margin membranous, inner and dorsal surfaces covered with many small dark spines. Ninth tergum incised along basal margin forming light membranous hemispherical area, median sclerotized portion narrow. Terga 8 to 5 with hemispherical membranous areas at base, membranous areas becoming smaller toward anterior portion of abdomen.

FEMALE TERMINALIA (Figure 115).—Seventh sternum little produced, extending only slightly onto

eighth sternum, with broad lightly sclerotized area along posterior margin. Eighth sternum broad, mostly sclerotized, median area developed into narrow sclerotized subgenital plate which reaches to posterior margin of sternum, small dark triangular patch located near genital opening, large triangular sclerotized patches extending from basolateral margins of sternum to midline, broad sclerotized bands on posterolateral margins. Cerci small, membranous and unmodified. Paraprocts small and triangular, with rounded corners.

NYMPH.—Gills: absent but with small single membranous gill-like nubs on outside of lateral cervical sclerites, base of cervical sclerites very broad. Forelegs (Figure 166): tibia slightly longer than femur, whole leg covered with many medium-sized spines; femur with numerous long spines scattered along posterior margin; tibia with fringe of long thin hairs along posterior margin. Pronotum with numerous small spines scattered over surface but without a definite lateral fringe. Mesonotum and metanotum with scattered small spines. Abdominal terga covered with numerous small spines, with fringes of small spines along distal margins. Cerci with whorls of spines at distal margins of segments, areas between segmental joints with a few large spines, number of spines increasing from base to apex of cerci.

DISCUSSION.—*Shipsa* is a very distinctive genus, especially in the male terminalia. The tenth tergum is produced into long terminal projections, 1 on each side of the epiproct (Figures 112–113). The epiproct is modified with the ventral sclerite extending to the dorsal surface and terminating in a prominent forcep-shaped structure (Figures 108–110). The nymphs have a definite fringe of long hairs along the posterior margins of the tibiae (Figure 166).

It is common in eastern and northern North America in the early spring.

DISTRIBUTION AND SPECIES LIST.—Nearctic (North America). This genus contains a single known species:

rotunda (Claassen) 1923, eastern and northern North America

Soyedina Ricker

FIGURES 116–123, 152, 170, 184

Nemoura (*Soyedina*) Ricker, 1952:50. [Type-species: *Nemoura vallicularia* Wu.]

Soyedina.—Illies, 1966:247.

ADULT.—Length: medium (6–12 mm). Wings (Figure 152): macropterous, venation altered so that A_1 and A_2 of forewings merge slightly before wing margin, generally hyaline, with scattered fumose areas, without definite mottled pattern, veins dark and distinct. Gills: absent but with single membranous gill-like nubs outside of lateral cervical sclerites.

MALE TERMINALIA.—Hypoproct (Figure 122): broadest at base, quite long and thin, extending distally to base of paraprocts, apical third bent abruptly upward, terminating in a very narrow tip; vesicle present. Paraprocts (Figure 119): consisting of 2 lobes (inner lobe sometimes difficult to observe); inner lobes lightly sclerotized, short and narrow, closely applied to inner margin of outer lobes, often completely hidden by hypoproct; outer lobes large and darkly sclerotized, with small membranous area along inner margin and near apex, very broad at base and extending around cerci, apical half elongate and rectangular in shape, sometimes with serrated margin or blunt process near apex, usually completely enclosing epiproct laterally. Cerci (Figures 120–122): small, simple and membranous. Epiproct (Figures 116–118): mostly sclerotized, short thin and asymmetrical in both dorsal and lateral views, not completely recurved, but directed at an oblique angle upward and backward from longitudinal axis of abdomen, left half similar but smaller than right half; dorsal sclerite broad at base of epiproct, extending toward apex, becoming abruptly very narrow near base and then broad again in apical two-thirds, covering most of dorsal and lateral aspects, most heavily sclerotized areas at base and directly ahead of basal cushion, apical area lightly sclerotized but covered with numerous small spines or scalelike plates; basal sclerites as 2 large elongate rectangular patches located near basolateral corners of epiproct; ventral sclerite heavily sclerotized, broad at base, with small lateral knobs at basolateral corners, becoming narrower toward apex, forming 2 parallel bars, 1 on each side of midline, each bearing a row of spines, narrow projection extending inward and upward to dorsal surface near apex, projection ending in single tube-shaped process or double asymmetrical processes. Tenth tergum (Figure 120) moderately produced, mostly sclerotized, forming a large flat area anterior to base of epiproct, surface naked or with a few very small hairs

or spines. Ninth tergum sclerotized but not produced, sclerotized portion very narrow near midline, sometimes with very small hairs or spines. Anterior abdominal tergites sometimes modified as elevated knobs or projections.

FEMALE TERMINALIA (Figure 123).—Seventh sternum enlarged and extended distally, covering part or all of eighth sternum, produced area lightly sclerotized. Eighth sternum narrow and excavated at midline, mostly membranous but with a distinct darkly sclerotized patch at genital opening. Paraprocts triangular and pointed at apex. Cerci short, simple and membranous.

NYMPH.—Gills: absent but with very small single nubs outside of lateral cervical sclerites on each side of midline. Forelegs (Figure 170): femur and tibia of approximately equal length, whole leg usually covered with small spines or hairs; femur with randomly scattered large spines dorsally on distal portion, extending from anterior to posterior margin, with a few long hairs intermingled along posterior margin; tibia with rows of large spines somewhat randomly distributed on anterior, posterior, and dorsal surfaces, ventral inner surface naked or with a few small spines. Pronotum not completely square or rectangular, with definite notch on lateral margins, basal third somewhat narrower, fringe of short stubby spines on all margins. Mesonotum and metanotum with sparse fringe of small spines on lateral margins of wingpads. Abdominal terga with fringe of short spines along distal margins, often with lateral rows of single long hairs. Cerci with whorls of spines at distal margins of segments, intermediate segmental spines very small, sparse and located near base of cerci.

DISCUSSION.—*Soyedina* is the only genus in Nemouridae where the shape of the epiproct is always asymmetrical. The epiproct is bisected down the middle and the right half is larger than the left half (Figures 116–118). The paraprocts are also greatly enlarged and highly modified into ventrolateral structures which often nearly enclose the epiproct (Figures 119, 122). The character that veins A_1 and A_2 of the forewings are joined (Figure 152) does not always hold true. Sometimes only one wing exhibits this character and rarely neither wing.

This genus is usually found in clear cold streams

at high elevations and emerges in the spring or early summer.

DISTRIBUTION AND SPECIES LIST.—Nearctic (North America). The following species are known in the genus *Soyedina*:

carolinensis (Claassen) 1923, southeastern United States
interrupta (Claassen) 1923, northwestern North America
nevadensis (Claassen) 1923, California, Nevada
potteri (Baumann and Gaufin) 1971, Idaho, Montana
producta (Claassen) 1923, northwestern North America
vallicularia (Wu) 1923, eastern North America
washingtoni (Claassen) 1923, northeastern North America

Visoka Ricker

FIGURES 124–131, 146, 168, 185

Nemoura (*Visoka*) Ricker, 1952:53. [Type-species: *Nemoura cataractae* Neave.]
Visoka.—Illies, 1966:249.

ADULT.—Length: small to medium (5–8 mm). Wings: macropterous, venation typical for family, clear or slightly cloudy around veins, which are dark and distinct. Gills (Figure 146): 1 branched gill on each side of midline, between labium and submentum, gill branches 5, divided nearly to base.

MALE TERMINALIA.—Hypoproct (Figure 130): broad at base, tapering to narrow apex, extending distally over inner lobes of paraprocts and sometimes to base of epiproct; vesicle present. Paraprocts (Figure 127): divided into 2 lobes; inner lobes darkly sclerotized, naked, narrow and sickle-shaped, closely applied to midline, sometimes completely hidden by hypoproct; outer lobes darkly sclerotized at broad triangular base, apical half bluntly rounded and membranous, covered with small hairs. Cerci (Figures 128–130): heavily sclerotized dorsally and with a large distinct spine at the inner apical margin, lightly sclerotized laterally, membranous ventrally and covered with small hairs, tip with a small light area which encircles the small brown segment remnant. Epiproct (Figures 124–126): elongate and narrow in dorsal view, bilaterally symmetrical, elongate and recurved in lateral view, with widest area at bend; dorsal sclerite broad but very short at base, apical portion narrow, lateral arms extending dorsolaterally toward apex, arms thin and narrow extending under large lightly sclerotized area near base; basal sclerites, as 2 thin triangular plates,

located at basolateral margins of epiproct; ventral sclerite heavily sclerotized, broadest at base, tapering to narrow apex, forming total epiproct at apex (apical third), ventral keel-shaped ridge naked of conspicuous spines. Tenth tergum (Figure 128) mostly sclerotized, forming a large flat dorsal area, with rounded membranous area under apex of epiproct, median sclerotized patch located beyond tip of epiproct, lateral margins produced and slightly angular. Ninth tergum mostly sclerotized, narrow at midline, slightly produced, bearing small hairs.

FEMALE TERMINALIA (Figure 131).—Seventh sternum produced and lightly sclerotized, extending over half or more of segment eight and covering the genital opening, forming a large nipplelike structure in lateral aspect. Eighth sternum narrow and with a distinct darkly sclerotized patch over genital opening. Ninth sternum wide and only lightly sclerotized but with more darkly sclerotized areas near lateral margins. Cerci lightly sclerotized, truncate at apex, with a small projection on inner apical margins.

NYMPH.—Gills (Figure 146): 1 branched gill on each side of midline between labium and submentum, gill branches 5, all divided nearly to base. Forelegs (Figure 168): femur and tibia of approximately equal length, most of leg covered with small fine hairs; femur with fringe of small hairs along posterior margin, with a diagonal whorl of long irregular spines on distal half; tibia with row of very long spines along posterior margin, with many long hairs intermingled, a row of small spines along anterior margin, with an occasional large spine in between. Pronotum with irregular fringe of spines along lateral margins (Figure 146). Abdominal terga with very sparse fringes of hairs along distal margins, composed mostly of long hairs in longitudinal rows. Cerci with whorls of spines at distal margins of segments, areas between joints with occasional small spines.

DISCUSSION.—*Visoka* is the only genus in the Nemouridae that has submental gills (Figure 146). The structure of the cerci and epiproct is similar to some species in the Cercispinosa Complex of *Nemoura*, but those species have simple bulbous paraprocts and *Visoka* has a narrow sclerotized inner lobe and a broad outer lobe, which has a membranous apex (Figure 127).

Visoka is known only from scattered localities in western North America.

DISTRIBUTION AND SPECIES LIST.—Nearctic (North America). The genus *Visoka* contains one species: *cataractae* (Neave) 1933, western North America

Zapada Ricker

FIGURES 1, 132-139, 147, 150, 172, 186

Nemoura (*Zapada*) Ricker, 1952:54. [Type-species: *Nemoura haysi* Ricker.]
Zapada.—Illies, 1966:250.

ADULT.—Length: small to large (5-14 mm). Wings (Figure 150): macropterous or brachypterous, venation typical for family in macropterous species, fumose or mottled, veins dark and distinct. Gills (Figure 147): 2 simple cervical gills on each side of midline, 1 arising inside and 1 outside of lateral cervical sclerites, usually unbranched but with 3 or 4 branches in *Z. cinctipes* (branches arising beyond gill base).

MALE TERMINALIA.—Hypoproct (Figure 138): broad at base, tapering to pointed apex, extending distally over inner lobes of paraprocts, tip extending nearly to base of epiproct; vesicle present. Paraprocts (Figure 135): consisting of 2 lobes; inner lobes sclerotized, long narrow and closely applied at midline, usually completely hidden by hypoproct; outer lobes sclerotized ventrally and membranous dorsally, very large and almost square or rectangular-shaped. Cerci (Figures 136-138): membranous, short and unmodified. Epiproct (Figures 132-134): completely recurved, mostly sclerotized, bilaterally symmetrical, short and broad in dorsal aspect, short and broad to narrow laterally, apex narrow; dorsal sclerite very large and broad at base of epiproct, extending dorso-laterally, becoming narrow around lateral knobs and then very large and triangular, often completely covering lateral portions of epiproct, most darkly sclerotized areas at base and near posterior end immediately ahead of basal cushion, anterior area lightly sclerotized and usually composed of many small overlapping scales or plates; basal sclerites as 2 broad triangular or rectangular patches located near basolateral corners of epiproct; ventral sclerite heavily sclerotized, broad at base, with lateral knobs at basolateral cor-

ners, becoming gradually narrower toward apex, forming a flat or convex base, bearing rows of long spines along lateral ridges, often covered by dorsal sclerite near apex, sometimes extending inside epiproct to dorsal margin, extended portion paired and sometimes visible in lateral view. Tenth tergum (Figure 136) mostly sclerotized, forming a large flat or concave area anterior to base of epiproct, bearing hairs and small spines, especially near proximal margin. Ninth tergum sclerotized but not produced, sclerotized portion narrow and with a few hairs and small spines.

FEMALE TERMINALIA (Figure 139).—Seventh sternum enlarged and extended at distal margin forming large pregenital plate, covering most or all of eighth sternum, produced area heavily sclerotized. Eighth sternum narrow, with a dark sclerotized patch over genital opening. Cerci short membranous and unmodified. Paraprocts broad and somewhat triangular.

NYMPH (Figure 1).—Gills (Figure 147): 2 cervical gills on each side of midline, 1 arising inside and 1 outside of lateral cervical sclerites, usually single and elongate, sometimes constricted but with 3 or 4 branches arising beyond gill base in *Z. cinctipes*. Forelegs (Figure 172): femur and tibia of approximately equal length; femur with a whorl of long spines near distal end, spines arranged in rows, with small space between dorsal and ventral arcs, with a few scattered spines along dorsoposterior margin; tibia with row of long spines along dorsoposterior margin; often with long hairs intermingled, ventral surface with rows of long spines along anterior and posterior margins. Whorls of spines present on femora of middle and hindlegs. Pronotum (Figure 1) with fringe of large stout spines on lateral margins which often completely encircle the outer margins. Mesonotum and metanotum (Figure 1) with fringes of long stout spines along lateral margins. Abdominal terga (Figure 1) with fringes of spines along distal margins, often with some enlarged and arranged in longitudinal rows. Cerci (Figure 1) with whorls of large spines at distal margins of segments, intermediate segmental spines absent or rare near apex of cercus.

DISCUSSION.—*Zapada* is the most common genus of Nemouridae in western North America. *Zapada cinctipes* Banks is found in almost every flowing-water habitat and sometimes emerges throughout

the year as recorded by Hales and Gaufin (1971). The genus is not uncommon in Alaska and could also be present in eastern Asia. Most species emerge very early in the year and are collected along with the winter Capniidae.

Zapada is a very distinctive genus in both the adult and nymphal stage. The combination of a single, simple gill on each side of the lateral cervical sclerites (Figure 147), large angular outer paraproctal lobes (Figures 135) and a short, broad epiproct with the dorsal sclerite well developed (Figures 132–134) serves to separate this from all other Nemouridae. The nymphs have whorls of large spines on all femora (Figure 1).

DISTRIBUTION AND SPECIES LIST.—Nearctic (North America). The following species are in the genus *Zapada*:

- chila* (Ricker) 1952, Tennessee
- cinctipes* (Banks) 1897, western North America
- columbiana* (Claassen) 1923, western North America
- cordillera* (Baumann and Gaufin) 1971, western North America
- frigida* (Claassen) 1923, western North America
- glacier* (Baumann and Gaufin) 1971, Montana
- haysi* (Ricker) 1952, western North America
- oregonensis* (Claassen) 1923, western North America

Species Incertae Sedis

The generic placement of the following species of the family Nemouridae is uncertain at this time. In most cases the original description and drawings are very poor, and fresh specimens were not available for study. Sometimes the species is only known from the type-specimen, which is in very poor condition.

Although some of these species have been placed in other genera by some authors, I am simply listing them as they were originally described.

- **Amphinemura microcercia* Wu 1938, China
- **Nemoura asakawae* Kohno 1941, Japan
- Nemoura babai* Kawai 1966c, Japan
- **Nemoura bituberculata* Kimmins 1950b, Assam
- Nemoura denticulata* Kawai 1954, Japan
- Nemoura elephas* Zwick 1974, Taiwan
- **Nemoura grandicauda* Wu 1973, China
- **Nemoura hangchowensis* Chu 1928, China
- Nemoura spinosa* Kawai 1960, Japan
- Nemoura stratum* Kawai 1966c, Japan
- Nemoura wahkeena* Jewett 1954, Oregon
- Protonemura cherrapunjii* Aubert 1967, Assam
- **Protonemura chinonis* Okamoto 1922, Japan

- Protonemura filigera* Kawai 1969, Thailand
- Protonemura longiplata* Wu 1949, China
- Protonemura recurvata* Wu 1949, China
- Protonemura scutigera* Kimmins 1950b, Assam
- Protonemura trifurcata* Wu 1949, China

Phylogeny

This study of the phylogeny of the Nemouridae is based on Hennig's (1966) method of "phylogenetic systematics." Hennig's method is of the cladistic type and is as follows: taxa to be monophyletic must be based upon synapomorphic character states. Character states are identified as either apomorphic or plesiomorphic and a system of monophyletic taxa is established. Within this system, two monophyletic taxa form a sister-group pair if each taxon exhibits a different apomorphic character state that is plesiomorphic in the other, and if they share a third apomorphic character state. The two taxa are then sister groups of each other. The method is to search for the sister group (Brundin, 1965; Munroe, 1974).

A similar phylogenetic study was done by Zwick (1973a) for the order Plecoptera. He included some information on the Nemouridae but refrained from a detailed analysis because he knew that I was revising the family Nemouridae.

The following synapomorphic character states were cited by Zwick (1973a) for the family Nemouridae:

1. The structure of the internal male sex organs. The testes are large and long and radiate from the anterior bend of the vas deferens in the shape of a star.
2. The reduction of the abdominal ganglia to only five.
3. The large, round flat shape of the last segment of the labial palpi.
4. The shape and site of insertion of the coxae.

APOMORPHIC CHARACTER STATES

The following list of apomorphic character states was used in detecting the phylogenetic relationships between the genera of Nemouridae as shown in the Argumentation Scheme (Figure 2). After each character state I give my reasons for deciding that it is apomorphic. The numbers refer to those used in the Argumentation Scheme.

TABLE 1.—Plesiomorphic (primitive) and apomorphic (derived) conditions of some characters of *Nemouridae*

Character	Plesiomorphic	Apomorphic
Head		
submental gills	absent	present
Thorax		
cervical gills	present simple	absent branched
Legs (nymphs)		
spines	absent irregular	present whorls
Wings		
veins A ₁ and A ₂	separate	fused
terminal costal crossveins.....	joining R	joining Sc
Abdomen (male)		
vesicle	present	absent
terga 4 to 8	simple	enlarged or modified
tergum 9	slightly produced symmetrical	greatly enlarged
Tergum 10	flat or concave	asymmetrical enlarged and modified
sclerotized bars	naked single	spines or prongs double
Male genitalia		
epiproct	symmetrical completely recurved	asymmetrical directed upward
dorsal sclerite	fused through- out	divided longi- tudinally
base	large	small
basal cushion	normal	dorsal
ventral sclerite	absent	present
flagellum	narrow and keel-shaped	broad and flat
lateral knobs	absent	present
paraprocts	naked	spines or prongs
lobes	simple short	modified elongate
inner lobes	two	three or one
	small lightly sclerotized	large heavily sclerotized
Female genitalia		
pregenital plate	absent	present
subgenital plate	present lightly sclerotized	absent heavily sclerotized
vaginal lobes	small	large
posterior margin	straight	bifurcate
Cerci	short membranous	elongate sclerotized
mesobasal lobe	absent	present
ventrobasal lobe	absent	present
spines or hooks	absent	present

At the base of the diagram, the four synapomorphies of the Nemouridae given by Zwick (1973a) are shown but not numbered.

1. *Division of male paraprocts into three lobes.* The plesiomorphic state of the male paraprocts in Plecoptera is a single, large, lightly sclerotized lobe. I suggest that the hypothetical stem nemourid had already developed a small poorly developed inner lobe like is present in most of the Nemourinae today. The subsequent development of an outer or cervical lobe is the apomorphic character state that separates the Amphinemurinae as a subfamily and unites the genera in the Amphinemurinae as a monophyletic lineage.

2. *Male paraprocts armed with spines or prongs.* The majority of the Plecoptera have paraprocts naked of spines or prongs. I conclude that spines or prongs on the middle or outer paraproctal lobes, found in all genera of Amphinemurinae, is an apomorphic state.

3. *Ventral sclerite of epiproct enlarged and with a very broad base.* The plesiomorphic condition is a thin, sclerotized keel-shaped sclerite that connects at the base as a narrow sclerotized band. This derived modification unites the Nemourinae as a monophyletic lineage.

