

Contribution to the Systematics of *Leucrocuta*, *Nixe*, and Related Genera (Ephemeroptera: Heptageniidae)

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ABSTRACT

Taxa that are comparatively treated belong to basal clades within a monophyletic subset of genera of Heptageniidae having, for example, an apically adenticulate outer incisor and scattered setae ventrally on the galealacinia. The genus *Ecdyonurus* Eaton is restricted and a distinct Holarctic subgroup within it (the *simplicioides* species group) is defined and shown to be equivalent to previous concepts of *Afghanurus* Demoulin, *Paracinygmula* Bajkova, and *Akkarion* Flowers. The Nearctic genus *Leucrocuta* Flowers is detailed. The Holarctic genus *Nixe* Flowers is restricted (as the prior subgenus *Nixe* s.s.) and detailed. The Palearctic genus *Siberionurus*, n. gen., is described and shown to be a sister genus to *Leucrocuta*. New combinations for strictly Western Hemisphere species include *Ecdyonurus bellus* (Allen and Cohen), n. comb., which is also shown to be the first species of this broader subset of genera to be found in the Neotropics, *E. criddlei* (McDunnough), n. comb., and *Nixe kennedyi* (McDunnough), n. comb. The only Holarctic species recombined is *E. simplicioides* (McDunnough), recomb. Strictly Asian species recombined include *E. klugei* Braasch, recomb., *E. rubrofasciatus* Brodsky, recomb., *N. subspinosa* Braasch and Soldán, recomb.; and new combinations include *Siberionurus asperus* (Kluge), n. comb., and *S. inversus* (Kluge), n. comb.

The genera *Ecdyonurus* Eaton, *Leucrocuta* Flowers, and *Nixe* Flowers and at least seven others share numerous characteristics, such as an apomorphic apically adenticulate outer mandibular incisor, that define them as a major subgroup within Heptageniidae. In addition in this subgroup, the ventral surface of the galealacinia retains some scattered setae and in the adults, the medial depression of the mesothoracic furcasternum is parallel sided. *Heptagenia* Walsh, where all North American species of the group once resided, is not a member of this group. Other taxa that do belong to this group include for example, *Afronurus* Lestage, *Asionurus* Braasch and Soldán, *Atopopus* Eaton, *Electrogena* Zurwerra and Tomka, *Notacanthurus* Tshernova, and *Thalerosphyrus* Eaton. Kluge (1988) essentially considered all of the lineages making up this group to belong to the genus *Ecdyonurus*; however, that highly conservative classification has not been generally followed by mayfly workers.

Within this natural group of genera, *Leucrocuta* and a distinctive new sister genus described below constitute a basal clade. *Nixe* and the complex genus *Ecdyonurus* belong to another even more basic clade. Details of the phylogeny, higher classification, and keys for these and all other Heptageniidae are being taken up elsewhere by McCafferty, T.-Q. Wang and J. M. Webb. The main purpose of the current paper is to establish the generic integrity and known composition of those genera that impact the North American fauna.

SYSTEMATICS

ECDYONURUS (SIMPLICIOIDES SPECIES GROUP)

Background and Diagnosis

Afghanurus Demoulin (type: *A. vicinus* Demoulin) was originally established by Demoulin (1964) for two Palearctic species known only as adults. Kluge (1980) redescribed what he identified as the adult of *A. vicinus*, described the larva of that species, recombined the species with *Ecdyonurus* (type: *Ephemera venosa* Fabricius), and thus placed *Afghanurus* as a synonym of a conceptually very broad *Ecdyonurus*. *Ecdyonurus* (including both Demoulin's and Kluge's concepts of *Afghanurus*), however, can be distinguished phylogenetically in a much stricter sense as a separate lineage among those in its subgroup of genera in having highly reduced or no dorsolateral spine on the penes lobes and lacking well-developed whorls of spines on the larval caudal filaments. Within this subgroup, *Ecdyonurus* is distinguished by having well-developed dorsal sclerotization of the penes that includes an extensive, medially expanded lateral sclerite on the dorsum of each penes lobe (e.g., Fig. 98 [Traver 1935], Fig. 4g [Demoulin 1964], Figs. 103, 106 [Jensen 1966]).

