Compliments of author: Eugene W. Hamilton

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REVIEW OF EPHEMERIDAE (EPHEMEROPTERA) IN THE MISSOURI RIVER WATERSHED WITH A KEY TO THE SPECIES[1]

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This paper deals with the mayflies of the Missouri River watershed; a watershed draining all or parts of the states of Montana, Wyoming, Colorado, North Dakota, South Dakota, Nebraska, Kansas, Iowa, and Missouri. Since specimens of mayflies were not obtained from South Dakota, this state is not included in the present study.

Specimens have been returned to the respective institutions from which they were borrowed. The material from Nebraska is being retained in the Entomology division of the Nebraska State Museum at the College of Agriculture. With extremely few exceptions, the records listed for a state are preserved at institutions in that state.

A proposed reclassification of the order by Edmunds and Traver (1954) is reminiscent of the one followed by Spieth (1933), but until the reasons for this grouping are forthcoming, it seems advisable to follow a more generally used classification such as is used by Needham, Traver, and Hsu (1935) or Burks (1953). Burks' arrangement of the Ephemeridae is identical to that proposed by Needham, except that the Neoephemera of Needham is placed in a new family, Neoephemeridae. Neoephemerids have not been found in the Missouri River Basin. The subfamilies of the Ephemeridae recognized by Burks are Campsurinae, Ephorinae, Potamanthinae, Ephemerinae, and Palingeniinae, an exotic group.

The 100th meridian, which traverses the middle of the Dakotas and the western portions of Nebraska and Kansas, is apparently the approximate geographical limit of many species of eastern and western Ephemeroptera. Examples of this limitation will be noted in the discussion of the species involved.

EPHEMERIDAE

Ephemerids are medium to large mayflies that include the largest representatives of the Ephemeroptera. Their wings have numerous cross-veins and, except in the Campsurinae, a network of marginal veinlets (Figs. 3-8). Veins Cu_1 and M_2 in the basal area of the fore wing curve strongly away from the nearly straight veins M_1 and R_4+R_5 (Figs. 3-8). In all other mayfly families (except Neoephemeridae) Cu_1, M_2, M_1, and R_4+R_5 of the fore wing are nearly straight or only moderately curved and but slightly divergent in the basal area (Figs. 1, 2). Veins R_4 and R_5

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of the ephemerids are fused in the hind wing and form a fork in the fore wing. The uniformly faceted compound eyes are usually divided by a nearly horizontal line into dark and light areas of equal size. In Ephorinae and Campsurinae, the middle and hind legs are either extensively reduced or absent; in the other subfamilies the legs are normally developed. Male fore tarsi are five-segmented with the basal tarsal segment very short. All hind tarsi of both sexes have four freely movable segments with the almost indiscernible fifth segment fused to the tibia.

In all species, the nymphs (Figs. 29, 30) have mandibular tusks (Figs. 29-30) and biramous plume-like gills on abdominal segments 1-7 (Figs. 37-40) that are held in either a dorsal or lateral position. Most species have a frontal process (Figs. 30-36) on the head. Nymphs of this family are generally digging forms that sprawl or bury themselves in the silt and fine sand of the larger lakes and rivers.

Key to the Species

Adults

Subfamily differentiation, which is based on wing venation and genitalic differences is relatively simple. Separation of the species is based in great part on color patterns and male genitalia. Intraspecific color variation is pronounced in the species of Hexagenia and the key couplets for this genus are workable only for typical specimens.

1. Median caudal filament as long as or longer than distance from segment 8 to base of filament 2
   Median caudal filament vestigial, much shorter than distance from segment 8 to base of filament. 8
2. Hind tibia longer than femur; wings normally with a variable pattern of dark spots (Figs. 6, 7) (Ephemerinae). 3
   Hind tibia shorter than femur; wings without dark spots or blotches. 5
3. Sterna unmarked; terga with a dark median band (Fig. 28); usually four black spots from bulla posteriorly across wing (Fig. 7); penes tube-like (Fig. 12). . . . . *Pentagenia vittigera*
   Dark markings on sterna; terga with dark marks, but not as above; dark spotting on wings more extensive (Fig. 6); penes short, truncate (Fig. 13). 4
4. Paired, subparallel, longitudinal, black, linear streaks on abdominal terga 3-8; black submedian streaks on each sterna. . . . . *Ephemera compar*
   Large dark blotches laterally on each abdominal terga; dark, oblong, submedian triangles on each sterna. . *Ephemera simulans*
5. Cubital intercalaries simple, four long; wing heavily cross-veined (Fig. 4) (Ephorinae).... female . . . . . *Ephoron album*
   Cubital intercalaries one or two, long and deeply forked; wing less heavily veined (Fig. 5) (Potamanthinae). 6
6. Eyes of male separated by 2.5 times width of eye as seen from above; cross-veins of fore wing pale in both sexes. 7

Eyes of male separated approximately by width of eye; cross-veins of female fore wing blacksih, of male hyaline. . . . . Potamanthus verticis

7. Lateral dusky pink spots on each abdominal tergite. . . . . Potamanthus rufus
   Lateral spots very rarely present. . . . . Potamanthus myops

8. Marginal veinlets absent (Campsurinae)(Fig. 3). Tortopus primus
   Marginal veinlets present. 9

9. Four long, unforked cubital intercalaries (Fig.4); penes strongly divergent apically, truncate (Fig.10). . . . male. . . . . Ephoron album
   Short, shallow forked cubital intercalaries, more like marginal veinlets; genitalia not as above (Ephemerinae) . . . 10

10. Sterna with a narrow median streak (Figs. 22b, 24b). 11
    Sterna not marked as above. 12

11. Median streaks present on abdominal terga 3-6 (Fig. 22a). . . . . Hexagenia limbata limbata
    Median streaks absent on abdominal terga 3-6 (Fig. 24a) . . . . . Hexagenia limbata venusta

12. Triangular areas medially on abdominal sterna (Fig. 23b). . . 13
    Markings on abdominal sterna not triangular. 15

13. Markings on abdominal terga 3-6 very dark (Fig.23a); penes as in Fig.15 . . . . . Hexagenia limbata occulta
    Markings on abdominal terga lighter; penes not as above . . . 14

14. Markings on abdominal terga 3-6 as in Fig. 27a; penes long, slender (Fig. 17). . . . . Hexagenia rigida
    Markings on abdominal terga 3-6 chevron-like (Fig.20); penes short, broad (Fig.14). . . . . Hexagenia atrocaudata

15. Truncate triangular markings on sterna (Figs. 25b, 26b); penes similar to those of H. limbata (Fig.16). 16
    Sterna not marked as above; penes otherwise. 17

16. Abdominal terga 3-6 dark medially (Fig. 25a). . . . . Hexagenia munda affiliata
    Abdominal terga 3-6 pale medially (Fig. 26a). . . . . Hexagenia munda munda

17. Abdominal sterna 3-6 broadly dark-banded, usually with a lighter median triangular area (Fig. 21b); penes beak-like (Fig. 19). . . . . Hexagenia bilineata
    Abdominal sterna 3-6 light with diffuse markings (Fig. 27b); penes long, slender, almost straight (Fig.17). . Hexagenia rigida

Nymphs

Many of the ephemerid nymphs are either undescribed or have been difficult to associate accurately with adults. The following key (couplets 6-9 modified from Burks, 1953) is given as an aid to identification of the known nymphs.

1. Frontal process absent (Fig. 29). 2
   Frontal process present (Figs. 30-36) 3

2. Fore tibia slender and longer than femur (Fig. 29). . Potamanthinae
   Fore tibia almost as broad and flat as, and shorter than, the femur (Fig. 30). . . . . Campsurinae
3. Frontal process bifid (Figs. 32, 33). 4
   Frontal process varying but not bifid. 5
4. Mandibular tusks crenate on outer margin (Fig. 32); labial palp 2-segmented. . . . . *Pentagenia vittigera*
   Mandibular tusks smooth on margins (Fig. 33); labial palp 3-segmented. . . . . *Ephemera* spp.
5. Frontal process truncate, often slgihtly emarginate (Fig. 34). . . . . *Hexagenia atrocaudata*
   Frontal process apically rounded or angled. 6
6. Mandibular tusks converging; frontal process conical (Fig. 31). . . . . *Ephoron album*
   Mandibular tusks diverging; frontal process not as above. . . . 7
7. Frontal process rounded (Fig. 30). . . . . *Hexagenia limbata*
   Frontal process conical or apically angled. 8
8. Frontal process as in Fig. 35; mid-tarsal claw thick near tip (Fig. 41). . . . . *Hexagenia bilineata*
   Frontal process apically angled but not as above; mid-tarsal claw slender near tip. 9
9. Mid-tarsal claw long and slender (Fig. 43). . . . . *Hexagenia rigida*
   Mid-tarsal claw slender near tip, broad at base (Fig. 42). . . . . *Hexagenia munda*

Subfamily Campsurinae

Species of this subfamily are superficially similar to the Ephorinae. However, the following venational characters differ from those found in other Ephemeridae: marginal veinlets lacking in both wings; Sc and R_1 of the fore wing curving around the apical edge of fore wing; and fork R_4+R_5 of the fore wing longer than fork R_2+R_3 (Fig. 3).

Tortopus Needham and Murphy, and *Campsurus* Eaton are the only generic representatives of this subfamily in the Nearctic Region. Although these two genera are well represented in Central and South America, only four species are found in America north of Mexico. Species of Campsurinae in North America not found in the Missouri River watershed are *Campsurus decoloratus* (Hagen) from Texas, *C. circumfluus* Ulmer from Texas, and *C. puella* (Pictet) from Louisiana. *C. puella* may fall as a synonym of *T. primus* when it can be studied more carefully.

Tortopus Needham and Murphy

Tortopus Needham and Murphy, 1924, 23: Burks, 1953, 28.

This genus differs from *Campsurus* in that the middle and hind legs of *Tortopus* are complete, although reduced in size, while those of *Campsurus* are absent beyond the trochanter. There are also some differences in wing venation that are not reliable (Ulmer, 1942).

The nymphs of *Tortopus* are unknown.

Type of genus: Tortopus igaranus Needham and Murphy (by original designation).

Tortopus primus (McDunnough)

Campsurus primus McDunnough, 1924a, 7; Needham and Murphy, 1924, 15; McDunnough, 1926, 185 (in discussion of C. puella Pictet); Needham, Traver, and Hsu, 1935, 287.