4. *Two highly branched cervical gills present, one on each side of lateral cervical sclerites.* The plesiomorphic state of nemourid gills is the single fingerlike condition. This synapomorphy unites the genera *Amphinemura* and *Malenka*.

5. *Female subgenital plate developed into large sclerotized median lobe which overlaps vaginal lobes.* The plesiomorphic state in Amphinemurinae is paired vaginal lobes and no median plate. The development of a large sclerotized median plate is the synapomorphic condition that combines *Indonemoura*, *Mesonemoura*, and *Protonemura* in a monophyletic lineage.

6. *Mesobasal lobe present on dorsolateral margins of male cerci.* Most male nemourids have simple membranous cerci. Formation of a specialized mesobasal lobe is the apomorphic state that separates *Malenka* from its sister-genus *Amphinemura*.

7. *Cervical gill branches all extending to gill base.* Although branched gills represent a derived character state, most branching is partial and incomplete. Numerous thin branches that all extend to the gill base is an apomorphic character state

that distinguishes *Amphinemura* as a distinct genus.

8. *Outer cervical gills with a single deep fork.* The plesiomorphic state is a single, simple gill on each side of the lateral cervical sclerites. This forked condition of the outer gill represents an apomorphic state that serves to separate the genus *Protonemura*.

9. *Inner cervical gills absent or reduced to small nubs.* The plesiomorphic state is a single, simple gill on each side of the lateral cervical sclerites. The loss of the gills inside the lateral cervical sclerites is a synapomorphic condition that unites *Mesonemoura* and *Indonemoura* as a monophyletic sister-group pair.

10. *Male cerci elongate.* Most male Nemouridae have very short cerci. This synapomorphic state helps unite the genera *Mesonemoura* and *Indonemoura*.

11. *Epiproct with large epiproctal flagellum.* Although the other genera in this lineage occasionally have a small epiproctal projection, the remainder of the Nemouridae are without one. The species of *Mesonemoura* all have a large well-developed epiproctal flagellum, and this distinguishes *Mesonemoura* as a separate genus.

12. *Median lobes of male paraprocts greatly enlarged and bearing large apical prongs.* The plesiomorphic condition in the Amphinemurinae is median paraproctal lobes of moderate size with spines or small prongs. This apomorphic state separates the genus *Indonemoura*.

13. *Lateral knobs present on base of ventral sclerite of epiproct.* The plesiomorphic condition of the basolateral corners of the ventral sclerite is a simple broadening at the junction of the sclerotized portion of the tenth tergum. Modification into definite hingelike knobs is one synapomorphic character state that unites the genera *Zapada*, *Illiesonemoura*, *Nemoura*, and *Soyedina*.

14. *Basal cushion present on dorsal base of epiproct.* The lateral arms of the dorsal sclerite bend inward and form a cavity where the basal cushion forms. This structure is absent from the rest of the Nemouridae. I conclude that the presence of this large membranous cushionlike structure immediately in front of the horseshoe-shaped base of the dorsal sclerite unites *Nemoura* and the other genera in this monophyletic lineage.

15. *Ventral sclerite forming entire ventral sur-*

face of *epiproct* and extending over much of lateral and dorsal aspects. The plesiomorphic condition is a narrow ventral sclerite, which is slightly en-

larged at the base and extends upward between the folds of the dorsal sclerite. This enlarged modified state unites the genera in this lineage.

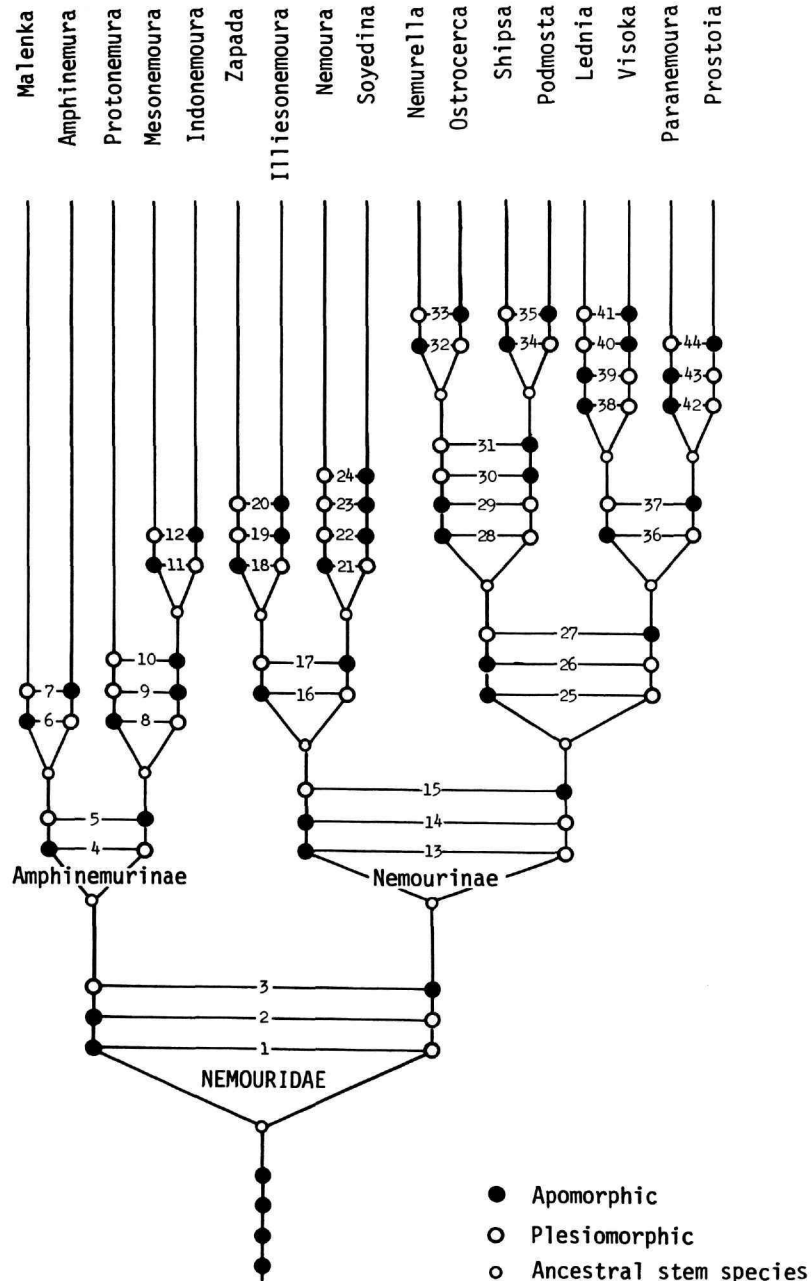


FIGURE 2.—Argumentation scheme for the hypothetical phylogeny of the family Nemouridae.

16. *Distinct whorls of femoral spines present on forelegs of nymphs.* Although the nymphs of most genera have femoral spines, they are seldom arranged in definite fringes or whorls a single spine wide. This synapomorphic state unites *Zapada* and *Illiesonemoura* as sister genera and separates them from *Nemoura* and *Soyedina*.

17. *Cervical gills absent.* The primitive condition is the presence of cervical gills. The absence of cervical gills is an apomorphic condition that serves as a synapomorphic character state to unite *Nemoura* and *Soyedina*.

18. *Whorls of femoral spines present on all nymphal leg pairs.* Since the presence of whorls of femoral spines has been stated to be apomorphic, the transformation of this character state to all leg pairs represents a further apomorphic modification.

19. *Inner cervical gills absent.* Gills both inside and outside of the lateral cervical sclerites is considered the plesiomorphic state. The loss of the inner gills is an apomorphic state.

20. *Outer lobe of male paraprocts with large inward-directed process near apex.* The primitive state of the male paraprocts in the Nemouridae is a large unmodified outer lobe and a small inconspicuous inner lobe. I suggest that this addition of an inward-directed process on the inner margin of the outer lobe is an apomorphic character state that serves to separate the genus *Illiesonemoura*.

21. *Male cerci enlarged, sclerotized, and usually bearing large terminal spines or hooks.* The plesiomorphic condition in Nemouridae is for the cerci to be simple and membranous or lightly sclerotized. The modification of the male cerci into sclerotized, hook-bearing structures is an apomorphic character state.

22. *Male paraprocts with outer lobes elongate and greatly enlarged.* The plesiomorphic state is simple, angular outer lobes. This modification into large modified, sclerotized structures is an apomorphic character state of *Soyedina*.

23. *Epiproct asymmetrical.* Most Nemouridae have a bilaterally symmetrical epiproct. I deduce that an asymmetrical condition produced by the reduction in size of the left half represents a derived character state.

24. *Veins A_1 and A_2 fused near margin of forewings.* The plesiomorphic condition is for veins A_1 and A_2 to run parallel to the margin of the

forewings. This fusion of the anal veins in the forewing is an apomorphic condition.

25. *Dorsal and ventral sclerites separated apically in a longitudinal plane.* The plesiomorphic structure of the epiproct is for the dorsal and ventral sclerites to be joined throughout the length of the epiproct. This division of the two sclerites represents a derived condition. This synapomorphic character state combines *Nemurella*, *Ostrocerca*, *Shipsa*, and *Podmosta* in a monophyletic lineage.

26. *Male tenth tergum joined to epiproct by two lateral sclerotized bars.* The rest of the Nemouridae have the epiproct joined to the tenth tergum by a single, median, sclerotized bar. I suggest that two sclerotized bars joining the epiproct is an apomorphic character state.

27. *Anterior lightly sclerotized portion of dorsal sclerite greatly reduced or absent.* The plesiomorphic state in Nemouridae is for the anterior portion of the dorsal sclerite to cover the entire anterodorsal surface. I suggest that this reduction in the anterior portion of the dorsal sclerite is an apomorphic character development. It is the synapomorphic state that unites the genera *Prostoia*, *Paranemoura*, *Lednia*, and *Visoka*.

28. *Male paraprocts with enlarged darkly sclerotized inner lobes.* The primitive condition is small, lightly sclerotized inner lobes. This modification of the inner lobes of the paraprocts is an apomorphic character state.

29. *Base of dorsal sclerite situated on top of epiproct.* Since the primitive condition is for the horseshoe-shaped base of the dorsal sclerite to be located at the base of the epiproct, this represents a derived condition. This apomorphic character state helps to further unite *Nemurella* and *Ostrocerca*.

30. *Laterodistal margins of male tenth tergum enlarged and bearing hairs or spines.* The lateral margins of the tenth tergum are slightly enlarged in *Nemurella* and *Ostrocerca*, but this is related to their enlarged, sclerotized cerci. This modification of the distal margins is an apomorphic character state that unites *Shipsa* and *Podmosta*.

31. *Inner lobes of male paraprocts absent.* The primitive condition is a large outer lobe and a small thin, sclerotized inner lobe. This loss of the inner lobe helps to combine *Shipsa* and *Podmosta*.

32. *Male cerci with large ventrobasal lobe.* Primitive cerci are simple and unmodified. The cerci of

Ostrocerca are elongate and have sclerotized points at the apex but are unmodified at the base. I suggest that this formation of a ventrobasal lobe in *Nemurella* represents an apomorphic character state that divides it from *Ostrocerca*.

33. *Male cerci elongate, heavily sclerotized, and pointed at apex.* Modifications of the cerci represent apomorphic states in the Nemouridae. The highly modified cerci of *Ostrocerca* are used in separating it from *Nemurella*.

34. *Male tenth tergum with very large sclerotized terminal projections.* The tenth tergum of most Nemouridae is essentially unmodified. The sister genus in this branch, *Podmosta*, also has an enlarged tenth tergum, but it is only partially modified in this direction. These enlarged, highly modified projections of the tenth tergum are an apomorphic condition in *Shipsa*.

35. *Female seventh and eighth sterna not modified into plates.* Most Plecoptera have either the seventh or eighth sternum modified into a genital plate. The plesiomorphic condition is for the eighth sternum to be modified but in the Nemourinae the seventh sternum is usually modified. I submit that a reduction to essentially no genital plate is a derived condition. This apomorphic character state unites the species in *Podmosta* and separates it from *Shipsa*.

36. *Male paraprocts with large darkly sclerotized inner lobes.* The plesiomorphic character state is small, lightly sclerotized inner lobes. This modification of the paraprocts is an apomorphic character state that unites *Lednia* and *Visoka* as a monophyletic sister group.

37. *Ventral sclerite curving upward laterally and forming most of epiproct.* The plesiomorphic state is for the ventral sclerite to be in a ventral or comparable position. The dorsal sclerite is also reduced, but this occurs in other genera without a corresponding modification of the ventral sclerite. This implied synapomorphic state unites *Paranemoura* and *Prostoia* as a monophyletic pair.

38. *Lateral margins of male tenth tergum modified as long narrow upward projections.* The usual condition in primitive Plecoptera and most Nemouridae is a broad flat tenth tergum. These distinct spine-bearing projections represent an apomorphic character state that helps to separate the genus *Lednia*.

39. *Vesicle absent from male ninth sternum.*

Most Nemouridae have a vesicle on the hypoproct or anterior margin of the ninth sternum. The absence of the vesicle represents an apomorphic state that helps separate *Lednia* from *Visoka*.

40. *Branched submental gills present.* Submental gills are not present in any other genera of Nemouridae. Submental gills are present in some other Plecoptera families, but they are usually simple and attached to the base of the submentum as in many Perlodidae. I submit that the presence of branched submental gills, attached between the labium and submentum, is an apomorphic character state that delineates *Visoka* as a distinct genus.

41. *Male cerci sclerotized and highly modified.* The plesiomorphic condition of cerci in Nemouridae is simple, membranous, and unmodified. This modification into short flat cerci with an apical spine is an apomorphic character state. I submit that this occurrence of sclerotized cerci with an apical projection similar to those in *Nemoura* is a result of convergence.

42. *Terminal costal crossvein of forewings joining Sc.* The plesiomorphic state is for the terminal costal crossvein of the forewings to join R. This apomorphic character state separates the genus *Paranemoura*.

43. *Vesicle absent from male ninth sternum.* The primitive condition is for the vesicle to be present on the ninth sternum of the male. The presence of this apomorphic condition in a second genus in this branch of the phylogenetic scheme is explained as an example of convergence. The genetic basis for the loss of the vesicle must have been present in the hypothetical ancestor and has occurred twice in separate genera.

44. *Lateral margins of ventral sclerite fused dorsally, forming dorsal and ventral surfaces of epiproct.* The plesiomorphic state is with the ventral sclerite forming essentially only the ventral aspect of the epiproct, although dorsal projections are often present. This apomorphic character state distinguishes *Prostoia* as a separate genus.

Zoogeography

The Nemouridae are distributed throughout the Northern Hemisphere. The sister family, Notoemouridae, has an extreme Southern Hemisphere or Gondwanian distribution pattern (Illies, 1965).

I suggest that the prenemourids or stem nemourids were present when there was still a distributional connection between Laurasia and Gondwanaland. This would make them approximately 120 million years old (Wilson, 1963).

The family Nemouridae developed on the northern landmass Laurasia. Fossil evidence in the form of fossilized Plecoptera in Baltic amber shows that some of the nemourid genera were present in the lower Oligocene epoch (Illies, 1965). These fossils indicate that the family Nemouridae is at least 25 million years old. When the family split into subfamilies is not known, but it must have been while there was still a good connection between North America and Eurasia, because both subfamilies are well represented by genera in both the Palearctic and Nearctic regions.

The Nemouridae radiated throughout the Northern Hemisphere with evolutionary centers in south central Asia and western North America. These centers correspond generally with the Himalayan Mountains and the Rocky Mountains. These areas presently contain the most extant genera with seven and ten respectively. They also have the most endemic genera with three each (Figure 3).

The subfamily Amphinemurinae contains four genera besides *Amphinemura*, three are found in the Oriental and Palearctic regions, and one is endemic to the Nearctic region. *Protonemura* is widely distributed in the Old World, but *Mesonemoura* and *Indonemoura* are restricted to central Asia. *Malenka* is only found in western North America. *Amphinemura* is the most widely distributed genus in the Nemouridae, it is present throughout the Holarctic region and has also radiated southward into the Oriental region.

The subfamily Nemourinae contains eleven genera besides *Nemoura* and with the exception of *Podmosta*, which is present in both North America and eastern Asia, they are all restricted to either the Oriental and Palearctic regions or the Nearctic region. Two genera, *Nemurella* and *Illiesonemoura*, are only found on the Eurasian continent, and their sister genera *Ostrocerca* and *Zapada* are only found in North America. The six remaining genera—*Lednia*, *Paranemoura*, *Prostoia*, *Shipsa*, *Soyedina*, and *Visoka*—are only known from North America. This does, however, reflect the fact that more research has been done on the North American nemourid fauna. When an adequate study of the Nemouridae of Asia is completed a

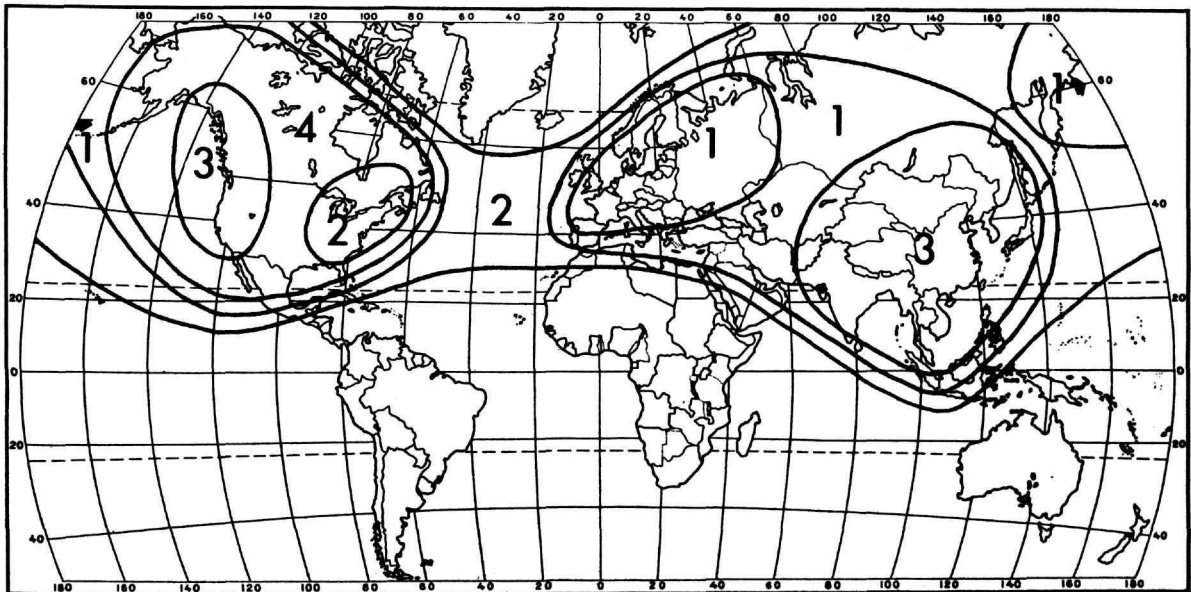


FIGURE 3.—Distribution map of the family Nemouridae. Numbers indicate the numbers of endemic genera occurring within the outlined areas.

better overall understanding will be possible. The species complexes in *Nemoura*—*Cercispinosa* and *Ovocercia*—may quite possibly represent distinct genera endemic to Asia.

Some genera have very interesting distribution patterns. Four genera in Nemourinae—*Ostrocerca*, *Prostoia*, *Soyedina*, and *Zapada*—have a disjunct pattern. They are found in extreme western North America and then again in eastern North America. They probably once ranged all across northern North America but are now absent in the central area. Most eastern species are rare and restricted to high mountain areas that are known to contain relict populations of plants and animals.

Podmosta has a similar disjunct distribution pattern in North America but has also been collected in eastern Asia. *Podmosta weberi* Ricker is known from northern Alaska and the Soviet Far East. This can be best explained by the fact that a land connection existed between Alaska and eastern Asia quite recently in geologic time. *Nemoura arctica* Esben-Petersen is another species that supports this fact because of its widespread holarctic distribution. There was much faunal exchange between North America and Asia in the Pleistocene epoch. This exchange was via the Bering Bridge which served as a major distributional track in the sense of Croizat et al. (1974).

Indonemoura is common in the Himalayan Mountains and then occurs again in the Sunda Islands. It is highly possible that collecting in Burma and Thailand will fill in this distribution gap.

Lednia is only known from two localities in Glacier National Park, Montana. This area of the northern Rocky Mountains was collected intensively over a ten-year period by Dr. Arden R.

Gaufin and others while studying the Plecoptera of Montana (Gaufin et al., 1972), but further records were not obtained. This simply shows that much more collecting needs to be done before our knowledge of the Nemouridae will be complete.

