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TWO NEW GENERA OF NEARCTIC HEPTAGENIIDAE (EPHEMEROPTERA)

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ABSTRACT

The Nearctic species of *Heptagenia* Walsh are herein divided into 3 genera: *Heptagenia*; *Leucrocuta* Flowers, n. gen.; and *Nixe* Flowers, n. gen. *Leucrocuta* corresponds to the *maculipennis* group of *Heptagenia* while *Nixe* corresponds to the *lucidipennis* and *simpliciodes* groups (all as originally discussed by Traver). The *lucidipennis* and *simpliciodes* groups represent subgenera of *Nixe* s.s. and *Akkarion* Flowers, n. subgen. Descriptions and keys to male imago and mature nymphs are provided.

Recent research has confirmed what has long been suspected by many mayfly workers: the widespread Northern Hemisphere genus *Heptagenia* Walsh is polyphyletic. Bogoescu and Tabacaru (1962) transferred a number of European species from *Heptagenia* to *Ecdyonurus*. Flowers (1980) showed that there are substantial morphological differences among the Nearctic species of *Heptagenia*. Careful study of imaginal, nymphal, and egg characters revealed that those species treated as the *maculipennis*, *lucidipennis*, and *simpliciodes* groups of *Heptagenia* by Traver (1933) have closer affinities to *Ecdyonurus* and its allied genera than to the remaining Nearctic *Heptagenia*, which were termed the *flavescens-pulla-elegantula* group by Traver (1933).

As treated herein, the 10 species of the *maculipennis* group represent 1 new genus and the 11 species of the *lucidipennis* and *simpliciodes* groups represent a second new genus with 2 distinct subgenera. *Heptagenia* (Fig. 1, 4, 7, 10, 13-14, 19, 22-24) in the Nearctic is now considered to include the following species: *H. adequata* McDunnough, *H. cruenta* Walsh, *H. diabasia* Burks, *H. dolosa* Traver, *H. elegantula* (Eaton), *H. flavescens* (Walsh), *H. julia* Traver, *H. marginalis* Banks, *H. patoka* Burks, *H. pulla* (Clemens), *H. solitaria* McDunnough and *H. townesi* Traver. All these species (the *flavescens-pulla-elegantula* group of Traver) show close affinities to *H.*

flavescens, the genotype of *Heptagenia*, and morphological studies indicate that this group is monophyletic.

Three species currently placed in *Heptagenia* (*H. bella* Allen, *H. kennedyi* McDunnough and *H. manifesta* (Eaton)) are not well enough known to permit reliable generic assignment. Until more is known, *H. bella* (known only from nymphs) and *H. manifesta* (known only from its early descriptions) are best left in *Heptagenia*. *Heptagenia kennedyi*, known only from imagos, is clearly not a *Heptagenia*. I have seen only male imagos of this last species, whose characters indicate a close relationship to *Nixe*; however, additional study will be necessary to confirm this and allow proper sub-generic placement.

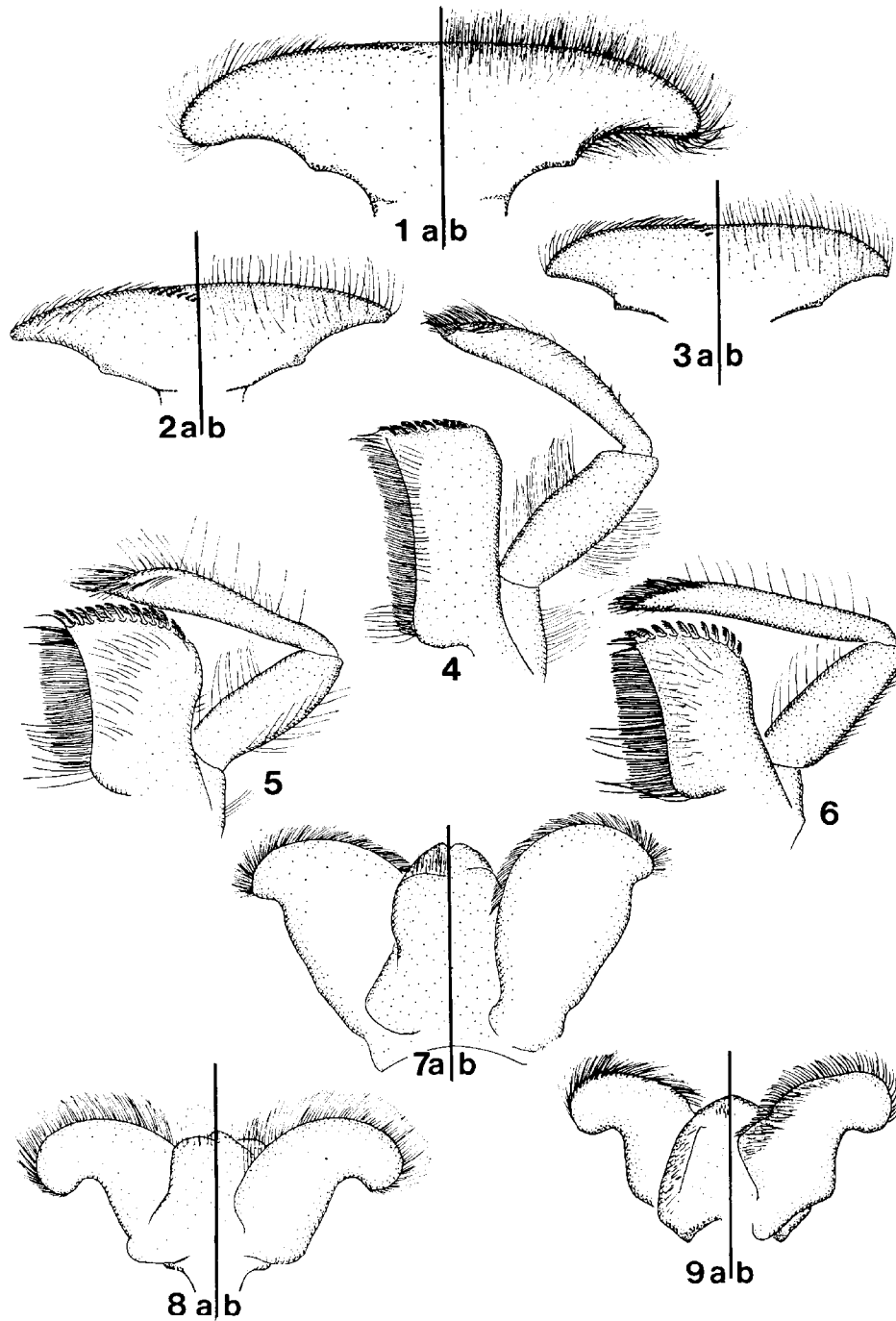
In the following descriptions, length measurements of imaginal and nymphal leg segments follow Jensen (1974). The forceps of these genera have 4 apparent segments, although the basal 2 may appear fused in some specimens. Terminology of egg characters is based on Koss and Edmunds (1974).