Campsurus incertus Traver, 1935 (in Needham, Traver, and Hsu), 286; Berner, 1950, 97.

Campsurus manitobensis Ide, 1941, 155.

Tortopus primus, Burks, 1953, 28.

An examination of the types of T. primus indicates that Burks' (1953) synonymy for this species is accurate. In the holotype and paratypes the genitalia appears as in Fig. 18. Mrs. L. K. Gloyd (Ill. Nat. Hist. Survey), after examining a series of 75 pinned specimens bearing the same accession number as the types, states in correspondence, "If one rotates the tip of the (genital) structure about 60°, turning the beak-like point toward you, you get Burks' (1953) view as in (his) Fig. 60. Now turn the 'beak' downward a little, as would happen if the two mesal processes (penes) were brought closer together, and then draw the outline of the shrunken inside tissue and you have McDunnough's figure—especially if in inking it you would let your pen go to the outside of your original sketch of the tip." Her viewpoint agrees with and confirms that held by the author of this paper. In the same manner, it is possible that the slight genitalic variance mentioned by Ide (1941) in his description of C. manitobensis is a result of a different deformation of the genitalia caused by drying and shrinkage. Burks' (1953) synonymy of C. manitobensis and T. primus is thus also believed to be correct although no reason was given by Burks for the synonymy.

Recorded distribution: Alabama, Arkansas, Florida, Georgia, Illinois, Kansas, Manitoba, Missouri, Nebraska, Ontario, Tennessee, and Texas.

New records: IOWA, Story Co., Ames - 1♂. KANSAS, Osborne, Co., Osborne - 1♂. NEBRASKA, Buffalo Co., Kearney (G. Edmunds); Dawson Co., Cozad, 29-VII-1949, at light (E.W. Hamilton) - 5♀♀; Madison Co., Monroe, 18-VI-1950, at Tri-County canal (E.B. Burcham) - 11♀♀.

Note: All known records are east of the 100th meridian.

Ephorinae

This group superficially resembles the Campsurinae. Only one genus, Ephoron Williamson, is present in North America.

The generic name Ephoron is derived from a neuter Greek adjective which in Latinized form is ephorum or ephorus. Ephori is the genitive of ephoron; hence the correct spelling of the subfamily name is Ephorinae. The spelling Ephoroninae is to be regarded as a lapsus calami and corrected.

Ephoron Williamson

Ephoron Williamson, 1802, 71; Ulmer, 1932, 205-8; Needham, Traver, and Hsu, 1935, 241; Ide, 1935, 113; Lestage, 1938, 381-94; Spieth, 1940, 109-111; Burks, 1953, 32.
Polymitarcys Eaton, 1868, 84; Eaton, 1871, 60; Eaton, 1883, 43; Ulmer, 1920, 209; Needham, 1920, 288; Spieth, 1933, 347.

McDunnough (1926) synonymized Polymitarcys Eaton and Ephoron Willaimson, a synonymy that has been accepted by the majority of present-day ephemeropterists. Spieth (1940) gives a very able and conclusive discussion of the evidence involved.

Only two species of this genus are found in North America, Ephoron album (Say) and E. leukon Williamson. E. leukon is an eastern species.

In the species of Ephoron, each wing is profusely cross-veined and bordered posteriorly with a net-like series of marginal veinlets (Fig. 4). As in Tortopus, the posterior two pairs of legs are reduced and useless.

Nymphs of both species have been described.

Type of genus: Ephoron leukon Williamson (by monotypy).

Ephoron album (Say)

Baetis alba Say, 1823, 305; Hagen, 1863, 170; Eaton, 1871, 124.
Palingenia alba, Hagen, 1861, 40.
Polymitarcys albus, Hagen, 1873, 391; Eaton, 1883, 47; Banks, 1894, 178; Howard, 1905, 60; Needham, 1920, 285.
Ephoron album, McDunnough, 1926, 184; Needham and Christenson, 1927, 16; Neave, 1932b, 54; Ide, 1935, 113 (in discussion); Needham, Traver, and Hsu, 1935, 243; Spieth, 1940, 110 (in discussion); Edmunds, 1948, 12; Burks, 1953, 35.
Cloe sp. (A), Walsh, 1863, 191 (synonymy after Traver, 1935).

Edmunds (1948) described and figured the nymph of this species.

Recorded distribution: Illinois, Iowa, Kansas, Ohio, Utah, and Washington.

New records: IOWA, Story Co., Ames (Quayle) - 2 ♀♀ ; Henry Co., Mt. Pleasant, 24-IX-1935 (C. Horn) - 1 ♀ , 14-VII-1949 (C. Yoshimoto) - 1 ♀. KANSAS, Douglas Co., August, at light (U. of Kan. Col. Lots 83 and 91) - 7 ♀♀ ; Ellis Co., 19-VII-1912, 2000 feet (F.X. Williams) - 7 ♂♂ (with the following additional label "Polymitarcys alba Say, Det. Nathan Banks" on two specimens). MONTANA, Gallatin Co., 23-XI-1947, Madison-Jefferson Rivers near junction with Gallatin River (R.A. Hayes) - ♂♂ . NEBRASKA, Cherry Co., Snake River Falls, 5-VIII-1948, Snake River (M.H. Muma) - 1 nymph; Dawson Co., Cozad, 15-VI-1950, at light (E.W. Hamilton) - 2 ♂♂, 12♀♀; Dundy Co., Rock Creek Hatchery; Frontier Co., Curtis, 2-VIII-1949, light trap (J. Lomax) - 11♀♀; Scotts Bluff Co., Scottsbluff, 27-IX-1951, at canal (E.W. Hamilton) - 6♂♂, 4♀♀; Sioux Co., University Lake, 25-VIII-1949, at light (E. Laird) - 3♀♀.

Potamanthinae

The subfamily Potamanthinae is represented by only one Nearctic genus.

Potamanthus Pictet

Potamanthus Pictet, 1845, 197; Eaton, 1868, 86; Eaton, 1871, 76; Eaton, 1884, 78; Banks, 1907, 16; Morgan, 1911, 99; Needham, 1920, 287; Ulmer, 1920, 110; Argo, 1927, 320; Spieth, 1933, 345; Needham, Traver, and Hsu, 1935, 277; Ide, 1935, 117; Berner, 1950, 79; Burks, 1953, 30.

Mayflies belonging to this genus are the smallest species of the Ephemeridae. Burks (1953) writes, "Adult specimens of Potamanthus should be studied when freshly killed, as the faint color markings fade rapidly after death." Genitalia of all species are nearly identical in form (Fig. 11). There is no good method for distinguishing the females. The nymphs of this genus have not been satisfactorily separated.

Type of genus: Ephemera luteus Linnaeus (by subsequent selection, Eaton, 1868).

Potamanthus myops (Walsh)

Ephemera myops Walsh, 1863, 207; Eaton, 1871, 71; Eaton, 1883, 72; Banks, 1907, 16.
Potamanthus myops, McDunnough, 1926, 186; Argo, 1927, 320, 322, 323; Needham, Traver, and Hsu, 1935, 281; Burks, 1953, 31.
Potamanthus medius Banks, 1908, 259; McDunnough, 1926, 186; Argo, 1927, 321; Needham, Traver, and Hsu, 1935, 281. (Synonymy after Burks, 1953).

See remarks under P. rufus Argo regarding possible synonymy of rufus and myops.

The nymph has not been described.

Recorded distribution: Illinois, Indiana, Iowa, Kansas, Michigan, and Wisconsin.

Note: All records are east of the 100th meridian.

Potamanthus rufus Argo

Potamanthus rufus Argo, 1927, 323; Ide, 1935, 121; Needham, Traver, and Hsu, 1935, 282.

Specimens from Kansas and Missouri have been identified, possibly in error, as P. rufus. Besides having the lateral dusky spots, as in P. rufus, the Missouri specimens (all subimagoes) also have lateral dusky shading on the abdominal terga distinctly visible from above as a continuous band, but almost indiscernible on most individuals in the lateral view. The lateral abdominal spots on the imagoes from Kansas look more like faint, short dashes.

P. rufus is closely related to P. myops with only slight differences between them being noted by Argo (1927). P. inequalis Needham (1908), another form that apparently represents an intermediate condition between P. rufus and P. myops, is, as McDunnough (1926) mentions, "... very close to, if not identical with, myops Wlsh.;"

In his redescription of P. myops, Burks (1953) states, "abdomen without lateral, salmon-pink spots or stripes, or, rarely, with small, faint, lateral spots discernible in living specimens;" Needham (1908) in speaking of P. inequalis mentions "faint opaque brownish areas on each tergite, and Argo (1927) in his characterization of P. rufus describes "fuscous spots" laterally on each tergite. The genitalia of each species is nearly identical. It is possible that a comparison of the types of these three species would indicate that there is actually only one species.

A nymphal description is given by Ide (1935).

Recorded distribution: New York, Ontario.

New records: KANSAS, Douglas Co., June, at light (U. of K. Col. Lot 47) - 1♀; July, at light (U. of K. Col. Lots 64, 67, 69, 71, 81) - 3♂♂, 13♀♀. MISSOURI, Pike Co., Louisiana, 15-VI-1953, at light, - 32♂♂, 9♀♀, all subimagoes.

Note: All records are east of the 100th meridian.

Potamanthus verticis (Say)

Baetis verticis Say, 1839, 42; Walker, 1853, 562; Hagen, 1861, 46; Walsh, 1863, 204 (in discussion); Eaton, 1871, 121.

Ecdyurus verticis, Eaton, 1885, 278.

Heptagenia verticis, Banks, 1907, 21; Banks, 1910, 201.

Potamanthus verticus, McDunnough, 1926, 186; Needham, Traver, and Hsu, 1935, 283; Berner, 1953, 31.

Ephemera flaveola Walsh, 1862, 377; Hagen, 1863, 178; Eaton, 1871, 70; Eaton, 1883, 71. (synonymy after McDunnough, 1926).

Heptagenia flaveola, Eaton, 1871, 149.

Potamanthus flaveola, Banks, 1907, 16; Needham, 1920, 287; Ide 1935, 119, 120.

Potamanthus bettini, Morgan, 1913, Pl. XLIV, Fig. 7 (in part-nymph only).