Bajkova (1975) described the Palearctic genus *Paracinygmula* Bajkova (type: *P. zhiltzovae* Bajkova). Shortly thereafter, Tshernova (1978), indicating that the type of *Paracinygmula* was not related to *Cinygmula* McDunnough, placed it in synonymy with *Ecdyonurus*. Because the name *E. zhiltzovae* was preoccupied, the species was renamed *E. bajkovae* Kluge in Tshernova et al. (1986). *Paracinygmula* is characteristic of the restricted concept of *Ecdyonurus* given above and thus its synonymy is here recognized.

Flowers (1980) divided his genus *Nixe* (type: *Ecdyonurus lucidipennis* Clemens) into two subgenera, *Nixe* s.s. and *Akkarion* Flowers (type: *Heptagenia simplicioides* McDunnough). *Akkarion* is also equivalent to *Ecdyonurus* as restricted above and therefore that part of a previous synonymy of *Nixe* with *Ecdyonurus* (Tshernova et al. 1986) is recognized. *Nixe* s.s., however, is phylogenetically separable from the restricted *Ecdyonurus* (see below), and therefore that part of the synonymy is not recognized.

Within this restricted concept of *Ecdyonurus*, two primary sub-groupings can be easily differentiated. These include a *simplicioides* species group equivalent to the concept of *Afghanurus* (= *Paracinygmula*, = *Akkarion*), and *Ecdyonurus* s.s. Differences in these particular groups include, for the most part, highly specialized apomorphies in *Ecdyonurus* s.s., such as a uniquely developed posteriorly produced lateral aspect of the pronotum in the larvae (e.g., Figs. 196-210 [Bauernfeind and Humpesch 2001]), and in the adult highly distinctive penes lobes each with a prominent apical sclerite dorsally that continues basally along the median margin of each lobe (e.g., Figs. 474-483, 489-495 [Bauernfeind and Humpesch 2001]). (This concept of *Ecdyonurus* s.s. has been further divided into informal species groups, particularly in Europe [see e.g., Bauernfeind and Humpesch 2001].) Although *Ecdyonurus* s.s. demonstrates apomorphies defining it as monophyletic, no consistent apomorphy for the relatively plesiomorphic *simplicioides* species group has yet been found. Thus, although the latter group is phenetically distinct, it is not relegated to subgeneric status (potentially as subge-

nus *Afghanurus*) at this time because of the possibility of it being paraphyletic and because of the idealistic goal of keeping within a strictly phylogenetic higher classification for the Ephemeroptera (McCafferty 1991), when possible.

For the purposes of recognizing *Ecdyonurus* in North America, i.e., the *simplicioides* species group of *Ecdyonurus*, especially from the closely related genera *Leucrocuta* and *Nixe*, it may be diagnosed as having generally plesiotypic larvae with well-developed male eyes, an unmodified pronotum, a gill tuft with two or more filaments present at base of gill lamella 6 (usually well-developed), and the three caudal filaments with well-developed interfacing setae; and in the adults, as having proximate male eyes, in addition to having penes (e.g., Fig. 98 [Traver 1935], Fig. 4g [Demoulin 1964], Figs. 103, 106 [Jensen 1966]) with divergent lobes that have spines present ventrally, a medially extended lateral sclerite dorsally, narrowly attenuate titillators, and that lack developed dorsolateral spines. (For additional larval characterization to consistently diagnose *Ecdyonurus* from *Nixe* in North America, see comments under *Nixe*, below.)

The absence of a pronotum with posteriorly distended lateral aspects in the larvae, and absence of dorsal apical sclerites of the penes lobes that extend along the medial margin of the lobes, clearly distinguish the *simplicioides* species group from other *Ecdyonurus* in the Eastern Hemisphere.

