THE BURROWING MAYFLIES (EPHEMEROPTERA: EPHEMEROIDEA) OF THE UNITED STATES

BY

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INTRODUCTION

The Ephemeroidea constitute a world-wide superfamily of Ephemeroptera which are commonly referred to as the "burrowing mayflies". Although most Ephemeroidea do burrow into the substrate of lakes or streams throughout most of their lives as aquatic larvae, the colloquial name applied to them in general is somewhat of a misnomer since some groups of species are adapted primarily to "sprawling" rather than burrowing. Approximately 250 species are presently known.

The Ephemeroidea are easily distinguished as larvae from all other mayflies. The paired abdominal gills on segments 2-7 are each forked into two elongated trunks or lamellar branches which are fringed laterally with slender filaments (Figs. 1, 3, 12, 20, 26, 28, 31, 34, and 36). Although these gills may be directionally oriented differently or vary in morphological detail from one group to the next, they are always diagnostic of ephemeroid larvae. Additionally, almost all Ephemeroidea have the mandibles modified into anteriorly projecting tusks to some degree (Figs. 3, 12, 20, 26, 28, 31, 34, and 36); however, if the tusks are completely absent then the anterolateral angles of the head possess a dense crown of spines (Fig. 1).

Currently 9 genera and 30 species of Ephemeroidea (Table 1) are recognized as occurring in the United States (none is known from Alaska or Hawaii). Of these species occurring in the United

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[1] Based in part on the author's presentation, Ephemeroptera Symposium, North American Benthological Society, March, 1974.

[2] Published with the approval of the Director of the Purdue University Agricultural Experiment Station as Journal Series No. 5674.

TABLE 1. — Alphabetical List of the Genera and Species of Ephemeroidea Known from the United States and Canada.

Campsurus
† * * *decoloratus* (Hagen)
Dolania
† * *americana* Edmunds and Traver
Ephemera
† * *blanda* Traver
† *compar* Hagen
* *guttulata* Pictet
* *simulans* Walker
† *traverae* Traver
† *triplex* Traver
* *varia* Eaton
Ephoron
† * *album* (Say)
* *leukon* Williamson
Hexagenia
* *atrocaudata* McDunnough
* *bilineata* (Say)
* *limbata* (Serville)
* *munda* Eaton
* *rigida* McDunnough
Litobrancha
* *recurvata* (Morgan)
Pentagenia
† *robusta* McDunnough
† * *vittigera* (Walsh)
Potamanthus
† * *diaphanus* Needham
† * *distinctus* Traver
† *inequalis* Needham
† * * *myops* (Walsh)
† *neglectus* Traver
* *rufous* Argo
* *verticis* (Say)
* *walkeri* Ide
Tortopus
† *circumfluus* Ulmer
† * *incertus* (Traver)
primus (McDunnough)

* Species in which the larvae have been described previously or have been known from the literature in some respect previously.

** Species formally described as larvae for the first time herein.

† Not known to occur in Canada.

States, 13 are also found in Canada (Table 1); however, no ephemeroid species are unique to Canada. These species make up an important component of the benthic community in many lentic and lotic habitats throughout North America. The biology and/or economic and applied aspects have been documented for a small number of species (e.g. Britt, 1962; Clemens and Bigelow, 1922; Cooke, 1952; Fremling, 1960, 1968, 1970; Henson, 1966; Hunt, 1953; Leonard, 1947; Lyman, 1944; and Neave, 1932). The vast majority of the species in the United States, however, have not been studied to any extent biologically and several remain unknown in the immature stage (see Table 1).

Most of the published morphological and ecological data concerning the Ephemeroidea of North America are fragmentary and

widely dispersed throughout the literature. Only a few works have dealt with summarizing certain limited information regarding these mayflies and often as a part of a larger treatment (e. g., Berner, 1959; Edmunds and Allen, 1957; Hamilton, 1959; Needham, 1920; and Needham et al., 1935). The obvious need for synthesizing the available data concerning the Ephemeroidea larvae of the United States and Canada, incorporating additional new information, and delineating basic research needs has prompted the present work. Hopefully this paper will serve as an appropriate starting point for those workers undertaking research on the North America Ephemeroidea, and also provide a set of reference data for aquatic ecologists who must deal with these insects.

Genera are presented in roughly phylogenetic sequence and following Edmunds' (1973) interpretation of familial relationships. Species are treated alphabetically under each genus. Family and subfamily designations have not been used herein since there remains some unresolved controversy concerning hierarchial status of the taxa and placement of certain genera[3]. More importantly, such designations are not particularly necessary to this work since the superfamily in this case (in which the study is restricted geographically) is an adequate and definitive working category.

The major emphasis has been to characterize comparatively the genera and species, and to completely update and augment the state of knowledge concerning the Ephemeroidea of the United States. The study is certainly applicable, however, to Canada in addition. A dichotomous taxonomic key to the larval genera and species has been appended to the discussion. It is necessarily somewhat incomplete because a few species are not known as larvae; and it is tentative in some respects where morphological criteria have not been tested with time. Most cited material upon which new state records are based are deposited in the Laboratory of Insect Diversity, Purdue University, West Lafayette, Indiana (PU). Other depositions are more specifically noted.

[3] I and G. F. Edmunds, Jr. will take up the subject of the familial status of *Pentagenia,* in the light of recent foreign discoveries, in another publication.

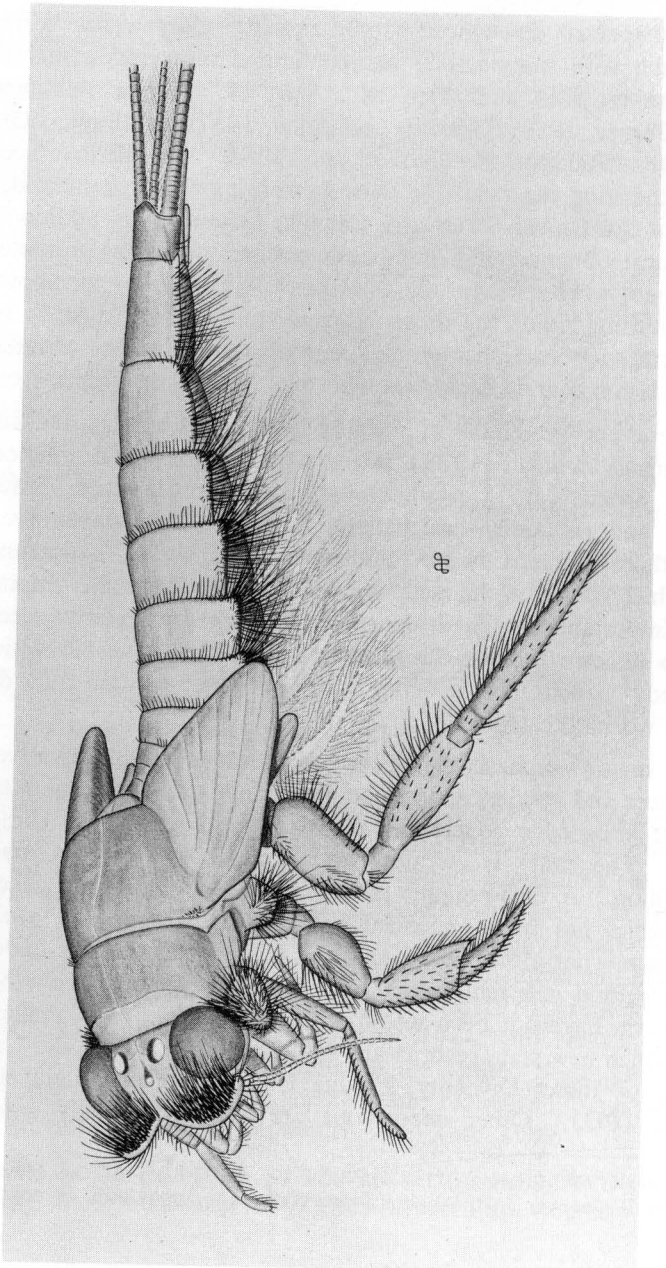


FIGURE 1. — *Dolania americana* Edmunds and Traver.

Genus DOLANIA Edmunds and Traver
Figure 1

This monospecific genus was originally described by Edmunds and Traver (1959) on the basis of four larvae from the Savannah River and its tributaries in South Carolina[4]. The genus along with its Old World counterpart, *Behningia* Lestage, constitute one of the least known groups of mayflies and one of the most atypical in terms of larval morphology and habit.

Dolania is conspicuously different in the larval stage from all other Ephemeroidea in the United States in that it lacks the specialized mandibular tusks, and in that both the anterolateral angles of the head and pronotum possess crowns of short dense spines. Other diagnostic features include the presence of modified labial palpi which resemble the short prothoracic legs, the lack of tarsal claws, and the ventrally oriented abdominal gills.

Dolania americana Edmunds and Traver

The most complete account of *D. americana* is found with its original description (Edmunds and Traver, 1959). Since the

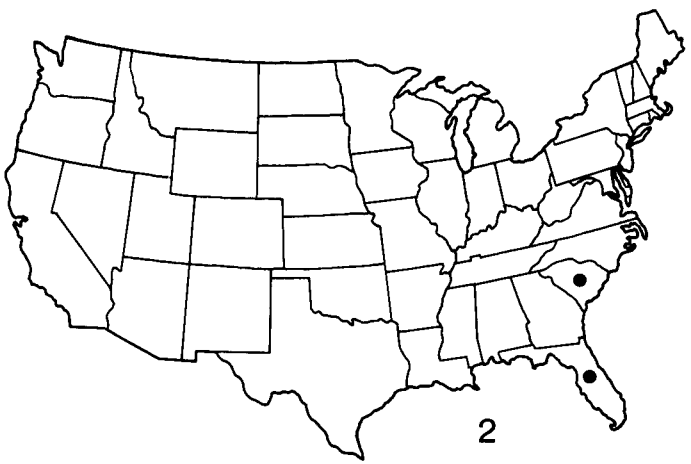


FIGURE 2. — Distribution of *Dolania americana*.

[4] The adults of *Dolania* are being described by Dr. George F. Edmunds, Jr., University of Utah.

species was first taken in South Carolina, it has been discovered in similar habitats in northern Florida[5] (Fig. 2). Very little has been reported on the biology of *D. americana,* although the larvae are apparently found in the clean shifting sand substrate of primarily cool spring-fed rivers. Laboratory observations which I have made indicate that the larvae burrow straight down in the sand to a depth of from 4-12 inches and may orient themselves in any direction. Although a burrow cannot be maintained in this type of substrate, the body and legs of an individual will form a protected cavity underneath the body in which the gills beat rapidly.

Genus POTAMANTHUS Pictet
Figure 3

This genus is Holarctic in distribution, with one species being doubtfully reported from India. The greatest number of species occur in the eastern half of North America. W. E. Howard (in Needham et al., 1905) was the first to describe North American *Potamanthus* larvae, but misidentified the material as *Polymitarcys albus* Say. *Potamanthus* is the North American representative of the so-called sprawling Ephemeroidea, in that larvae do not actively burrow throughout most of their existence. The larvae are most commonly found on rocks and gravel of streams and rivers.

The mandibular tusks of North American *Potamanthus* are well developed, curved inward, and somewhat sickle-shaped. Many other morphological adaptations which are usually associated with the fossorial habit are not found in this genus, but rather the body is flattened with long, narrow, outspread legs; there is no pronounced frontal process; and, the gills are oriented laterally.

Potamanthus diaphanus Needham

Needham (1908) described both the adults and larvae of this species, and this remains the only morphological treatment of the

[5] Dr. William L. Peters, Janice G. Peters, Florida A & M University, and Dr. Philip T. P. Tsui, formerly of Florida A & M University, have all conducted extensive work on the biology of *D. americana* which is to be published.