Argo's (1927) specimens (erroneously identified as P. verticis) belong to the species P. neglectus Traver (1935). The large eyes of P. verticis are markedly different from the small eyes of P. neglectus.

On each tergite of the specimens from Missouri, is a lateral dot with an arched to triangular mark above. Traver (1935) mentions these same markings. A lateral dusky shading similar to that described on specimens of P. rufus is also present.

Nymphs of P. verticis have been described or figured by Morgan (1913, P. bettini), Needham (1920, P. flaveola), and Ide (1935, P. flaveola).

Recorded distribution; Hudson Bay, Illinois, Indiana, Michigan, New York, Ontario, and Tennessee.

New records: MISSOURI, Pike Co., Louisiana, 15-VI-1953, at light - 7♂♂,, 10♀♀,, all subimagoes.

Note: All records are east of the 100th meridian.

Ephemerinae

Pentagenia Walsh

Pentagenia Walsh, 1863, 196; Eaton, 1868, 85; Eaton, 1883, 75; Ulmer, 1920, 109; Needham, 1920, 282; Spieth, 1933, 347; Needham, Traver, and Hsu, 1935, 255; Burks, 1953, 37.

Only two species of this genus are known in North America; one of them is found in the area studied. Their life histories are unknown.

Type of genus: Palingenia vittigera Walsh (by subsequent selection - Eaton, 1868).

Pentagenia vittigera (Walsh)

Palingenia vittigera Walsh, 1862, 373; Hagen, 1863, 174.
Pentagenia vittigera Walsh, 1863, 197; Eaton, 1868, 85; Eaton, 1871, 63; Eaton, 1883, 76; Needham, 1920, 282; McDunnough, 1926, 185; Needham, Traver, and Hsu, 1935, 257; Berner, 1950, 96; Burks, 1953, 37.
Pentagenia quadripunctata Walsh, 1863, 198; Eaton, 1871, 64; Eaton, 1883, 77; Banks, 1894, 178. (synonymy after Needham, 1920).

At the time of his erection of the genus Pentagenia, Walsh (1863) described two forms, P. vittigera and P. quadripunctata. Needham (1920) considered P. quadripunctata "only a variant." His synonymy has been generally accepted.

The nymph has been described by Needham (1920) and Spieth (1941).

Recorded distribution: Alabama, Arkansas, Florida, Illinois, Indiana, Iowa, Kansas, Manitoba, Missouri, Tennessee, and Texas.

New records: IOWA, Clinton Co., Clinton, 28-VIII-1943 (D.T. Jones) - 2♀♀; Des Moines Co., Burlington, 14-VIII-1925 (H.M. Harris) - 1♀, 20, 21-VI-1951 (Newby) - 2♀♀; Dickinson Co., 10-VIII-1939 (H. E. Jaques) - 1♀; Henry Co., Mt. Pleasant, 24-IX-1935 (C. Horn) - 1♀, 18-VI-1938 (M. Cornick), 19-VII-1939) (Staebler), 13-VII-1948 (S. Statler), 20-VI-1949 (Donovan Orman), 14-VI-1941 (B.J. Luke), 23-VI-1951 (Widmer), 2-VII-1941 (Ben Luke) - 3♂♂, 7♀♀; Muscatine Co., 12-VI-1936 and 22-VI-1937 (Bernard Berger) - 1♂, 1♀; Van Buren Co., 14-VIII-1949 (M. Schwabauer) - 1♀, Keosauqua, 1-IX-1953, at light (W.S. Craig) - 1♀; Washington Co., 2-VIII-1947 (Toker) - 2♀♀. KANSAS, Douglas Co., June (U. of K. Col. Lots 43, 58) - 1♀, July, (U. of K. Col. Lot 69) - 1♀ subimago, July, (U. of K. Col. Lot 83) - 1♀, August, (U. of K. Col. Lot 97) - 1♀ subimago (all taken at lights); Douglas Co., Lawrence, 25-V-1922, at light (W.J. Brown) - 1♂ subimago. MISSOURI, Boone Co., Columbia, 15-VIII-1953, at lights (W. R. Enns) - 1♀; Lincoln Co., Clarksville, 15-VI-1953, at light - about 30 imagoes, subimagoes, both sexes; Pike Co., Louisiana, 15-VI-1953, at light - about 100 imagoes, subimagoes, both sexes. NEBRASKA, Madison Co., Norfolk, 10-VIII-1949, at light (R.E. Hill) - 1♀; Platte Co., Columbus, 2-VII-1950, at light (E.W. Hamilton) - 5♂♂, 4♀♀. WISCONSIN, Dane Co., 20-VII-1947 - 1♀.

Note: All records are east of the 100th meridian.

Ephemera Linnaeus

Ephemera Linnaeus, 1758, 546; Leach, 1815, 137; Eaton, 1868, 85; Eaton, 1871, 68; Eaton, 1883, 58; Ulmer, 1920, 109; Needham, 1920, 283; Spieth, 1933, 347; Needham, Traver, and Hsu, 1935, 246; Burks, 1953, 35.

Type of genus: Ephemera vulgata Linnaeus (by subsequent selection, Eaton, 1868).

Ephemera compar Hagen

Ephemera compar Hagen, 1875, 578; Eaton, 1883, 65; Needham, Traver, and Hsu, 1935, 249.

This species has not been collected since the original description. Traver (1935) writes "it is apparently close to E. simulans, but slightly larger."
Recorded distribution: Colorado.

Ephemera simulans Walker

Ephemera simulans Walker, 1853, 536; Hagen, 1863, 38; Eaton, 1883, 67; Needham, 1908, 261; Morgan, 1911, 100; Clemens, 1913, 332; Clemens, 1915, 116; Ide, 1930, 206; Needham, Traver, and Hsu, 1935, 252; Spieth, 1940, 325, 326, 327; Berner, 1950, 94; Burks, 1953, 36.
Palingenia natata Walker, 1853, 551.
Ephemera natata, Hagen, 1863, 39; Hagen, 1863, 177; Hagen, 1873, 384; Hagen, 1875, 580. (synonymy after Eaton, 1883)
Ephemera decora Walker, 1853, 536; Walsh, 1862, 376; Hagen, 1863, 177. (synonymy after Eaton, 1883)
Ephemera varia, Needham, 1920, 271 (in part—nymph only).

The nymph has been described and figured by Needham (1920) and incorrectly identified as E. varia.
Recorded distribution: Alberta, Colorado, Connecticut, Florida (?), Hudson Bay, Idaho, Illinois, Maine, Manitoba, Michigan, Minnesota, Montana, New York, Ohio, Ontario, Pennsylvania, Saskatchewan, Utah, Virginia, and Wyoming.

Hexagenia Walsh

Hexagenia Walsh, 1863, 197; Eaton, 1868, 85; Eaton, 1871, 64; Eaton, 1883, 48; Ulmer, 1920, 108; Needham, 1920, 278; Ulmer, 1921, 233; McDunnough, 1924b, 90; Traver, 1931, 591; Lestage, 1931, 39; Spieth, 1933, 347; Needham, Traver, and Hsu, 1935, 258; Spieth, 1941, 233; Berner, 1950, 78; Burks, 1953, 38.

The great color variations within and small genitalic differences between the species of this genus have caused universal confusion in the taxonomy of this group. Because of this confusion many synonyms have

been incorrectly applied. At various times Hagen (1861, 1863), Eaton (1871, 1883), and Needham (1920) placed H. limbata and its subspecies H. l. limbata, H. l. occulta, H. l. venusta, and H. l. viridescens as synonyms of H. bilineata. Needham (1920), for example, wrote, "A good many names have been applied to the different forms of this genus, but after a careful study of a good bit of material from many localities I am unable to recognize more than two good and distinct species in the eastern United States—a lowland species from lakes and rivers, Hexagenia bilineata Say, and an upland bog-species, H. recurvata Morgan." However, Walsh (1863) considered H. limbata and H. bilineata distinct at the time he described this genus. On other occasions authorities such as Walker (1853), Eaton (1883), McDunnough (1924, 1927), and Traver (1931, 1935), though usually lacking large series of specimens, took the opposite view and described many species on the basis of slight color and genitalia variations.

Spieth in 1941 proposed a much needed revision of this genus relegating several species to subspecific rank and synonymizing many others. He thus reduced the 18 Nearctic species of Traver (1935) to 6 species and 10 subspecies. Though agreeing in general with Spieth's (1941) revision, Burks (1935) did not recognize Spieth's "subspecific segregates within the species limbata and munda."

Type of genus: Ephemera limbata Serville (by subsequent selection, Eaton, 1868). Eaton (1883) in a later paper contradicted his original type selection by listing Baetis bilineata Say as the type of the genus. Traver (1935) and Spieth (1941) apparently overlooked Eaton's earlier (1868) paper and erroneously followed the later type selection given by Eaton in 1883.

Hexagenia atrocaudata McDunnough

Hexagenia atrocaudata McDunnough, 1924b, 92; McDunnough, 1927, 117; Traver, 1931, 611; Needham, Traver, and Hsu, 1935, 262; Spieth, 1941, 240; Burks, 1953, 39.

Contrary to the usual wide specific color variation encountered in this genus, this species (Spieth, 1941) has a "remarkably constant" color pattern.

The nymph has been described by Traver (1931).

Recorded distribution: Georgia, Illinois, Indiana, Maryland, Michigan, Missouri, New York, North Carolina, Ohio, Ontario, Pennsylvania, Virginia, and West Virginia.

Note: All records are east of the 100th meridian.

Hexagenia bilineata (Say)

Baetis bilineata Say, 1824, 303.

Palingenia bilineata, Hagen, 1861, 41; Walsh, 1862, 373; Hagen, 1863, 174; Walsh, 1863, 199-202.

Hexagenia bilineata, Eaton, 1871, 66; Eaton, 1883, 50; Clemens, 1913, 331; Needham, 1920, 278; Ulmer, 1921, 235; McDunnough, 1924b, 90; Wiebe, 1926, 267; McDunnough, 1927, 116; Traver, 1931, 591 (in

discussion), 611 (in key), 615 (nymph); Traver, 1937, 76; Needham, Traver, and Hsu, 1935, 263; Spieth, 1941, 242; Berner, 1950, 93; Burks, 1953, 38.