Composition

In the Western Hemisphere, *Ecdyonurus* remains unknown from Eastern North America and South America. It can now, however, be shown to occur in the northern extremes of the Neotropical region (extreme southern Mexico and Guatemala) (see Material Examined, below) so that in the Western Hemisphere it extends from Alaska to Central America. In the Eastern Hemisphere, the *simplicioides* species group is known essentially from Asia. Species include *E. bajkova* (Korea and Russia); *E. bellus* (Allen and Cohen), n. comb. (Mexico and Central America); *E. criddlei* (McDunnough), n. comb. (western Canada, western USA and northern Mexico); *E. flavus* Takahashi (Japan); *E. kibuensis* Imanishi (Asia); *E. klugei* Braasch, recombination (Mongolia); *E. rubrofasciatus* Brodsky, recombination (Uzbekistan); *E. simplicioides* (McDunnough), recombination (Holarctic, in North America: Alaska, western Canada and western USA); *E. tigris* Imanishi (Japan); and *E. vicinus* (Afghanistan, ?Russia).

Flowers (1980) had not been able to place *Heptagenia bella* to any genus; however, it was informally considered in *Nixe* by McCafferty et al. (1992) and later newly combined with *Nixe* by Edmunds and Murvosh (1995). The species, however, had not been placed to subgenus. Although unknown as an adult, the restudy of newly acquired larvae of this species (see material examined, below) shows that it belongs to the *simplicioides* species group of *Ecdyonurus*.

Flowers (1986) synonymized the Palearctic species *Ecdyonurus werestschagimi* Tshernova (also known as *Rhithrogena imanica* Bajkova) under *E. simplicioides* [as *Nixe* (Akkarion)]. In addition, a number of recent specific synonymies involving *E. simplicioides* and *E. criddlei* (again as *Nixe*) in North America were given by McCafferty (2001) and Jacobus and McCafferty (2002). Based on available descriptions and figures (e.g., Imanishi 1936), the Asian *E. flavus*, *E. kibuensis*, *E. klugei*, *E. rubrofasciatus*, and *E. tigris* all appear to fit the concept of *simplicioides* species group, but are subject to further review.

Additional Eastern Hemisphere *Ecdyonurus* species may eventually be shown to belong to this species group, especially when workers in Asia are able to make stage associations and restudy local populations.

LEUCROCUTA Flowers

Background and Diagnosis

Flowers (1980) established the genus *Leucrocuta* (type: *Heptagenia maculipennis* Walsh) for the North American species that had been known as the *Heptagenia maculipennis* species group of *Heptagenia* (e.g., see Burks 1953). *Leucrocuta* was considered a synonym of *Ecdyonurus* by Tshernova et al. (1986); however, it constitutes a distinct, separable monophyletic group of species.

The male adults of *Leucrocuta* have relatively well-separated compound eyes (e.g., see Fig. 20 [Flowers 1980]) and have penes lobes with highly developed posterolateral spines together with apicomarginal discal spines and variously developed dorsal spines in combination with well-developed medioapical lobules or extensions (e.g., Figs. 374-380 [Burks 1953]). Dorsal sclerotization is not developed on the penes as in *Ecdyonurus* and *Nixe*. In addition to these distinctive features, the larvae have caudal filaments with reduced lateral setae, unlike those of *Ecdyonurus* and *Nixe*. Although such reduction of lateral setae on the caudal filaments is not unique to *Leucrocuta*, it does aid in distinguishing the larvae of this genus from other North American Heptageniidae larvae that are three tailed and lack the tuft on gill lamellae 7. The fact that segment 3 in relation to segments 2 and 4 of the male genital forceps of *Leucrocuta* is not elongate compared to the relatively long forceps segment 3 of *Nixe*, for example, is another diagnostic feature of some value.

The relatively broad head of the larvae compared to the pronotum in *Leucrocuta* is consistent but can be found in certain species of related genera in North America. Also, the presence of developed gill tufts on lamella 6 in the larvae is also consistent, but alone cannot always be used to distinguish *Leucrocuta* from certain species of *Nixe* (see comments under *Nixe*, below). Other features associated with *Leucrocuta*, including egg characteristics, may be found in Flowers (1980).