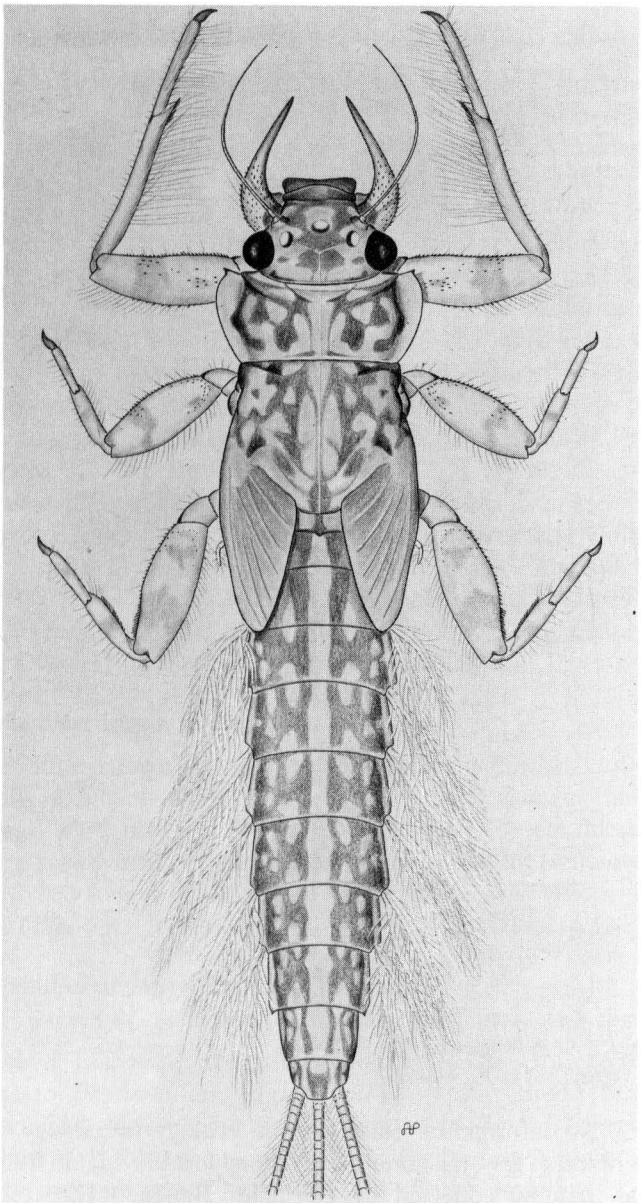
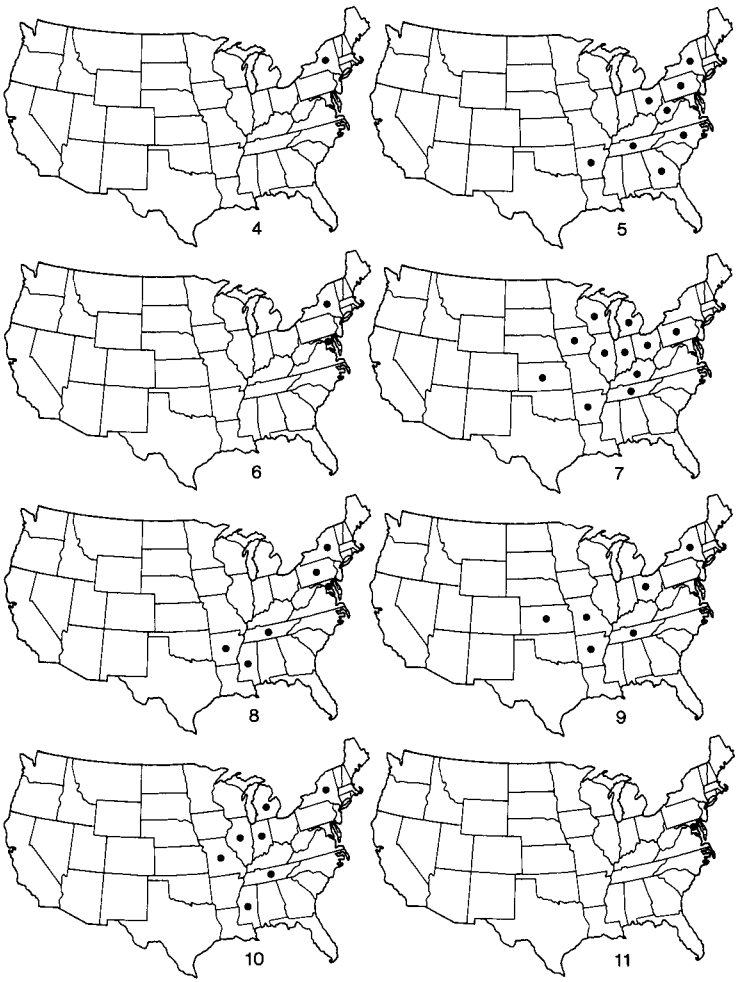


FIGURE 3. — *Potamanthus myops* (Walsh).



FIGURES 4-11. — 4. Distribution of *Potamanthus diaphanus*. 5. *P. distinctus*. 6. *P. inequalis*. 7. *P. myops*. 8. *P. neglectus*. 9. *P. rufous*. 10. *P. verticis*. 11. *P. walkeri*.

larvae. No information exists on the ecology or biology of the larvae except for the brief collection locality data from the original material collected by Cornelius Betten. The restricted distribution is shown in Figure 4.

Potamanthus distinctus Traver

This species was originally described by Traver (in Needham et al., 1935). The larvae of this species were also first described by Traver (1937), the species determination having been confirmed by rearing. Traver's morphological description is the only datum pertaining to the larvae of *P. distinctus*. Habitat data are quite scanty from available adult collection records. It appears that mature larvae may be expected in late June or July. The few remarks concerning the biology of *Potamanthus* larvae in North Carolina by Traver (1932) may refer to this species. The state distribution is shown in Figure 5. The West Virginia record is somewhat questionable, and new state records are based on the following: 1 male imago, PENNSYLVANIA, Crawford Co., Sugartown, VII-24-1973, G. R. Finni, PU. 4 male imagos and 7 female imagos, GEORGIA, White Co., Helen, VII-19-1945, P. W. Fattig, deposited in the P. W. Fattig Collection, University of Georgia, Athens. 30 male imagos and 30 female imagos, TENNESSEE, Sevier Co., Pigeon Forge, VII-24-1957, C. D. Hynes, deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

Potamanthus inequalis Needham

This little known species was described on the basis of adults only by Needham (1909) and has been touched on in the literature only very briefly since then. Argo (1927) considered this to be a synonym of *P. diaphanus*. The larvae are unknown and the species' known distribution is limited to the eastern United States (Fig. 6).

Potamanthus myops (Walsh)

Walsh (1863) described this species from Illinois in the genus *Ephemera* Linnaeus, and McDunnough (1926) transferred the species to *Potamanthus*. *Potamanthus medius* Banks has been synonymized with *P. myops* by Burks (1953). The recorded distribution of this species is shown in Figure 7. Additional new state records are added herein for this species as follows: 7 male imagos and 9 female imagos, OHIO, Shelby Co., Miami R., Hwy.

47, Sidney, VI-26-1953, A. R. Gaufin, PU. 1 female imago, TENNESSEE, Davidson Co., Stones R. at Coochville Pike Bridge, VI-28-1955, S. W. Edwards, deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

Although the adults of *P. myops* have been known for sometime, larvae have never been definitely associated with the adults and so have not been described up to this time. I have been able to successfully rear *P. myops* in our laboratory, and therefore provide the following description of the larvae. The dorsal view of a mature *P. myops* larva is figured (Fig. 3).

Mature larva. — Length of body including tusks and excluding caudal filaments, 18 mm. Caudal filaments, 8 mm.

Head. — Frons with large pale maculation anterior to median ocellus. Smaller median pale spot on clypeus. Vertex brown and pale patterned throughout. Anterior margin of labrum nearly straight with very slight emargination medially. Mandibular tusks tapering gradually to apices, with slight abrupt constriction along lateral margin at approximately mid-length of tusk, inner margin evenly curved, densely spuriferous in basal half, spurs becoming much less dense distally, dorsal surface with large brown basomedial spot.

Thorax. — Pronotum with anterolateral angles each forming small acute spine. Dorsal surface of femora of prothoracic legs with broad subapical light brown band and small subproximal light brown spot.

Abdomen. — Abdominal tergites with pale median longitudinal streak ending at mid-length of terminal tergite; each tergite with pair of submedian anterior pale maculations and pair of submedian posterior pale maculations, becoming fused in terminal tergite; additional pale pattern lateral of submedian maculations. Segment 8 with short acute posterolateral spines; segment 9 without such spines. Caudal filaments pale with very light brown annulations evident inconsistently on every few segments in basal half.

Material examined. — 1 larva, Indiana, Montgomery Co., Sugar Crk. at Deers Mill, VI-1-1973, W. P. McCafferty, A. V. Provonsha, and K. Black. 7 larvae, Ind., Tippecanoe Co., Wabash R. at Fort Ouiatenon, X-22-1973, B. L. Huff, Jr. 2 larvae, Ind., Elkhart Co., Elkhart R. 1 mi SE Millersburg, V-25-1973, A. V. Provonsha and K. Black. 1 larva, Ind., Warren Co., Mud Pine Crk. 1.5 mi W Rainsville, V-31-1973, A. V. Provonsha and K. Black. 5 larvae, Ind., Grant Co., Mississinewa R. at Marion, IV-18-1974, A. V. Provonsha. All material deposited in the Laboratory of Insect Diversity, Purdue University, West Lafayette, Indiana.

Remarks. — Measurements and coloration are based on a

mature male larva. Color pattern is extremely variable with age in the larvae of this species with the body becoming less fused with pale markings as the larvae mature. The larvae of *P. myops* can be distinguished from the larvae of either *Potamanthus verticis* (Say) or *Potamanthus walkeri* Ide[6] by the possession of the much more evenly curved and less apically constricted tusks. As would be predicted from study of the adults, the larvae of *P. myops* are most similar to those of *Potamanthus rufous* Argo. On the basis of the limited material available to me, however, there are distinct diagnostic characteristics which can be used to differentiate the larvae of these species. Most conspicuous is the difference in ground color between the two species. Although the color patterns are nearly identical, *P. myops* is a much darker cinnamon-brown (near sepia) while *P. rufous* is a lighter reddish-brown. In addition, the tusks may be slightly more constricted in *P. myops*. *P. rufous* apparently lacks the dark basal spot on the dorsal surface of the femora of the prothoracic legs which is found in *P. myops*.

P. myops larvae have been taken in gravel substrate in a moderate current of medium sized to large rivers, oftentimes under rocks or logs. In Indiana, this species probably overwinters as larvae with emergence of adults taking place predominantly in July. Young larvae have been taken in October and middle instar larvae have been taken in May.

On the basis of the figures given in Needham et al. (1905) under the name *Polymitarcys albus* and the description by W. E. Howard under the name *Polymitarcys albus,* it is possible that the larval material Howard referred to was *P. myops*. Also important is the fact that the larval material Howard referred to was evidently from northern Illinois.

Potamanthus neglectus Traver

Traver (in Needham et al., 1935) described this species on the basis of adults only, and some of these were from material that Argo (1927) had previously called *Potamanthus verticis*

[6] I have examined the larval material of *Potamanthus rufous* Argo, *P. verticis* (Say), and *P. walkeri* Ide that formed the basis of Ide's (1935a) study of this group.

(Say). The larvae remain unknown. Burks (1953) indicated that this was an "Atlantic Seaboard" species. Koss (1970), however, has reported specimens from Arkansas (Fig. 8). Furthermore, *Potamanthus* larvae taken from Benton County, Arkansas, are not exactly like any known larvae, and more than likely will prove to be *P. neglectus.* In addition, the following new state records indicate its more extensive range: MISSISSIPPI: 1 male imago and 2 female imagos, Lowndes Co., Columbus, VI-11-1956, L. Berner; 1 male imago and 5 female imagos, Pike Co., Bayou Chitto R., VIII-18-1954, C. D. Hynes. TENNESSEE: 1 male imago, Lincoln Co., Fayetteville, VII-22-1956, C. D. Hynes; 1 female imago, Cheatham Co., Harpeth R. at Kingston Springs, VII-2-1954, S. W. Edwards. All Mississippi and Tennessee specimens are deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

Potamanthus rufous Argo

This species was originally described by Argo (1927). The original and most complete description of the larvae of this species was given by Ide (1935a). The biology and ecology of the larvae of *P. rufous* is virtually unknown. Hamilton (1959) reported *P. rufous* from Kansas and Missouri but noted that the specimens may have been identified in error. I have recently studied specimens from Arkansas which definitely fit the present concept of *P. rufous* and therefore I can assume Hamilton's identification to be correct. The total known state distribution of this species is shown in Figure 9, and includes the following new state records: ARKANSAS: 6 male imagos and 10 female imagos, Montgomery Co., Ouachita R. at Rocky Shoals Boat Camp at US Hwy 270, VI-1-1974, W. P. McCafferty, A. V. Pronvonsha, and L. Dersch, PU; 2 larvae, Washington Co., VI-20-1966, Carter, deposited in the University of Arkansas Entomological Collection, Fayetteville. 4 male imagos and 6 female imagos, OHIO, Warren Co., Little Miami R. at Morrow, VI-28-1953, A. R. Gaufin, PU. 3 male imagos and 10 female imagos, TENNESSEE, Hamilton Co., 5 mi E Chattanooga, VIII-11-1956, C. D. Hynes, deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

Potamanthus verticis (Say)

This was the earliest discovered species of North American *Potamanthus* (Say, 1839). First reference to the larvae was made by Morgan (1913) in the form of a whole figure labeled *Potamanthus bettini*[7]. The most complete description of the larvae was given by Ide (1935a) under the name *Potamanthus flaveola* (Walsh). McDunnough (1926) synonymized *P. flaveola* with *P. verticis*. The few biological notes by Morgan (1913) concerning *Potamanthus* probably referred to this species; otherwise the biology and ecology of the larvae have not been reported. State distribution is shown in Figure 10, and includes the following new state record: MISSISSIPPI: 2 male imagos and 1 female imago, Lowndes Co., Columbus, VI-21-1947, no collector indicated, deposited in the Tulane University Collection, New Orleans, Louisiana; 1 female imago, Lawrence Co., Pearl R., VIII-16-1954, C. D. Hynes, deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

Potamanthus walkeri Ide

Adults and larvae of this species were originally described from Ontario by Ide (1935a). Traver (1937) discovered several larvae which she identified as *P. walkeri* from the Potomac River. The figures labeled as *Polymitarcys albus* by Needham (1920) were very possibly drawn from *P. walkeri* larvae. No information on the biology or ecology of the larvae is presently available. The limited, known distribution of this species in the United States is shown in Figure 11.

Discussion of Potamanthus spp.