This is a very dark species whose abdomen, in the lateral view, appears to be striped. Darker markings may completely obscure the paler median ventral triangles (Fig. 21b). H. limbata occulta has often been confused with this species but the abdominal markings (Fig. 23) and genitalia (Fig. 15) of H. l. occulta are quite different from that of H. bilineata (Figs. 18, 21).

Baetis angulata Walker, at one time listed as a synonym of H. bilineata by Eaton (1883), is discussed under the subspecies H. limbata occulta.

The nymph has been described by Needham (1920) and Traver (1931).

Recorded distribution: Alabama, District of Columbia, Georgia, Illinois, Indiana, Iowa, Kentucky, Lousiana, Maryland, Minnesota, Mississippi, Missouri, New Mexico, Ohio, Oklahoma, Tennessee, Texas, and Virginia.

New Records: IOWA, Butler Co., 6-VII-1940 (U.W.) - 1♂; Des Moines Co., Burlington, 4-VIII-1926 (H.M. Harris) - 2♀♀; Henry Co., Mt. Pleasant, 4-VII-1928 and 11-VII-1928 (Van Horn), 16-VII-1930 (H. Knight), 15-VII-1942 (A. Pidgeon) - 4♀♀, 13-VII-1948 (S. Statler) - 1♀, 18-VI-1949 (C. Yoshimoto) - 1♀, 20-VI-1949 (Orman Donovan) - 1♂ (very pale), 25-VI-1949 (P. Kautsky) - 1♀, 19-VII-1951 (Newby) - 2♀♀, 20-VII-1941 (Miller) - 1♀, 25-VII-1951 (R. Newby) - 1♀, 31-VII-1951 (Clegg) - 1♀ (D. Prickett) - 1♀; Lee Co., 24-VII-1929 (Farris) - 1♀; Muscatine Co., Muscatine, 12-VII-1894 (H.C.) - 2♀♀, 14-VI-1934 (H.E. Jaques) - 1♀ (subimago), 4-VII-1951 (Newby) - 1♂ (subimago); Scott Co., LeClaire 2♀♀. KANSAS, Douglas Co., 7-VII-1920 and 9-VII-1920 (William E. Hoffman) - 4♀♀; Riley Co., Manhattan, 2-VII-1949 (L. Edelblute) - 2♀♀, July, at light (U. K. Col. Lot 66, 73, 82) - 1♂, 2♀♀, September, at light (U. K. Col. Lot 115) - 1♂ (pale). MISSOURI, Lincoln Co., Clarksville, 22-VI-1953 about 200♀♀ and ♂♂; Taney Co., Hollister, 20-VII-1930 (H.H. Knight) - 10♀♀. WISCONSIN, Dane Co., 21-VI-1947, 24-VII-1947, and 27-VII-1947 - 3♀♀.

Note: All records are east of the 100th meridian except for a single specimen from New Mexico.

Hexagenia limbata (Serville) complex

Spieth's (1941) subspecies H. l. limbata, H. l. occulta, and H. l. venusta meet in a broad area of intergrades across Nebraska, Kansas, Iowa, northern Missouri, southern Minnesota, southern Wisconsin, Illinois, Indiana, and Ohio; H. l. occulta and H. l. viridescens intergrade in the Great Lakes region (Fig. 44). H. l. viridescens is not found in the area studied, and thus its synonymy, distribution, and records are not discussed. However, each subspecies is a quite distinct entity in its own region; typical H. l. limbata being found in the northwest, H. l. venusta in the south, H. l. occulta in the northeast, and H. l. viridescens just north of H. l. occulta. If these forms were not considered subspecies (Burks, 1953), the resulting H. limbata would consist of an

extremely variable population in the center of its geographical area, with different and distinct color phases in the northeast, south, and northwest. Since these populations at the geographical extremes of H. limbata are distinct and rather constant, the subspecific concept of Spieth (1941) is retained, although in the broad, central geographic area it is impossible to assign specimens to a particular subspecies.

Since the distributional information concerning the subspecies of this group is being added to, new subspecific records outside of the Missouri River watershed are included.

Hexagenia limbata limbata (Serville)

Ephemera limbata Serville, in Guérin Méneville, 1829, 384.
Palingenia limbata, Pictet, 1843, 146; Walker, 1853, 548; Hagen, 1861, 41; Walsh, 1862, 373; Hagen, 1863, 176; Provancher, 1876, 265.
Hexagenia limbata, Walsh, 1863, 197; Eaton, 1868, 85; Eaton, 1871, 65; Hagen, 1890, 11; Needham, 1920, 279; McDunnough, 1924b, 90; McDunnough, 1927, 119; Traver, 1931, 611 (in keys); Needham, Traver, and Hsu, 1935, 265; Burks, 1953, 39.
Hexagenia limbata limbata, Spieth, 1941, 246.
Hexagenia variabilis Eaton, 1883, 55 (in part).

The distribution and hybridization of H. l. limbata is shown in Fig. 44. The abdominal color pattern of H. l. limbata (Fig. 22) is intermediate between that of H. l. occulta (Fig. 23) and H. l. venusta (Fig. 24).

The nymph has not been described.

Recorded distribution of H. l. limbata; British Columbia, Colorado, Idaho, Illinois, Michigan, Oregon, Utah, and Washington.

Recorded distribution of hybrids: H. l. limbata x occulta - Illinois, Manitoba; H. l. limbata x venusta - Iowa, Kansas, Utah; H. l. limbata x occulta x venusta - Illinois.

New records of H. l. limbata: IOWA, Clayton Co., 13-VI-1932 (Russel) - 1♀, 12-VIII-1932 (M.W.J.) - 1♀; Dickinson Co., 28-VI-1935 (Gould Warren) - 1♀, 2-VII-1936 (P. Travis) - 2♂♂, 26-VII-1935 (R. Huizinga) - 1♂, 2-VIII-1938 (J.B.J.) - 1♀; Floyd Co., Charles City, 21-VIII-1918 (E.V. Walter) - 1♀; Franklin Co., Hampton, 17-VIII-1942 (W.W. Darlington) - 1♀; Henry Co., 19-V-1948 (Griffen) - 1♀, 12-VI-1951 (Herb Miller) - 1♀, 17-VI-1951 (Widmer) - 1♀, 27-VI-1947 (Toker) - 1♀, 13-VII-1948 (S. Statler) - 1♀ (subimago), 23-VII-1948 (S. Statler) - 1♀, 15-IX-1951 (Oppenheimer) - 1♀; Muscatine Co., 7-VI-1936 (Bernard Berger) - 1♀; Story Co., Ames, 29-III-1949 (Shoenhair) - 1♀, 28-V-1933 (Ruth Madden) - 1♀, no data - 1♂, 7-VI-1925 and 9-VI-1925 (C.W.M.) - 3♀♀, 18-VII-1946 (J. Laffoon) - 1♀, Gilbert, 16-VI-1928 (G. Hendrickson) - 1♀. KANSAS, Douglas Co., 14-VI-1921 (W.J. Brown) - 1♀. MICHIGAN, Ingham Co., East Lansing, 28-VI-1899, Lot 138, Sub. 10 - 3♀♀; 15-VI-1898 - 1♂, 26-VII-1890 - 1♂, 20-VII-1897 - 1♀, 25-VI-1895 - 1♀, all in Lot 129, Sub. 41 (det. by Nathan Banks), Aurelius, 10-VII-1938 - 5♀♀. MINNESOTA, Crow Wing Co., Nisswa, Pelican Lake, 12-VII-1912 (L. Bruner) - 1♀; Stearns Co., Sauk Center, 7-VIII-1954, at light (E.W. Hamilton) - 2♀♀. NEBRASKA, Buffalo Co., Kearney, 13-VI-1952, at light (E.W. Hamilton) - 1♂; Keith Co.,

Ogallala, 2-VII-1954, at light (E.W. Hamilton) - 1♀; Madison Co., Norfolk, 14-VII-1949, at light (M.H. Muma) - 1♂; Platte Co., Columbus, 26-VI-1950, on stream surface (E.W. Hamilton) - 1♀; Scotts Bluff Co., Mitchell, 14-VII-1915 (L.M. Gates) - 1♂. WISCONSIN, Dane Co., 17-VI-1946 and 13-VII-1946 (J.R.D.) - 2♀♀, 15-VIII-1947 - 1♀.

New records of H. l. limbata x occulta: IOWA, Clay Co., 5-VI-1933 (Maurer) - 1♂; Clayton Co., 3-VIII-1932 (M.W.J.) - 1♂, 9-VIII-1932 (Cronn) - 1♂ subimago; Dickinson Co., 19-VI-1936 (D. Millspaugh) - 1♂, 3-VII-1936, 9-VII-1936, 28-VII-1936, and 9-VII-1937 (H.E. Jaques) - 4♂♂, 13-VII-1936 (M.E. Barres) - 1♂; Henry Co., 9-VII-1947 (Swanson) - 1♀. MINNESOTA, Crow Wing Co., Nisswa, Pelican Lake, 12-VII-1912 (L. Bruner) - 2♂♂. 1♀. WISCONSIN, Dane Co., 16-VIII-1947 - 1♀.