Leucrocuta Flowers, NEW GENUS

(Fig. 2, 5, 8, 11, 15-16, 20, 25-26, 30-31, 36a)

IMAGO: *Length of* ♂ : body, 4.5-8.2 mm; fore wings, 5.0-10.0 mm. *Length of* ♀ : body, 4.4-8.2 mm; fore wings, 5.8-9.0 mm. Eyes of ♂ moderate in size, separated dorsally by 4-5 times width of median ocellus (Fig. 20); eyes of ♀ separated dorsally by 6-7 times width of median ocellus. Frontal margin of head with shallow median emargination. Fore wings with basal costal cross veins well developed, stigmatic cross veins slightly slanted; costal and subcostal cross veins often with dark pigmentation. Hind wings with obtuse costal projection, 1 cubital intercalary; length 0.25-0.32 as long as fore wings. *Fore legs of* ♂ : tibiae (1.6-3.8 mm) 1.2-1.4 times length of femora; tarsi 1.6-1.9 times length of femora, 0.6-0.8 times length of tibiae; tarsal segments in order of descending length: 2, 3, 4, 1, 5 or 2, 3, 4, 5, 1; basal tarsal segment 0.17-0.31 times length of segment 2. Hind legs: tibiae (0.9-1.5 mm) 0.6-0.8 times length of femora; tarsi 0.3-0.5 times length of femora, 0.4-0.7 times length of tibiae; tarsal segments in order of descending length: 5, 1=2, 3, 4 or 5=1, 2, 3, 4 or 5=1=2, 3, 4; basal tarsal segment 1.0-1.3 times length of segment 2. Claws of all legs dissimilar; 1 blunt, pad-like, 1 hooked. *Male genitalia* (Fig. 25-26): posterior margin of subgenital plate evenly convex or concave; combined segments 3 and 4 of forceps $2/5$ - $2/3$ length of segment 2; penes slightly divergent, fused in basal $3/5$ - $2/3$; dorsolateral spines prominent (as in Fig. 24), discal spines present, median titillators smooth, slender. Ninth sternum of ♀ evenly convex or obtusely pointed. Cerci 2-2 $1/2$ times length of body.

MATURE NYMPH: *Length of body*, 4.2-6.2 mm. Head capsule $1\frac{1}{2}$ - $1\frac{2}{3}$ times as wide as long; anterior and lateral margins smoothly convex; posterior margin slightly concave. *Mouthparts* (Fig. 2, 5, 8, 11, 15-16): Labrum (Fig. 2) $1/2$ width of head capsule, greatest width about twice basal width, anterior margin straight; densely setaceous dorsally, a row of subapical spines ventrally. Mandibles (Fig. 15-16): outer incisor longer, serrate; prosthecae consisting of tuft of 3-5 long setae; apical margin between incisor and molar areas smooth, lateral margins setaceous. Maxillae (Fig. 5): galea-lacinia with 11-18 pectinate spines on crown, ventral setae scattered; palpi with



Mouthparts of mature nymph. Fig. 1-3, labrum (a- ventral; b- dorsal): 1, *Heptagenia flavescens*; 2, *Leucrocuta hebe*; 3, *Nixe (Nixe) lucidipennis*. Fig. 4-6, left maxilla, ventral: 4, *Heptagenia flavescens*; 5, *Leucrocuta hebe*; 6, *Nixe (Nixe) lucidipennis*. Fig. 7-9, hypopharynx (a- ventral; b- dorsal): 7, *Heptagenia flavescens*; 8, *Leucrocuta hebe*; 9, *Nixe (Nixe) lucidipennis*.