Composition

Leucrocuta is apparently confined to the Nearctic region and currently consists of the following species, some of which are questionably valid: *L. aphrodite* (McDunnough) (eastern Canada and eastern USA), *L. hebe* (McDunnough) (far northern Canada and eastern Canada and eastern USA), *L. jewetti* (Allen) (northwestern USA and central Canada), *L. juno* (McDunnough) (eastern Canada and eastern USA), *L. maculipennis* (Walsh) (throughout USA and far northern and eastern Canada), *L. minerva* (McDunnough) (eastern Canada and eastern USA), *L. petersi* (Allen) (western USA), *L. thetis* (Traver) (eastern USA), *L. umbratica* (McDunnough) (eastern Canada and USA), and *L. walshi* (McDunnough) (eastern Canada and northeastern USA).

NIXE Flowers

Background and Diagnosis

Nixe (type: *Ecdyurus lucidipennis* Clemens) was established by Flowers (1980) for several distinctive species of North American Heptageniidae that had been known as the *Heptagenia lucidipennis* and *simplicioides* species groups (e.g. see Traver 1935, Burks 1953). Because the *simplicioides* group was given subgeneric status as *Akkarion* by Flowers (1980) and that group is herein shown to be encompassed by the genus *Ecdyonurus* (see above), only the *lucidipennis* species group applies to the newly restricted concept of *Nixe*. This is a highly distinct, separable monophyletic genus, which nonetheless was synonymized under a very broad concept of *Ecdyonurus* by Tshernova et al. (1986).

Nixe can be distinguished from its sister genus *Ecdyonurus* by numerous characteristics, including a poor development of dorsal penes sclerites that when evident are confined to marginal areas of the penes lobes (see e.g., Figs. 370,371,373 [Burks 1953]), and in the larvae of most species, by the absence or reduction to a single filament of the gill tuft associated with lamellae 6. The latter characteristic, however, has proven to be unstable (Flowers 1986) (as has the presence or absence of gill tuft on lamellae 7 in some other genera). In North America, the still undescribed larvae of *N. rusticalis* (McDunnough) have been found to have developed tufts on lamella 6 (J. Webb, pers. comm.). I have also found developed tufts on lamella 6 in *N. perfida* (McDunnough). In these instances, and as is the case for all other known North American *Nixe* larvae, they may be distinguished from North American *Ecdyonurus* larvae by their well-developed patterning on most abdominal terga, and their distinct pair of pale, narrowly separated (clearly within the antennal base separation) but discontinuous spots anteriorly on the head capsule (see e.g., Fig. 385 [Burks 1953], Figs. 1, 3 [McCafferty 1977]). This latter larval character is of particular use for *Nixe* with developed tufts on lamella 6, and in regions where *Nixe* and *Ecdyonurus* are known to overlap geographically, i.e., in central Canada (J. Webb, pers. comm.). In North America, *Nixe* is further distinguished from *Ecdyonurus* (*simplicioides* species group) by non-attenuated, somewhat spindle shaped titillators of the penes, which also tend to be spiculate apically. The larvae of *Nixe* have caudal filaments with well-developed interfacing lateral setae, which distinguish them from *Leucrocuta* in North America and a new genus from Asia closely related to *Leucrocuta* (see below). Male adults (and mature male larvae) have well developed proximate eyes and have forceps with a relatively elongated segment 3 compared to segments 2 and 4, thus differing from those of *Leucrocuta*. The penes tend to be compact; lobes are not divergent as in many other genera, and they do not have well-developed posterolateral spines as do *Leucrocuta* and the new genus described below. A distally extended apical lobule of the penes lobes is generally not developed in *Nixe*, but when it is (Fig. 372 [Burks 1953]), the penes are otherwise considerably different than that typical of the plesiomorphic penes of *Leucrocuta* and the new genus described below. Additional characterization, including egg characteristics, may be found in Flowers (1980) under *Nixe* s.s. In particular, *Nixe* eggs have a chorion with meshlike reticulate ridging, and are not tuberculate as is typical of closely related North American genera.