It will also be extremely helpful when the species placed in incertae sedis are studied and assigned to their proper places in the phylogenetic scheme.

Distribution maps are provided for all genera in Figures 173–186, and detailed distribution data are given for each species in the "Distribution and Species List" sections under each genus.

Epilogue

The basis for this revision was to organize the present knowledge of the family Nemouridae, analyze and define the morphological characters available for taxonomy, and construct a hypothetical phylogeny for use in further studies. With this accomplished, the foundation has been laid for detailed studies of the Nemouridae at the specific level.

I plan to do complete revisions of all the genera in Nemouridae over the next decade, including the species incertae sedis. These revisions will include studies of the internal anatomy and will incorporate further analysis of external features using a scanning electron microscope. Ecology and dynamic zoogeographic factors will be studied, especially when dealing with the nymphal or aquatic life stage.

My goal upon completion of the detailed generic revisions is to complete a special study on the phylogeny and zoogeography of the family Nemouridae.

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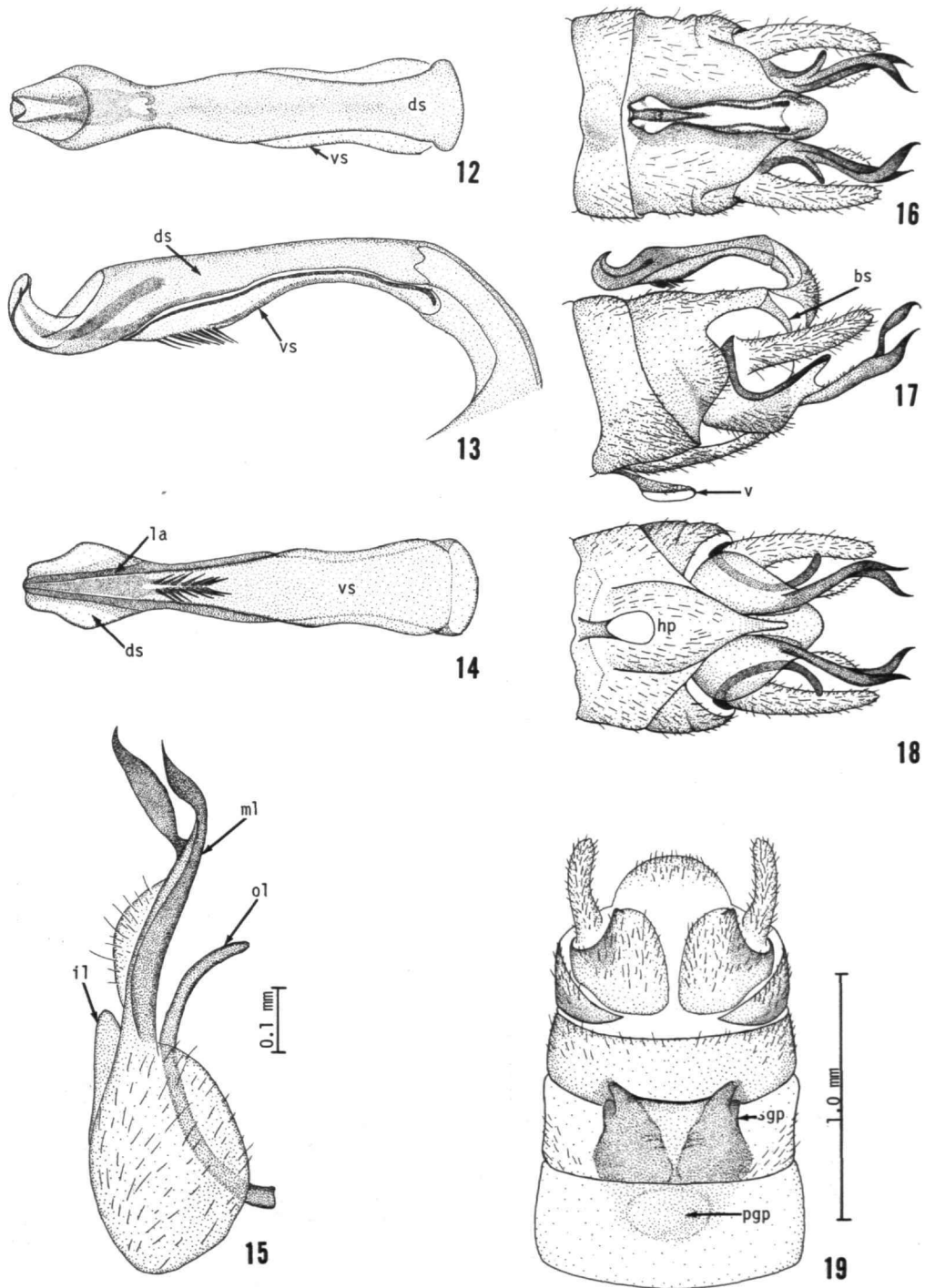
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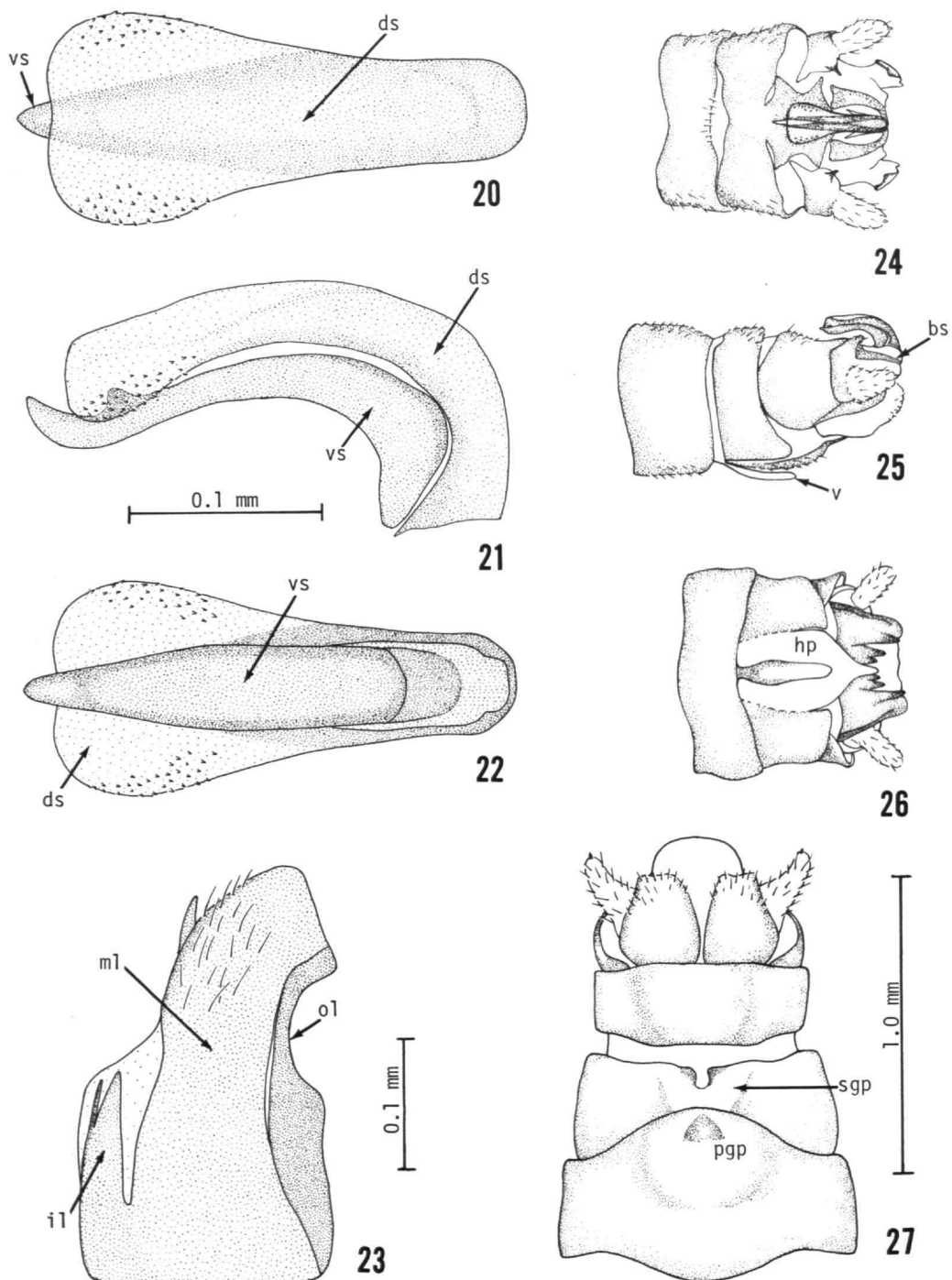
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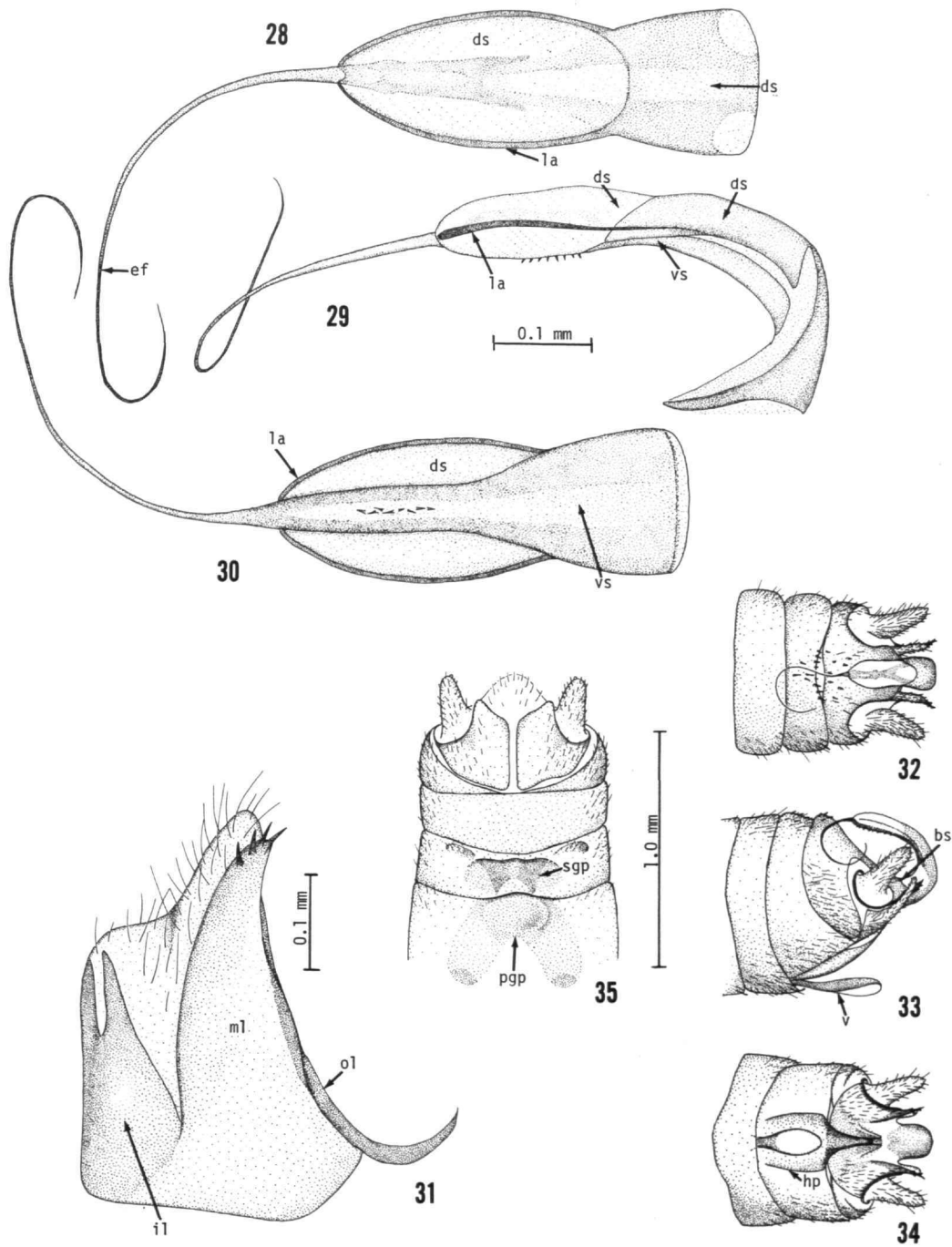
FIGURES 4-11.—*Amphinemura delosa* (Ricker): 4, epiproct, dorsal; 5, epiproct, lateral; 6, epiproct, ventral; 7, male paraproct, right; 8, male terminalia, dorsal; 9, male terminalia, lateral; 10, male terminalia, ventral; 11, female terminalia, ventral.



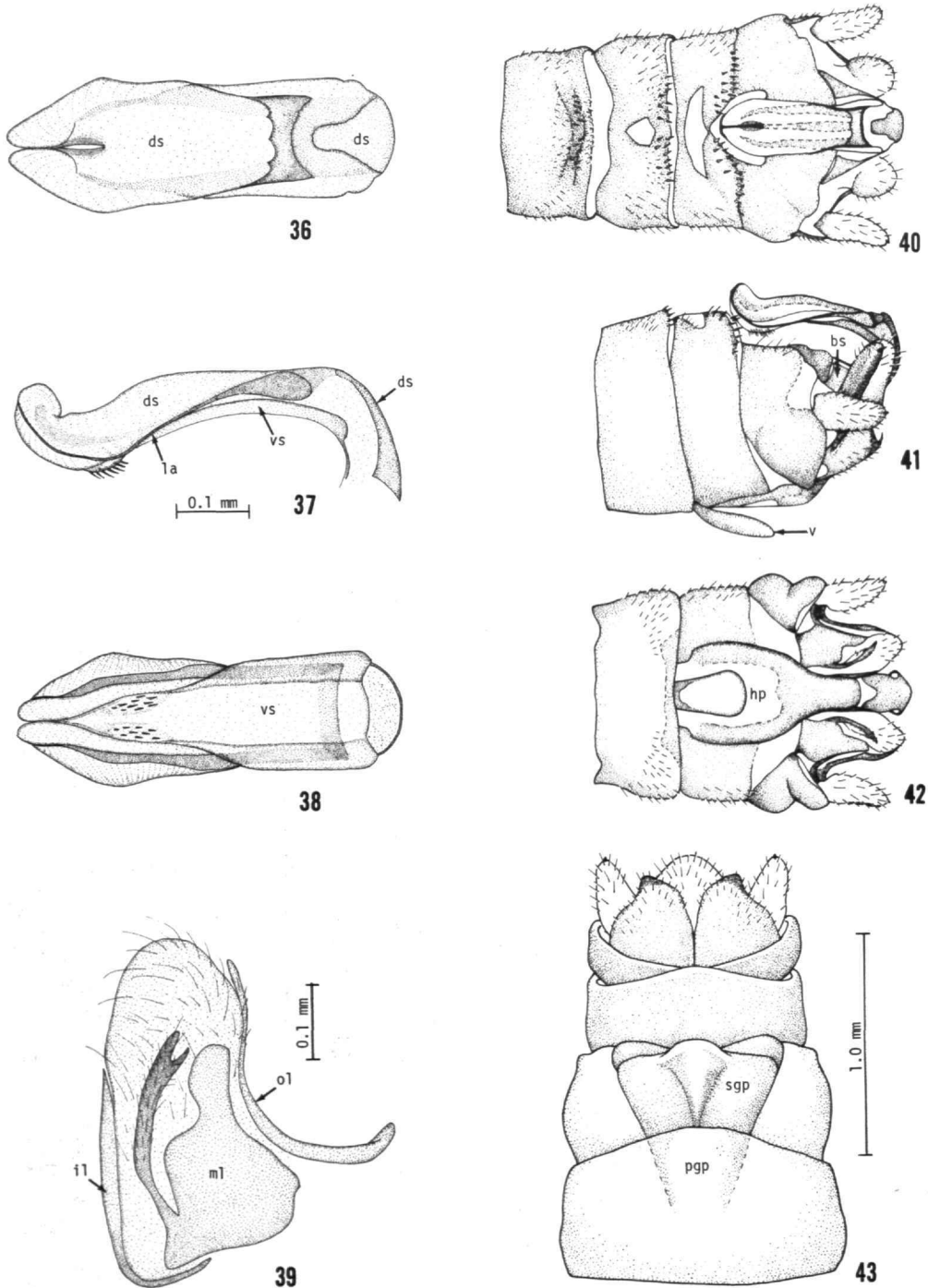
FIGURES 12-19.—*Indonemoura indica* (Kimmins): 12, epiproct, dorsal; 13, epiproct, lateral; 14, epiproct, ventral; 15, male paraproct, right; 16, male terminalia, dorsal; 17, male terminalia, lateral; 18, male terminalia, ventral; 19, female terminalia, ventral.



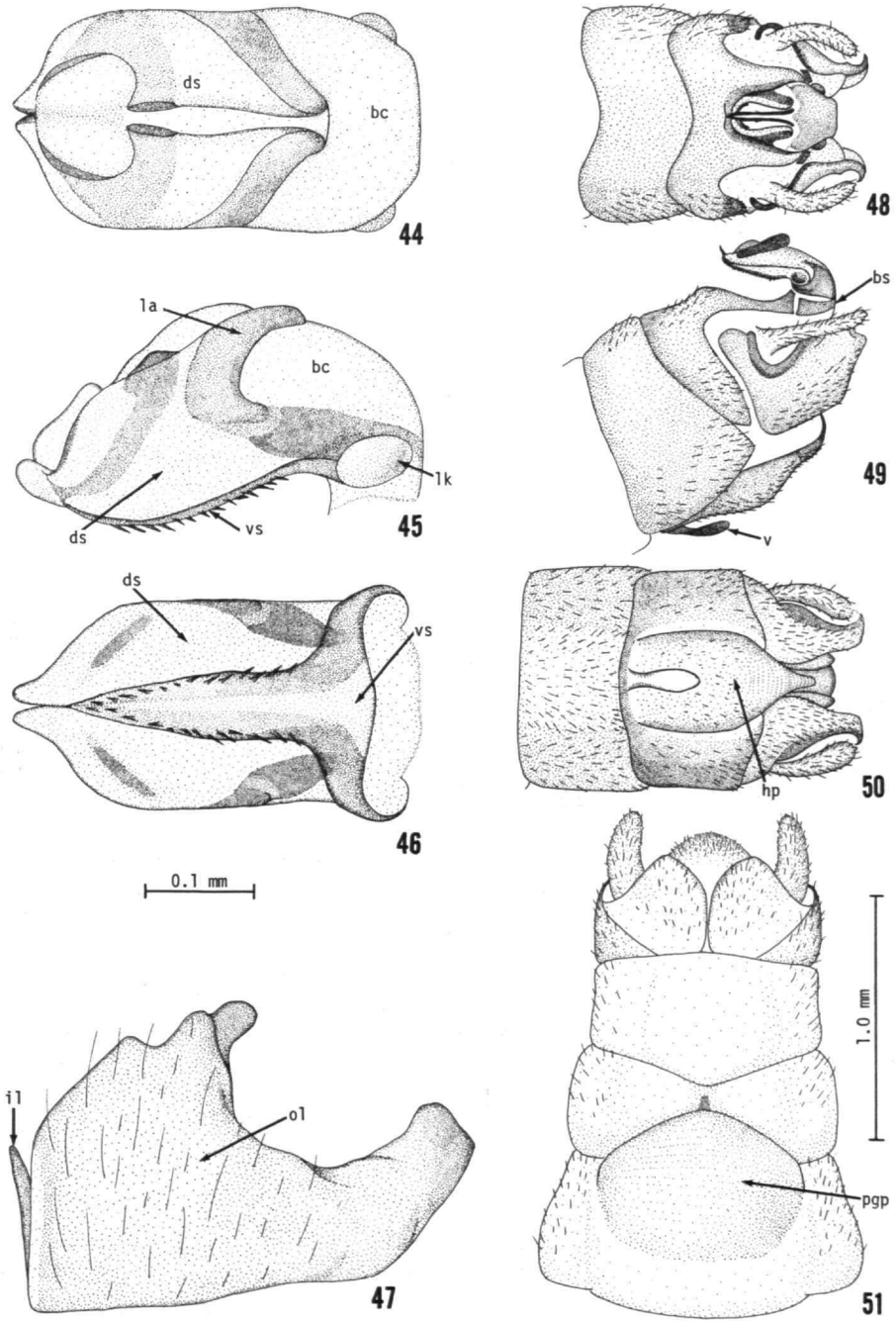
FIGURES 20-27.—*Malenka californica* (Claassen): 20, epiproct, dorsal; 21, epiproct, lateral; 22, epiproct, ventral; 23, male paraproct, right; 24, male terminalia, dorsal; 25, male terminalia, lateral; 26, male terminalia, ventral; 27, female terminalia, ventral.