segments 2 and 3 fused, 1 1/2-2 times length of segment 1. Hypopharynx (Fig. 8) with lingua conical at apex, superlingua with lateral arms well developed. Labium (Fig. 11) with broad U-shaped separation of glossae; glossae oval, stalked; paraglossae laterally elongated; apical segment of palpi acutely pointed, subequal in length to basal segment. Pronotum widest at middle, strongly produced laterally, posterior margin with shallow median emargination. *Fore legs*: femora with small spines on anterior (leading) margin and dorsal surface, posterior margin with fringe of long setae; tibiae with row of setae on outer margin, small spines scattered on surface; tarsi with sparse setae; tibiae 0.8-1.0 times length of femora; tarsi 0.3-0.4 times length of femora and 0.3-0.4 times length of tibiae. *Middle and hind legs*: similar to fore legs in armature; hind legs with tibiae 0.7-0.8 times length of femora; tarsi 0.2-0.3 times length of femora and 0.3-0.4 times length of tibiae. Claws with 2-4 small subapical denticles. Gills with lamellae broad on abdominal segments 2-6, narrower on segments 1 and 7; fibrilliform portion of gills 1-5 well developed, reduced on gill 6 and absent on gill 7. Abdomen with posterolateral projections on segments 2-8. Caudal filaments with whorls of spines at articulations, intersegmental setae absent.

EGG: Elongate oval; chorion densely ornamented with small tubercles; knob-terminated coiled threads concentrated at poles or evenly distributed (Fig. 30-31).

ETYMOLOGY: Feminine; *Leucrocuta*, L., a fabulous beast (Pliny).

TYPE-SPECIES: *L. maculipennis* (Walsh), n. comb. (originally in *Heptagenia*).

SPECIES INCLUDED: *L. aphrodite* (McDunnough), n. comb.; *L. hebe* (McDunnough), n. comb.; *L. jewetti* (Allen), n. comb.; *L. juno* (McDunnough), n. comb.; *L. minerva* (McDunnough), n. comb.; *L. petersi* (Allen), n. comb.; *L. thetis* (Traver), n. comb.; *L. umbratica* (McDunnough), n. comb.; *L. walshi* (McDunnough), n. comb.

SPECIES EXAMINED: *L. aphrodite*, ♂ and ♀ imagos; *L. hebe*, ♂ and ♀ imagos, nymph; *L. juno*, ♂ and ♀ imagos; *L. thetis*, ♂ imago; *L. umbratica*, ♂ imago; *Leucrocuta* spp., numerous nymphs from southeastern United States.

DISCUSSION: *Leucrocuta* adults can be distinguished from *Heptagenia* and *Nixe* by the wide separation of the male eyes (Fig. 20) and the presence of discal and large dorsolateral spines on the penes (Fig. 25-26). Except for *L. umbratica*, all species have the costal and subcostal cross veins heavily margined with brown. Eggs of this genus are similar to those of *Heptagenia* (Flowers 1980). Nymphs of *Leucrocuta* differ from those of *Heptagenia* and *Nixe* by the absence of intersegmental setae on the caudal filaments.

Nixe Flowers, NEW GENUS

(Fig. 3, 6, 9, 12, 17-18, 21, 27-29, 32-35, 36b)

IMAGO: *Length of ♂*: body, 4.0-8.0 mm; fore wings, 5.8-8.5 mm. *Length of ♀*: body, 4.0-7.5 mm; fore wings 6.0-8.7 mm. Eyes of ♂ large, dorsally contiguous or separated by less than width of median ocellus; eyes of ♀ separated dorsally by 4-6 times width of median ocellus. Frontal margin of head with shallow median emargination. Fore wings with basal costal cross veins weak, stigmatic cross veins slightly slanted. Hind wings with obtuse costal projection; 1 cubital intercalary; length 0.28-0.37 as long as fore wing. *Fore legs of ♂*: tibiae (1.3-2.4 mm) 1.1-1.3 times length of femora; tarsi 1.2-1.7 times length of femora, 1.0-1.4 times length of tibiae; tarsal segments in order of