New records of H. l. limbata x venusta: IOWA, Davis Co., Floris, 9-VIII-1941 (Calhoun) - 1♀; Dickinson Co., 23-VI-1934 (W.E. Dodds) - 1♀, 28-VI-1935 and 5-VII-1935 (Mabel Jaques) - 2♀♀, 2-VII-1935 and 5-VIII-1935 (H. Huizinga) - 1♂, 1♀, 3-VII-1936, 13-VII-1936, 2-VIII-1937, and 8-VIII-1935 (H.E. Jaques) - 3♀♀, 1♀ subimago, 2-VII-1934 (H.C. Knutson) - 1♂ subimago, 7-VII-1937 (George Crane) - 1♂; Henry Co., 20-VII-1937 (Donovan Orman) - 1♂ subimago, 28-VI-1951 (Benjamin Luke) - 1♀, Mt. Pleasant, 29-VII-1942 (L. Wright) - 1♀ subimago, 5-VIII-1942 (A. Pidgeon) - 1♀ subimago; Story Co., 28-V-1941 (L. Polter) - 1♀, 4-VI-1949 (Totemeier) - 1♂, 12-VI-1953 and 19-VI-1953 (W.S. Craig)- 1♂, 2♀♀, 1♂ subimago, 9-VII-1948 (W. Luginbuhl) - 1♀ subimago. NEBRASKA, Brown Co., Johnstown, 4-VIII-1950, Plum Creek (E.G. Burcham) - 1♀; Buffalo Co., Kearney, 13-VI-1952, at light (L.W. Quate) - 1♀; Cherry Co., Valentine, 30-VIII-1954, at light (E.W. Hamilton)- 1♂, 2♀♀, 30-VIII-1954, at light (L.W. Quate) - 1♂, 1♀; Dawson Co., Lexington, 28-VI-1950, at light (O.S. Bare) - 6♂♂, Willow Island, 15-VII-1954, on potatoes (R.E. Hill) - 1♂; Douglas Co., Omaha, 5-VIII-1913 and 12-VIII-1913 (L.T. Williams)- 1♂, 1♂ subimago; Keith Co., Ogallala, 2-VIII-1954 and 10-VIII-1955, at light (E.W. Hamilton)- 1♀, 1♂ subimago; Lincoln Co., North Platte, 30-VII-1949, at light (E.W. Hamilton) - 1♀; Madison Co., Norfolk, 25-VI-1913 (L.T. Williams) - 1♂, 1♀, 15-VI-1949, at light (D. Scott) - 5♂♂ subimagoes, 16-VI-1949, at light (M.H. Muma) - 1♂, 30-VI-1949, at light (M.H. Muma)- 2♂♂, 3♀♀, 14-VII-1949, at light (M.H. Muma)- 1♀; 5-VIII-1949, at light (M.H. Muma) - 1♂; Platte Co., Columbus 2-VII-1950, at light (E.W. Hamilton) - 1♂; Scotts Bluff Co., Scottsbluff, 10-VI-1952, at light (E.W. Hamilton) - 1♂, 26-VIII-1949, at light (J. Weimer) - 1♀; Thomas Co., Halsey, 13-VIII-1912 (J.T. Zimmer) - 1♂. NORTH DAKOTA, Cass Co., 4-VII-1930 (Adrian Fox) - 1♀, 21-VI-1941, 4-VII-1941, at light (H.S. Telford) - 1♂, 1♀, no date - 3♀♀. WYOMING, Goshen Co., Torrington, 27-VIII-1947 and 2-IX-1948 (R.E. Pfadt) - 3♂♂, 2♀♀.

Hexagenia limbata occulta (Walker)

Palingenia occulta Walker, 1853, 551.
Hexagenia limbata var. occulta, McDunnough, 1927, 119.
Hexagenia occulta, Traver, 1931, 611 (in key); Needham, Traver, and Hsu, 1935, 267.
Hexagenia limbata occulta, Neave, 1932a, 182; Neave, 1932b, 54; Spieth, 1940, 327; Spieth, 1941, 250.
Hexagenia variabilis (in part) Eaton, 1883, 55; Hagen, 1890, 12; Needham, 1901, 427; Needham, 1908, 262; Morgan, 1911, 99.
Hexagenia mingo Traver, 1931, 597; Needham, Traver, and Hsu, 1935, 267. (synonymy after Spieth, 1941)
Hexagenia rosacea Traver, 1931, 607; Needham, Traver, and Hsu, 1935, 273. (synonymy after Spieth, 1941)

Spieth in his discussion of the North American species of Francis Walker (1940, p. 332) writes, "A careful study of the eye size, the remaining abdominal color pattern and the coloration of the head, cerci and wings indicates that (Baetis) angulata Walker is a synonym of H. viridescens Walker instead of H. bilineata Say as indicated by Eaton, or H. l. occulta Walker as McDunnough and Traver have held." Since Spieth (1941) in his revision did not include B. angulata Walker in the synonymy of H. viridescens, it is mentioned here to clarify its standing.

The distribution and hybridization of H. l. occulta is shown in Fig. 44. Dark specimens of H. l. occulta are practically indistinguishable from H. viridescens, a subspecies of the Great Lakes region. One must be careful also not to confuse H. l. occulta (Figs. 15, 23) with H. bilineata (Figs. 19, 21) as has often been done.

The nymph has been described by Neave (1932) and Spieth (1941).

Recorded distribution of H. l. occulta: District of Mackenzie, Illinois, Indiana, Kentucky, Manitoba, Michigan, Minnesota, New Brunswick, New York, North Carolina, North Dakota, Ohio, Ontario, Province of Quebec, Saskatchewan, West Virginia, and Wisconsin.

Recorded distribution of hybrids: H. l. limbata x occulta - Illinois, Manitoba; H. l. limbata x occulta x venusta - Illinois; H. l. occulta x venusta - Illinois, Indiana, Manitoba, Minnesota, Ohio.

New records of H. l. occulta: IOWA, Clayton Co., 10-VI-1938 (Harold Beery) - 3♂♂; Dickinson Co., 19-VI-1936 and 30-VII-1937 (H. E. Jaques) - 1♂, 1♀, 19-VI-1936 (D. Millspaugh) - 1♂; Henry Co., 17-VI-1951 (Widmer) - 1♂; Lee Co., 21-V-1949 (Ivor Koch) - 1♂ subimago; Linn Co., 19-VI-1934 (H.C. Knutson) - 1♂; Lyon Co., 27-VI-1940 (H.E. Jaques) - 1♂, Beloit, 27-VII-1928 (G. Hendrickson) - 1♂; Plymouth Co., 2-VIII-1921 (L.S.) - 1♂; Story Co., Ames, ?-V-1940 (Ellis Hicks)-1♂ (very purplish), 4-VII-1946 (J. Laffoon) - 1♂ (#701), 30-V-1949 (Shoenhair) - 1♂. MANITOBA, Hartney, 31-VII-1937 (C. L. Johnson) - 1♂. MICHIGAN, Bay Co., Bay City, 28-VI-1899 - 21♂♂, 2♀♀; Cheboygan Co., Douglas Lake, ?-VI-1927 (Leonora K. Gloyd) - 2♂♂ subimagoes. MINNESOTA, Crow Wing Co., Nisswa, Pelican Lake, 12-VII-1912 (L. Bruner) - 8♂♂, 2♀♀, 3♂♂ subimagoes. NORTH DAKOTA, Cass Co., Fargo, no other data - 4♂♂, 1♀.

WISCONSIN, Dane Co., 3-VIII-1946 (J.R.D.) - 1♂, 8-VIII-1947 - 2♂♂; Vilas Co., Eagle River, 3-VII-1952, at light (H.J. Ball) - 3♂♂, 3♀♀.

New records of H. l. occulta x venusta: IOWA, Davis Co., Floris, 9-VIII-1941, (Calhoun) - 2♂♂; Dickinson Co., 23-VI-1934 (W.E. Dodds) - 1♂, 5-VII-1935, 3-VII-1936, 13-VII-1936, and 27-VII-1936 (H. E. Jaques) - 4♂♂; Emmet Co., 24-VII-1932 (Iles) - 1♂; Muscatine Co., Muscatine, 23-VI-1953, at light (W.S. Craig) - 1♂, 1♀; Story Co., Ames, ?-V-1940 (Ellis Hicks) - 1♂, 23-V-1941 (Levi Mohler) - 1♀, 30-VI-1948 (R.E. Nelson) - 1♀. NEBRASKA, Platte Co., Columbus, 2-VII-1950, reared from swift stream (E.W. Hamilton) - 1♂. WISCONSIN, Dane Co., 3-VIII-1947 - 1♂.

Hexagenia limbata venusta Eaton

Hexagenia venusta Eaton, 1883, 54; Ulmer, 1921, 235, 237, 239; McDunnough, 1927, 119 (in discussion of H. affiliata); Traver, 1931, 611 (in key); Needham, Traver, and Hsu, 1935, 274; Spieth, 1941, 88.

Hexagenia limbata venusta, Spieth, 1941, 253.

Hexagenia pallens Traver, 1935, (in Needham, Traver, and Hsu) 271 (synonymy after Spieth, 1941).

The distribution and hybridization of H. l. venusta is shown in Fig. 44, its abdominal color pattern in Fig. 24.

The nymph has been described by Spieth (1941).

Recorded distribution of H. l. venusta: Illinois, Iowa, Kansas, Mississippi, Missouri, Nebraska, Oklahoma, Tennessee, and Texas.

Recorded distribution of hybrids: see H. l. limbata and H. l. occulta.

New records of H. l. venusta: IOWA, Dickinson Co., 29-VI-1934 (H.C. Knutson), 28-VI-1935 (Gould Warren), 9-VII-1937, 2-VIII-1937, and 8-VIII-1935 (H.E. Jaques) - 3♂♂ (1 subimago), 2♀♀; Henry Co., 20-VII-1951 (Miller) - 1♀, 25-VII-1951 (Ginkens) - 1♀; Iowa Co., Lake Amana, 23-VI-1928 (G.O. Hendrickson) - 1♂; Story Co., Ames, 4-VI-1930 (H.E.G.), 1-VIII-1939 (E. Buren), no date (Osborn) - 2♂♂, 1♀. KANSAS, Douglas Co., Lawrence, ?-VI-? (H.T. Martin) - 1♂ (#7 determined by N. Banks), ?-VII-? (U. of K. Col. Lot 66 and 71) - 2♀♀. ?-VII-? (U. of K. Col. Lot 97) - 1♀ (all taken at lights); Ellis Co., 14-VII-1912, 2000' (F.X. Williams) - 1♂; Franklin Co., 1-VII-1912 (H.K. Gloyd) - 2♀♀; Gove Co., no date, 2813' (F.X. Williams) - 1♀ subimago; Graham Co., 16-VIII-1912, 2130' (F.X. Williams) - 2♂♂; Greenwood Co., 31-VII-1923 (Beamer - Lawson) - 3♀♀; Pratt Co., 6-VI-1950 (J.G. Rozen) - 1♀ subimago; Reno Co., 21-VII-1947 - 7♀♀, 21-IX-1949 - 1♀; Riley Co., Manhattan, 6-VI-1949, at light (R.L. Fischer) - 6♀♀, 10-VI-1942, on alfalfa (Roger C. Smith) - 1♂, 1♀, ?-VII-1929 (T.F. Winburn) - 1♀, 2-VII-1941, on alfalfa (Roger C. Smith) - 1♀; Rooks Co., 9-VIII-1912, 1775' (F.X. Williams) - 1♂, 1♀; Scott Co., 20-VI-1925 (H.O. Deay) - 1♀. MICHIGAN, Ingham Co., East Lansing, 8-VI-1900 - 12♀♀, 7-VI-1899 and 18-VI-1899 - 4♀♀. MISSOURI, Boone Co., Columbia, 28-VI-1953, at light (W.R. Enns) - 3♀♀, 2♀♀ subimagoes; Pike Co., Louisiana, 15-VI-1953 (W.R. Enns) - 2♂♂, 2♀♀ (all subimagoes), Clarksville, 15-VI-1953, at light (W.R.