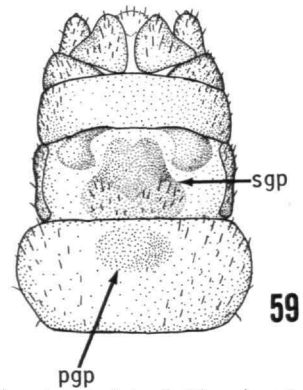
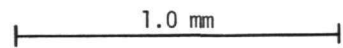
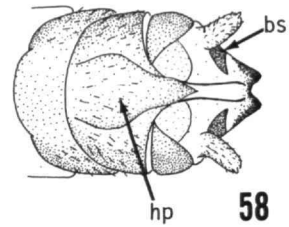
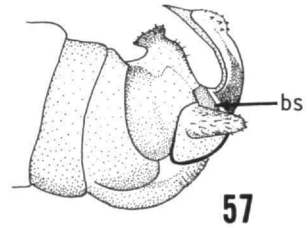
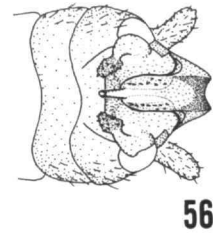
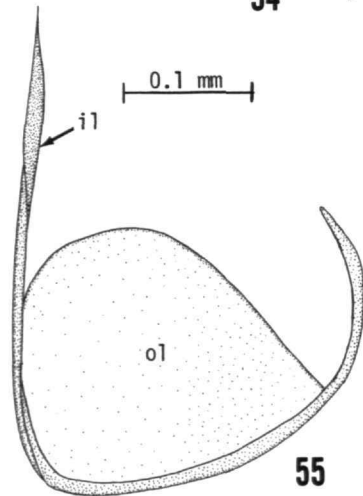
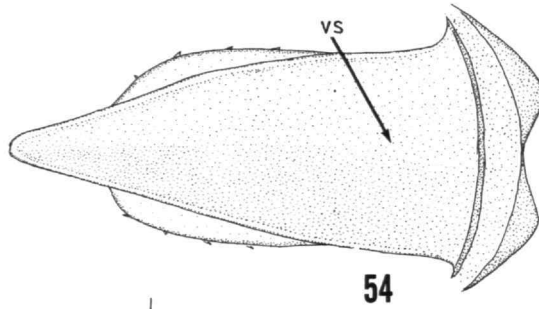
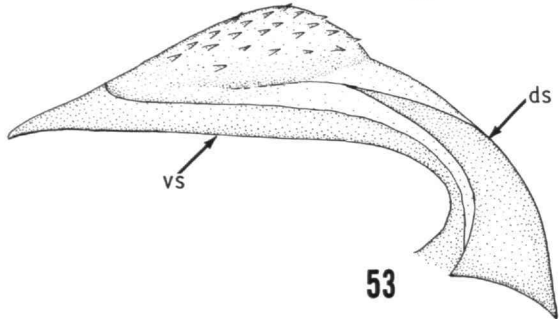
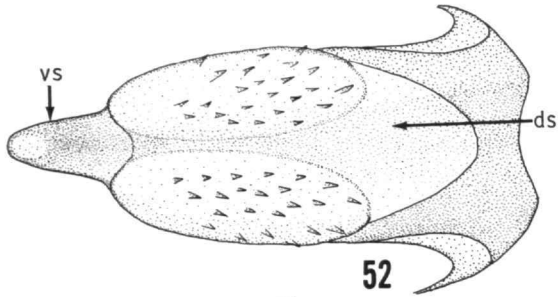
FIGURES 28-35.—*Mesonemoura vaillanti* (Navás): 28, epiproct, dorsal; 29, epiproct, lateral; 30, epiproct, ventral; 31, male paraproct, right; 32, male terminalia, dorsal; 33, male terminalia, lateral; 34, male terminalia, ventral; 35, female terminalia, ventral.



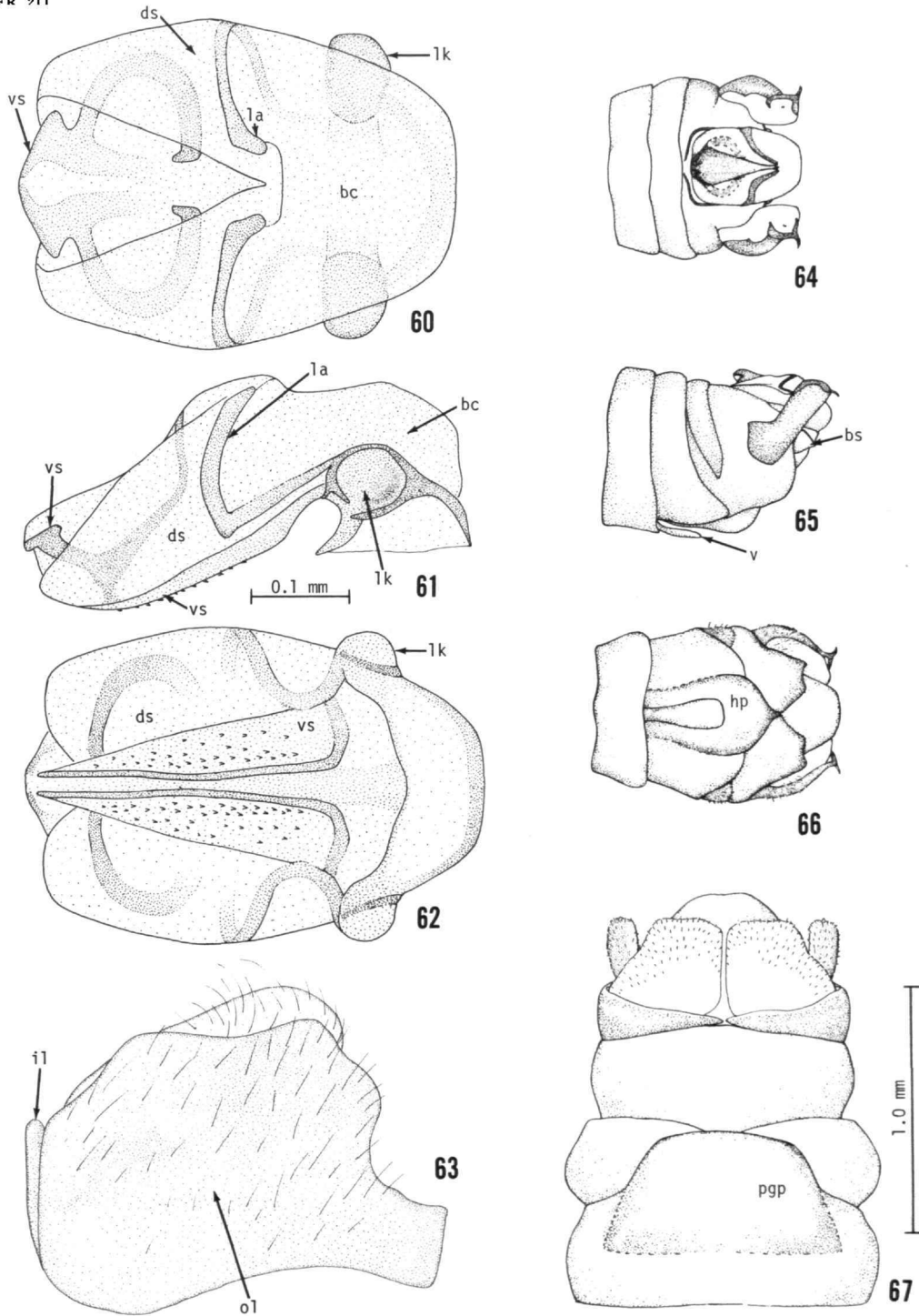
FIGURES 36-43.—*Protonemura nitida* (Pictet): 36, epiproct, dorsal; 37, epiproct, lateral; 38, epiproct, ventral; 39, male paraproct, right; 40, male terminalia, dorsal; 41, male terminalia, lateral; 42, male terminalia, ventral; 43, female terminalia, ventral.



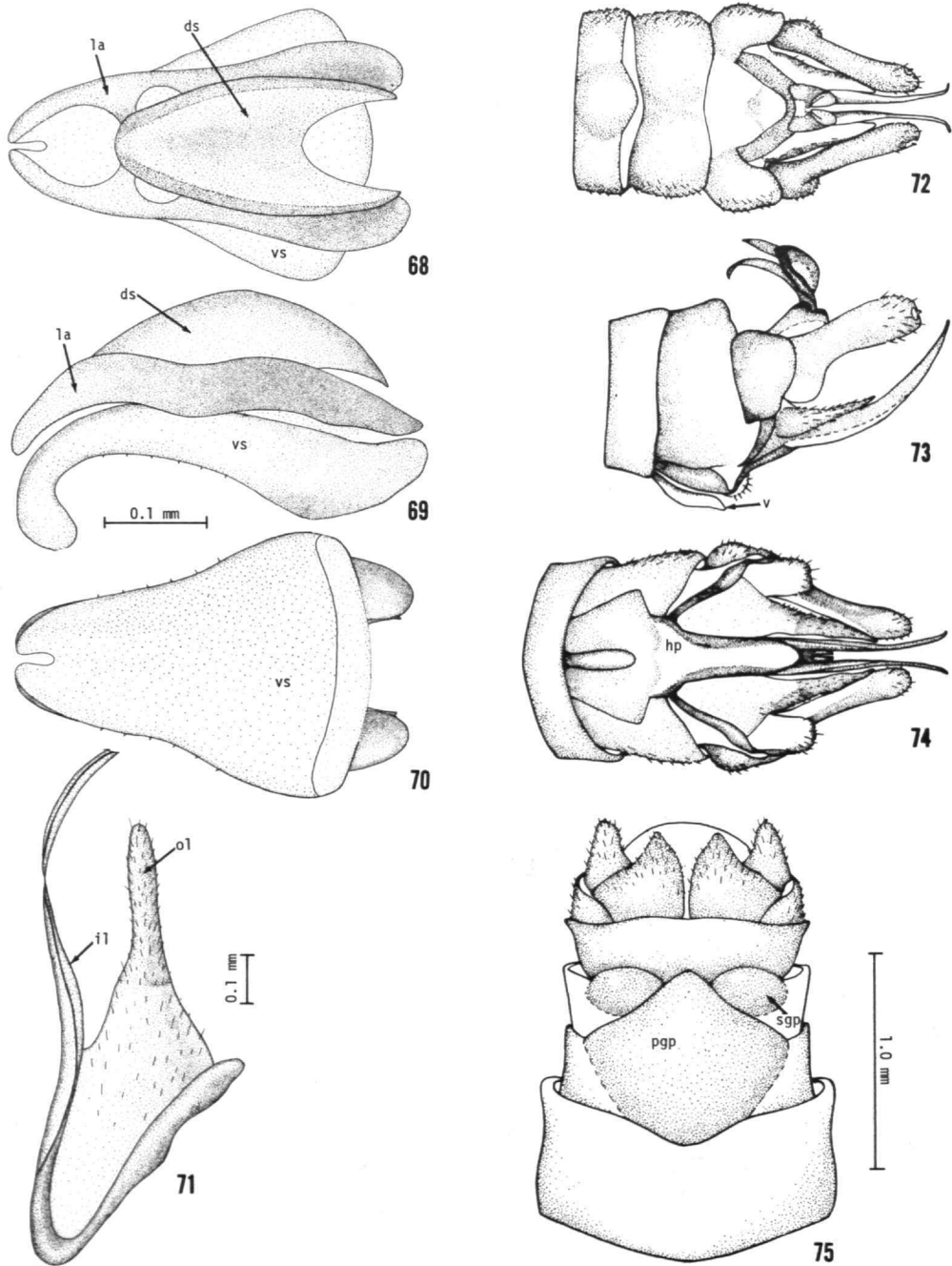
FIGURES 44-51.—*Illiesonemoura punctata* (Jewett): 44, epiproct, dorsal; 45, epiproct, lateral; 46, epiproct, ventral; 47, male paraproct, right. *Illiesonemoura cordata* (Jewett): 48, male terminalia, dorsal; 49, male terminalia, lateral; 50, male terminalia, ventral. *Illiesonemoura punctata*: 51, female terminalia, ventral.



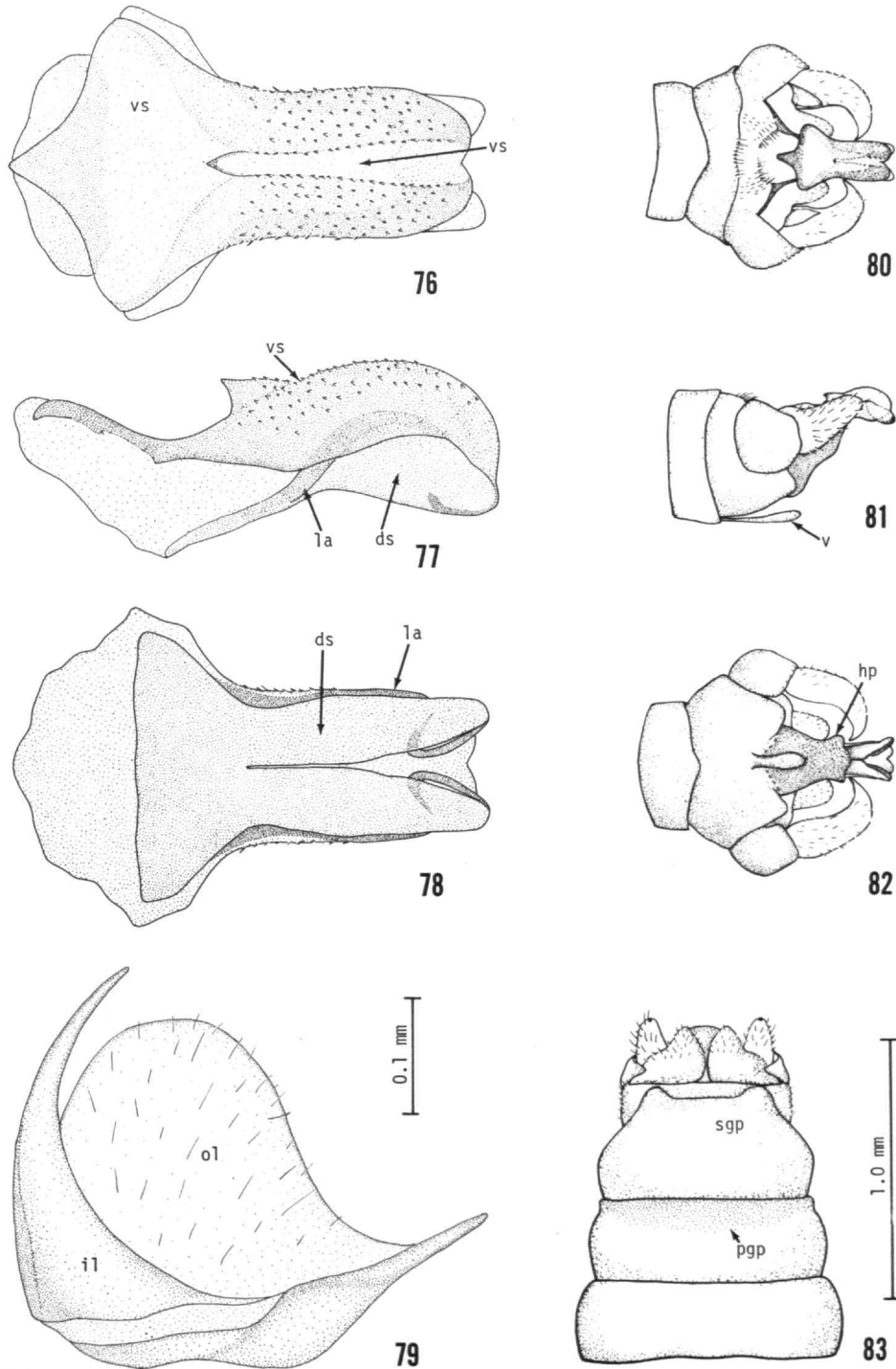
FIGURES 52-59.—*Lednia tumana* (Ricker): 52, epiproct, dorsal; 53, epiproct, lateral; 54, epiproct, ventral; 55, male paraproct, right; 56, male terminalia, dorsal; 57, male terminalia, lateral; 58, male terminalia, ventral; 59, female terminalia, ventral.



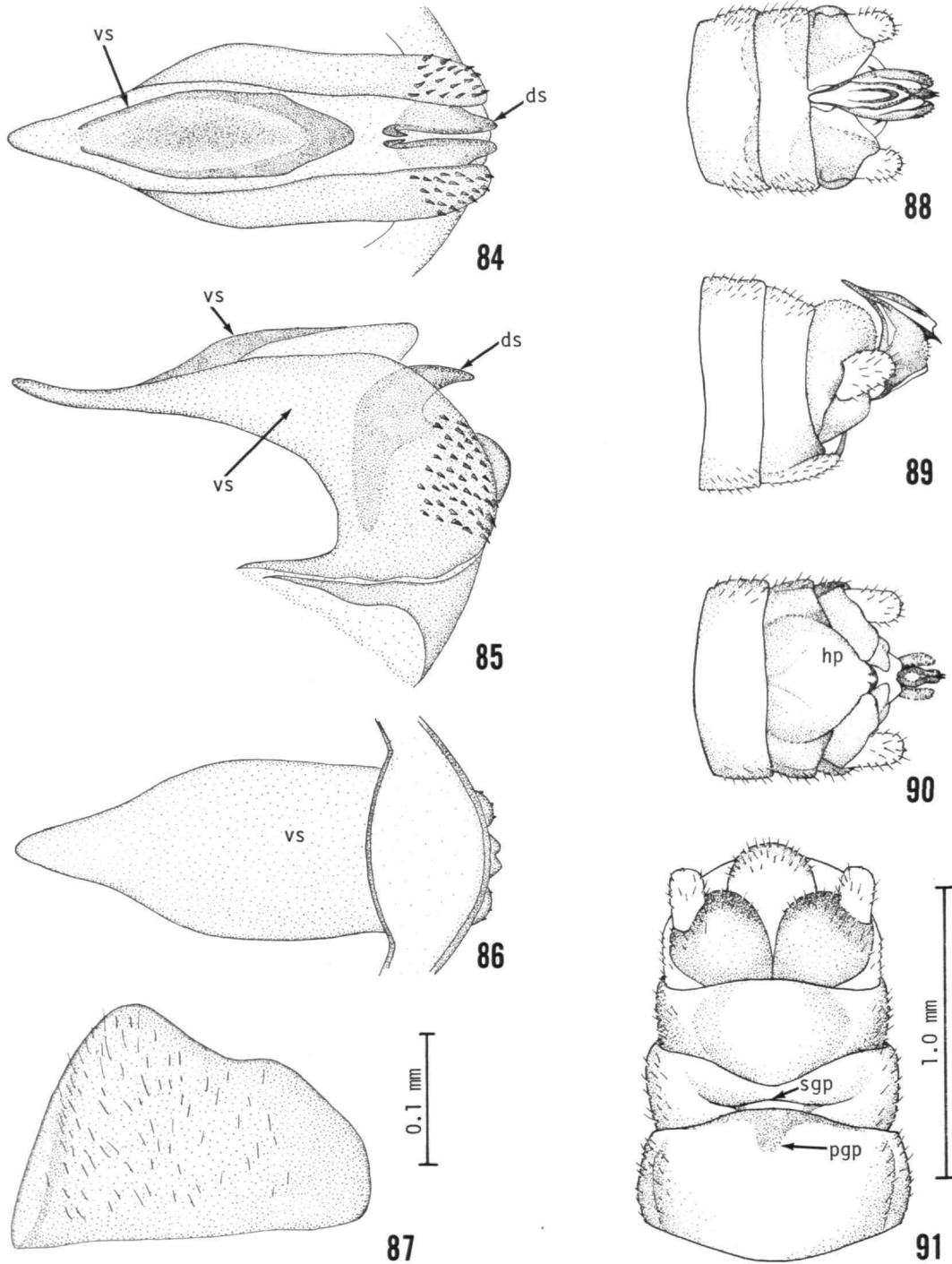
FIGURES 60-67.—*Nemoura trispinosa* Claassen: 60, epiproct, dorsal; 61, epiproct, lateral; 62, epiproct, ventral; 63, male paraproct, right; 64, male terminalia, dorsal; 65, male terminalia, lateral; 66, male terminalia, ventral; 67, female terminalia, ventral.