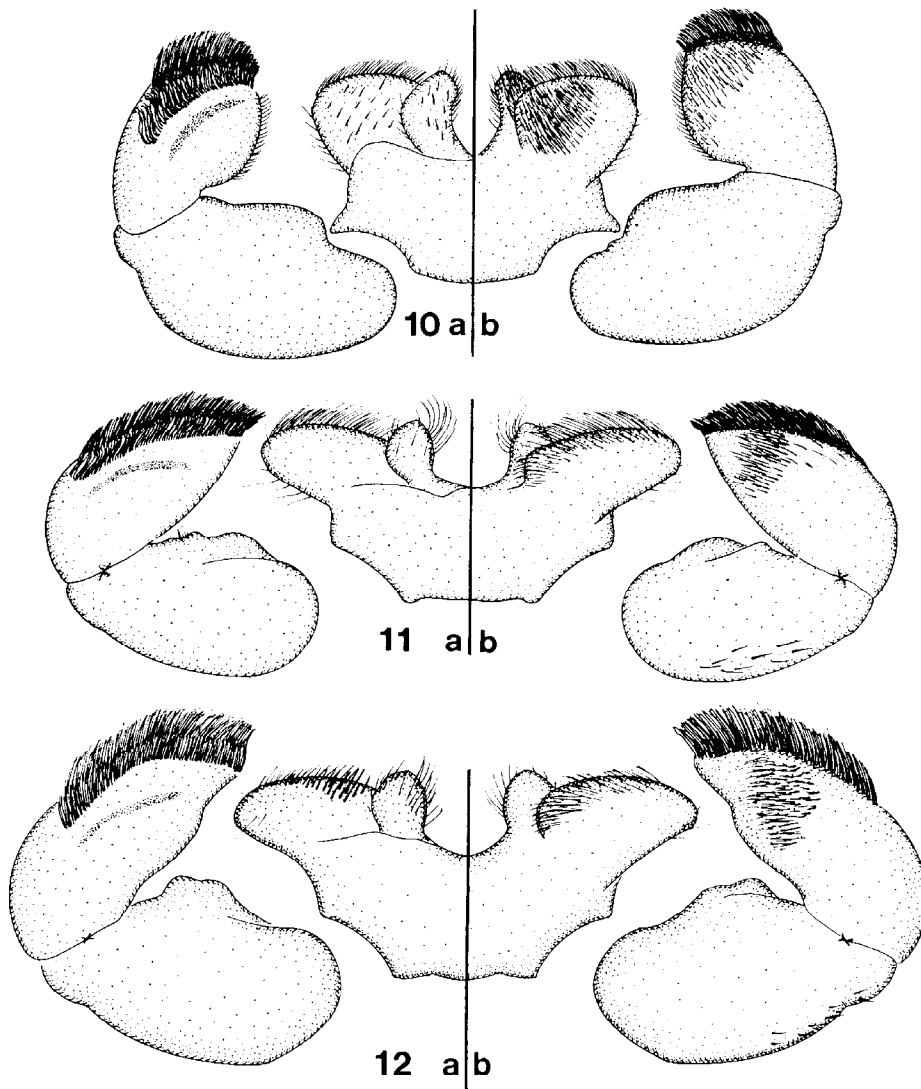


Fig. 10-12, labium of mature nymph (a- ventral; b- dorsal): 10, *Heptagenia flavescens*; 11, *Leucrocota hebe*; 12, *Nixe (Nixe) lucidipennis*.

descending length: 2, 3, 4, 1, 5 or 2, 3, 4, 5, 1 or 2=3, 4, 5, 1; basal tarsal segment 0.12-0.50 times length of segment 2. *Hind legs*: tibiae (1.0-1.8 mm) 0.7-0.8 times length of femora; tarsi 0.3-0.5 times length of femora, 0.4-0.7 times length of tibiae; tarsal segments in order of descending length: 5, 1, 2, 3, 4 or 5, 1=2, 3, 4 or 5=1, 2, 3, 4; basal tarsal segment 1.0-1.2 times length of segment 2. Claws of all legs dissimilar; 1 blunt, pad-like, 1 hooked. *Male genitalia* (Fig. 27-29): posterior margin of subgenital plate obtusely pointed or evenly convex; combined segments 3 and 4 of forceps subequal to length of segment 2; penes not or slightly divergent, fused in basal 4/5-9/10; dorsolateral spines minute, discal spines present or absent, median titillators slender, or swollen and spiculate at apex. Ninth sternum of ♀ evenly convex or obtusely pointed. Cerci $1\frac{1}{4}$ - $1\frac{3}{4}$ times length of body.

MATURE NYMPH: *Length of body*, 5.2-9.1 mm. Head capsule $1-1\frac{3}{4}$ times as

wide as long; anterior and lateral margins convex, posterior margin straight or slightly concave. *Mouthparts* (Fig. 3, 6, 9, 12, 17-18): Labrum (Fig. 3) 1/3 as wide as head capsule, greatest width 1 1/2-2 times basal width; anterior margin straight, densely setaceous dorsally, a row of strong subapical setae ventrally. Mandibles (Fig. 17-18) with incisors subequal in length, outer incisors serrate; prosthecae consisting of tuft of 3-5 long setae; apical margin between incisor and molar areas smooth; lateral margins setaceous. Maxillae (Fig. 6): galea-lacinia with 10-15 pectinate spines on crown, ventral setae scattered; palpi with combined segments 2 and 3 fused, 1 1/3-2 times length of segment 1. Hypopharynx (Fig. 9) with lingua conical at apex, superlingua with lateral arms well developed. Labium (Fig. 12) with broad U-shaped separation of glossae; glossae oval, stalked; paraglossae laterally elongated; apical segment of palpi acutely pointed, subequal in length to basal segment. Pronotum widest anterior to middle, not strongly produced laterally, posterior margin with shallow median emargination. *Fore legs*: femora with small spines on anterior (leading) margin and dorsal surface, posterior margin with fringe of long setae; tibiae with row of setae on outer margin and small spines scattered on surface; tarsi with sparse setae; tibiae 0.9-1.0 times length of femora; tarsi 0.3-0.5 times length of femora and 0.4-0.6 times length of tibiae. *Middle and hind legs*: similar to fore legs in armature; hind legs with tibiae 0.6-0.8 times length of femora; tarsi 0.2-0.4 times length of femora and 0.3-0.6 times length of tibiae. Claws with 2-4 small subapical denticles. Gills with lamellae broad on segments 2-6, narrower on segments 1 and 7; fibrilliform portion present on gills 1-5, present or absent on gill 6, absent on gill 7. Abdomen with posterolateral projections on segments 2-8. Caudal filaments with whorls of spines on articulations; intersegmental setae on both sides of terminal filament and mesal sides of cerci.

EGG: Oval to elongate oval; chorion ornamented with ridges or small tubercles; knob terminated coiled threads evenly distributed (Fig. 32-35).

ETYMOLOGY: Feminine; Nixe, Ger., a water sprite.