Enns) - 3♀♀. NEBRASKA, Buffalo Co., Kearney, 13-VI-1952 (L.W. Quate) - 1♀; Dawson Co., Johnson Lake, 25-VIII-1955, at light (O.S. Bare) - 1♂ subimago, Lexington, 28-VI-1950, at light (O.S. Bare) - 4♀♀, 7-VII-1955, on potatoes (R.E. Hill) - 1♂; Douglas Co., Omaha, 12-VII-1913 and 5-VIII-1913 (L.T. Williams) - 2♂♂, 2♀♀; Keith Co., Ogallala, 2-VIII-1954, at light (E.W. Hamilton) - 2♀♀, 19-VII-1955, at light (D. Scott) - 2♂♂ subimagoes; Lancaster Co., Lincoln, 20-X-1949, in pond (E.W. Hamilton) - 2 nymphs, 3-VII-1950, at light (E.W. Hamilton) - 1♂; Lincoln Co., North Platte, 11-VII-1955, at light (E. W. Hamilton) - 3♂♂; Madison Co., Norfolk, 16-VII-1949, at light (M. H. Muma) - 1♀; Platte Co., Columbus, 26-VI-1950 and 2-VII-1950, at light (E.W. Hamilton) - 1♂, 1♀; Scotts Bluff Co., Scottsbluff, 10-VI-1952, at light (E.W. Hamilton) - 1♀; Seward Co., Milford, 3-VII-1954, at light (E.W. Hamilton) - 1♀, Seward, 15-VIII-1949, at light (E.W. Hamilton) - 1♂, 5♀♀ subimagoes, 26-VI-1950, at light (E.W. Hamilton) - 1♀. TEXAS, Eastland Co., Cisco, 19-VI-1947 (A.C. Michener) - 6♀♀, Wiley, 2-IX-1920 (Grace Olive) - 1♀.

Hexagenia munda Eaton complex

This species has not been found in the Missouri River watershed, but is reported from Iowa and Missouri in the Mississippi drainage. The complex is distinguishable from H. limbata (Serville) only by very slight genitalic differences (Fig. 17) and by a uniform umber pigmentation of the costal membrane with the costal cross-veins not margined.

Hexagenia munda affiliata McDunnough

Hexagenia affiliata McDunnough, 1927, 118; Traver, 1931, 611 (in key); Needham, Traver, and Hsu, 1935, 261.
Hexagenia munda affiliata, Spieth, 1941, 257.

This subspecies is very close to H. l. occulta in its dorsal abdominal maculations (Fig. 25a). It can be distinguished from H. l. occulta and other species by its costal pigmentation, penes (Fig. 16), and abdominal pattern (Fig. 25).

The nymph is undescribed.

Recorded distribution: Connecticut, Indiana, Iowa, Maine, Michigan, Minnesota, New Hampshire, New Jersey, New York, Ohio, Ontario, Pennsylvania, and Quebec.

New records: IOWA, Delaware Co., 10-VI-1932 (Moore) - 1♂; Linn Co., 19-VI-1934 (H.C. Knutson) - 1♂.

Note: All records are east of the 100th meridian.

Hexagenia munda munda Eaton

Hexagenia munda Eaton, 1883, 53; McDunnough, 1927, 118; Needham, Traver, and Hsu, 1935, 268; Burks, 1953, 41.
Hexagenia munda munda, Spieth, 1941, 263.

The nymph has not been described.

Recorded distribution: Illinois, Missouri, Oklahoma.
Note: All records are east of the 100th meridian.

Hexagenia rigida McDunnough

Hexagenia rigida McDunnough, 1924b, 90; McDunnough, 1927, 117 (in discussion); Traver, 1931, 611 (in key); Neave, 1932a, 1; Neave, 1932b, 54; Needham, Traver, and Hsu, 1935, 272; Spieth, 1941, 267; Burks, 1953, 41.

This is another species that can be confused with H. l. occulta, particularly the females. Quite often the ventral abdominal markings (Fig. 27b) become obscured by dark pigmentation, the pattern thus looking more like that of H. l. occulta (Fig. 23b). Some light specimens of H. l. occulta have the ventral abdominal pattern approaching that of H. rigida. However, the eggs of the two species (Neave, 1932), the nymphs, and the male genitalia are quite different.

The nymph has been described by Neave (1932) and Spieth (1941).

Recorded distribution: Illinois, Iowa, Kansas, Manitoba, Michigan, Missouri, New Brunswick, New York, Ohio, Oklahoma, Ontario, Pennsylvania, Quebec, and Vermont.
Note: All records are east of the 100th meridian.

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Literature Cited

Argo, Virgil. 1927. The North American species of the genus Potamanthus, with a description of a new species. N. Y. Ent. Soc. 35: 319-328.

Banks, Nathan. 1894. On a collection of neuropteroid insects from Kansas. Ent. News 5:178.

_____. 1907. Catalog of the neuropteroid insects of U.S. (except Odonata). Amer. Ent. Soc. Phila., pp. 1-53.

_____. 1908. Neuropteroid insects—Notes and descriptions. Trans. Amer. Ent. Soc. 34:259.

_____. 1910. Notes on our eastern species of the mayfly genus Heptagenia. Canad. Ent. 42:197-202.

Berner, Lewis. 1950. The mayflies of Florida. Univ. Florida Studies, Biol. Sci. Ser. 4:vii-267.

Burks, B.D. 1953. The mayflies, or Ephemeroptera, of Illinois. Bull. Ill. Nat. Hist. Surv. 26:1-216.

Clemens, W.A. 1913. New species and new life histories of Ephemeridae or mayflies. Canad. Ent. 45:246-262, 329-341.

_____. 1915. Rearing experiments and ecology of Georgian Bay Ephemeridae. Contr. Canad. Biol., Paper 39b:114-143.

Eaton, A.E. 1868. An outline of a re-arrangement of the genera of Ephemeridae. Ent. Mo. Mag. 5:82-91.

_____. 1871. A monograph on the Ephemeridae. Trans. Ent. Soc. of London, 1871:1-158.

_____. 1883. A revisional monograph of recent Ephemeridae or mayflies. Trans. Linn. Soc. London, Ser. 2, Zool. 3:1-352.

Edmunds, George F., Jr. 1948. The nymph of Ephoron album (Ephemeroptera). Ent. News 59:12-14, 2 figs.

_____ and Jay R. Traver. 1954. An outline of a reclassification of the Ephemeroptera. Ent. Soc. Wash. 56:236-240.

Hagen, Hermann. 1861. Synopsis of the Neuroptera of North America, with a list of South American species. Smith. Misc. Coll. 38-55.

_____. 1863. Observations on certain N.A. Neuroptera (translated from the original French MS. and published by Benj. D. Walsh with the permission of the author containing notes and descriptions of about twenty new N. A. species of Pseudoneuroptera). Proc. Ent. Soc. Phila. 2:169-179.

_____. 1873. Notes on the Ephemeridae (compiled, with remarks, by the Rev. A. E. Eaton). Trans. Ent. Soc. London, 1873:381-406.

_____. 1875. Report on the Pseudoneuroptera and Neuroptera collected by Lieut. W. L. Carpenter in 1873 in Colorado. Ann. Rept., U.S. Geol. Surv. of the Territories for 1873. Part III, Ephemerina, pp. 578-583. Washington.

_____. 1890. Unser gegenwartige Kentniss der Ephemeriden. Stett. Ent. Zeit. 51:11-13.

Howard, W.E. 1905. Polymitarcys albus Say, pp. 60-62. In James G. Needham - Ephemeridae. In James G. Needham, Kenneth J. Morton, and O.A. Johannson - Mayflies and Midges of New York. New York State Mus. Bull. 86.

Ide, F.P. 1930. The nymph of the mayfly genus Cinygma Eaton. Canad. Ent. 62:42-45.

_____. 1935. Life history notes on Ephoron, Potamanthus, Leptophlebia, and Blasturus with descriptions (Ephemeroptera). Canad. Ent. 67: 113-125.

_____. 1941. Mayflies of two tropical genera, Lachlania and Campsurus, from Canada with descriptions. Canad. Ent. 73:153-156.

_____. 1955. Two species of mayflies representing southern groups occurring at Winnipeg, Manitoba. Ann. Ent. Soc. Amer. 48:15-16.

Leach, William E. 1815. Entomology in Brewster's Edinburgh Encyclopedia 9:57-172.

LeConte, John L., editor. 1891. The complete writings of Thomas Say on the entomology of North America, I. II. A.E. Foote, Philadelphia.

Lestage, J.A. 1931. Contribution à l'étude des Éphéméroptères, VIII. Soc. Ent. Belg. Bul. et Ann. 71:39-60.

_____. 1938. Contribution à l'étude des Éphéméroptères, XVI-XXI. Soc. Ent. Belg. Bul. et Ann. 78:381-394.

Linnaeus, Carolus. 1758. Systema Naturae. Tenth Ed., pp. 1-826. Holmiae.

Lyman, F. Earle. 1943. Note regarding authorship of Hexagenia limbata (Serville) (Ephemeroptera). Ent. News 54:248.

McDunnough, J. 1924a. New Ephemeridae from Illinois. Canad. Ent. 56:7-9.

_____. 1924b. New Canadian Ephemeridae with notes, II. Canad. Ent. 56:90-98.

_____. 1926. Notes on North American Ephemeroptera with description of new species. Canad. Ent. 58:184-196.

_____. 1927. Notes on the species of the genus Hexagenia with description of a new species (Ephemeroptera). Canad. Ent. 59:116-120.

Morgan, Ann H. 1911. Mayflies of Fall Creek. Ann. Ent. Soc. Amer. 4:93-119.