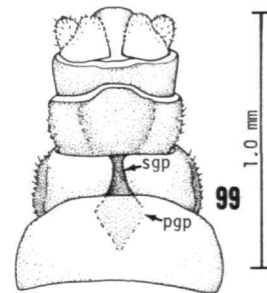
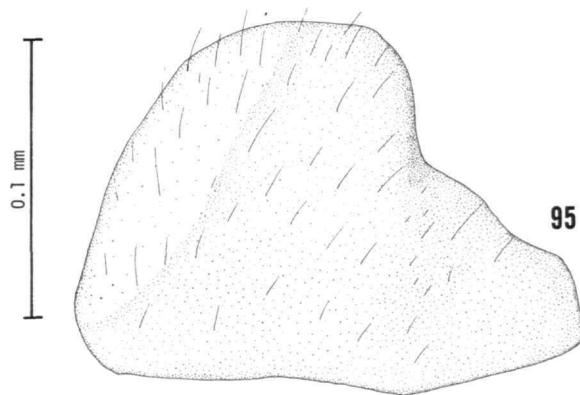
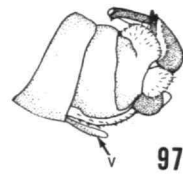
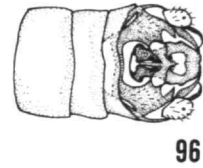
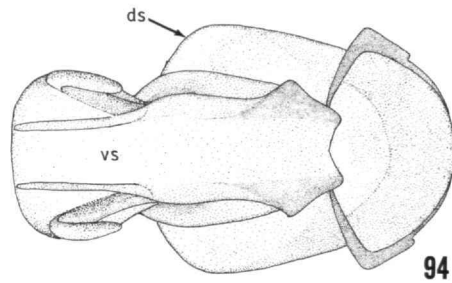
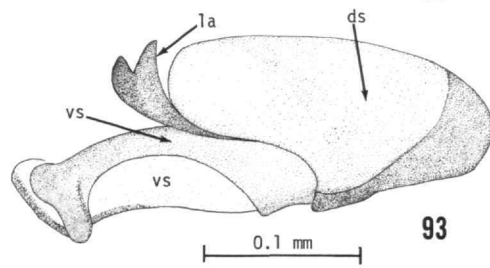
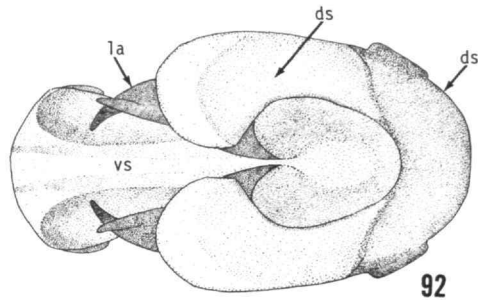
FIGURES 68-75.—*Nemurella pictetii* Klapálek: 68, epiproct, dorsal; 69, epiproct, lateral; 70, epiproct, ventral; 71, male paraproct, right; 72, male terminalia, dorsal; 73, male terminalia, lateral; 74, male terminalia, ventral; 75, female terminalia, ventral.



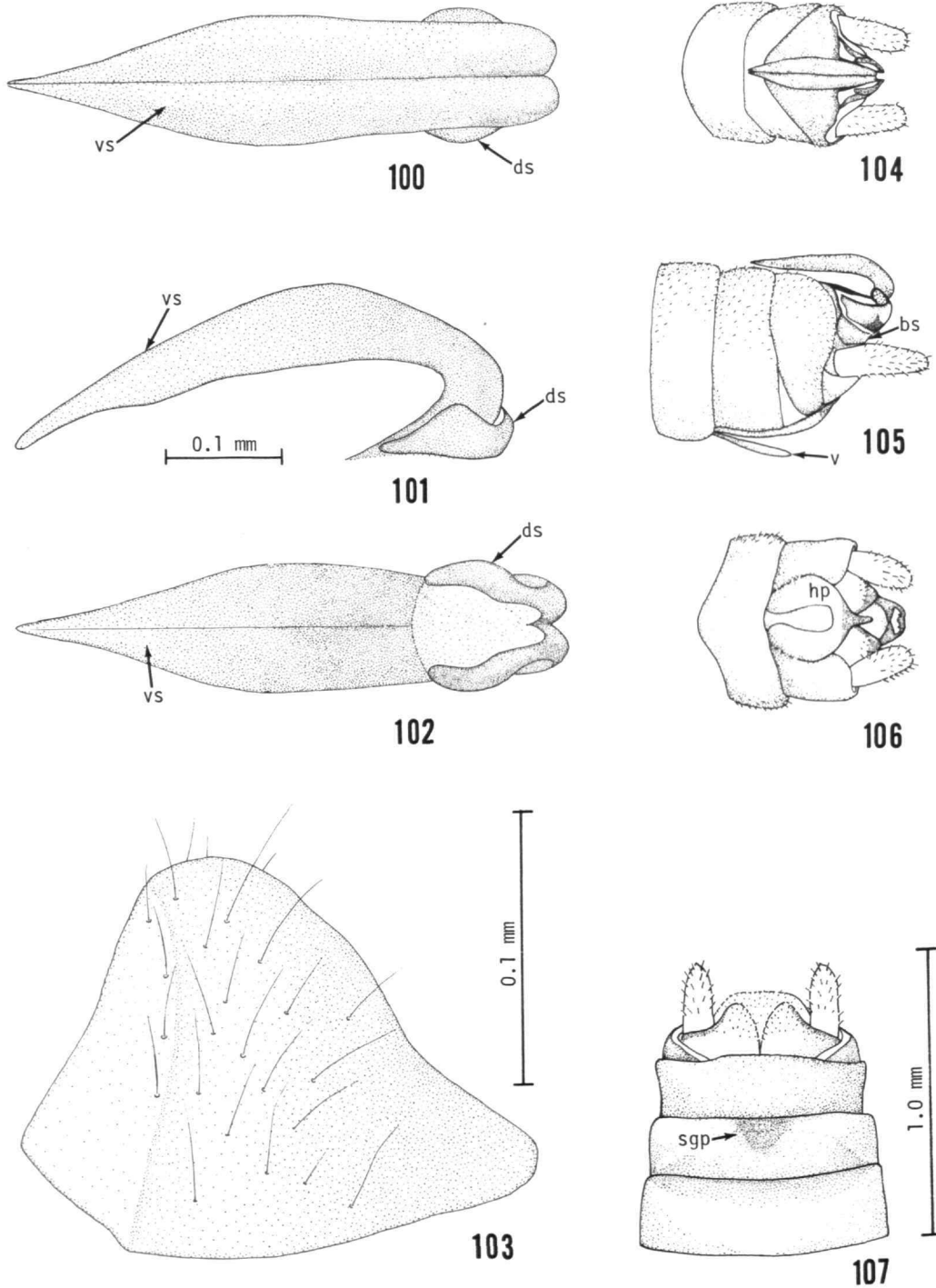
FIGURES 76-83.—*Ostrocerca truncata* (Claassen): 76, epiproct, ventral; 77, epiproct, lateral; 78, epiproct, dorsal; 79, male paraproct, right; 80, male terminalia, dorsal; 81, male terminalia, lateral; 82, male terminalia, ventral; 83, female terminalia, ventral.



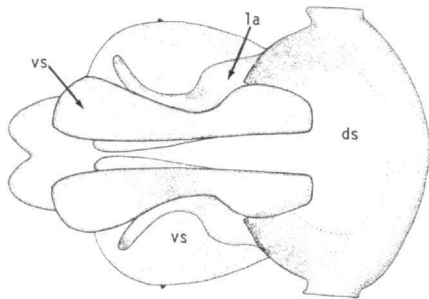
FIGURES 84-91.—*Paranemoura perfecta* (Walker): 84, epiproct, dorsal; 85, epiproct, lateral; 86, epiproct, ventral; 87, male paraproct, right; 88, male terminalia, dorsal; 89, male terminalia, lateral; 90, male terminalia, ventral; 91, female terminalia, ventral.



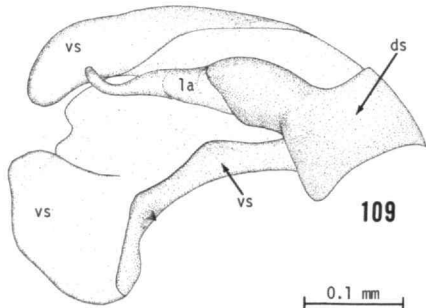
FIGURES 92-99.—*Podmosta delicatula* (Claassen): 92, epiproct, dorsal; 93, epiproct, lateral; 94, epiproct, ventral; 95, male paraproct, right; 96, male terminalia, dorsal; 97, male terminalia, lateral; 98, male terminalia, ventral; 99, female terminalia, ventral.



FIGURES 100-107.—*Prostoia besametsa* (Ricker): 100, epiproct, dorsal; 101, epiproct, lateral; 102, epiproct, ventral; 103, male paraproct, right; 104, male terminalia, dorsal; 105, male terminalia, lateral; 106, male terminalia, ventral; 107, female terminalia, ventral.

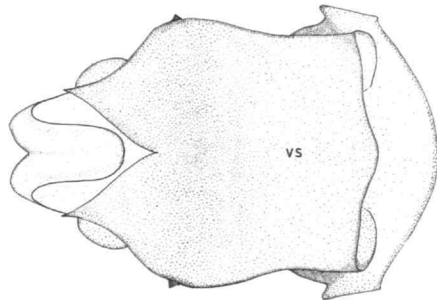


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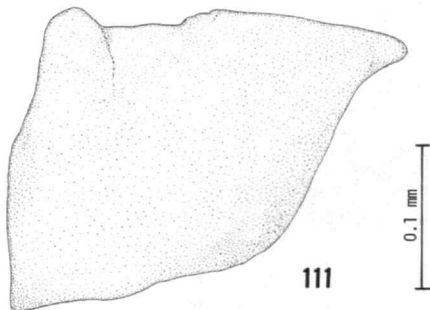


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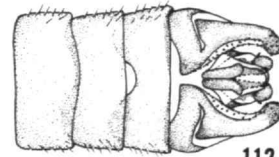


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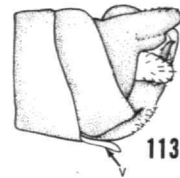


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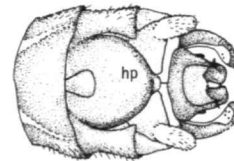
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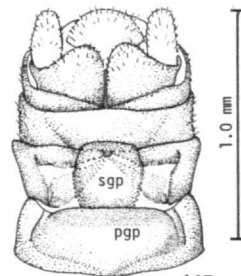
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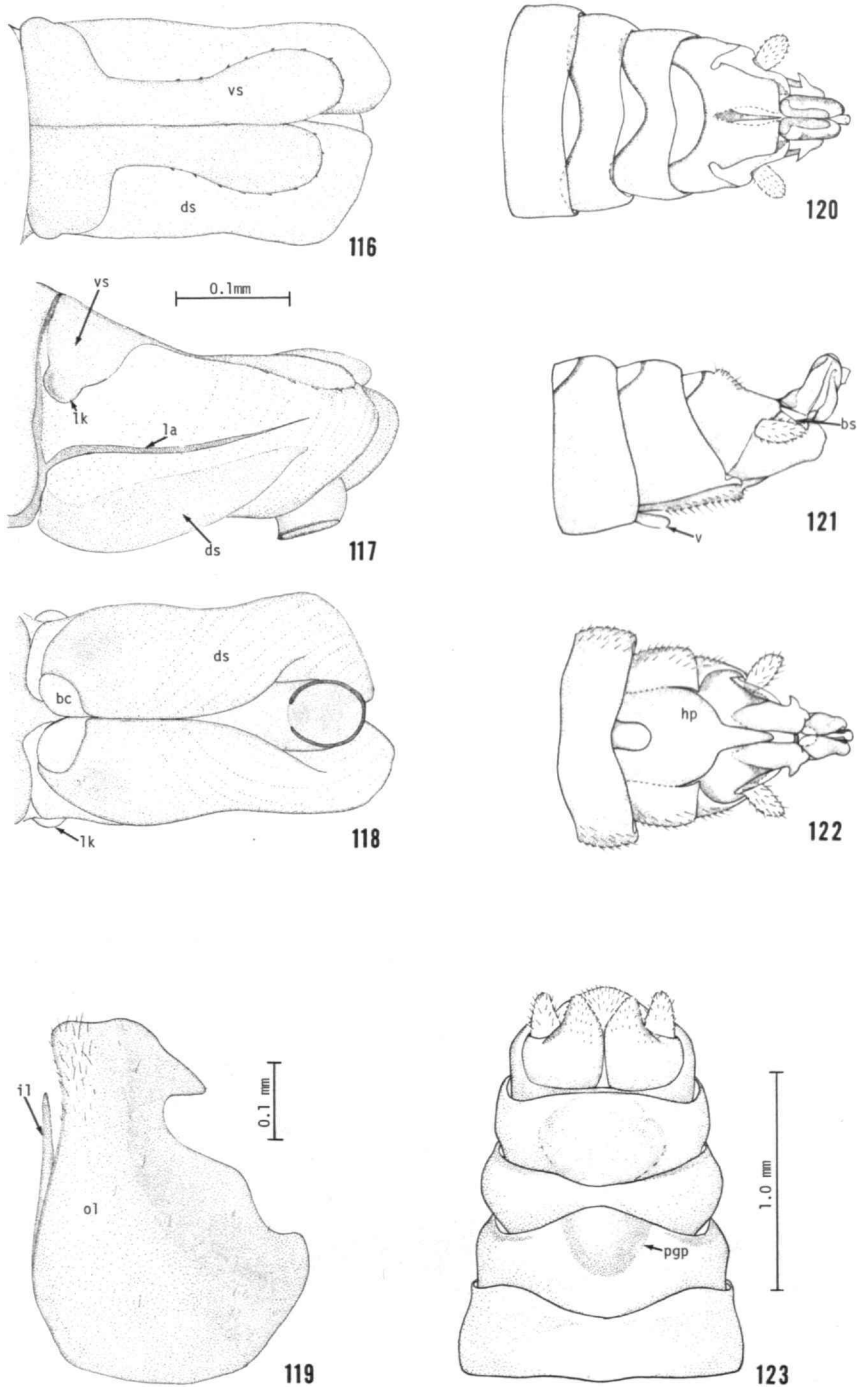
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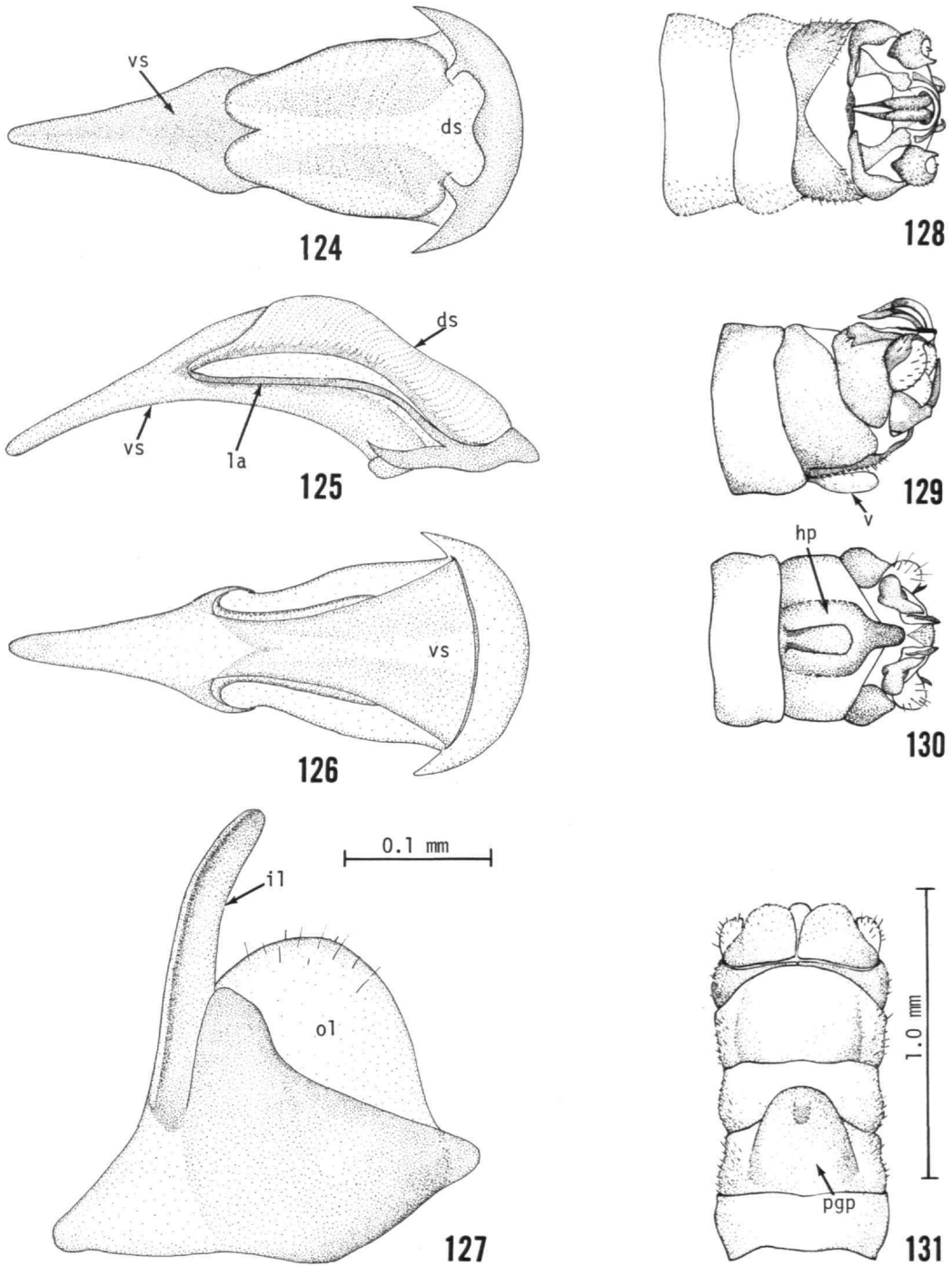
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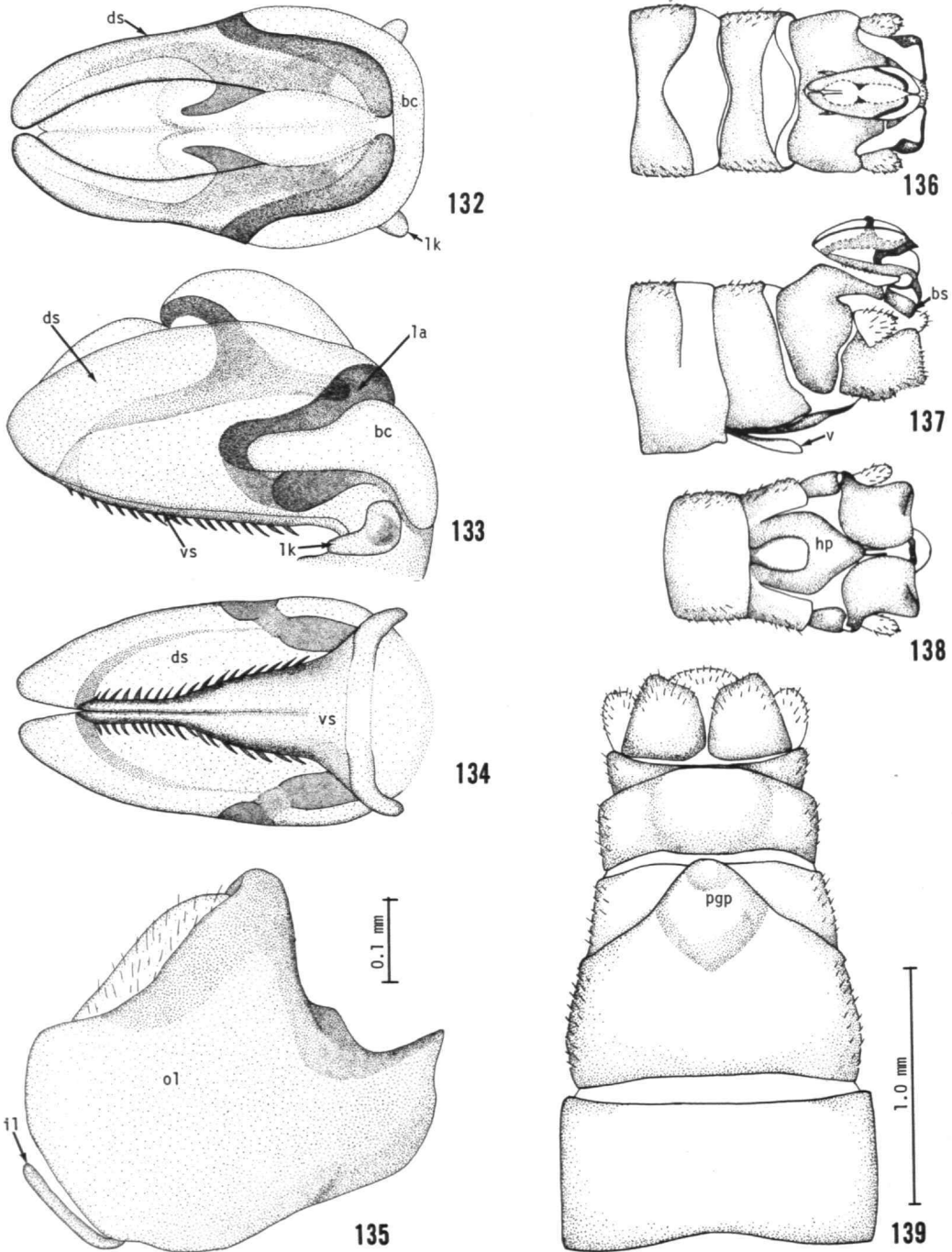
FIGURES 108-115.—*Shiptsa rotunda* (Claassen): 108, epiproct, dorsal; 109, epiproct, lateral; 110, epiproct, ventral; 111, male paraproct, right; 112, male terminalia, dorsal; 113, male terminalia, lateral; 114, male terminalia, ventral; 115, female terminalia, ventral.