TYPE-SPECIES: *Nixe lucidipennis* (Clemens), n. comb. (originally in *Ecdyonurus*).

DISCUSSION: *Nixe* can be distinguished from *Leucrocota* and *Heptagenia* in the adult stage by the eyes of the male which meet or almost meet on the vertex (Fig. 21), penes which have small dorsolateral spines (Fig. 28-29), and the elongation of segments 3 and 4 of the forceps (Fig. 27). Nymphs of this genus differ from *Heptagenia* nymphs in lacking a fibrilliform portion on gill 7 and in the structures of the mouthparts, and from *Leucrocota* nymphs in having fine setae on the caudal filaments.

Nixe (*Nixe*) Flowers, NEW SUBGENUS
(Fig. 3, 6, 9, 12, 17-18, 21, 27-28, 32, 33)

IMAGO: *Length of ♂*: body, 4.0-6.6 mm; fore wings, 5.8-7.0 mm. *Length of ♀*: body, 4.0-6.7 mm; fore wings, 6.0-8.7 mm. Eyes of ♂ (Fig. 21) large, dorsally contiguous or separated by less than width of median ocellus. Hind wings 0.28-0.35 as long as fore wings. *Fore legs of ♂*: tibiae (1.3-2.0 mm) 1.2-1.3 times length of femora; tarsi 1.4-1.7 times length of femora, 1.1-1.4 times length of tibiae; basal tarsal segment 0.12-0.5 times as long as segment 2. *Hind legs*: tibiae (1.0-1.2 mm) 0.7-0.8 times as long as femora; tarsi 0.3-0.5

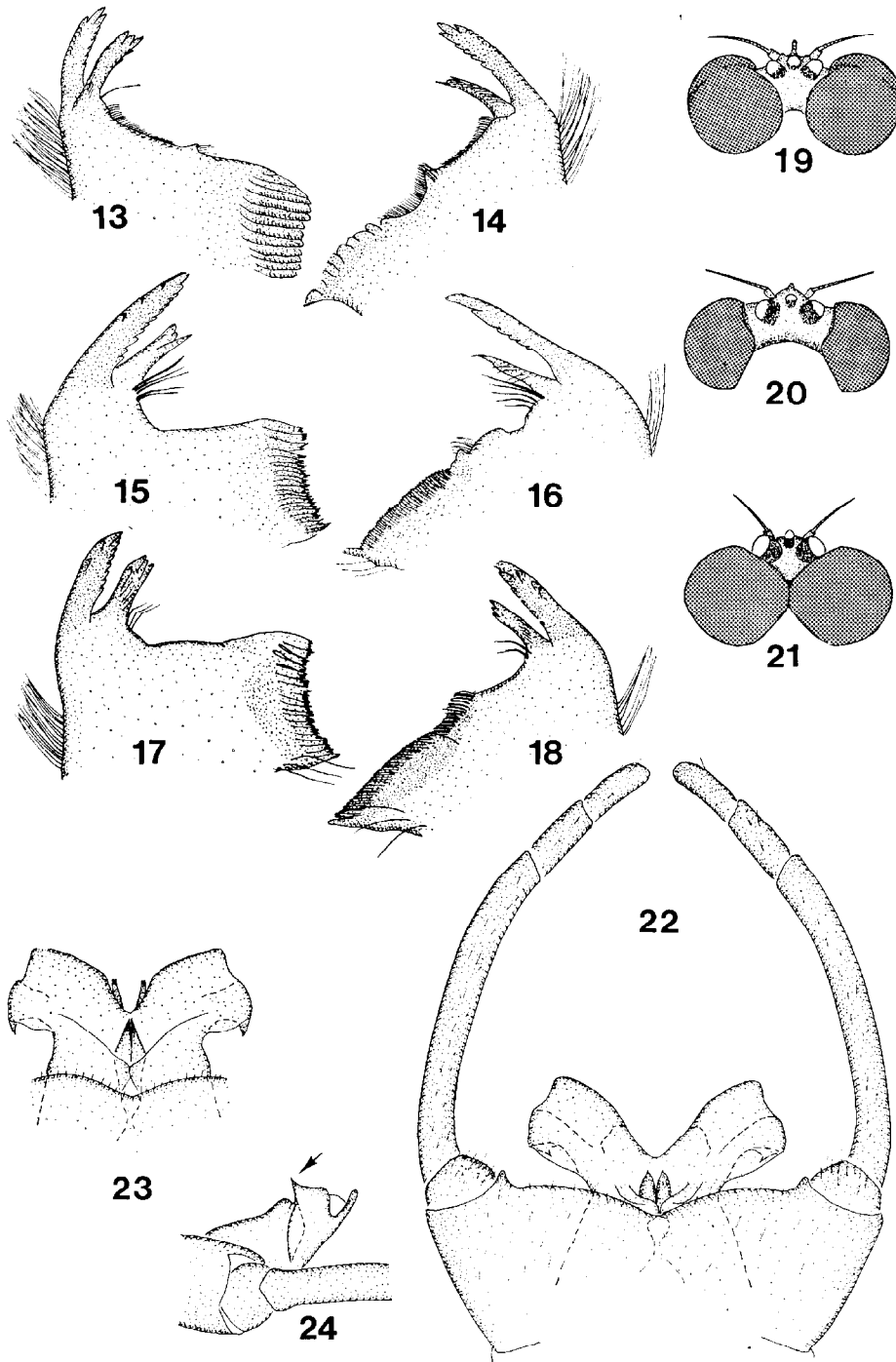


Fig. 13-18, apical half of mandibles (left and right) of mature nymph: 13-14, *Heptagenia flavescens*; 15-16, *Leucrocuta hebe*; 17-18, *Nixe (Nixe) lucidipennis*. Fig. 19-21, male imago. Fig. 19-21, head, dorsal view: 19, *Heptagenia flavescens*; 20, *Leucrocuta hebe*; 21, *Nixe (Nixe) lucidipennis*. Fig. 22-24, genitalia and detail of penes: 22, *Heptagenia flavescens*, ventral view; 23-24, *Heptagenia pulla* (23-ventral; 24-lateral).