The paucity of information regarding the individual species of *Potamanthus* in the larval stage makes a complete comparative analysis impossible at this time. *P. inequalis* and *P. neglectus* remain unknown in the aquatic stage and little can be said about them. I would suspect, however, on the basis of adult similar-

[7] A complete discussion of the nomenclatural status of this species name has been treated elsewhere (McCafferty, 1975).

ities, that the larvae of *P. inequalis* would be similar to *P. myops* or *P. rufous* and that *P. neglectus* would be of the *P. verticis* type.

Characteristics of the larvae which appear at this time to have specific diagnostic value are as follows: the contour of tusks (Figs. 43-45), the distribution of spurs on the tusks, the relative length of the tusks, the shape of the lateral margin of the pronotum, and the presence or absence of dark crossveins in the fore wing pads. In addition to these, color pigment and color patterns may be used. A caution must be given, however, first, that color patterns are extremely variable with age in *Potamanthus,* and therefore only the mature larvae (with darkened wing pads) can be determined with any degree of confidence; and color qualities may be altered by certain fluid preservatives. Patterns of the head, prothoracic legs, and dorsal abdomen may be useful. It could be interpreted from Ide's (1935a) figures of *P. rufous, P. verticis,* and *P. walkeri* that there are differences in the anterior margin of the labrum or clypeus. This is not the case, however, since apparent differences in the figures are a result of these regions of the heads having been in slightly different perspective as they were drawn. Also, although it may appear as such from the abdominal drawings, there is no significant structural difference in the posterolateral regions of the ninth tergites. Further study of material is necessary before thoroughly adequate keys can be constructed. The comparison of *P. rufous* and *P. myops* herein, and Ide's (1935a) discussion of *P. walkeri, P. rufous,* and *P. verticis* are of particular importance in studying larval species of this genus at this time.

North American *Potamanthus* are found primarily east of the Mississippi River except for records from Arkansas and very sparse records from Missouri, Kansas and Iowa (Figs. 4-11). *P. verticis* (Fig. 10) and *P. myops* (Fig. 7) are predominant Midwestern species in the group, while *P. distinctus* (Fig. 5) is the most common Eastern species. Interestingly, those *Potamanthus* species which have been taken west of the Mississippi River are also always found in the far eastern United States.

This genus is in great need of revision, and any such revision must take into account the morphology of mature larvae associated with adults via rearing. It is very possible that some of the now

recognized species will eventually fall into synonymy. For example, the following synonymies have been at least suggested by workers in the past. *P. inequalis* may prove to be either a synonym of *P. diaphanus* (Argo, 1927) or *P. myops* (Traver in Needham et al., 1935). *P. neglectus* may prove to be a synonym of *P. verticis* (Traver in Needham et al., 1935). Possible larvae of *P. neglectus* (see discussion under that species), if confirmed, however, would not substantiate this latter possible synonymy. These suggestions had all been made on the basis of knowledge of the adults only.

On the basis of larval information (primarily tusks type), I am able to place the currently recognized species in two groupings. The first is the *myops* grouping, and along with *P. myops* this would include *P. rufous, P. distinctus,* and tentatively *P. inequalis.* The second is the *verticis* grouping, and along with *P. verticis* this would include *P. diaphanus, P. walkeri,* and tentatively *P. neglectus.* Adult characterization would tend to corroborate these groupings.

Aside from the obvious need for taxonomic revision, the biology and ecology of *Potamanthus* species should be investigated. It would also be of much interest to ascertain the function of the mandibular tusks and to determine whether or not burrowing activity occurs at any time in the larval stage.[8]

Genus EPHEMERA Linnaeus

Figure 12

This genus and its subgenera have recently been treated comprehensively by McCafferty and Edmunds (1973). On a world basis, this is the largest genus of Ephemeroidea; however, in North America there are only seven currently recognized species and no species are found in the Neotropical Region. All of the North American species are members of the subgenus *Ephemera* s.s. Larvae was first described from the United States by Needham (1901). The larvae typically burrow in silt and sand deposits and are found in streams, rivers, and lakes throughout much of North America.

[8] Very early instar larvae have recently been taken in our Tippecanoe R. studies from substrate core samples at an 11 cm depth.

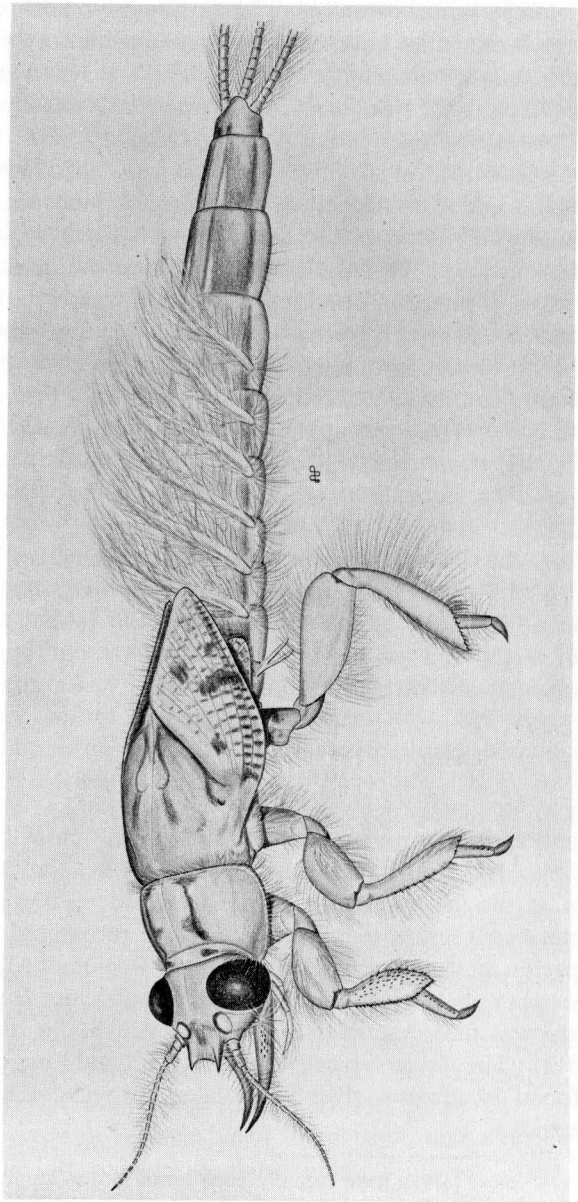


FIGURE 12. — *Ephemera simulans* Walker.

A few characteristics taken in combination will serve to differentiate *Ephemera* larvae from those of other Ephemeroidea. They possess a pronounced, bifurcate frontal process; antennae with long whorled setae over most of their lengths; and prothoracic legs having the tibiae distally rounded and with no processes. The long upward curved tusks that are spuriferous only at the base are unique to the larvae of this genus in North America.

Ephemera blanda Traver

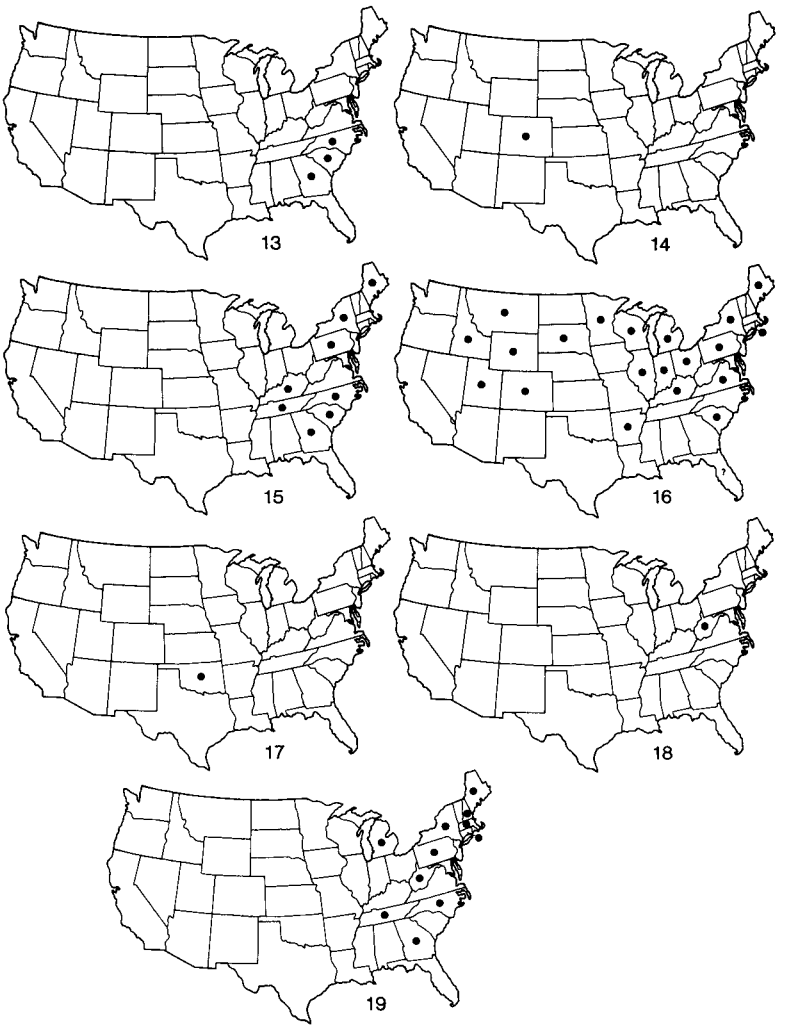
Traver (1932) described both the larvae and adults of this species from North Carolina, and this remains the most complete morphological treatment of the larvae. Positive correlation of the stages was established by rearing. Traver also gave some information on the larval habitat. The known distribution of *E. blanda* is shown in Figure 13.

Ephemera compar Hagen

This little known yet distinctive species was described by Hagen (1875). It is known only from adult type material taken from Colorado (Fig. 14).

Ephemera guttulata Pictet

This species was the first of the North American *Ephemera* to be described (Pictet, 1843). This is perhaps the most striking North American ephemeroid as an adult because of the black thorax and wings, and the contrasting snow-white abdomen. The original and most complete description of the larvae of this species was given by Kennedy (1926). In the work, Kennedy included notes regarding the biology and ecology of the larvae. Burks (1953) pointed out that the species occurred only in the Northeast. Consideration of Traver's (1937) record from North Carolina and new records from South Carolina, Georgia, and Kentucky indicate that *E. guttulata* is also definitely a Southeastern species (Fig. 15). New distribution records are as follows: 2 male imagos, SOUTH CAROLINA, Oconee Co., Chattooga R. nr. Mountain Rest, VI-6-1970, W. P. McCafferty, PU. Several male and female imagos were taken by W. P. McCafferty, A. V. Provonsha,



FIGURES 13-19. — 13. Distribution of *Ephemera blanda*. 14. *E. compar*. 15. *E. guttulata*. 16. *E. simulans*. 17. *E. traverae*. 18. *E. triplex*. 19. *E. varia*.

and K. Black from each of the following localities in KENTUCKY: Jackson Co., War Frk. Station Camp Crk., VI-7-1973, PU; Bath

Co., Trib. of Salt Lick Crk. at Clear Crk. Furnace Campground, VI-4-1973, PU; and McCreary Co., Indian Crk. at St. Hwy. 1045, 2.7 mi W Jnct. 90-1045, VI-6-1973, PU. 1 male imago, GEORGIA, Lumkin Co., Neel Gap, Chestatee Crk., V-30-1945, P. W. Fattig, deposited in the P. W. Fattig Collection, University of Georgia, Athens.

Ephemera simulans Walker

This relatively widespread and well known North American species was first described by Walker (1853) from Quebec. Larvae of *E. simulans* were first studied in Ontario by Clemens (1915); however, no description of them was given. Ide (1935b) has presented the most complete morphological treatment of the larval instars of this species. Spieth (1936) first reported the life history on lake dwelling populations from Indiana. Britt (1962) summarized the ecological and biological data regarding *E. simulans* up to that time, and Eriksen (1966) has shown the relationship of respiration and substrate preference as it pertains to this burrowing species.

This species is found throughout most of the United States (Fig. 16), excepting its absence in the Southwest and possibly extreme Southeast[9]. In the terms of Allen and Brusca (1973), it would be considered a boreal-lower north temperate species. The following constitute new state records for the United States: 1 female subimago, SOUTH CAROLINA, Fairfield Co., Cedar Crk. at Hwy 215, IV-19-1955, L. Berner, deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville. 1 male imago and 4 female imagos, KENTUCKY, Jackson Co., War Frk., Station Camp Crk., VI-7-1973, W. P. McCafferty, A. V. Provonsha, and K. Black, PU.

Ephemera traverae Spieth

This species is known only from the adults which were described by Spieth (1938b). From the adult collecting data, nothing can be inferred concerning the possible larval habitat. All adults

[9] Dr. Lewis Berner, University of Florida, (personal communication, 1974) has indicated to me that he has been unable to confirm the presence of *E. simulans* in Florida and that this remains a very dubious record.

were taken in early or mid-June. The known restricted distribution is shown in Figure 17.

Ephemera triplex Traver

Traver described this species in Needham et al. (1935). The larvae remain unknown. This species is known only from the adult type material taken in July and early August in West Virginia (Fig. 18).