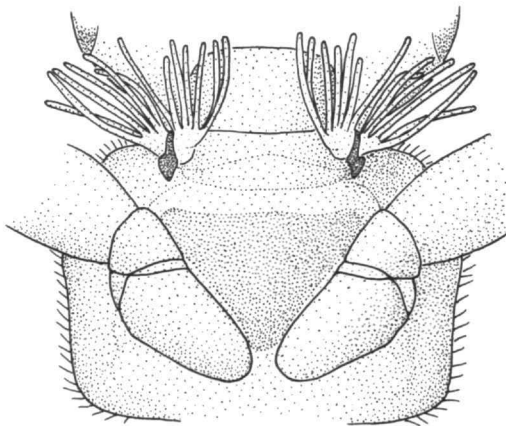
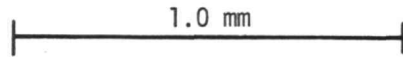
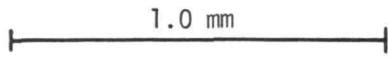
FIGURES 116-123.—*Soyedina producta* (Claassen): 116, epiproct, ventral; 117, epiproct, lateral; 118, epiproct, dorsal; 119, male paraproct, right; 120, male terminalia, dorsal; 121, male terminalia, lateral; 122, male terminalia, ventral; 123, female terminalia, ventral.



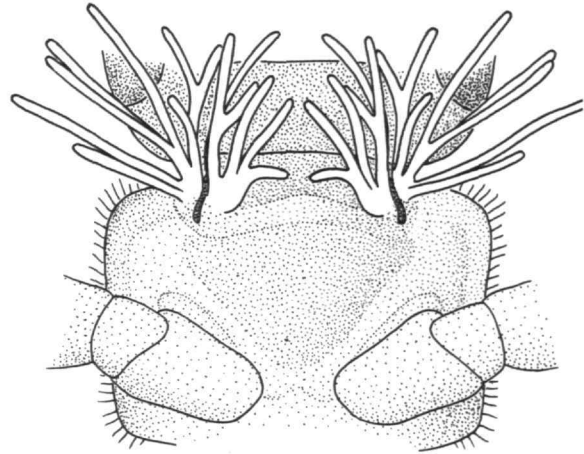
FIGURES 124-131.—*Visoka cataractae* (Neave): 124, epiproct, dorsal; 125, epiproct, lateral; 126, epiproct, ventral; 127, male paraproct, right; 128, male terminalia, dorsal; 129, male terminalia, lateral; 130, male terminalia, ventral; 131, female terminalia, ventral.



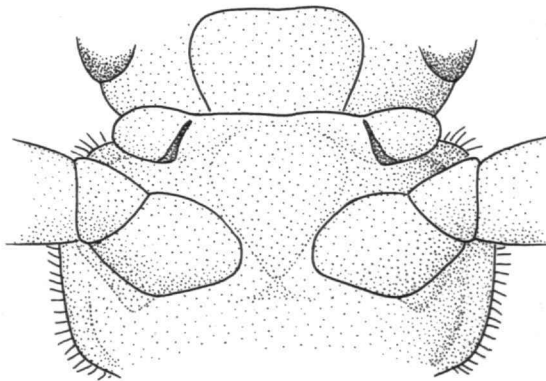
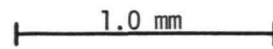
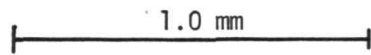
FIGURES 132-139.—*Zapada oregonensis* (Claassen): 132, epiproct, dorsal; 133, epiproct, lateral; 134, epiproct, ventral; 135, male paraproct, right; 136, male terminalia, dorsal; 137, male terminalia, lateral; 138, male terminalia, ventral; 139, female terminalia, ventral.



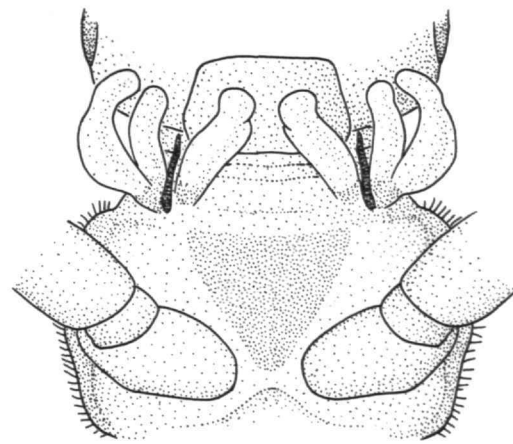
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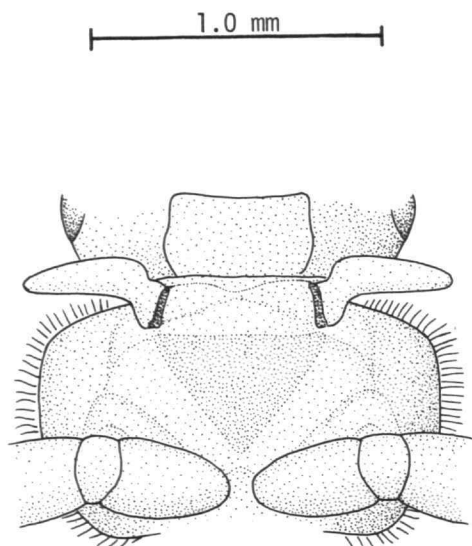


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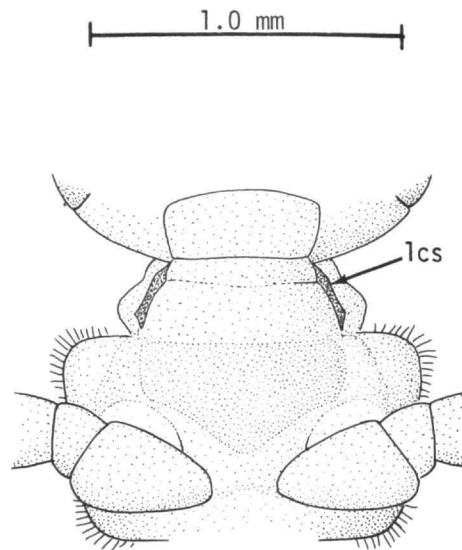


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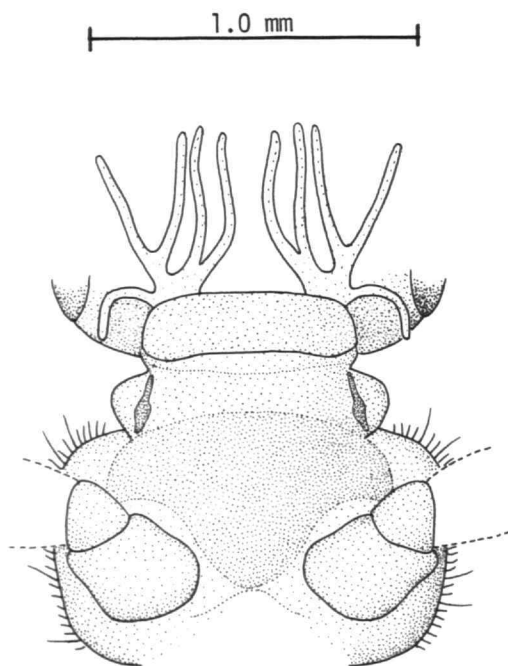
FIGURES 140-143.—Cervical region of nymphs: 140, *Amphinemura delosa* (Ricker); 141, *Malenka californica* (Claassen); 142, *Mesonemoura vaillanti* (Navás); 143, *Protonemura* sp.



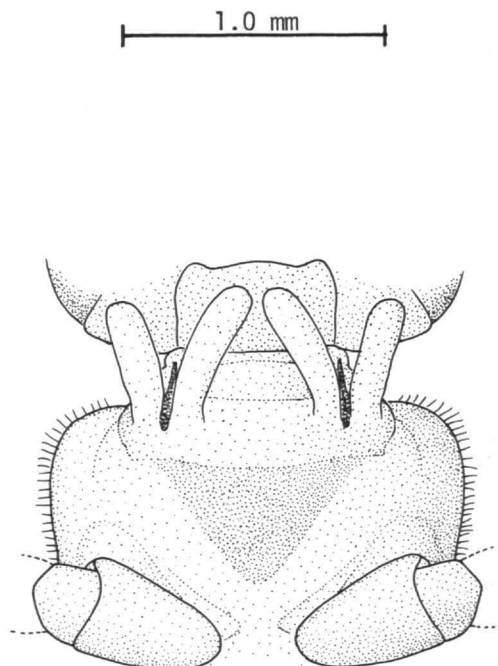
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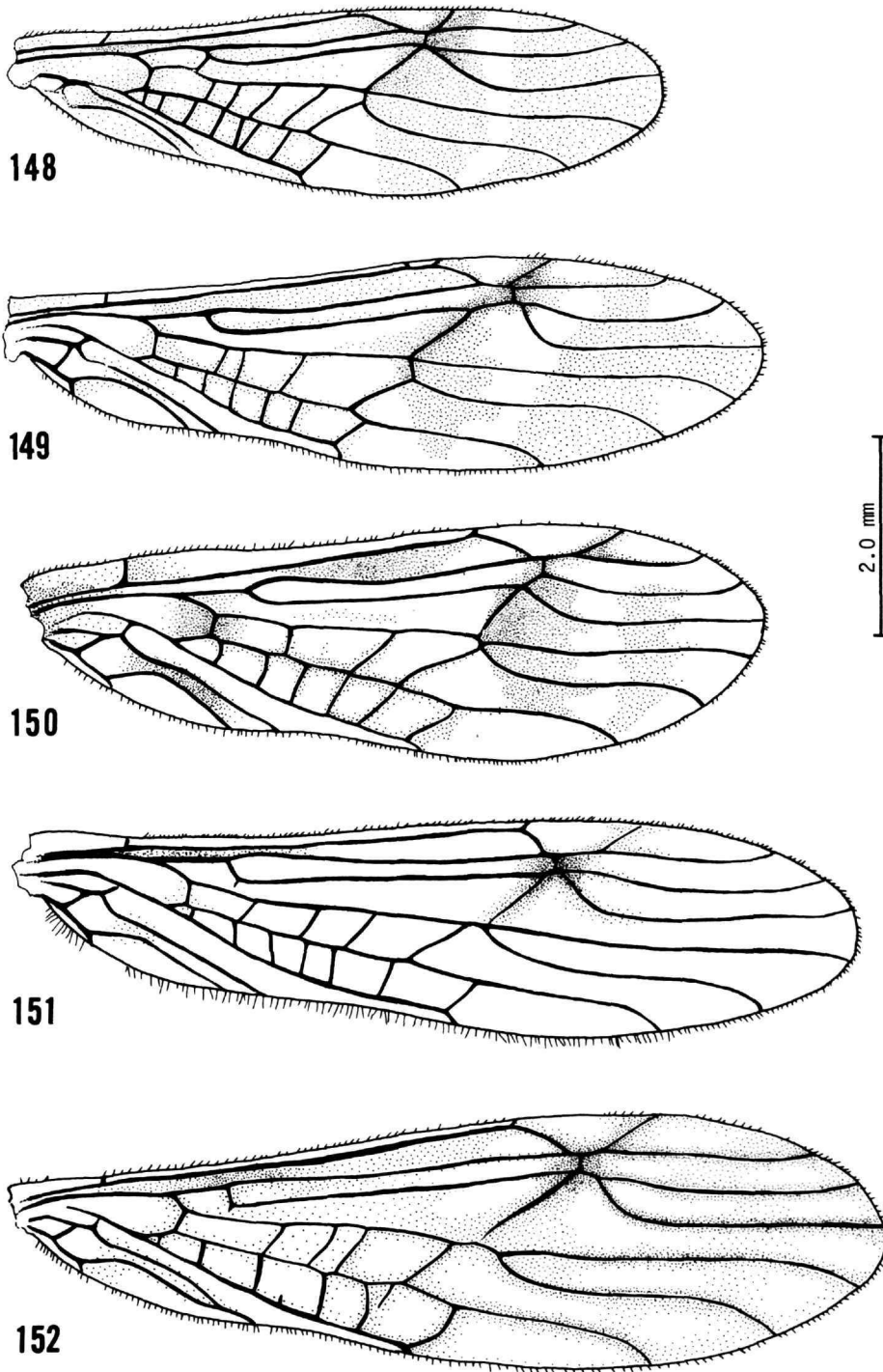


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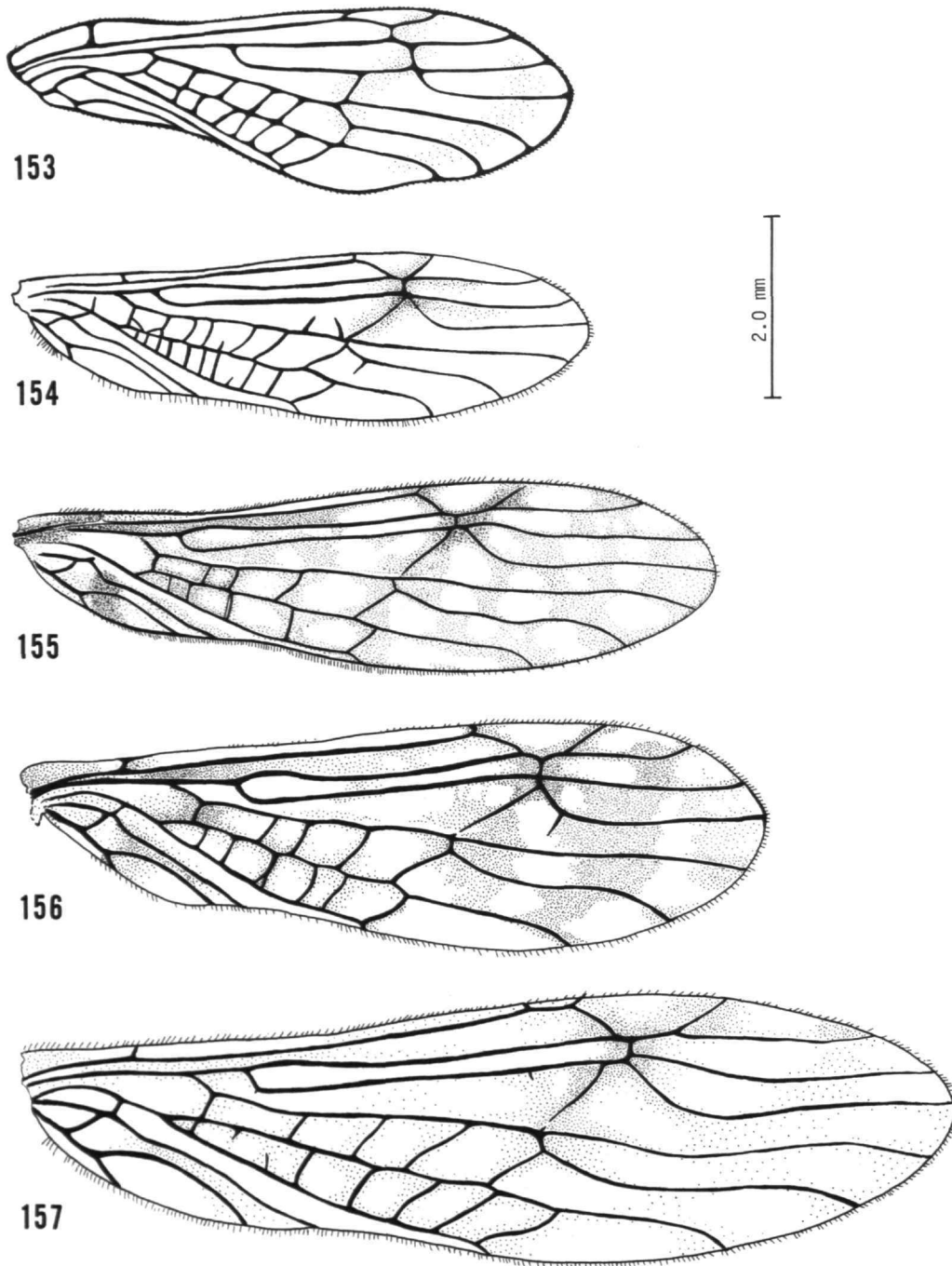


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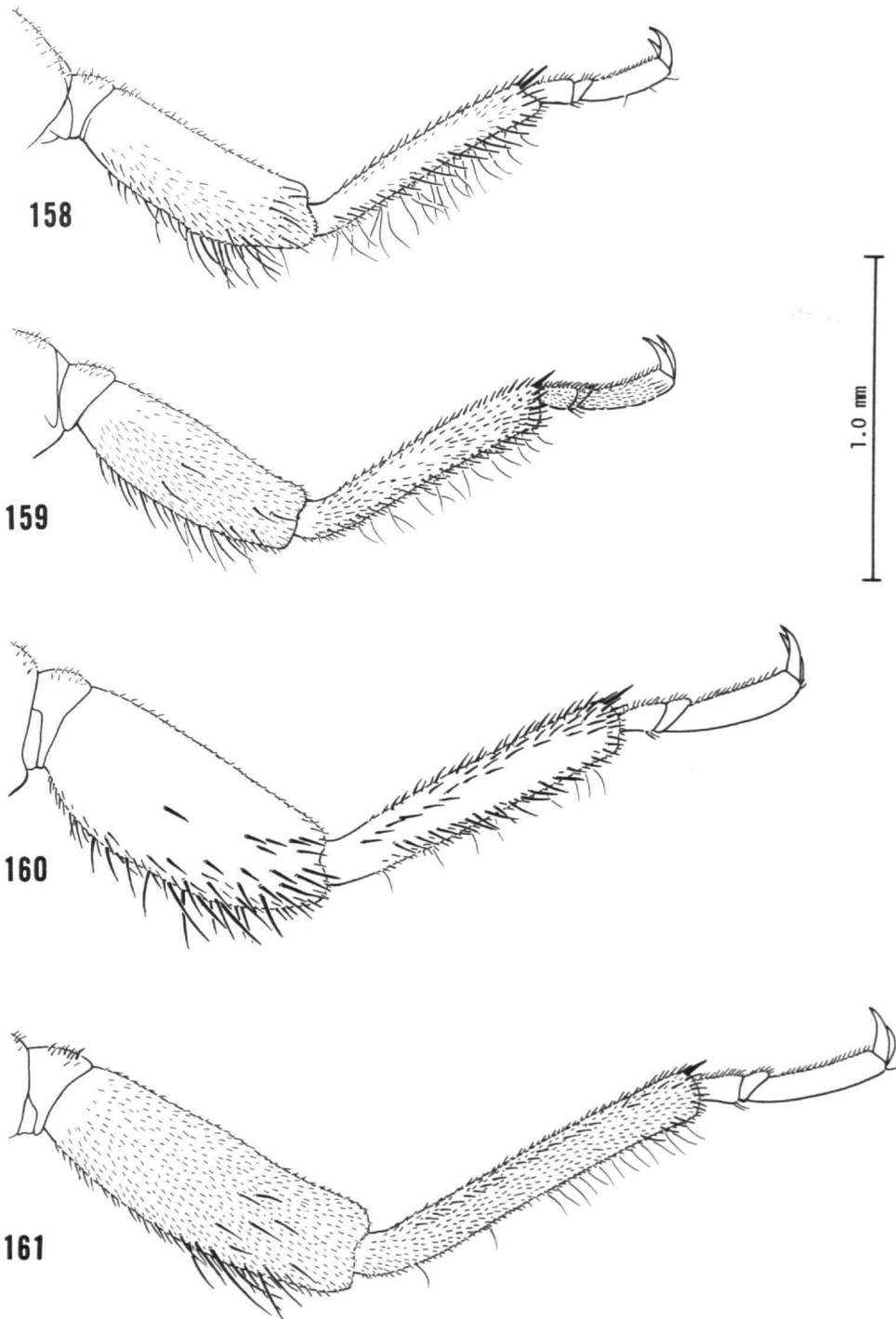
FIGURES 144-147.—Cervical region of nymphs: 144, *Illiesonemoura* sp.; 145, *Nemoura cinerea* (Retzius); 146, *Visoka cataractae* (Neave); 147, *Zapada hoyi* (Ricker).