times as long as femora, 0.4-0.7 times as long as tibiae. Basal tarsal segment 1.0-1.2 times as long as segment 2. *Male genitalia* (Fig. 27-28): penes with lobes not divergent and with median titillators swollen, spiculate at apex.

MATURE NYMPH: Length of body, 5.2-7.1 mm. Fibrilliform portion present on gills 1-5, absent on gills 6 and 7. Abdominal terga with extensive pale markings.

EGG: Chorion ornamented with mesh-like reticulate ridges (Fig. 32-33).

SPECIES INCLUDED: *N. (N.) horrida* (McDunnough), n. comb.; *N. (N.) inconspicua* (McDunnough), n. comb.; *N. (N.) lucidipennis* (Clemens), n. comb.; *N. (N.) perfida* (McDunnough), n. comb.; *N. (N.) rusticalis* (McDunnough), n. comb.; *N. (N.) spinosa* (Traver), n. comb.

SPECIES EXAMINED: *N. (N.) horrida*, ♂ imago; *N. (N.) inconspicua*, ♂ and ♀ imagos, nymph; *N. (N.) lucidipennis*, ♂ and ♀ imagos, nymph; *Nixe (N.)* spp., numerous ♂ and ♀ imagos and nymphs from eastern North America.

DISCUSSION: The subgenus *Nixe* s. s. is widely distributed from the Great Plains eastward. The eggs (Fig. 32-33) are very distinctive. Characters given above will distinguish other stages of *Nixe* s. s. from the subgenus *Akkarion*.

Nixe (Akkarion) Flowers, NEW SUBGENUS
(Fig. 29, 34-35)

IMAGO: Length of ♂: body, 6.4-8.0 mm; fore wings, 7.0-8.5 mm. Length of ♀: body, 7.0-7.5 mm; fore wings, 8.3 mm. Eyes of ♂ large, dorsally contiguous. Hind wings 0.31-0.37 as long as fore wings. *Fore legs of ♂*: tibiae (1.6-2.4 mm) 1.1-1.3 times length of femora; tarsi 1.2-1.4 times length of femora, 1.0-1.2 times length of tibiae; basal tarsal segment 0.25-0.38 times length of segment 2. *Hind legs*: tibiae (1.4-1.8 mm) 0.7-0.8 times length of femora; tarsi 0.3-0.4 times length of femora, 0.4-0.6 times length of tibiae; basal tarsal segment 1.2 times as long as segment 2. *Male genitalia* (Fig. 29): penes slightly divergent apically, median titillators slender, smooth.

MATURE NYMPH: Length of body, 6.5-9.1 mm. Fibrilliform portion present on gills 1-6, absent on gill 7. Abdominal terga with pale markings restricted. EGG: Chorion ornamented with irregular ridges (Fig. 34) or dense tubercles (Fig. 35).

ETYMOLOGY: Neuter; akko, Gr., meaning a bugbear; arion, Gr., diminutive. TYPE-SPECIES: *N. (A.) simpliciodes* (McDunnough), n. comb. (originally in *Heptagenia*).

SPECIES INCLUDED: *N. (A.) criddlei* (McDunnough), n. comb.; *N. (A.) otiosa* (McDunnough), n. comb.; *N. (A.) rodocki* (Traver), n. comb.; *N. (A.) rosea* (Traver), n. comb.; *N. (A.) salvini* (Kimmins), n. comb.

SPECIES EXAMINED: *N. (A.) criddlei*, ♂ and ♀ imagos, nymph; *N. (A.) rosea*, ♂ imago; *N. (A.) simpliciodes*, ♂ and ♀ imagos, nymphs.

DISCUSSION: The subgenus *Akkarion* is known to occur in the western United States and northern Mexico. The above characters will distinguish it from the subgenus *Nixe* s.s.

These new taxa will key to *Heptagenia* in Edmunds, Jensen and Berner (1976), Needham, Traver and Hsu (1935), Burks (1953) and Flowers and Hilsenhoff (1975). The following key should be used as a supplement to the above keys to separate the new taxa from *Heptagenia*.