Ephemera varia Eaton

This species was described by Eaton (1883), and this was the first species of *Ephemera* known in the larval stage from North America (Needham, 1901). Needham's (1920) later references to *E. varia* actually applied to *E. simulans*. Needham's original description of the larvae remains the most complete description to date. Biology of the larvae is unreported, except for a brief statement accompanying Needham's original description and his few, 1920 observations. The known distribution is shown in Figure 19, and includes new state records as follows: PENNSYLVANIA: 3 male subimagos and 4 female subimagos, Crawford Co., Woodcock Crk., VII-23-1973, W. Burgess, PU; 1 male imago, Crawford Co., Woodcock Crk., VII-10-1973, M. Davis, PU. 3 larvae, GEORGIA, Rabun Co., Coweeta Exp. Sta. nr. Dillard, VI-9-1953, M. J. Westfall. NORTH CAROLINA: 1 male imago and 2 female imagos, Macon Co., Cullasaja R. nr. Highlands, VIII-14-1948, L. Berner; 1 female imago, Macon Co., Cashiers, VIII-12-1948, L. Berner. The Georgia and North Carolina material are deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

Discussion of Ephemera spp.

The known larvae of *Ephemera* in North America can be distinguished morphologically from one another by modifying Burks' (1953) key which did not include *E. blanda*. The most reliable characteristics to use for the larvae are those of the adults which are evident in the later instars, i.e., color patterns of the abdomen and wings. Larvae of *E. guttulata* are easily told since they lack any color pattern on the abdominal sternites as do the adults. In

addition, the abdomen is quite different in appearance, being broader and more depressed than in the other species. *E. simulans* possesses a dark spotted color pattern in the hind wing pads. Both fore and hind pads are relatively free of dark blotches in *E. blanda,* whereas the fore wing pads alone are spotted in *E. varia* larvae. These latter two species are very similar in coloration; however, Traver in Needham et al. (1935) indicated a black lateral abdominal streak in *E. varia* but not in *E. blanda.*

The shape and proportional sizes of structures such as the mandibular tusks and frontal process as were used by Traver are unreliable as diagnostic characters. The extreme amount of variability in the frontal process was convincingly demonstrated by Macan (1958) for the British species of *Ephemera.*

E. guttulata and *E. blanda* appear to be more restricted in habitat to smaller, swifter streams than are either *E. simulans* or *E. varia. E. simulans* is common in lakes in addition to streams and rivers and is often found in close relationship with *Hexagenia limbata* (Serville), but evidently prefers a somewhat coarser substrate (Eriksen, 1966).

E. blanda is definitely a Southeastern species (Fig. 13), while the closely related *E. varia* is primarily a Northeastern species (Fig. 19) although, Wright and Berner (1949) reported it from eastern Tennessee, and new records have been presented herein for Georgia and North Carolina. It may be noted that all Southeastern records for *E. varia* are from high mountain areas and that little overlap occurs between the respective ranges of the latter two species. The very distinctive *E. guttulata* is more widespread throughout the Northeast and Southeast (Fig. 15). *E. simulans* ranges throughout much of the United States (Fig. 16) and along with the poorly known *E. compar* (Fig. 14) is represented in the western United States.

Other than the fact that three species are still unknown in the larval stage for this genus in the United States and require description, additional reliant structural characteristics should be found to separate the known larvae. Although the biology and ecology of *E. simulans* is relatively well known for North American ephemeroids, more intensive investigation is needed especially for *E. blanda* and *E. varia.*

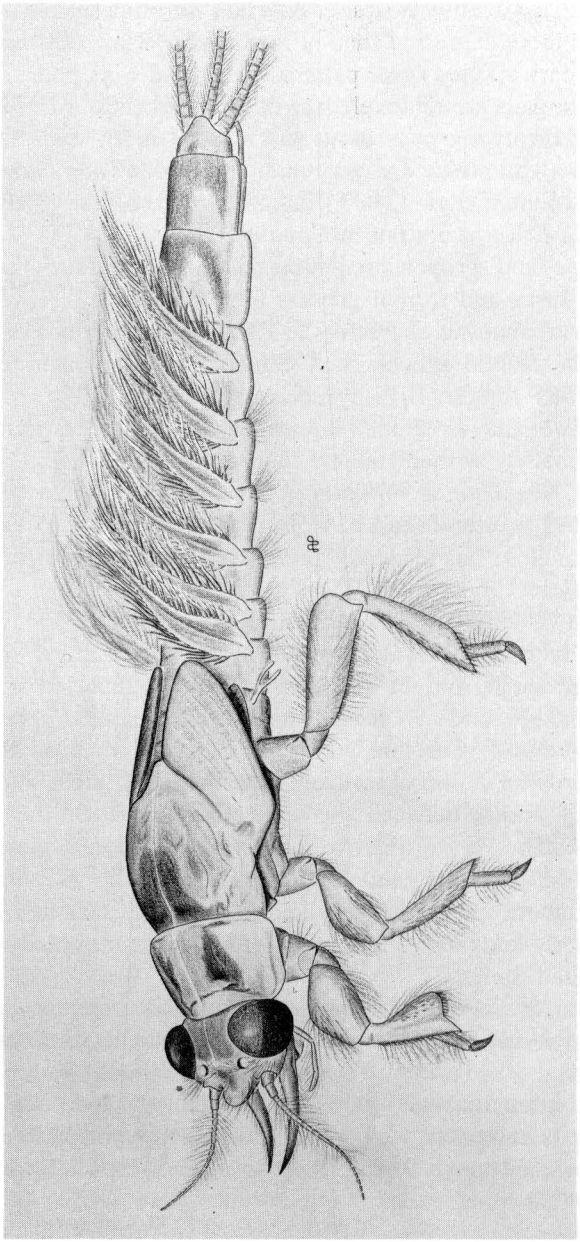


FIGURE 20. — *Hexagenia limbata* (Serville).

Genus HEXAGENIA Walsh
Figure 20

This relatively well known genus is distributed throughout most of the United States. McCafferty (1973) indicated that the occurrence of *Hexagenia* species outside of the Western Hemisphere was highly doubtful. The five currently recognized species in the United States are all members of the subgenus *Hexagenia* s.s., while the Neotropical species belong to the subgenus *Pseudeatonica* Spieth (McCafferty, 1968 and 1970). Adults of this group have been known since 1829, and the larvae were first comprehensively described by Eaton (1883) although no species as such were described as larvae. Morgan's (1913) reference and figures to *Hexagenia* larvae actually apply to *Litobrancha* McCafferty. Larvae are typically burrowers in fine silt and marl substrate of streams, rivers, and lakes of all sizes.

A combination of easily recognized characteristics may be used to identify *Hexagenia* larvae. On the head, the antennae possess long setae over most of their length and the distinct frontal process is more or less rounded with the lateral margins converging anteriorly. The long, upcurved mandibular tusks are without any spination or spurs. Tibiae of the prothoracic legs are emarginate, possessing two processes apically, and gill 1 is bifurcate.

Hexagenia atrocaudata McDunnough

This species was originally described from Ontario and Virginia by McDunnough (1924). Traver (1931) described the larvae of *H. atrocaudata* which had been reared by J. G. Needham. The most useful description of the larvae, however, was presented by Spieth (1941) in his revision of the genus *Hexagenia*. Little is known regarding the biology of the larvae, with only a brief comment given by Leonard and Leonard (1962) regarding its habitat in Michigan. The state distribution is shown in Figure 21, and includes the following new state record[10]: 1 female imago, WISCONSIN, Florence Co., VII-16-1959, R. L. Giese, PU.

[10] Hilsenhoff (1970) lists all species of U.S. *Hexagenia* as probably occurring in Wisconsin. The literature up to this time, however, substantiates only two of these with actual Wisconsin records. I am therefore including new Wisconsin records herein for the remaining three species.

FIGURES 21-25. — 21. Distribution of *Hexagenia atrocaudata*. 22. *H. bilineata*. 23. *H. limbata*. 24. *H. munda*. 25. *H. rigida*.

Hexagenia bilineata (Say)

This is the earliest known species of *Hexagenia* and was described by Say (1824) in the genus *Baetis* Leach. Walsh (1863) transferred it to *Hexagenia*. Clemens (1913) first described the larvae of this species from Canadian material, some individuals of which were reared. This remains probably the most complete morphological description to date although it is of little comparative value. Needham's (1920) description does not with certainty apply to the species and in fact some of his figures have been shown to be mislabeled (McCafferty, 1971). The most complete study of the biology of this species was presented by

Fremling (1960). *H. bilineata* is known generally from throughout the United States excluding the West and Northwest (Fig. 22). Specimens from the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville, have provided new state records as follows: NORTH CAROLINA: 1 female imago, Swain Co., Bryson City, VIII-13-1954, L. Berner; 1 female imago, Macon Co., Franklin, VI-29-1957, C. D. Hynes; 2 female imagos, Macon Co., Highlands, VII-14-19-1958, T. Howell. 7 female imagos, SOUTH CAROLINA, Aiken Co., Beulah Pond (Savannah R. Proj.), VII-1-29-1952, W. Cross. There are additional specimens from South Carolina deposited in the Clemson University Collection, Clemson, South Carolina, as follows: 1 male imago and 5 female imagos, Abbeville Co., Pelzer, VI-1934, no collector indicated.

Hexagenia limbata (Serville)

Serville (in Guerin-Meneville, 1829) described this species in *Ephemera,* but it was later transferred to *Hexagenia* by Walsh (1863). This geographically diverse species has had a rather confused taxonomic history up to the time Spieth (1941) clarified its taxonomic limitations and indicated its geographic variants as subspecies. The larvae of this species were the first to be described for the genus (Needham, 1901) and were treated under the synonym *Hexagenia variabilis* Eaton. An exhaustive description of the exoskeletal morphology of the larvae of this species is not present in the literature although it has been treated briefly by several authors. The subspecific variation in the larvae has not been studied to any extent. The most complete treatment of the life history, ecology, and economic importance of this mayfly was presented by Hunt (1953). This species is known to range over more of the United States than any other North American ephemeroid species (Fig. 23). The following new state records are herein added: 6 larvae, MONTANA, Flathead Co., Mud Crk., VII-15-1969, B. R. Oblad, deposited in the United States National Museum, Washington, D.C. 1 larva, VIRGINIA, Charlotte Co., Wards Fork (Roanoke Crk.), Madison and Cullen, no date, Myers and Abraham, deposited in the United States National Museum, Washington, D.C. 1 male subimago and 6 female sub-

imagos (*H. limbata venusta* Eaton), ALABAMA, Walker Co., Blackwater Crk., nr Jasper, VI-24-1954, C. D. Hynes, deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville. 1 male imago, (*H. l. venusta*), GEORGIA, Bartow Co., Cartersville, VI-14-1940, P. W. Fattig, deposited in the P. W. Fattig Collection, University of Georgia, Athens. 1 male imago and 1 female imago, (*H. l. venusta*), LOUISIANA, Vermilion Parish, Kaplan, VII-23-1952, E. J. Hebert, deposited in the Florida State Collection of Arthropods, Gainesville.

Hexagenia munda Eaton

This species was described in Eaton's monograph (1883-88) and presently possesses a number of synonyms most of which have been relegated to subspecific rank (Spieth, 1941). Larvae of this species were first formally described by Traver (1931) under the name *Hexagenia carolina* Traver. Other than Spieth's (1941) brief remarks concerning the larvae of *H. munda marilandica* Traver, there have been few descriptive accounts of the larvae. The ecology and biology of this species in Florida was treated in some detail by Berner (1950), and is similar in many respects to that of *H. limbata*. *H. munda* is also a relatively widespread species (Fig. 24), but may be considered the typical representative of the genus found in the South. It is composed of several subspecies and many intergrades of these. New distribution records are as follows: WISCONSIN: 1 male imago (*H. munda affiliata* McDunnough), Oneida Co., Snowden Lake, VI-20-1957, R. L. Giese, PU; 1 male imago, 1 female imago, 3 male subimagos, and 4 female subimagos, Chippewa Co., Brunet Island State Park, VII-26-1957, R. L. Giese, PU. ARKANSAS: 3 female imagos, Montgomery Co., Ouachita R. at Rocky Shoals Boat Camp at US Hwy 270, VI-1-1974, W. P. McCafferty, A. V. Provonsha, and L. Dersch, PU; 2 male subimagos, (*H. munda munda*), Boone Co., Bear Crk. at St. Rd. 14, 3 mi W Junct. 281 and 14, V-28-1974, W. P. McCafferty, A. V. Provonsha, and L. Dersch, PU. The following additional new state records (for *H. munda elegans* Traver) are represented by material in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville. LOUISIANA: 1 female imago, St. Tammany Parish, Covington, VI-2-

1956, C. D. Hynes; 1 male imago and 1 female imago, East Baton Rouge Parish, Baton Rouge, V-10-1948 and V-15-1956 respectively, no collector indicated. MISSISSIPPI: 1 male imago and 2 female imagos, Pike Co., Bayou Chitto R., VI-1-1956, C. D. Hynes; 5 male imagos, 5 female imagos, 20 male subimagos and 20 female subimagos, Lawrence Co., Pearl R. VIII-17-1954, C. D. Hynes. 12 male imagos and 2 female imagos, TENNESSEE, DeKalb Co., Caney Fork R. nr. Sparta, VII-26-1956, C. D. Hynes.