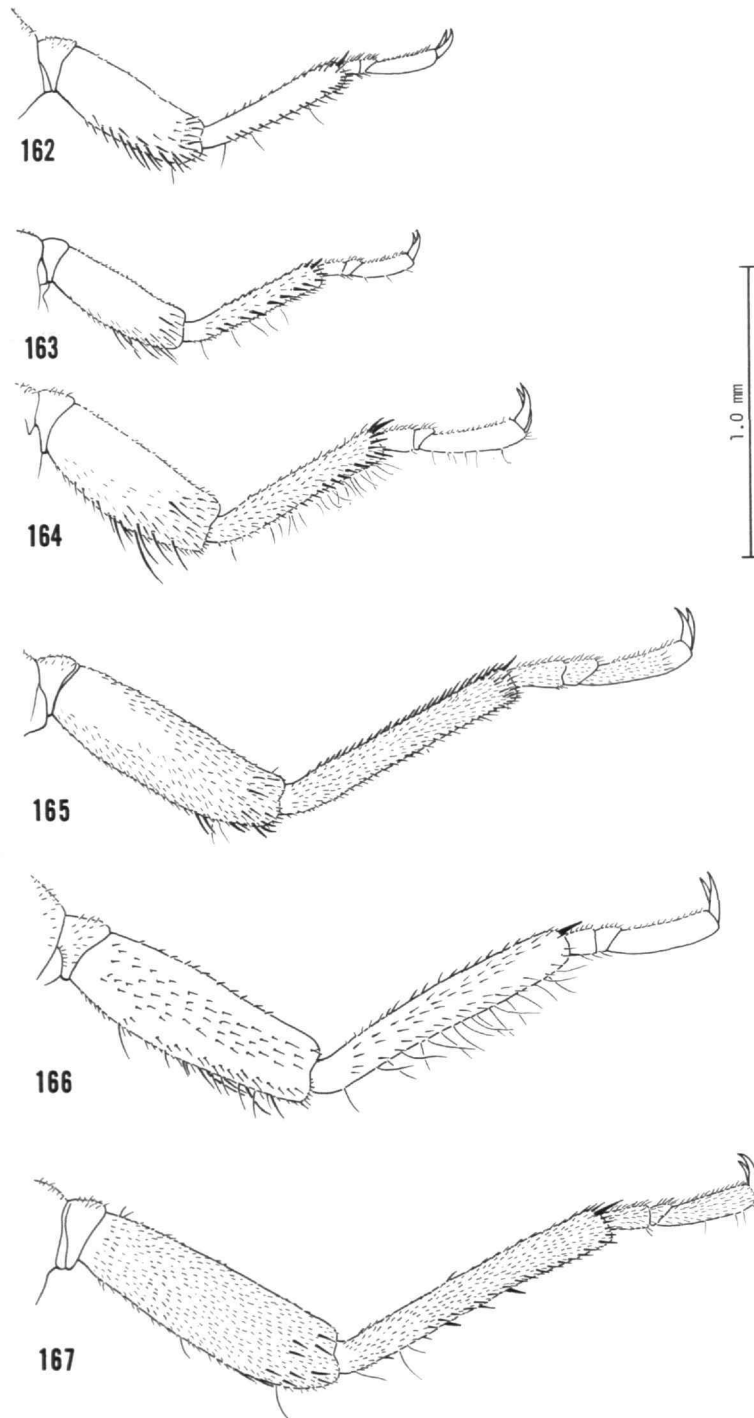
FIGURES 148-152.—Right forewings: 148, *Prostoia besametsa* (Ricker), female; 149, *Shipsa rotunda* (Claassen), female; 150, *Zapada columbiana* (Claassen), female; 151, *Malenka coloradensis* (Banks), female; 152, *Soyedina producta* (Claassen), female.



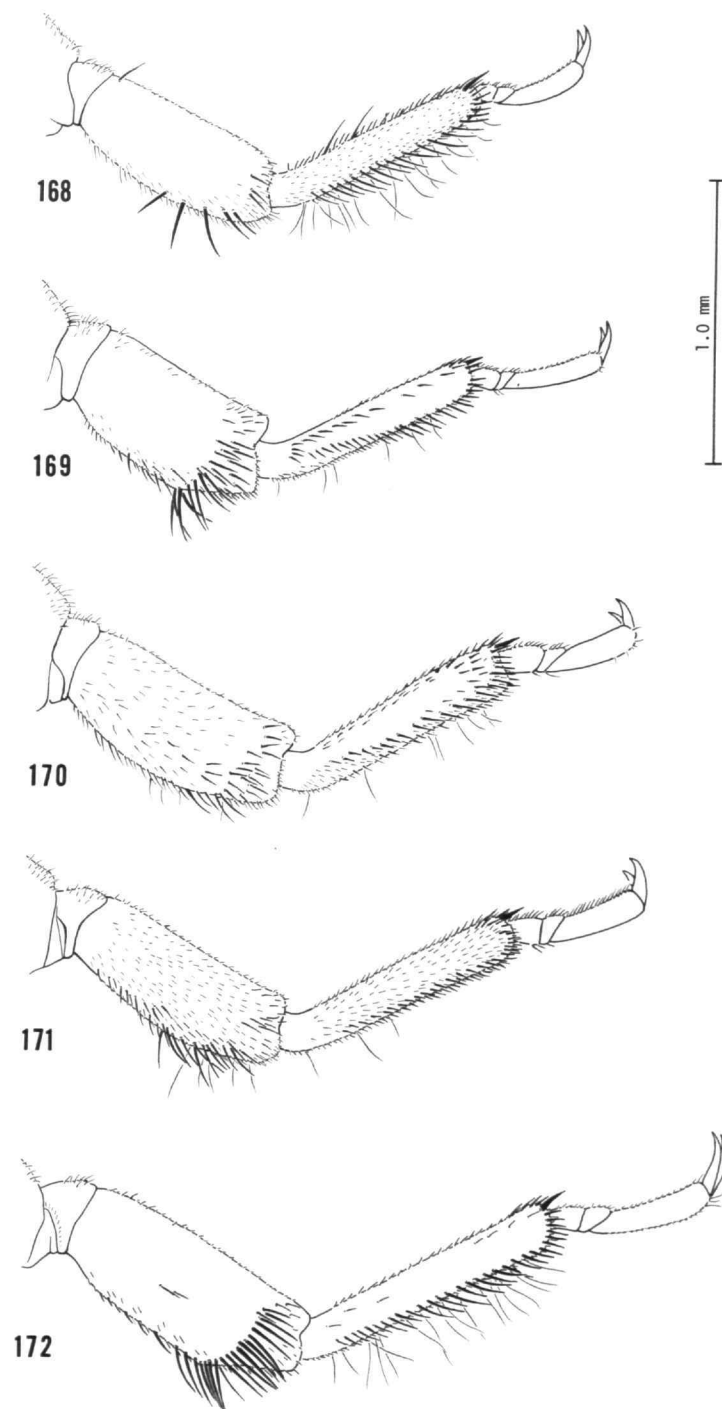
FIGURES 153-157.—Right forewings: 153, *Paranemoura perfecta* (Walker), male; 154, *Nemoura arctica* Esben-Petersen, female; 155, *Amphinemoura apache* Baumann and Gaufin, female; 156, *Illiesonemoura cordata* (Jewett), female; 157, *Protonemoura meyeri* (Pictet), female.



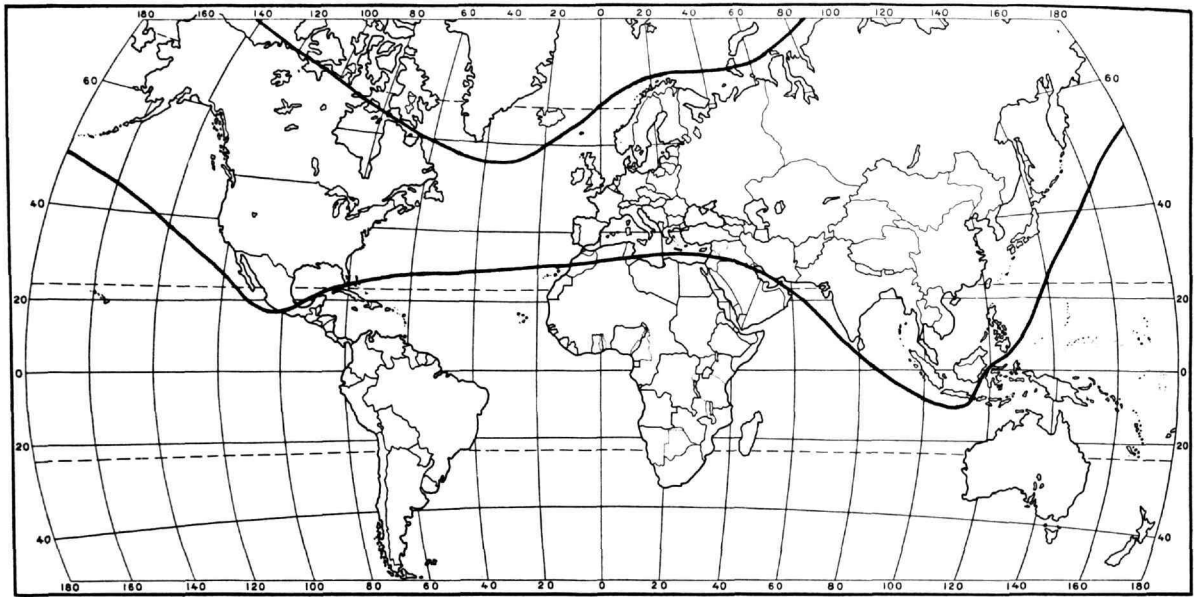
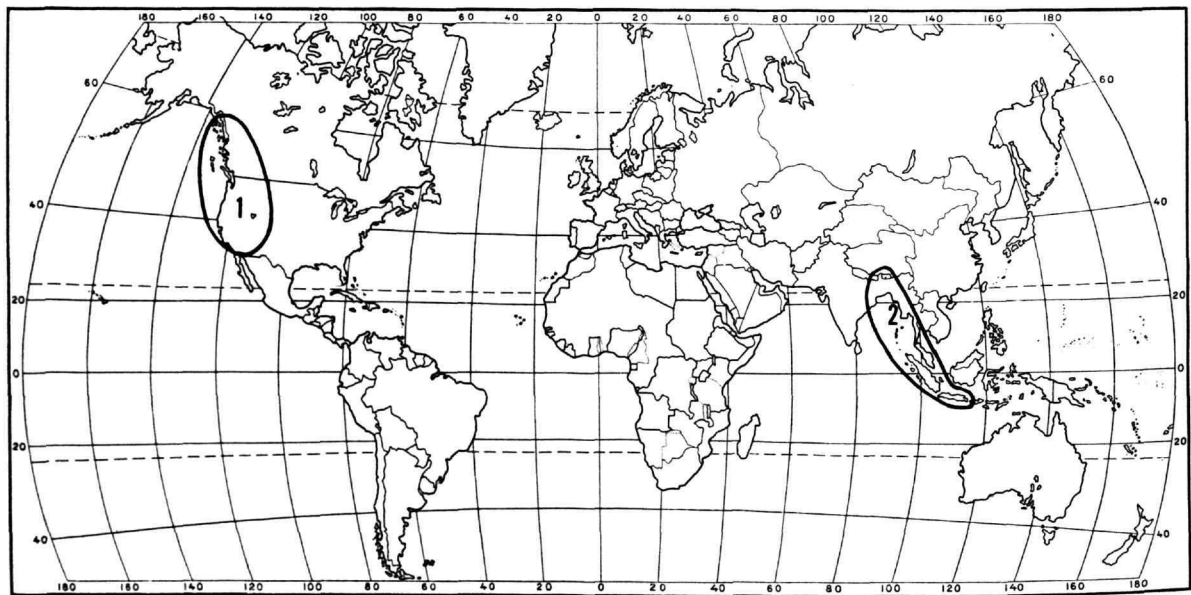
FIGURES 158-161.—Right forelegs of nymphs: 158, *Malenka californica* (Claassen); 159, *Amphinemura wui* (Claassen); 160, *Protonemura* sp.; 161, *Mesonemoura vaillanti* (Navás).



FIGURES 162-167.—Right forelegs of nymphs: 162, *Ostrocerca truncata* (Claassen); 163, *Podmosta decepta* (Frison); 164, *Prostoia besametsa* (Ricker); 165, *Paranemoura perfecta* (Walker); 166, *Shipsa rotunda* (Claassen); 167, *Nemurella pictetii* Klapálek.



FIGURES 168-172.—Right forelegs of nymphs: 168, *Visoka cataractae* (Neave); 169, *Illiesonemoura* sp.; 170, *Soyedina vallicularia* (Wu); 171, *Nemoura cinerea* (Retzius); 172, *Zapada haysi* (Ricker).

FIGURE 173.—Distribution map of *Amphinemura*.FIGURE 174.—Distribution map of *Malenka* (1) and *Indonemoura* (2).

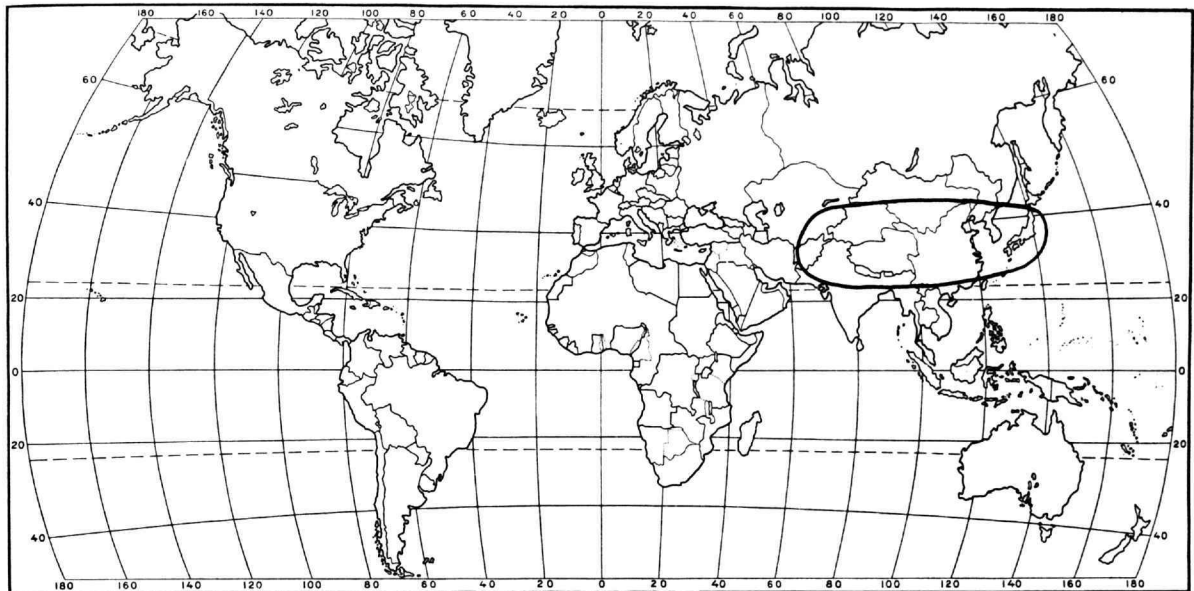


FIGURE 175.—Distribution map of *Mesonemoura*.

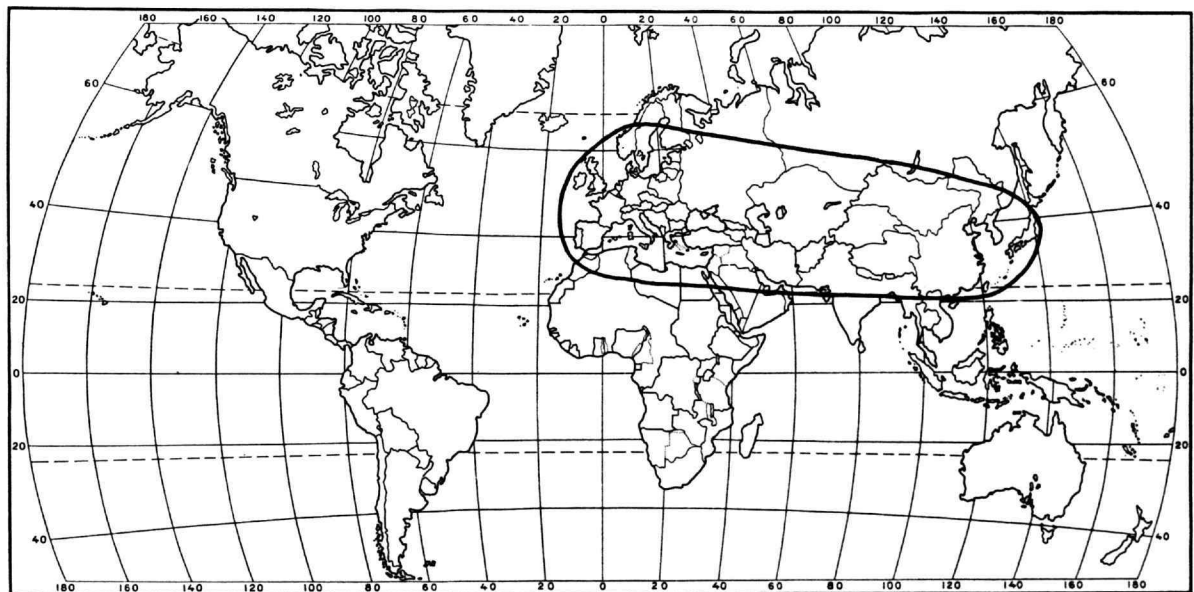


FIGURE 176.—Distribution map of *Protonemoura*.

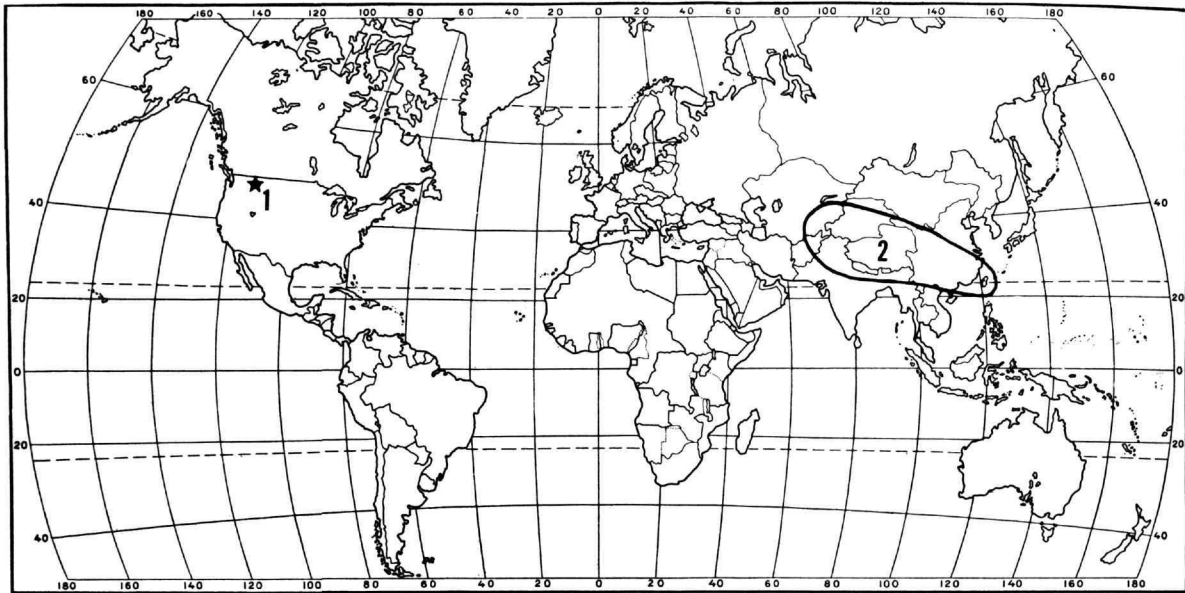


FIGURE 177.—Distribution map of *Lednia* (1) and *Illiesonemoura* (2).