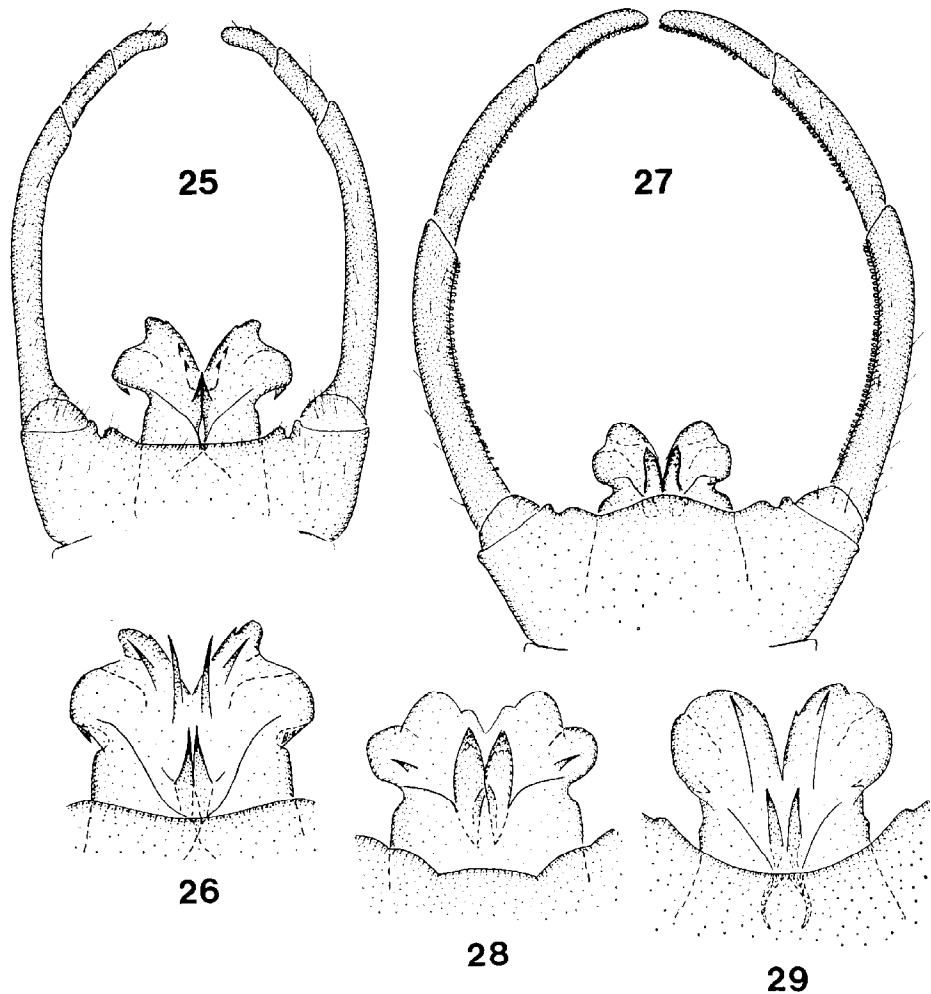


Fig. 25-29, ventral view of genitalia (or penes) of male imago: 25, *Leucrocuta thetis*; 26, *L. hebe*; 27, *Nixe (Nixe) rusticalis*; 28, *N. (N.) horrida*; 29, *N. (Akkarion) simpliciodes*.

Male Imagos

1. Penes with large dorsolateral spines (Fig. 24) and lacking discal spines (Fig. 22-23); hind tarsi usually with segment 1 shorter than segment 2; if subequal, then segment 1 of middle tarsi shorter than segment 2 *Heptagenia*.
- 1'. Penes with large or small dorsolateral spines; if large, discal spines also present (Fig. 25-29); middle and hind tarsi with segment 1 subequal to segment 2 2.
2. Eyes of ♂ separated by 3-5 times width of median ocellus (Fig. 20); penes with dorsolateral spines large (as in Fig. 24), discal spines present (Fig. 25-26); basal costal cross veins well developed *Leucrocuta*, n. gen.
- 2'. Eyes of ♂ separated by less than width of median ocellus or meeting on vertex (Fig. 21); penes with dorsolateral spines