Hexagenia rigida McDunnough

This distinctive species has been known since McDunnough (1924b) described it from Canadian specimens. Neave (1932) described the larvae and also presented the most complete data on the biology of this species. The distribution of this mainly Midwestern and Eastern species is shown in Figure 25, and includes the following new state records: INDIANA: 1 male imago and 3 female imagos, Cass Co., Wabash R. at Logansport at light, VII-16-1973, A. V. Provonsha and K. Black, PU; 1 male imago, Harrison Co., White Cloud, VII-30-1924, J. J. Davis, PU; 1 male imago, Tippecanoe Co., West Lafayette, VII-12-1974, A. V. Provonsha, PU. 2 male imagos, WISCONSIN, Dane Co., VIII-15-1947, no collector indicated, PU. 1 male imago, MARYLAND, Catonsville, VIII-2-1953, G. B. Vogt, deposited in the U.S. National Museum, Washington, D.C. 1 male imago and 2 female imagos, TENNESSEE, Hamilton Co., 5 mi E Chattanooga, VIII-11-1956, C. D. Hynes, deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

Discussion of Hexagenia spp.

Taxonomic keys to the larval species of *Hexagenia* have been written by Traver (in Needham et al., 1935) and Burks (1953). Both, however, are inadequate to various degrees. *H. atrocaudata* possesses perhaps the most distinctive frontal process (Fig. 48), it being more or less truncate and sometimes having a slightly emarginate anterior margin. *H. rigida* possesses a slightly pointed frontal process (Fig. 49), and in mature male larvae, the long,

almost straight, developing penes are most characteristic of this species. On the basis of material I have seen and other reports (e.g. Spieth, 1941), I must seriously question the applicability of Burk's (1953) figures of the frontal processes labeled as *H. bilineata, H. rigida,* and *H. munda.* As more material is studied we may find that due to variability the shape of the frontal process is of little value taxonomically in most of the species of *Hexagenia* as has been shown for *Ephemera.* The remaining three species can be somewhat difficult to differentiate from each other, and locality records may be of some help in identifying them. *H. munda* generally possesses a somewhat conical frontal process, and relatively long slender tusks. Traver (1931) first attempted to utilize the shape of the tarsal claws of the larvae to distinguish species in this genus, and Burks (1953) incorporated some of these into his key. Young larvae of *H. bilineata* and *H. limbata* are extremely difficult to distinguish from one another. Gooch (1967), however, has shown that in larvae over 16 mm in length, that the claws of *H. bilineata* (Fig. 50) are consistently swollen basally and that those of *H. limbata* (Fig. 51) are long and slender. The shapes of the frontal processes in these species are inconsistent. In addition, Fremling (1960) indicated that in the male larvae the cerci and median terminal filament are approximately the same length in *H. limbata,* while in *H. bilineata* the median terminal filament is shorter than the cerci. This situation is also inconsistent, however.

The above characters must be used with caution since for the most part they are applicable only to mature larvae. Adult characters which may be evident in the larvae can be utilized to some extent along with known (Figs. 21-25) or expected geographic distribution. Rearing the larvae through to identifiable terrestrial forms will obviously verify determinations; however, this technique is often impractical, and also larvae of *H. limbata* and *H. bilineata* often may be taken together in benthic samples.

I am in agreement with Spieth's (1941) revision of the N.A. species of *Hexagenia. H. limbata* and *H. munda* are highly variable and this variability appears to be based primarily on geographic populations. Thus these two species were each assigned several subspecies. Since designation of these subspecies, however, an

increasing number of intergrades have been found and are continuing to be found. The practical utility of the subspecies concept in these cases therefore becomes questionable. It is also doubtful that these populations would demonstrate statistically significant degrees of difference which may be expected to preclude subspecific categories (see Mayr, 1969). The extent of genetic intergradation would indicate that possible, once existent geographic gaps or other isolating mechanisms are deteriorating. At this point in time, I see no biological necessity for determining subspecies in *Hexagenia* larvae, although it may be important in the future as our understanding of these groups increases.

Few comparative studies of the biology and/or ecology of *Hexagenia* larvae on a species level have been reported. Neave (1932) compared *H. limbata* and *H. rigida,* and Fremling (e.g., 1973) has compared ecological factors influencing the distribution of *H. bilineata* and *H. limbata* on the Mississippi River. *H. bilineata* is primarily a "big river" mayfly, the larvae preferring large silted pool areas. It may also be common in lakes. It evidently possesses a one year life cycle. *H. limbata* is found in various bodies of water ranging from the Great Lakes to small streams with silt deposits. Larvae may reach maturity throughout the summer months often resulting in mass emergence. The length of the life cycle of *H. limbata* has been unresolved with reports indicating one, two, or even three year span of development. Spieth (1938a) believed that perhaps the species in the northern part of its range required two years to mature while those in the southern part would require only one. Interestingly, Hudson and Swanson (1972) have recently discovered both one-year and two-year life cycle individuals of *H. limbata* in Lewis and Clark Lake. Evidently those individuals completing the life cycle in one year resulted from eggs oviposited more toward mid-summer while those completing the life cycle in two years resulted from eggs deposited in late summer or early fall. Berner (1950) was able to key out three subspecies of *H. munda* and also *H. bilineata* in Florida on the basis of habitat and distribution. *H. munda orlando* was found restricted to deep water areas of sand bottom lakes where a small film of silt covered the sandy substrate.

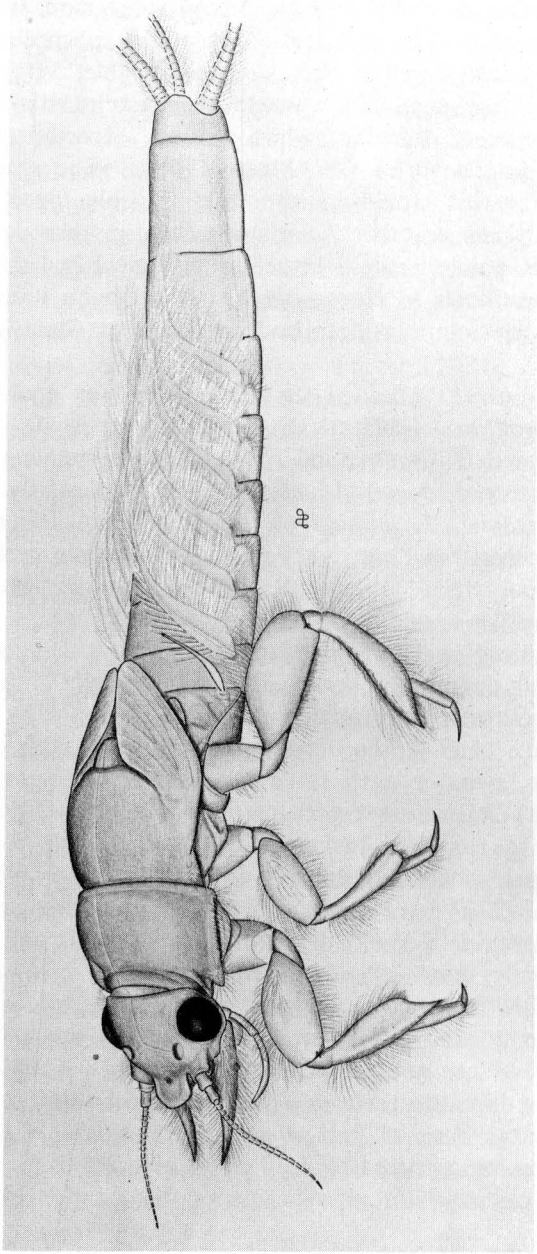


FIGURE 26. — *Litobrancha recurvata* (Morgan).

H. munda marilandica and *H. munda elegans* were found in silt deposits in streams. The life cycle is evidently one year long in *H. munda.* Little can be said regarding *H. rigida* except that it evidently is restricted to certain portions of lakes and has also been taken in rivers but appears to be absent in cold spring-fed water. It is much less abundant than either *H. limbata* or *H. bilineata.* Britt et al. (1973) stated that previous to 1953, *H. limbata occulta* and *H. rigida* had been the dominant bottom organism in the deeper, mud bottom portion of Lake Erie. Neave (1932) reported the life cycle of *H. rigida* in Lake Winnipeg to be two years. *H. atrocaudata* was reported by Leonard and Leonard (1962) to burrow in beaver ponds on cold, swamp fringed streams. It also is found in small numbers compared to other *Hexagenia.*

So few larvae have been studied morphologically on the species level in *Hexagenia* that those characters used must be viewed with caution. An obvious need is to find consistent structural attributes which can be used with confidence to differentiate the larvae. The species of *Hexagenia* would appear to be an excellent group in which to study speciation and North American biogeography. Additional biological information should be sought particularly for *H. atrocaudata, H. munda,* and *H. rigida.* It would be most interesting to know the extent of ecological differences between the subspecies of *H. munda.*

Genus LITOBRANCHA McCafferty

Figure 26

This genus was described by McCafferty (1971) for the species *Litobrancha recurvata* (Morgan) which had previously been treated in the genus *Hexagenia.* The genus is restricted in distribution to eastern North America.

Several easily studied characteristics can be used to separate the larvae of this genus from other Ephemeroidea larvae in the United States. The lateral margins of the non-bifurcate frontal process are angular and the antennal flagella lack long setae. The tusks are somewhat shorter in *Litobrancha* than in *Ephemera* and *Hexagenia,* and they lack spurs or spines. The prothoracic legs are basically similar to those of *Hexagenia* but

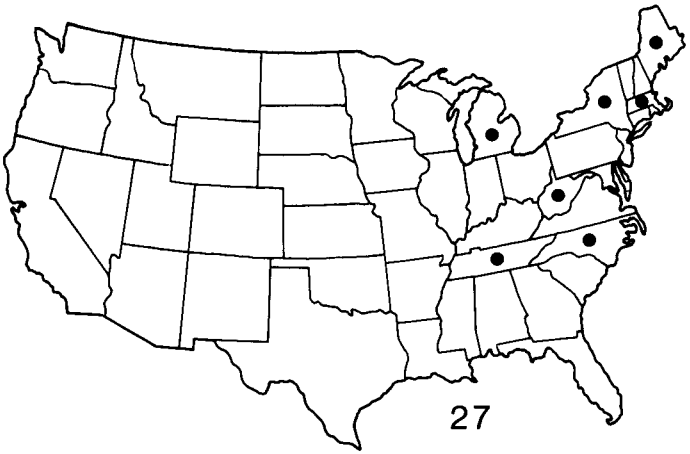


FIGURE 27. — Distribution of *Litobrancha recurvata.*

differ in certain details of the tibiae. The first abdominal gill is vestigial and unbranched; other than that the gills are well developed and dorsally oriented.

Litobrancha recurvata (Morgan)

First reference to this species was made by Morgan (1913). Morgan's comments in regards to *Hexagenia* larvae are actually applicable to this species. The most complete description of the larvae of this species was offered by Spieth (1941), although the morphological treatment of McCafferty (1971) of the monospecific genus is certainly useful as a specific account also. The biology of *L. recurvata* has been variously treated by Morgan (1913), Needham (1920), Morgan and Grierson (1932), Morgan and Wilder (1936), and Spieth (1941). Needham referred to this species as an upland bog-stream species, and in fact *L. recurvata* is usually associated with colder and swifter streams than are most other North American burrowing mayflies. As pointed out by Spieth, the relatively small populations of this species may be due to this restricted habitat. The species reportedly emerges during May and June. The known distribution in the United States of this species is indicated in Figure 27.

Genus PENTAGENIA Walsh

Figure 28

Pentagenia was erected by Walsh (1863). The genus is made up of two nominal species and occurs only in North America. Larvae of the genus were first described by Needham (1920). The most complete morphological treatment including figures was presented by McCafferty (1972). Although these mayflies can be abundant around large rivers, the larvae are most difficult to collect and are taken most commonly in drift samples.

Many distinctive morphological features distinguish *Pentagenia* larvae among North American Ephemeroidea. On the head the bifurcate frontal process is accompanied by a pair of similar looking but smaller processes above the bases of the antennae. The broadened tusks are toothed with spurs along most of their lateral margins. All of the mouthparts are rather unique (e.g. see Figure 40) but difficult to examine in the field. The tibiae of the prothoracic legs possess two distinctive apical processes. The gills are dorsally oriented.

Pentagenia robusta McDunnough

Our knowledge of this species is restricted to the original adult material upon which McDunnough (1926) based his original description. It has been taken only from Ohio (Fig. 29). The larvae most probably occurred in the Ohio River near Cincinnati.