_____. 1913. A contribution to the biology of mayflies. Ann. Ent. Soc. Amer. 6:371-413.

Neave, Ferris, 1932a. A study of the mayflies (Hexagenia) of Lake Winnipeg. Contr. Canad. Biol. and Fish. Nova Scotia 7:179-201.

_____. 1932b. The mayflies of Lake Winnipeg. Canad. Field-Nat. 46: 54-55.

Needham, J.G. 1901. Aquatic insects in the Adirondacks. New York State Mus. Bull. 47:418-429.

_____. 1908. Notes on the aquatic insects of Walnut Lake. Rep. of Geol. Surv. of Michigan for 1907. 259-263.

_____. 1920. Burrowing mayflies of our larger lakes and streams. Bull. U. S. Bur. Fish. 36:269-292.

Needham, J.G. and R.O. Christenson. 1927. Economic insects in some streams of northern Utah. Bull. Utah Agr. Exp. Sta. 201:6-16.

_____ and Helen E. Murphy. 1924. Neotropical mayflies. Bull. Loyd Libr. 24, Ent. Ser. 4:1-79.

_____, Jay R. Traver, and Yin-Chi Hsu. 1935. The biology of mayflies, pp. 1-759.

Pictet, F.J. 1843-45. Histoire naturelle, générale et particulière des Insectes Néuropterès. Seconde Monographie, Famille des Éphémèrines. Geneva and Paris, pp. 1-300, pls. 1-47.

Provancher, Léon. 1876. Petite faune entomologique de Canada, Névroptères, Fam. III, Éphémérides. Nat. Can. 8:264-268.

Say, Thomas. 1823. Long's Narrative, Appendix 2:162-163 (see Le Conte edition).

_____. 1824. Long's Expedition, 2:304-305 (see Le Conte edition).

_____. 1839. Descriptions of new North American neuropterous insects and observations on some already described. Jour. Acad. Nat. Sci. Phila. 8:9-46 (see Le Conte edition).

Serville, M. 1829. In Iconographie du regne animal de G. Cuvier (by F.E. Guérin-Méneville) 3:384.

Spieth, Herman T. 1933. The phylogeny of some mayfly genera. Jour. N.Y. Ent. Soc. 41:55-86, 327-390.

_____. 1940. The North American ephemeropteran species of Francis Walker. Ann. Ent. Soc. Amer. 33:324-338.

_____. 1941. Taxonomic studies on the Ephemeroptera. II. The genus Hexagenia. Amer. Midland Nat. 26:233-280.

Traver, J.R. 1931. Seven new southern species of the mayfly genus Hexagenia, with notes on the genus. Ann. Ent. Soc. Amer. 24:591-621.

_____. 1937. Notes on mayflies of the southeastern states (Ephemeroptera). Jour. Elisha Mitchell Sci. Soc. 53:27-86.

Ulmer, Georg. 1920. Uebersicht ueber die Gattungen der Ephemeropteran, Nebst Bemerkungen ueber einzelne Arten. Stett. Ent. Zeit. 81:97-144.

_____. 1921. Ueber einige Ephemeropteren-Typen älterer Autoren. Arch. f. Naturg. 87:229-267.

_____. 1932. Bemerkungen ueber die seit 1920 neu aufgestellten Gattungen der Ephemeropteran. Stett. Ent. Zeit. 93:204-219.

Walker, Francis. 1853. Catalogue of the species of neuropterous insects in the collection of the British Museum Pt. III, Termitides and Ephemeridae, pp. 533-585.

Walsh, Benjamin D. 1862. List of the Pseudoneuroptera of Illinois, contained in the cabinet of the writer, with descriptions of over forty new species, and notes on their structural affinities. Proc. Acad. Nat. Sci. Phila. 14:361-402.

_____. 1863. Notes (on Hagen's "Observations of certain N.A. Neuroptera" translated by Walsh in 1863). Proc. Ent. Soc. Phila. 2:182-272.

Wiebe, A.H. 1926. The first three larval stages of Hexagenia bilineata (Say). Ohio Jour. Sci. 26:267-275.

Williamson, Hugh. 1802. On the Ephoron leukon, usually called the white fly of Passaic River. Trans. Amer. Philos. Soc. 5:71-73.

PLATE I

Figure	Species	Character
1	*Heptagenia elegantula*	Wings
2	*Isonychia sicca*	"
3	*Tortopus primus*	"
4	*Ephoron album*	"
5	*Potamanthus verticis*	"
6	*Ephemera simulans*	"
7	*Pentagenia vittigera*	"
8	*Hexagenia bilineata*	"
9	Diagram showing wing fluting	

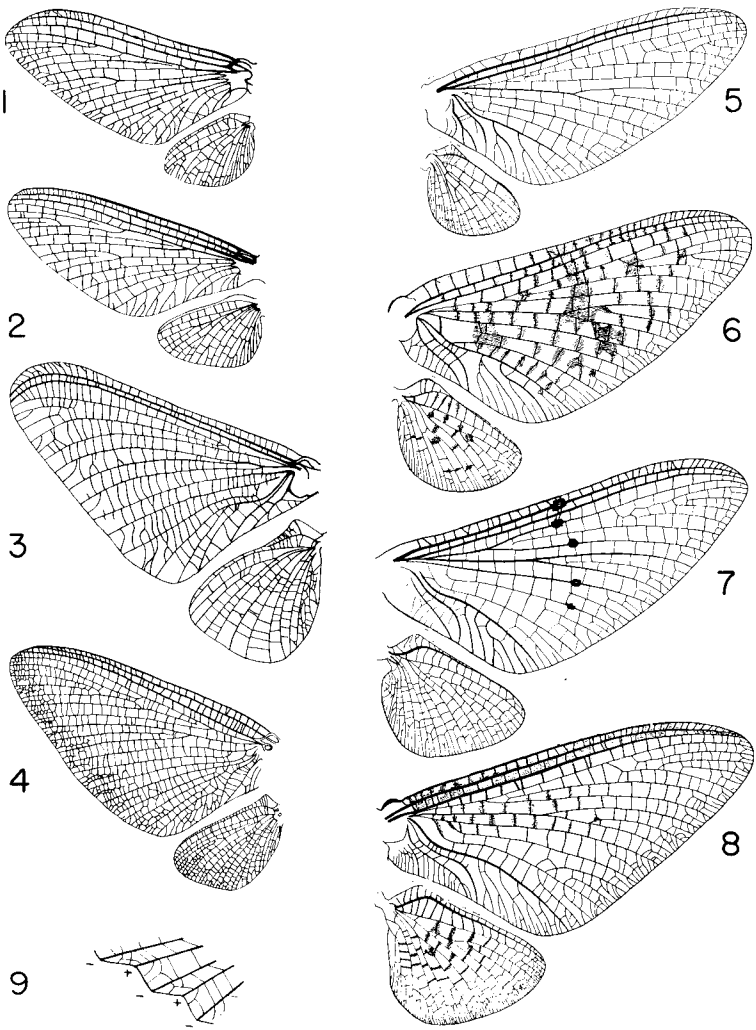
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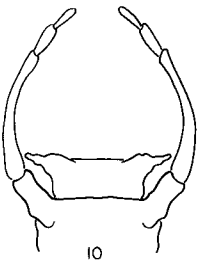
PLATE II

Figure	Species	Character
10	*Ephoron album*	Penes
11	*Potamanthus rufus*	"
12	*Pentagenia vittigera*	"
13	*Ephemera simulans*	"
14	*Hexagenia atrocaudata*	"
15	*Hexagenia limbata limbata*	"
16	*Hexagenia munda*	"
17	*Hexagenia rigida*	"
18	*Tortopus primus*	"
19	*Hexagenia bilineata*	"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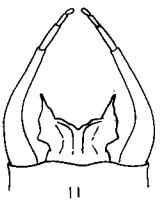
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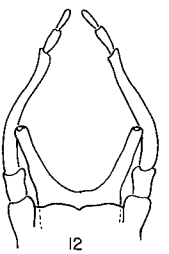
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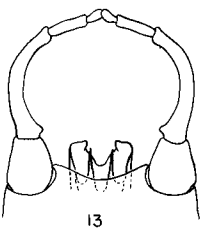
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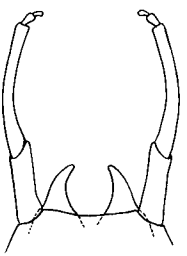
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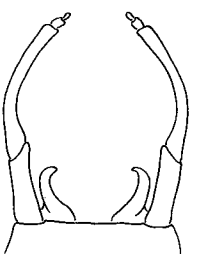
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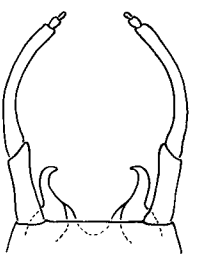
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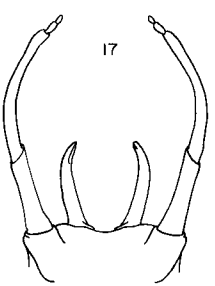
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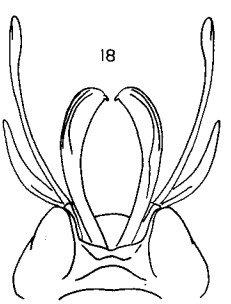
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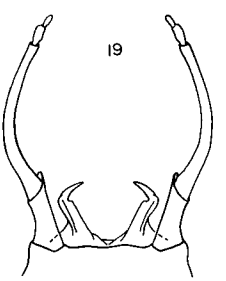
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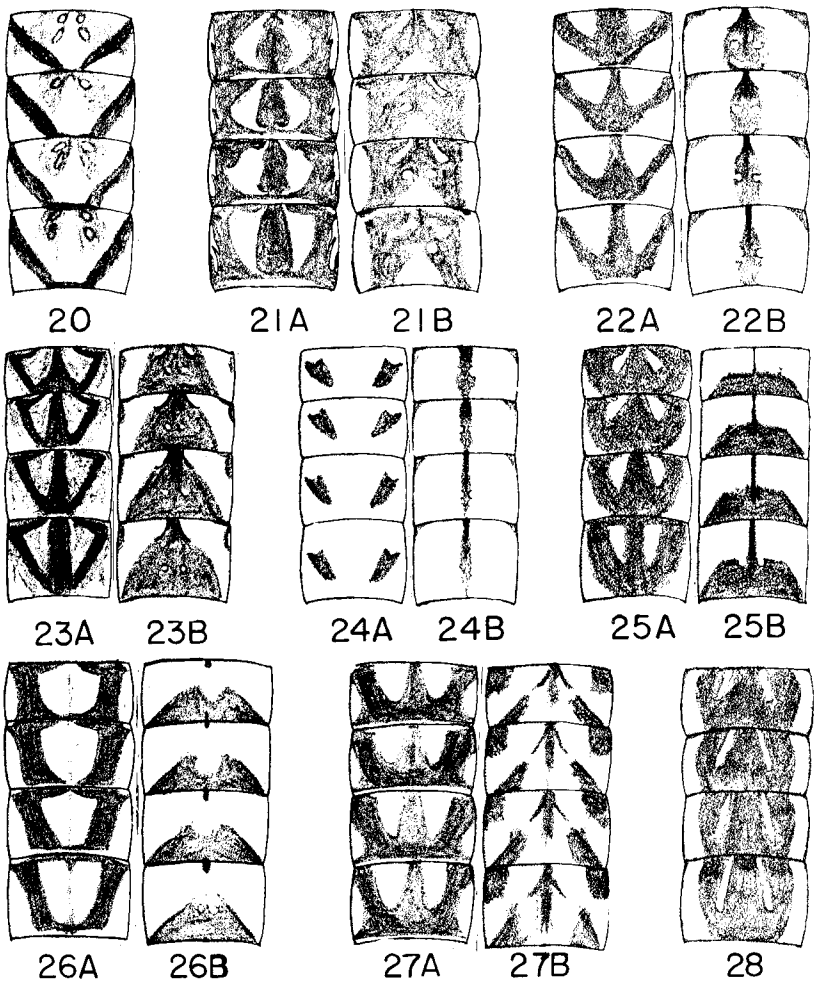
PLATE III