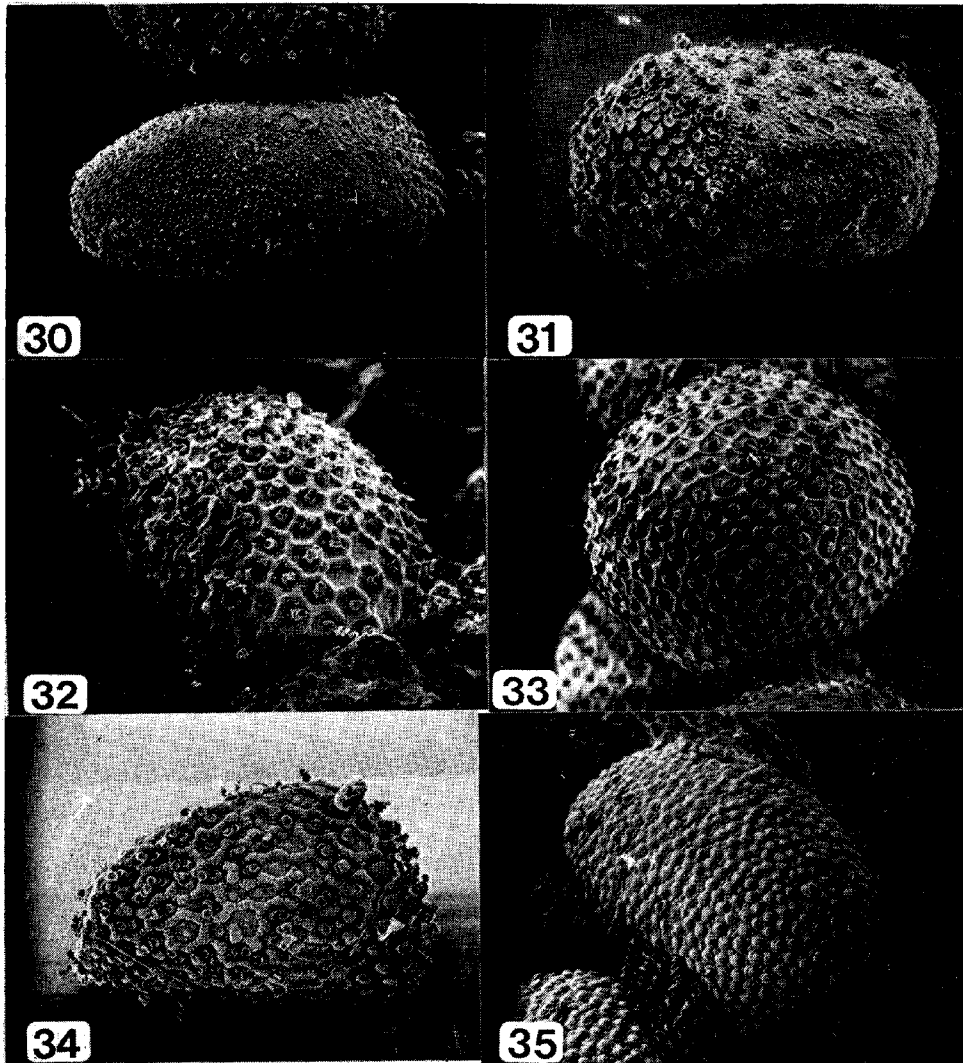


Fig. 30-35, eggs: 30, *Leucrocuta juno* (525X); 31, *L. aphrodite* (550X); 32, *Nixe (Nixe) inconspicua* (475X); 33, *N. (Nixe) sp* (450X); 34, *N. (Akkarion) simpliciodes* (455X); 35, *N. (A.) criddlei* (435X).

- minute, discal spines present or absent (Fig. 27-29); basal costal cross veins weak *Nixe*, n. gen. 3.
- 3. Penis lobes not divergent, median titillators large, thick and spiculate at apex (Fig. 27-28) *Nixe*, n. subgen.
- 3'. Penis lobes divergent, median titillators slender, smooth at apex (Fig. 29) *Akkarion*, n. subgen.

MATURE NYMPHS

- 1. Abdominal gill 7 with fibrilliform portion; tarsal claws lacking pectines; maxillae with submedian row of ventral setae on galealacinia (Fig. 4) *Heptagenia*.
- 1'. Abdominal gill 7 lacking fibrilliform portion; tarsal claws

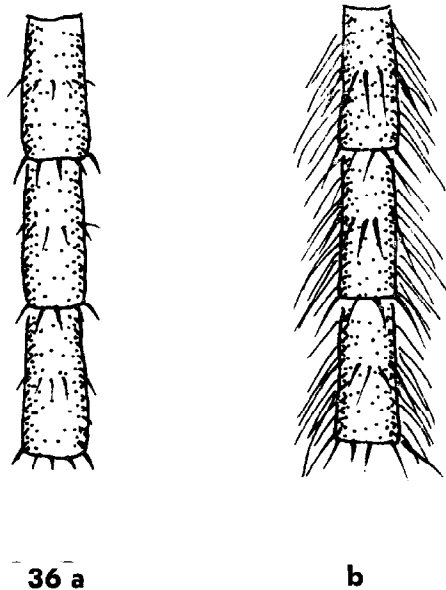


Fig. 36, Terminal filament of nymph: a, *Leucrocota hebe*; b, *Nixe* (*N.*) sp.

- pectinate; maxillae with ventral setae of galea-lacinia scattered (Fig. 5-6) 2
2. Caudal filaments with whorls of spines at articulations (Fig. 36a), intersegmental setae absent; eyes of ♂ nymphs separated by 3 times width of median ocellus *Leucrocota*, n. gen.
- 2'. Caudal filaments with intersegmental setae in addition to whorls of spines (Fig. 36b); eyes of ♂ nymphs separated by width of median ocellus *Nixe*, n. gen. 3.
3. Gill 6 lacking fibrilliform portion; pale markings on dorsum extensive; eastern and midwestern species *Nixe*, n. subgen.
- 3'. Gill 6 with fibrilliform portion; pale markings on dorsum restricted; western species *Akkarion*, n. subgen.

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MICROMORPHOLOGY OF BEETLE ELYTRA,
USING SIMPLE REPLICAS

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ABSTRACT

One of the simplest techniques in biology, an instant replica, utilized cellulose acetobutyratfolie and yielded transparent impressions that were examined directly and photographed by light microscopy. The resulting photographs were comparable to those of the scanning electron microscope at that magnification. Elytra of hundreds of species, belonging to various families of Coleoptera were examined. The microsculpture was somewhat different in almost every species possessing it. Taxonomists can routinely utilize this very simple method for a better understanding of the interrelationships between various taxa.

The stereoscope has been used routinely by entomologists for identification and classification. Coleopterists have used it to study the surface sculpture of beetles, especially that of elytra. Punctures, striae, sulci, setae, scales, etc., have been constantly compared in various taxa. However, there are finer micromorphological details that can be seen and utilized when resolution beyond that of the stereoscope is used.

Balfour-Browne (1940) attempted to study the surface sculpturing of the elytra of beetles. His method was the classical biological technique, including softening by boiling in caustic soda or potash, bleaching, dehydrating, clearing, and mounting in balsam. Balfour-Browne studied the sculpture only of the water beetles that belong to the suborder Adephaga. However,