Pentagenia vittigera (Walsh)

This species was originally described by Walsh (1862) in the genus *Palingenia* Burmeister. Walsh (1863) transferred it to *Pentagenia* and also described *Pentagenia quadripunctata* which was later shown to be a variant of *P. vittigera* by Needham (1920). At that time Needham also described the larvae of *P. vittigera.* The most complete comparative study of the larval morphology of this species was given by Spieth (1933). The illustrations presented in McCafferty (1972) pertain to this species. The biology of the larvae has been virtually unknown. Some ecological data on this species were presented by Fremling (1970) for Mississippi River adult populations, and indicates that the larvae may appar-

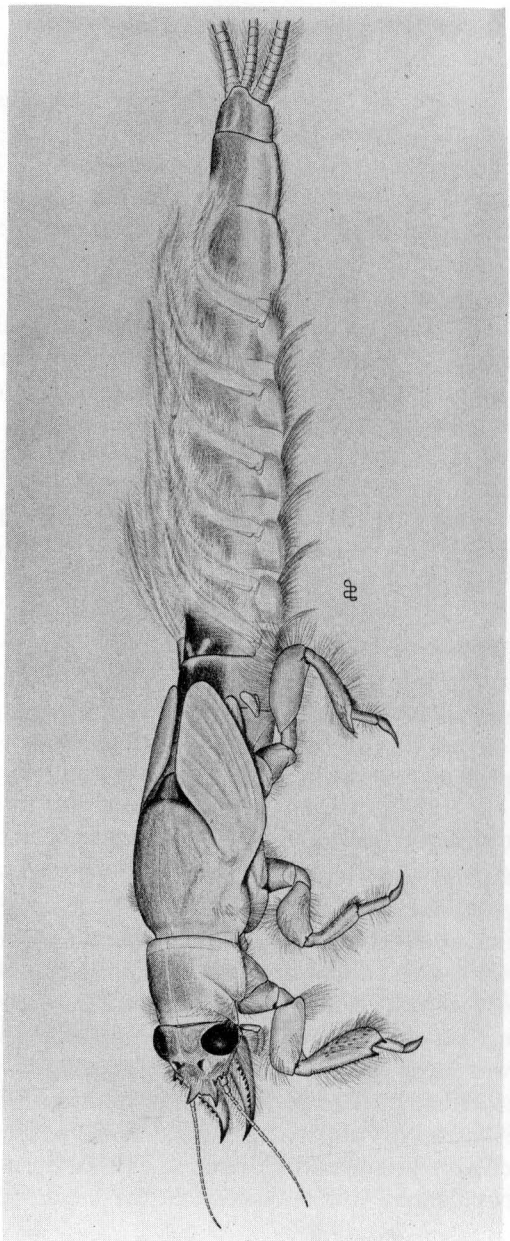
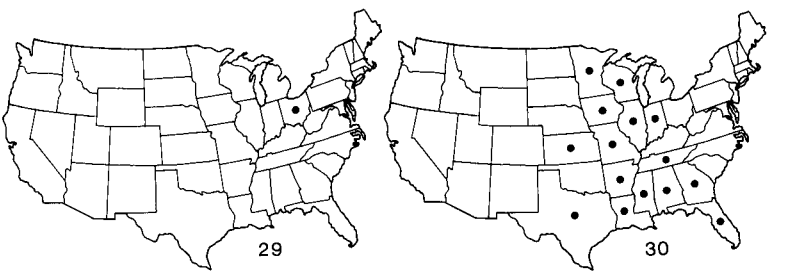


FIGURE 28. — *Pentagenia vittigera* (Walsh).



FIGURES 29 and 30. — 29. Distribution of *Pentagenia robusta.* 30. *P. vittigera.*

ently live in faster water areas than *Hexagenia bilineata* or *H. limbata,* and that under unpolluted conditions emergence may be expected throughout the summer.

We have recently (1974) collected *P. vittigera* larvae from the Wabash River at New Harmony, Indiana. Individuals were taken in hard clay banks at approximately three feet below the water level. The habitat and dense honeycomb burrows were very similar to those described for *Tortopus incertus* (Traver) from the Savannah River by Scott et al. (1959). On the basis of studying the functional morphology of *Hexagenia limbata* in regards to its fossorial behavior, McCafferty (1969) had predicted that *Pentagenia* larvae because of the somewhat different structure of the head, tusks, and prothoracic legs would be found in clay or relatively hard substrate. It was further predicted that the tusks of *Pentagenia* would be used as true digging organs rather than leverage organs. The latter prediction can now be demonstrated by the study of live larvae.

The distribution of this Central and Southeastern species is shown in Figure 30, and includes the following new state records: 2 male imagos, GEORGIA, Clark Co., Athens, VII-14-1970, W. P. McCafferty and T. L. Harris, PU. 3 male imagos, 1 female imago, 9 male subimagos, and 5 female subimagos, LOUISIANA, East Baton Rouge Parish, Baton Rouge, IX-3-1964, no collector indicated, deposited in the Tulane University Collection, New Orleans, Louisiana. 2 female imagos and 1 male subimago, MISSISSIPPI, Lawrence Co., Pearl R., VIII-17-1954, C. D.

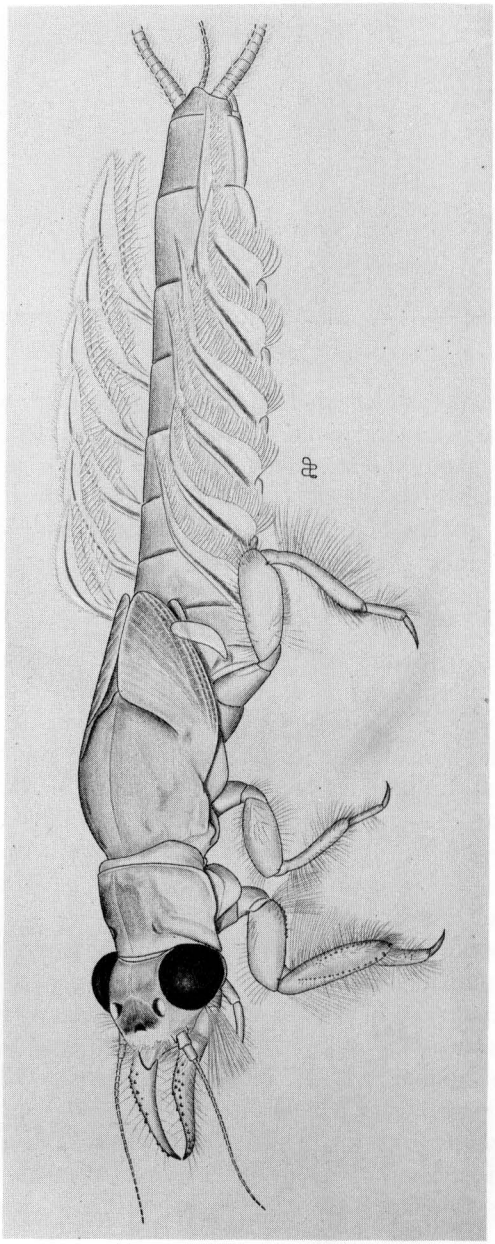


FIGURE 31. — *Ephoron album* (Say).

Hynes deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

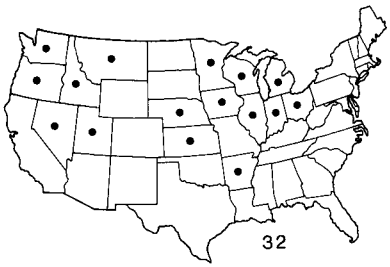
Genus EPHORON Williamson
Figure 31

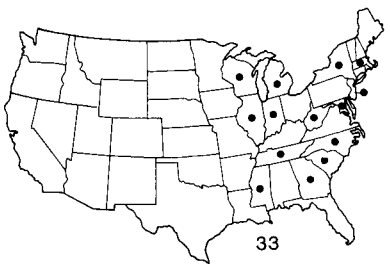
This genus was originally described by Williamson (1802), but has also been known in North America under the name, *Polymitarcys* (Eaton, 1868) which was synonymized by Spieth (1940). The genus presently contains 13 described species and is found in the Holarctic, Ethiopian, and Oriental Regions. Two species are known from North America. The larvae of this genus have been known in Europe since the Eighteenth Century (Reaumur, 1742), and the most complete larval description of the genus remains that of Eaton (1883). Larvae of *Ephoron* were first discovered in the United States by Needham and Christenson (1927) and Argo (1927), at which time Argo resolved the confusion that had been created in the literature previously between *Potamanthus* and *Ephoron* larvae in the United States.

The larval stage of this genus in North America can be briefly characterized as follows: The head possesses a small, narrow frontal process. The tusks are convergent and somewhat downcurved apically, and possess a number of spines scattered over the dorsal surface. The tibiae of the prothoracic legs are only slightly broadened and the tibiae of the metathoracic legs lack distinct, distally produced processes. The major abdominal gills are dorsally oriented.

Ephoron album (Say)

This species was originally described by Say (1824) as *Baetes alba*. The larvae were originally described by Edmunds (1948), and this remains the best description to date. Edmunds et al. (1956) studied the life history of this species in detail from Utah. Britt (1962) added considerable information concerning its biology based on Lake Erie populations. The United States distribution of this species is shown in Figure 32, and includes the following new state records: 5 larvae, NEVADA, Elko Co., Humbolt R. at Elko, VIII-29-1965, S. L. and J. W. Jensen, PU. INDIANA: 24 male imagos and 30 female imagos, Harrison Co.,





FIGURES 32 and 33. — 32. Distribution of *Ephoron album*. 33. *E. leukon*.

Blue R. 1 mi E White Cloud, VI-21-1972, W. P. McCafferty, A. V. Provonsha, and E. Levine, PU. 1 larva, Gibson Co., White R. at Cunningham's Ferry 5 mi NW Patoka, VII-11-1973, W. P. McCafferty, K. Black, and A. V. Provonsha, PU. 6 larvae, Marshall Co., Yellow R. at Hwy 17, 3 mi N of Culver, VII-27-1973, K. Black, PU. 8 larvae, Warren Co., Big Pine Crk., 3 mi SW Rainsville, VII-16-1973, A. V. Provonsha and K. Black, PU. 49 larvae, Carroll Co., Tippecanoe R. at Hwy 18, Springborrow, VII-2-1973, A. V. Provonsha, B. Huff, and K. Black, PU. 24 larvae, Martin Co., White R. at Shoals, VII-18-1973, K. Black, PU.

Ephoron leukon Williamson

This, the type species of the genus, was described by Williamson (1802). Ide (1935a) first described the larvae of this species from Canada. Both his published morphological and biological information on the larvae of this species are the most complete in existence. Figure 33 indicates the known distribution of *E. leukon* in the United States and includes the following new state records: 2 larvae, NORTH CAROLINA, Macon Co., Coweeta, Shope Fork, VI-4-1970, T. L. Harris and F. F. Sherberger, PU. INDIANA: 1 male imago, Fountain Co., Coal Crk. at Veedersburg, VII-30-1972, A. V. Provonsha, PU. 12 larvae, Carroll Co., Tippecanoe R. at Hwy 18, Springborrow, VII-2-1973, A. V. Provonsha, B. Huff, and K. Black, PU. GEORGIA: 2 male imagos, Cherokee Co., Etowah R. nr. Gober, VIII-13-1955, L. Berner; 3 female imagos, Cobb Co., nr. Marietta, VII-16-1955,

C. D. Hynes. MISSISSIPPI: 10 female imagos, Monroe Co., Bigbee, VII-24-1954, C. D. Hynes; 2 female imagos and 1 larvae, Itawamba Co., Ball Mnt. Crk., VII-26-1954, C. D. Hynes. SOUTH CAROLINA: 7 female imagos, Chesterfield Co., Cheraw, VII-27-1955, L. Berner; 1 female imago, Darlington Co., Hartsville, VII-28-1955, L. Berner. The Georgia, Mississippi, and South Carolina material is deposited in the Florida State Collection of Arthropods, Division of Plant Industry, Gainesville.

Discussion of Ephoron spp.

Both *E. album* and *E. leukon* are quite similar morphologically to the European species, *Ephoron virgo* (Olivier) (Vayssire, 1882). Edmunds (1948) has presented diagnostic characteristics which can be used to differentiate the two North American species from each other, and these have been modified somewhat as follows: There are 16-25 spines on each of the tusks of mature *E. album,* whereas there are about 28-39 spines in *E. leukon.* Tubercles are more extensive along the ventral margin of the femora of the prothoracic legs in *E. album* than they are in *E. leukon,* and the gills of *E. leukon* (Fig. 47) have darkly pigmented tracheal branches in freshly taken specimens, while those of *E. album* (Fig. 46) have only the tracheal trunk of each gill pigmented.

Sufficient data on the ecology and biology of *E. leukon* is not available presently to make a definitive comparison between the species on that basis. Where they occur together the habitat and rate of development appear to be similar. *E. album* appears to be much more ecologically diverse, being found in such places as clay banks of irrigation canals to fine silt deposits in rivers and lakes. *E. leukon* has only been taken in association with rocks in the riffle areas of streams.

E. album can be considered primarily a Western and Midwestern species (Fig. 32), whereas *E. leukon* is found primarily in the East (Fig. 33). The respective ranges apparently overlap in certain Midwestern states.

There is an obvious need to determine more of the biology and ecology of *E. leukon,* and to determine the ecological interrelationship of the two species where they occur together. Although there is some information on burrowing behavior in some North

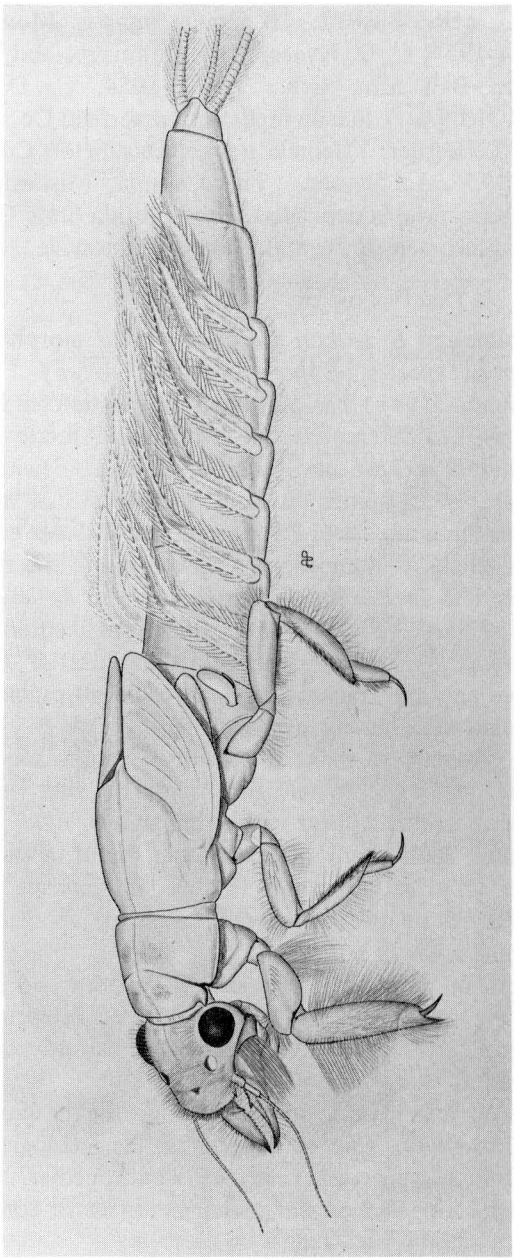


FIGURE 34. — *Campsurus decoloratus* (Hagen).

