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

E. W. Hamilton

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 Neopelmherera of Needham is placed in a new family, Neopelmhereridae. Neopelmhererids 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

Ephemerals 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 Cu1 and M2 in the basal area of the fore wing curve strongly away from the nearly straight veins M1 and R4+R5 (Figs. 3-8). In all other mayfly families (except Neopelmhereridae) Cu1, M2, M1, and R4+R5 of the fore wing are nearly straight or only moderately curved and but slightly divergent in the basal area (Figs. 1, 2). Veins R4 and R5

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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
2. Median caudal filament vestigial, much shorter than distance from segment 8 to base of filament ........................................ 8
3. Hind tibia longer than femur; wings normally with a variable pattern of dark spots (Figs. 6, 7) (Ephemerinae) .................. 3
4. Hind tibia shorter than femur; wings without dark spots or blotches ............................... 5
5. 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
6. Large dark blotches laterally on each abdominal terga; dark, oblong, submedian triangles on each sterna. .................. Ephemera simulans
7. Cubital intercalaries simple, four long; wing heavily cross-veined (Fig. 4) (Ephorinae) .............................. female Ephoron album
8. Cubital intercalaries one or two, long and deeply forked; wing less heavily veined (Fig. 5) (Potamanthinae) .............................. 6
9. 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 sternae (Fig. 23b). 13
Markings on abdominal sterne 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 sternae (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). 18
Abdominal terga 3-6 pale medially (Fig. 26a). Hexagenia munda affiliata
Abdominal terga 3-6 broadly dark-banded, usually with a lighter median triangular area (Fig. 21b); penes beak-like (Fig. 19). Hexagenia bilineata
Abdominal terga 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). 
Frontal process varying but not bifid. 

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 slightly emarginate (Fig. 34). Hexagenia atrocaudata
Frontal process apically rounded or angled. 

6. Mandibular tusks converging; frontal process conical (Fig. 31). Ephoron album
Mandibular tusks diverging; frontal process not as above. 

7. Frontal process rounded (Fig. 30). Hexagenia limbata
Frontal process conical or apically angled. 

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. 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 R₁ of the fore wing curving around the apical edge of fore wing; and fork R₄+R₅ of the fore wing longer than fork R₂+R₃ (Fig. 3).

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.


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 Ephorininae 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 Williamson, 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.


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 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 Wish."

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).


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 verticis, McDunnough, 1926, 186; Needham, Traver, and Hsu, 1935, 283; Bener, 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).


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).


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 decorata 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.


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

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
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, Louisana, Maryland, Minnesota, Mississippi, Missouri, New Mexico, Ohio, Oklahoma, Tennessee, Texas, and Virginia.


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 Hau, 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 hybrids: _H. l. limbata x occulta_ - Illinois, Manitoba; _H. l. limbata x venusta_ - Iowa, Kansas, Utah; _H. l. limbata x occulta x venusta_ - Illinois.


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 nympha 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. Millsap) - 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, 7-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, 7-VI-1927 (Leonora K. Gloyd) - 2♂♂ subimagos. MINNESOTA, Crow Wing Co., Nisswa, Pelican Lake, 12-VII-1912 (L. Bruner) - 8♂♂, 2♀♀, 3♂♂ subimagos. NORTH DAKOTA, Cass Co., Fargo, no other data - 4♂♂, 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.


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♀; Rocks 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♀♀ subimagos; Pike Co., Louisiana, 15-VI-1953 (W.R. Enns) - 2♂♂, 2♀♀ (all subimagos), Clarksville, 15-VI-1953, at light (W.R.
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.


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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REVIEW OF EPHEMERIDAE

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**PLATE VI**

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