Figure	Species	Character
20	Hexagenia atrocaudata	Abdominal terga 3-6
21a	Hexagenia bilineata	" " 3-6
b		" sterna 3-6
22a	Hexagenia limbata limbata	" terga 3-6
b		" sterna 3-6
23a	Hexagenia limbata occulta	" terga 3-6
b		" sterna 3-6
24a	Hexagenia limbata venusta	" terga 3-6
b		" sterna 3-6
25a	Hexagenia munda affiliata	" terga 3-6
b		" sterna 3-6
26a	Hexagenia munda munda	" terga 3-6
b		" sterna 3-6
27a	Hexagenia rigida	" terga 3-6
b		" sterna 3-6
28	Pentagenia vittigera	" terga 3-6



Redrawn from Smith (1941)

PLATE IV

Figure	Species	Character
29	*Potamanthus* sp.	Whole nymph
30	*Hexagenia limbata*	" "
31	*Ephoron album*	Nymph head and tusks
32	*Pentagenia vittigera*	" " " "
33	*Ephemera simulans*	" " " "
34	*Hexagenia atrocaudata*	" " " "
35	*Hexagenia bilineata*	" " " "
36	*Hexagenia munda*	" " " "

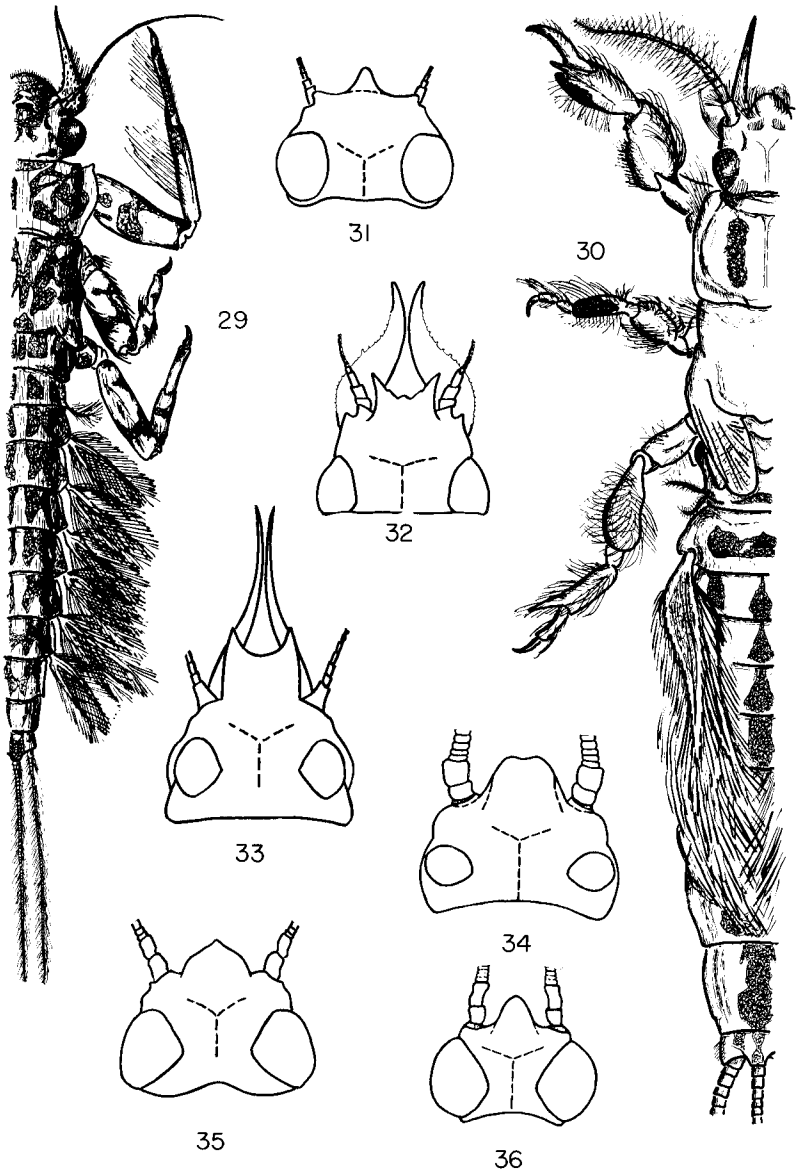

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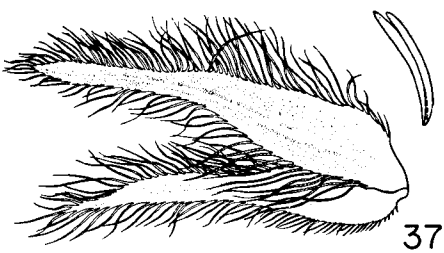
PLATE V

Figure	Species	Character
37	*Hexagenia limbata*	Nymph gills on 1-4
38	*Ephoron leukon*	" " " "
39	*Potamanthus myops*	" " " "
40	*Pentagenia vittigera*	" " " "
41	*Hexagenia bilineata*	Nymph mid-tarsal claw
42	*Hexagenia munda*	" " "
43	*Hexagenia rigida*	" " "



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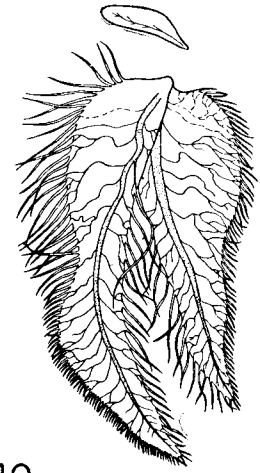

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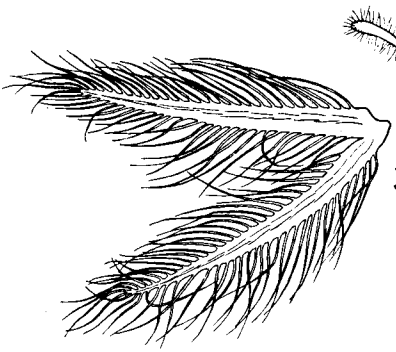

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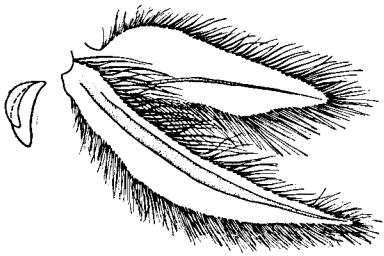

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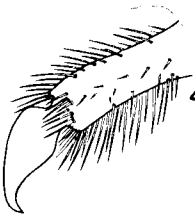

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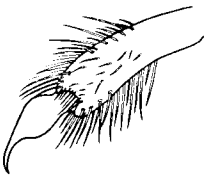

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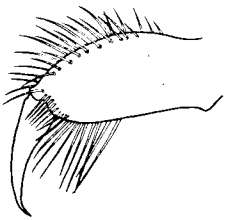

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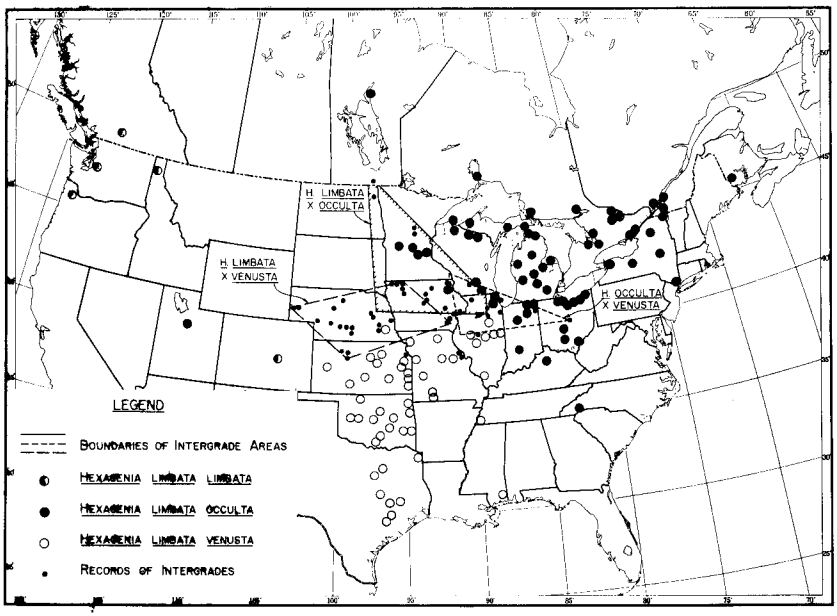

PLATE VI

Fig. 44. Hexagenia limbata. Distribution map of subspecies and apparent areas of intergradation.