American ephemeroids (Lyman, 1943), nothing is known of the mechanisms utilized by *Ephoron* larvae.

Genus CAMPSURUS Eaton
Figure 34

This relatively large ephemeroid genus is found commonly in Central and South America and extends northward only to southern Texas. Only one valid species has been reported from the United States. The genus was erected by Eaton (1868), and Ulmer (1920) first described larvae of this genus from South America. Needham and Murphy (1924) provided extensive figures of the larvae. Larvae from the United States have not been known previous to this time.

The larvae can be distinguished from the larvae of other genera by the tusks which are convergent apically and each possess a large median spine at about mid-length which is followed distally by a series of smaller spines. The head possesses a broad, rounded frontal shelf anteriorly. Claws of the prothoracic legs are paralleled by a long acute process anteriorly and the tarsi are obscure on these legs. The abdominal gills 2-7 are oriented dorsally and bent slightly, posteriorly at about mid-length; and gill 1 is branched.

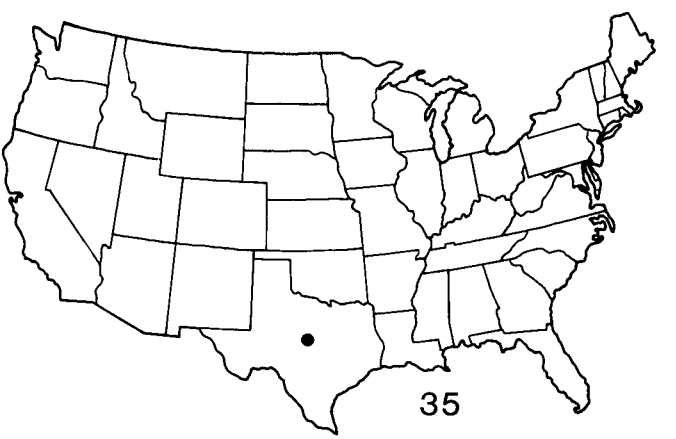


FIGURE 35. Distribution of *Campsurus decoloratus*.

Campsurus decoloratus (Hagen)

Hagen (1861) originally described this species in *Palingenia* and from Mexico. McDunnough (1924a) first confirmed the existence of this species in the United States (Fig. 35). The first description of the larvae of this species follows. A dorsolateral view of the whole larva of *C. decoloratus* is figured (Fig. 34).

Larva. — Length of body excluding tusks and caudal filaments, 20 mm. Cerci, 6 mm; median terminal filament, 7 mm. General body coloration ivory with slight gray markings on abdomen and gills. Setae yellow or gold.

Head. — Anterior margin of frontal shelf evenly convex and extending across entire width of head between antennal bases, margined with thick setae lengthening laterally and blending with group of long setae on antennal pedicels; lateral margins of frontal shelf extending anteriorly to level of distal margin of antennal scapes, with pair of large, upturned single spines at base of shelf laterally. Posterior margin of head capsule in dorsal view emarginate with median three-fourths straight and with margin posterior to compound eyes expanded. Flagella of antenna without setae. Mandibular tusks with large medial spine at mid-length of tusk followed anteriorly by 8-13 small median spines, apices of tusks slightly upturned, heavily sclerotized, and appearing spine-like; body of mandible with lateral, vertical band of very long setae near base and extending to approximately distal margins of antennal pedicels.

Thorax. — Pronotum with pair of anterolateral depressions receiving posteriorly expanded margin of head capsule posterior to compound eyes; lateral portions of depression formed by large, anteriorly directed spine. Tibiae of prothoracic legs with distinct ventral spine at bases of tarsi, dorsodistal processes nearly as long as tarsi. Tarsi of prothoracic legs slender, claw-like, and without true claws.

Abdomen. — Gill 1 very small and leaf-like with small secondary, posteromedial finger-like branch. Gills 2-7 bent posteriorly at mid-length. Cerci with long thick setae laterally along entire length, sparse setae medially along entire length. Median terminal filament with sparse setae along lateral margins for entire length.

Material examined. — 6 larvae, Texas, Guadalupe Co., Lake McQueeny, X-1-1970, G. Longley, deposited in the Florida A & M University collection, Tallahassee. 1 dissected larva (on slides), Texas, Guadalupe Co., Guadalupe R., at Seguin, VII-22-1952, S. S. Roback, deposited in the University of Utah collection, Salt Lake City.

Remarks. — Measurements are based on a nearly mature

individual. There is some indication that there may be an increase in the number of mandibular spines with age in the larvae.

Although larvae were not reared, adults of *C. decoloratus* are common in the Guadalupe River area of Texas. The larvae are obviously *Campsurus* and since *C. decoloratus* is the only species of the genus for some distance, I am most confident of the association of the stages.

Campsurus larvae are not well enough known at this time to be able to compare *C. decoloratus* with its Neotropical relatives. Biology and ecology of the larvae of this species are unknown, although it certainly must be a burrower. It is probably most similar to *Tortopus* in habit and habitat for which there is some data available.

Genus TORTOPUS Needham and Murphy
Figure 36

This genus was originally described by Needham and Murphy (1924) and based on a Peruvian species, *T. igaranus* Needham and Murphy. Eaton (1871) had evidently studied some *Tortopus* material from Texas which he considered *Asthenopus* Eaton (Traver, 1950). As is the case with the closely allied *Campsurus, Tortopus* is restricted to the Western Hemisphere. Three nominal species are Nearctic. I am recognizing the treatment of *Tortopus puella* (Pictet) as a *nomen dubium* after Edmunds and Allen (1957). Larvae of the genus were not described until quite recently (Scott et al., 1959). Proper generic disposition of the species (many of which were originally described as *Campsurus*) have been discussed by Ulmer (1932 and 1942) and Traver (1950).

Tortopus larvae are distinguishable from other ephemeroid larvae on the basis of the following characteristics: The tusks are robust, convergent apically, and possess a single, subapical, median spine. The frontal shelf of the head between the antennae is straight with a conically produced area below it and evident between the tusks. Gill 1 is not branched at least in the presently known species. Most other character states are similar to those of the genus *Campsurus*.

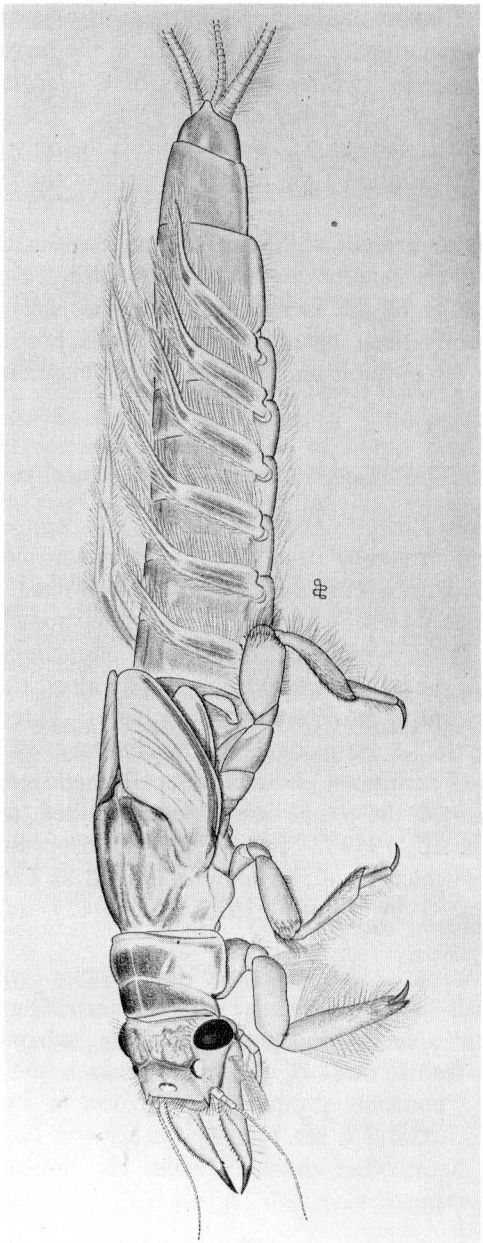


FIGURE 36. — *Tortopus incertus* (Traver).

Tortopus circumfluus Ulmer

This species was described from females by Ulmer (1942). The larvae are unknown. The restricted Southwestern distribution is shown in Figure 37.

Tortopus incertus (Traver)

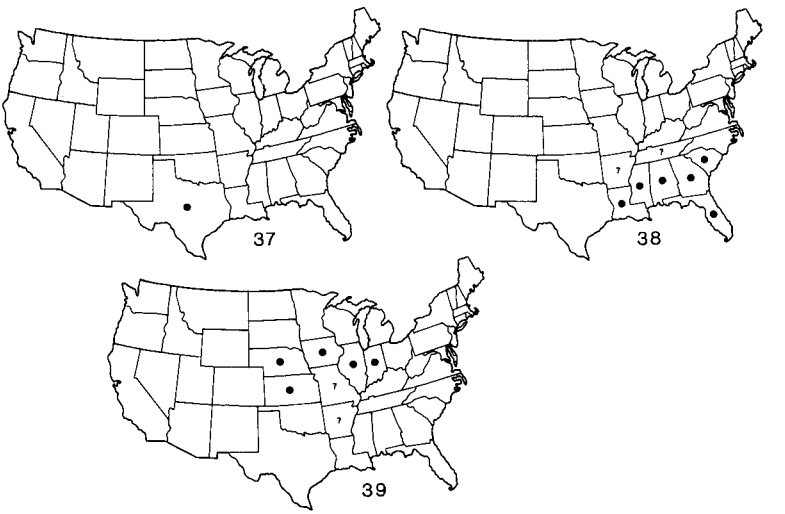
This species was originally described by Traver (in Needham et al., 1935) in the genus *Campsurus,* and later transferred to *Tortopus* by Ulmer (1942). Burks (1953) considered this species a synonym of *Tortopus primus* (McDunnough); however, I feel there is not sufficient comparative material available to base such a conclusion at this time, and would prefer to follow the specific recognition of Edmunds (1962)[11]. The larvae of this species have been described in some detail by Scott et al. (1959) and this remains the only species of *Tortopus* known in the larval stage[12]. The ecology and biology of this species in the Savannah River, Georgia, was also included along with the larval description. The larvae burrow in large numbers and close proximity into the clay banks, and burrows are found extensively along the river. The species reportedly require two years to reach maturity which occurs from July to September. Berner (personal communication, 1974) now believes, however, that there is a strong likelihood that there may be several broods each year in *Tortopus.* Embryology and early instar behavior has recently been studied by Tsui and Peters (1974). The larvae may be filter feeders similar to the related Old World genus, *Povilla* Navas. The confirmed distribution of this mainly Southeastern species is shown in Figure 38.

Tortopus primus (McDunnough)

McDunnough (1924a) described this species under the genus *Campsurus* and the species was later transferred to *Tortopus* by

[11] The specific makeup and biology of *Tortopus* is currently undergoing study by Mr. Paul H. Carlson, formerly of Florida A & M University.

[12] I have examined partially digested body parts of *Tortopus* larvae taken from fish stomach analysis in Kansas. Their condition prohibits determination or description at this time, although they could presumably be assigned to *T. primus* McDunnough on the basis of their distribution. I have also seen very immature larvae from Louisiana and again, on the basis of distribution records, they would tentatively be placed as *T. incertus.*



FIGURES 37-39. — 37. Distribution of *Tortopus circumfluus*. 38. *T. incertus*. 39. *T. primus*.

Ulmer (1942). Ide (1941) described this species from Canada as *Campsurus manitobensis* Ide which has since been transferred to *Tortopus* by Traver (1950) and subsequently synonymized by Burks (1953). The larvae of *T. primus* have not been described.

This species is the Midwestern representative of the genus in the United States (Fig. 39). Burks (1954) listed the states of Tennessee, Missouri, and Arkansas (with no further locality data) under the known distribution of *T. primus*. I have not found these records in the literature previous to this citation under any *Tortopus* spp. or synonyms, and presumably they had been newly recorded by Burks. In addition, I could not locate substantiating specimens at the Illinois Natural History Survey. It, therefore, cannot be determined whether these records were actually assignable to *T. primus* or *T. incertus* or some combination. Because these states (particularly Arkansas) may contain components of either the Midwestern, Mississippi River drainage or Southeastern mayfly fauna, these distribution records are not recorded definitively herein, but attention is drawn to their tentative and presently inapplicable nature. A new record for *T. primus* is herein estab-

lished as follows: 8 male imagos and 13 female imagos, INDIANA, Posey Co., Wabash R. at Old Dam, New Harmony, at light, VIII-12-1974, A. V. Provonsha and L. Dersch, PU.