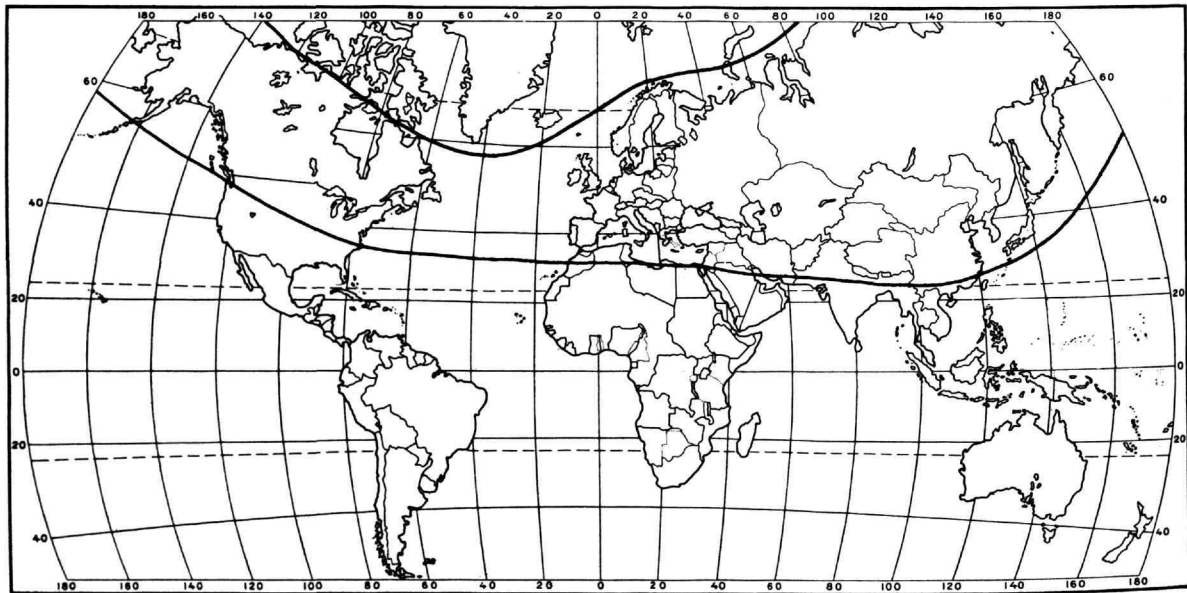


FIGURE 178.—Distribution map of *Nemoura*.

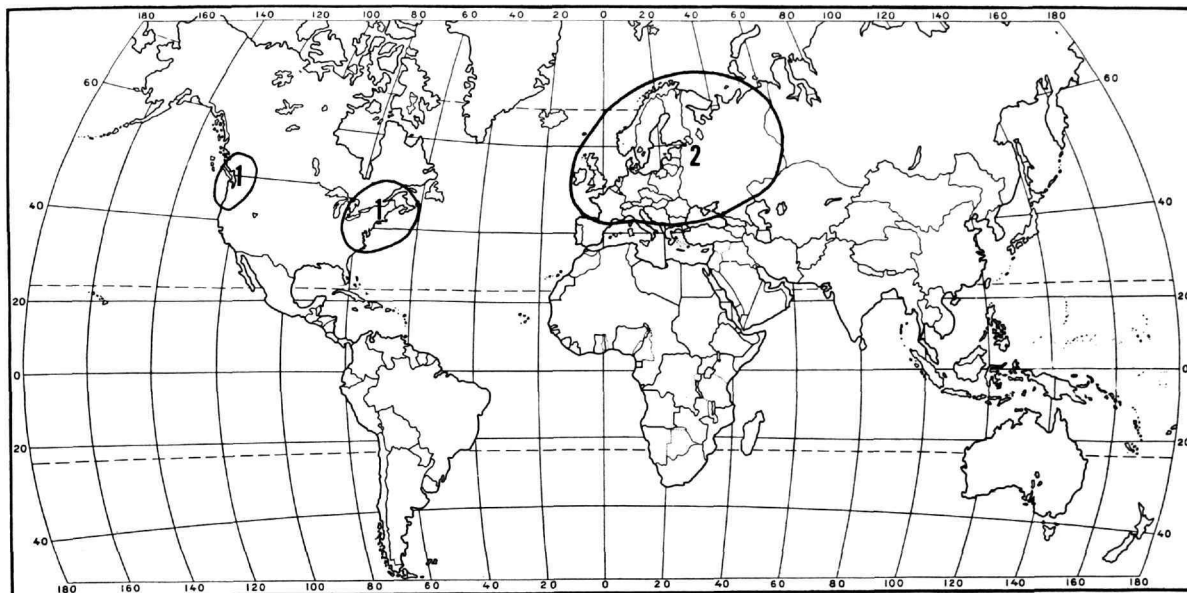


FIGURE 179.—Distribution map of *Ostrocerca* (1) and *Nemurella* (2).

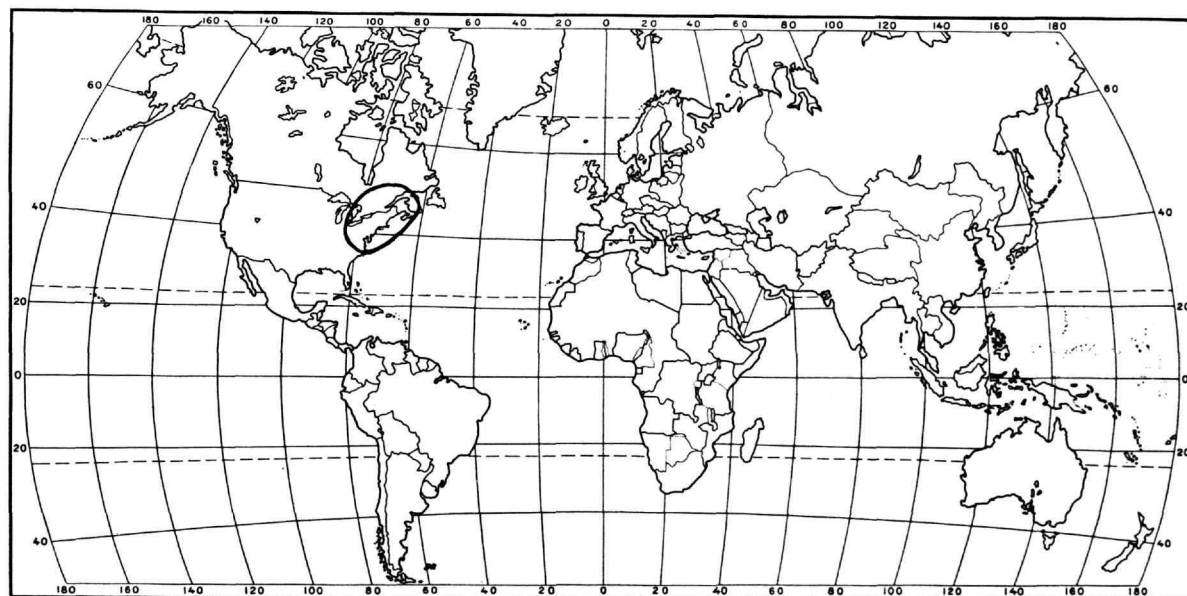
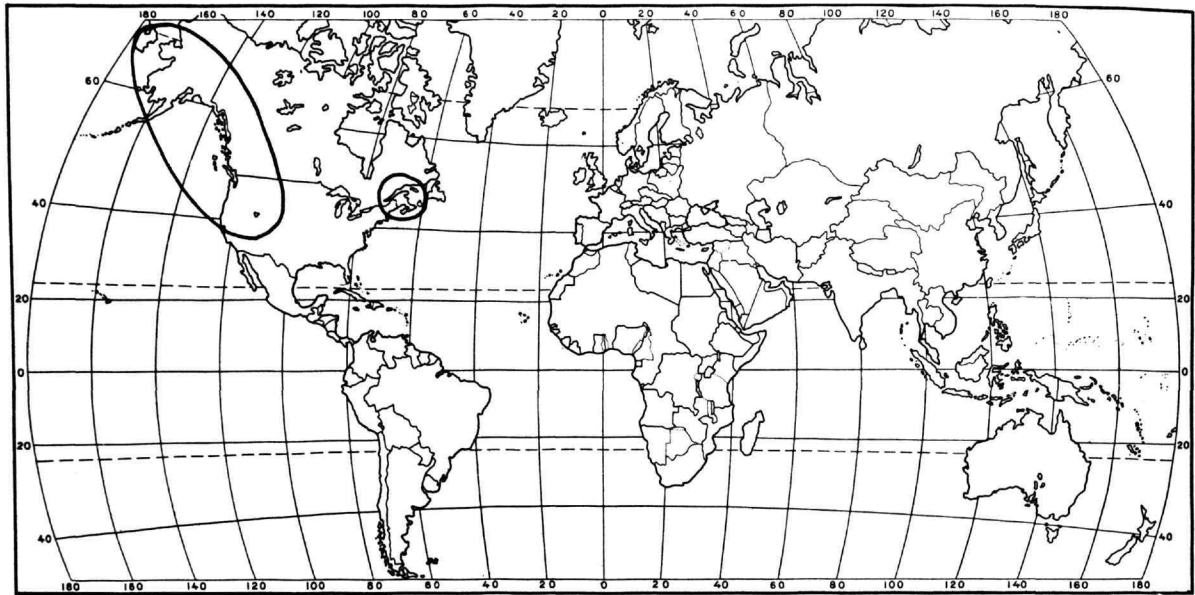
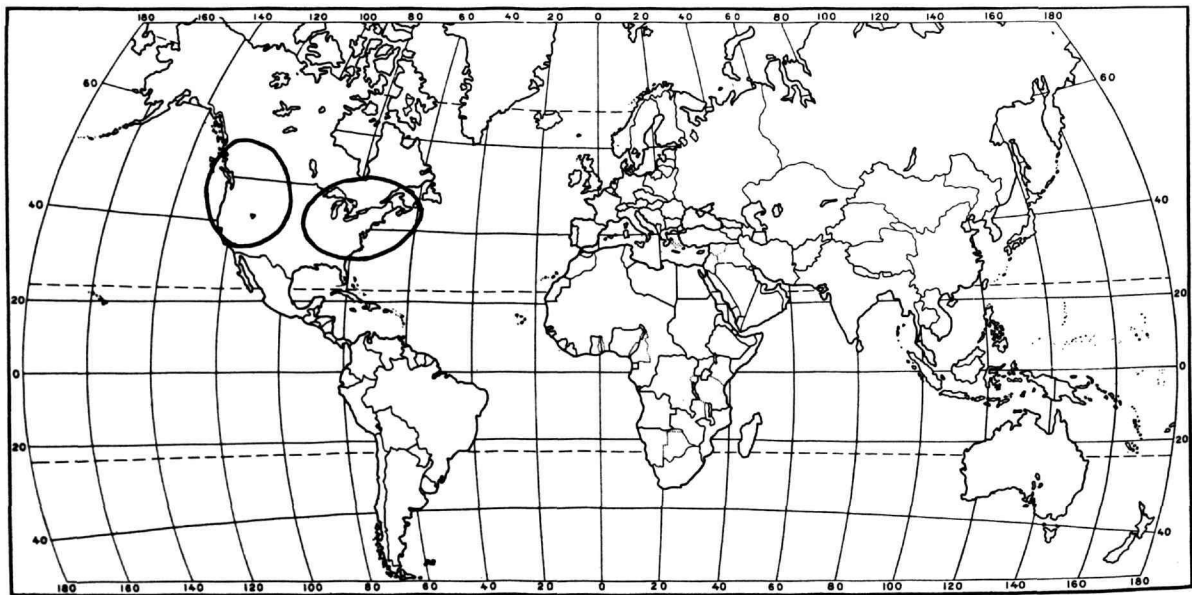


FIGURE 180.—Distribution map of *Paranemoura*.

FIGURE 181.—Distribution map of *Podmosta*.FIGURE 182.—Distribution map of *Prostoia*.

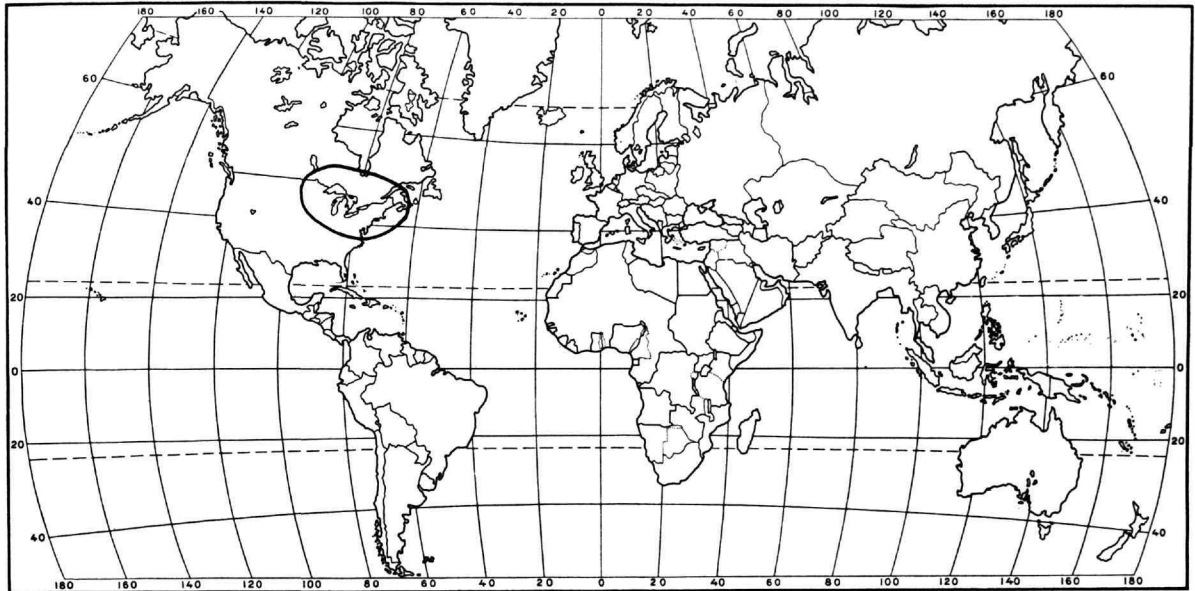


FIGURE 183.—Distribution map of *Shipsa*.

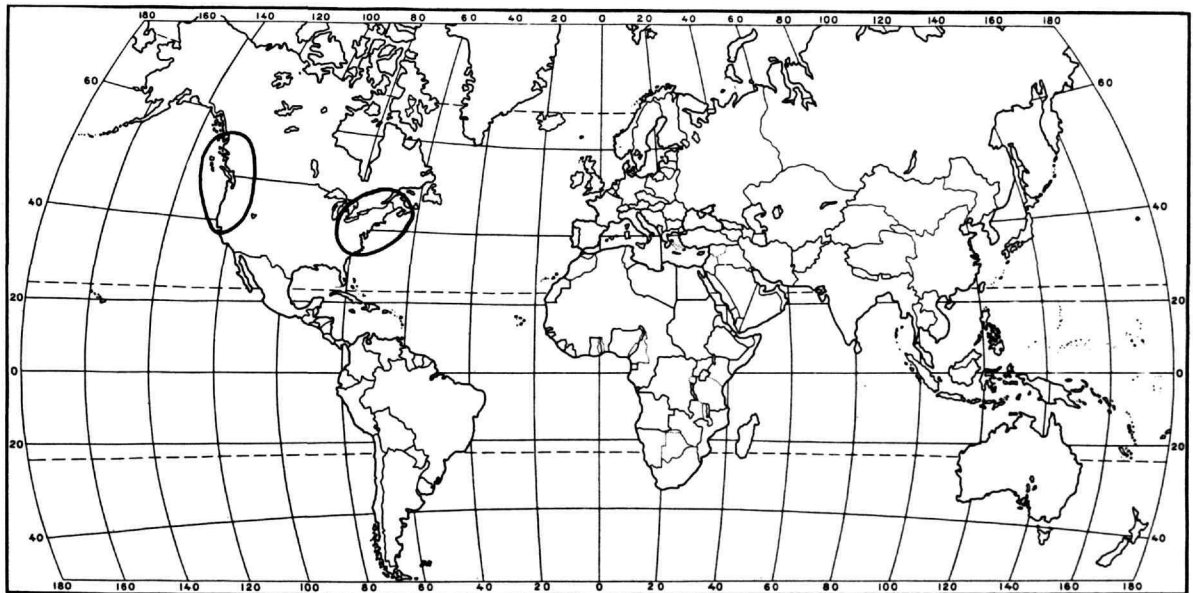
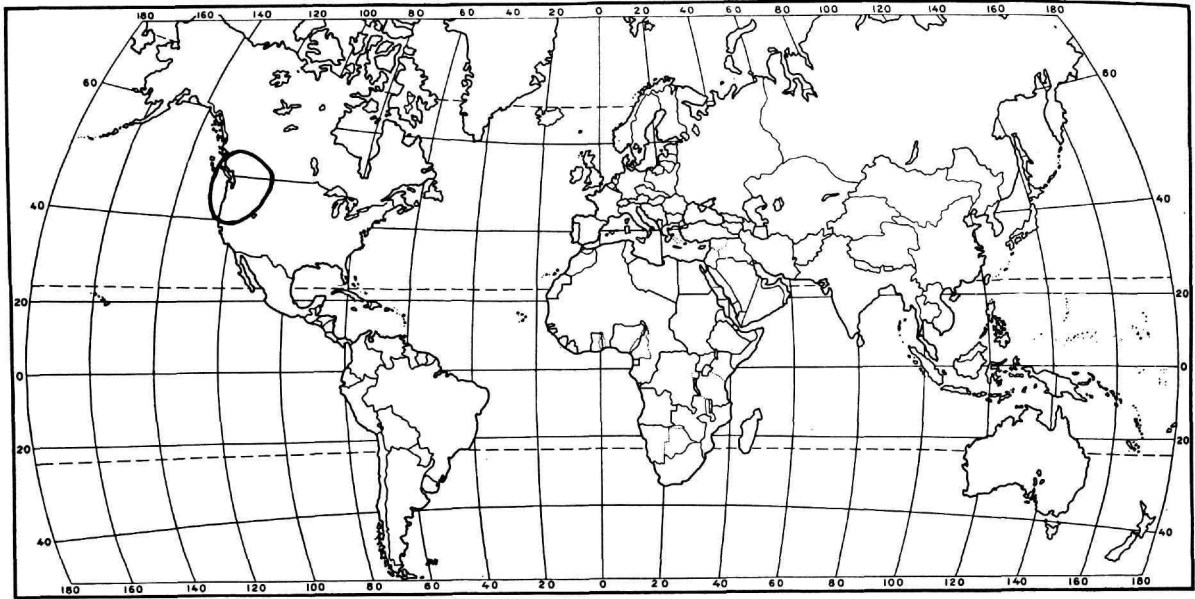
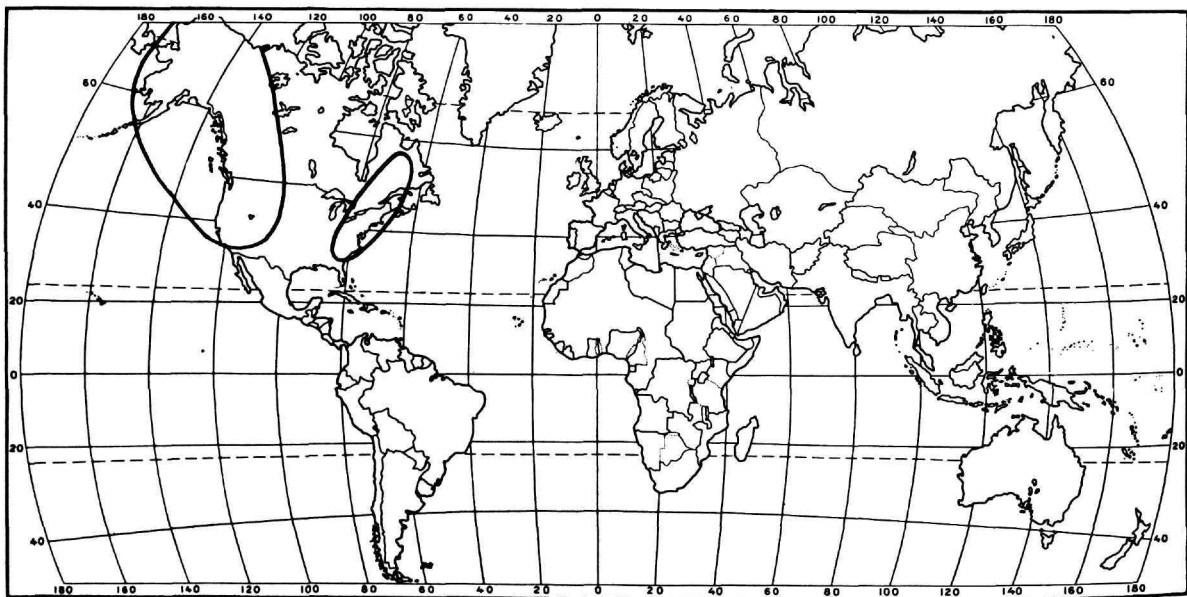


FIGURE 184.—Distribution map of *Soyedina*.

FIGURE 185.—Distribution map of *Visoka*.FIGURE 186.—Distribution map of *Zapada*.

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