I have examined a *Tortopus* larval head capsule from Fort Calhoun, Washington County, Nebraska, which on the basis of this locality can be presumed to be that of *T. primus.* Because of the lack of holomorphology and any association with adult material, the larvae of *T. primus,* however, still cannot be described. Comparing this supposed head capsule of *T. primus* with those from large samples of *T. incertus* has revealed the following difference which may eventually prove to be of importance in distinguishing *T. primus* larvae from those of *T. incertus.* In *T. incertus* the anterolateral horns (at the lateral edges of the frontal shelf) extend slightly beyond the margin of the antennal scapes as seen from above. In the supposed head capsule of *T. primus,* however, the anterolateral horns do not quite reach the margins of the antennal scapes as seen from above.

A Preliminary and Partial Key to the Genera and Species of Mature Larvae of Ephemeroidea Occurring in the United States and Canada[13]

1. Head and pronotum with distinctive crowns of short, robust setae (Fig. 1); mandibles not modified into tusks (Fig. 1); gills oriented ventrally (Fig. 1) ..... *Dolania americana*

   Head and pronotum without distinctive crowns of setae as above; mandibles variously modified into anteriorly projecting tusks; major gills not oriented ventrally (Figs. 3, 12, 20, 26, 28, 31, 34, and 36) 2

2(1). Legs long and slender (Fig. 3); head and body more or less flattened dorsoventrally (Fig. 3); gills and legs outspread laterally (Fig. 3). . . . *Potamanthus* 9

   Legs variously modified, tibiae often broadened and prothoracic legs often fossorial; head and body not greatly flattened dorso-

[13] The key is necessarily incomplete but will serve identification needs in most cases. It, however, should not be used at the exclusion of textual discussion herein, and particular attention should be paid to cautions regarding variability. Where color patterns are utilized, larval specimens must be mature. Use of established ranges of the various taxa should be extremely helpful in increasing the probability of accurate or more specific diagnosis in many cases.

ventrally; major gills oriented dorsally, with legs usually bent closer to body (Figs. 12, 20, 26, 28, 31, 34, and 36) 3

3(2). Femora of prothoracic legs produced posteroproximally ventral to trochanters as in Figure 28; tusks broadened laterally with armature consisting of row of spurs along lateral margins (Fig. 28); terminal segment of labial palpi club-shaped, being broadly rounded apically (Fig. 40) ..... *Pentagenia*

Femora of prothoracic legs not produced proximally as above (Figs. 12, 20, 26, 31, 34, and 36); tusks either slender (Figs. 12, 20, 26, and 31) or without singular row of spurs along lateral margins (Figs. 12, 20, 26, 31, 34, and 36); labial palpi not club-shaped, being either slightly rounded (Fig. 41), pointed, truncate, or falcate (Fig. 42) apically 4

4(3). Tusks convergent apically with spines present to various degrees in distal two thirds (Figs. 31, 34, and 36); labial palpi at right angles to body of labium as in Figure 41; tibiae without acute distal processes (Figs. 31, 34, and 36) 5

Tusks divergent and usually upcurved at apices, with armature not present in distal two thirds (Figs. 12, 20 and 26), but when present, basad only (Fig. 12); labial palpi lateral to body of labium (Fig. 42); metathoracic legs with tibiae produced distally posterior to tarsi to form acute tibial processes (Figs. 12, 20 and 26) 7

5(4). Tusks slender and with scattered spines dorsally (Fig. 31); frontal process of head narrowly produced (Fig. 31); prothoracic legs with tarsal claws not paralleled by long, acute processes, and tarsi distinctive (Fig. 31). . . . *Ephoron* 13

Tusks robust and with variable spines along median margins (Figs. 34 and 36); frons of head produced into no more than expanded shelf-like area (Figs. 34 and 36), with additional, lower, anteriorly produced clypeal shelf; prothoracic legs with tarsal claws each paralleled by long, acute, anterior process, and delineation of tarsi obscure (Figs. 34 and 36) 6

6(5). Tusks as in Figure 34, each with large, median spine followed distally by series of smaller spines; margin of frontal shelf between antennae rounded (Fig. 34); gill 1 branched (Fig. 34) ..... *Campsurus decoloratus*

Tusks as in Figure 36, each with single, large, subapical spine on median margins; anterodorsal margin of frontal shelf straight (Fig. 36); gill 1 not branched (Fig. 36) . . . . *Tortopus*[14] 14

[14] Although only one species of *Tortopus* is currently known positively in the larval stage, tentative identifications may be made on the basis of confirmed distribution records. Also, see the discussion under *T. primus* for a possible morphological difference between *T. primus* and *T. incertus*.

7(4). Frontal process of head distinctly bifurcate (Fig. 12); small group of spurs basally and laterally on tusks (Fig. 12); tibiae of prothoracic legs never emarginate apically and not greatly flattened (Fig. 12). . . . *Ephemera* 16

Frontal process of head complete (Figs. 20 and 26); tusks devoid of any spurs or spines (Figs. 20 and 26); tibiae of prothoracic legs slightly to distinctly emarginate along distal margin as in Figures 26 or 20 respectively 8

8(7). Antennae without whorls of long setae over most of length (Fig. 26); frontal process somewhat angulate with lateral margins slightly divergent from base (Fig. 26); gill 1 not branched (Fig. 26) ..... *Litobrancha recurvata*

Antennae with whorls of long setae over most of length of flagellae (Fig. 20); frontal process rounded (Fig. 20), conical (Fig. 49), or truncate (Fig. 48); gill 1 branched. . . . *Hexagenia* 19

9(2). Tusks more or less evenly rounded along lateral margins, and armature scattered over most of dorsal surface (Figs. 3, 44, and 45); lateral areas of abdominal tergites moderately patterned with pale maculations (Fig. 3). . . . *myops* grouping .. 10

Tusks somewhat constricted and devoid of armature in distal half (Fig. 43); lateral areas of abdominal tergites not or only very slightly patterned with pale maculations. . . . *verticis* grouping[15] 12

10(9). Ground color dark, cinnamon-brown, never with any tinge of reddish ..... *Potamanthus myops*

Ground color reddish-brown 11

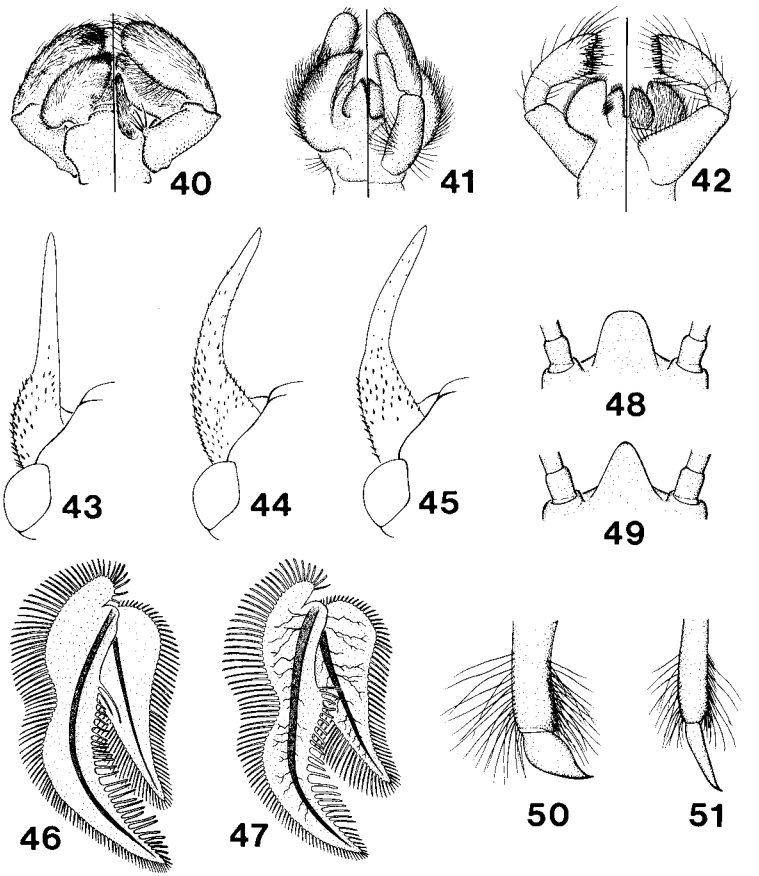
11(10). Tusks with some scattered spurs present nearly to tips, and with lateral margins smoothly rounded throughout (Fig. 44) ..... *Potamanthus rufous*

Tusks with spurs becoming very few in distal half, and with slight lateral constrictions at approximately mid-length (Fig. 45) ..... *Potamanthus distinctus*

12(9). Dorsum of abdomen with continuous, longitudinal, median, pale streak ..... *Potamanthus walkeri*

Dorsum of abdomen with longitudinal, median, pale markings, which are interrupted at middle third of tergites ..... *Potamanthus verticis*

[15] Because of the lack of morphological information concerning *P. diaphanus* it cannot be compared diagnostically with *P. verticis* and *P. walkeri*; it will, however, key to *verticis* grouping and may or may not fall with either of the latter two species on the basis of the present key. Unidentifiable larvae from Arkansas which may possibly be *P. neglectus*, but have not been reared for positive association, will key to *P. walkeri* on the basis of the color pattern character used in the pertinent couplet.



FIGURES 40-51. — 40-42. Labia. 40. *Pentagenia vittigera.* 41. *Tortopus incertus.* 42. *Ephemera simulans.* 43-45. Left tusk. 43. *Potamanthus verticis.* 44. *P. rufous.* 45. *P. distinctus,* redrawn from Traver (1937). 46-47. Gill. 46. *Ephoron album.* 47. *E. leukon.* 48-49. Frontal process. 48. *Hexagenia atrocaudata.* 49. *H. rigida.* 50-51. Mesotarsal claw. 50. *H. bilineata.* 51. *H. limbata.*

13(5). Tusks each with 16-25 spines; tracheal branches of gills 2-7 not darkly pigmented (Fig. 46) ..... *Ephoron album*
Tusks each with 28-39 spines; tracheal branches of gills 2-7 darkly pigmented (Fig. 47) ..... *Ephoron leukon*

14(6). Midwestern in distribution (Fig. 39) ..... *Tortopus primus*
Distributed in the southern U.S. (Figs. 37 and 38) 15

15(14). Southeastern in distribution (Fig. 38) ..... *Tortopus incertus*
Southwestern in distribution (Fig. 37) ..... *Tortopus circumfluus*

16(7). Abdomen generally lacking any color pattern, sternites without dark markings, and appearing relatively broadened and flattened dorsoventrally; caudal filaments more than one half of length of body ..... *Ephemera guttulata*
Abdomen with dark, longitudinal markings at least on some sternites, and not appearing flattened or broadened dorsoventrally; caudal filaments no more than one half of length of body 17

17(16). Both fore and hind wing pads heavily blotched with dark markings (Fig. 12) ..... *Ephemera simulans*
Hind wing pads without dark blotches. 18

18(17). Fore wing pads blotched with dark markings; dark, longitudinal streaks sometimes discernible laterally along abdomen ..... *Ephemera varia*
Both fore and hind wing pads relatively free of dark blotches, but sometimes shaded clouds apparent in fore wing pads; no dark longitudinal streaks laterally along abdomen ..... *Ephemera blanda*

19(8). Frontal process more or less truncate (Fig. 48), often slightly emarginate; pairs of round or somewhat elliptical, pale, dark margined spots sometimes apparent on both tergites and sternites ..... *Hexagenia atrocaudata*
Frontal process not truncate (Figs. 20 and 49), if anterior margin approaching straight, then lateral margins distinctly convergent anteriorly; never both abdominal tergites and sternites with pairs of pale, dark margined spots 20

20(19). Frontal process narrowly conical (Fig. 49); mature male larvae with distinctive, nearly straight, developing penes ..... *Hexagenia rigida*
Frontal process more or less rounded (Fig. 20) or broadly conical; developing penes of mature male larvae curved. 21

21(20). Tusks usually over one and one half times length of head and strongly upcurved in distal half; specific adult abdominal color pattern evident in late instars[16] ..... *Hexagenia munda*[17]
Tusks less than one and one half times length of head; specific adult color patterns when developed differing from that of above 22

[16] Reference should be made to the figures of Spieth (1941) for the abdominal color patterns of *Hexagenia* species.

[17] *H. munda orlando* does not possess the very long tusks, but its color pattern, relatively small size (15-22 mm), Southern distribution, and its lake dwelling habits will make its identification possible [see Spieth (1941) and Berner (1950)].

22(21).[18] Mesotarsal claws swollen for most of their length (Fig. 50); developing penes of mature male larvae angulate and beak-like; frontal process sometimes somewhat conical ..... *Hexagenia bilineata*

Mesotarsal claws slender for most of their length (Fig. 51); developing penes of mature male larvae more evenly curved; frontal process usually evenly rounded (Fig. 20) ..... *Hexagenia limbata*

ACKNOWLEDGMENTS

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[18] C. R. Fremling (personal communication, 1974) has indicated that populations of larvae of *H. limbata* and *H. bilineata* from the Mississippi River are inseparable morphologically in many instances. Obviously, then, these species may not always be identifiable by use of the present key.

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