Edmunds and Waltz (1996) in their larval key to North American mayfly

genera used "head width less than that of pronotum" and "absence of anterior spotting on the head capsule" in *Nixe* to distinguish *Nixe* from *Leucrocuta*. These features are inconsistent among North American species, and they can even be inconsistent within some species. The head capsule of some species, e.g., *N. flowersi* McCafferty and *N. inconspicua* (McDunnough), can be broader than the pronotum, and at least *N. inconspicua* has spotting typical of *Leucrocuta* (e.g., see Figs. 1,3 [McCafferty 1977]).

Composition

Nixe is Holarctic and consists of the following species: *N. flowersi* (midwestern and southeastern USA), *N. horrida* (McDunnough) (eastern Canada and northeastern USA), *N. inconspicua* (Canada and eastern USA), *N. joernensis* (Bengtsson) (Palearctic), *N. kennedyi* (McDunnough), n. comb. (northwestern USA), *N. lucidipennis* (Canada and northeastern USA), *N. littorosus* Kang and Yang (Taiwan), *N. mitificus* Kang and Yang (Taiwan), *N. obscurus* Kang and Yang (Taiwan), *N. perfida* (eastern Canada and eastern USA), *N. rusticalis* (eastern Canada and eastern USA), *N. spinosa* (Traver) (southeastern USA), and *N. subspinosa* Braasch and Soldán (Korea), recombination.

Flowers (1980) had not been able to place *Heptagenia kennedyi* to any genus; however, it began to be listed provisionally, with no formal new combination, as *Nixe* beginning with McCafferty (1996). A restudy of this species, known only as adults (see material examined, below), shows that it indeed belongs to *Nixe* as restricted here.

Flowers (1986) first showed that the Palearctic species *Ecdyonurus joernensis* (also known as *E. flavomaculatus* Aro, *H. mongolica* Bajkova and Varychanova or *E. mongolicus*, and *H. dentata* Braasch) belonged to *Nixe* s.s. This same new combination was also recognized, evidently independently, by Braasch and Soldán (1988).

SIBERIONURUS new genus

Description.—*Larva*. Head capsule (Figs. 52,65 [Kluge 1980]) slightly narrower to subequal in width to pronotum. Eyes of male well developed, with little separation. Maxillae (Fig. 58 [Kluge 1980]) with galealaciniae with scattered setae ventrally; palps with setae medially near base of segment 1. Pronotum (Figs. 52,56 [Kluge 1980]) not developed posteriorly in lateral aspects. Meso- and metathorax not produced into acute or subacute processes above bases of coxae. Forefemora (Figs. 52,56 [Kluge 1980]) only slightly broadened. Claws (Fig. 52 [Kluge 1980]) with single basal denticle. Gill lamellae (Figs. 52,56 [Kluge 1980]) bluntly pointed; lamellae 1 well developed; lamellae 6 with tuft basally; lamellae 7 not strongly narrow-elongate and without tuft. Median caudal filament well developed; cerci and median caudal filament (Figs. 52,56 [Kluge 1980]) lacking lateral interfacing setae.

Adult. Compound eyes of male not separated more than width of median ocellus. Genital forceps (Fig. 71 [Kluge 1980]) with segment 3 not much different in length than that of segment 4. Penes lobes (Figs. 63,64,71,73 [Kluge 1980]) each with apically extended lobule, well-developed dorsal, ventral, and dorsolateral spines, attenuate titillators, and without well developed sclerites dorsally.

Diagnosis.—*Siberionurus* appears to be a closely related sister genus to *Leucrocuta*, retaining fundamentally similar penes (with developed posterolateral and medioapical extensions and lacking evident sclerotization), and sharing the loss of developed lateral setae on the larval caudal filaments. These characteristics easily distinguish *Siberionurus* from *Ecdyonurus* and *Nixe* in Asia (see also diagnoses given above). Lateral caudal filament setae are lacking in some other related Old World genera, but are apparently derived independently, with these latter genera otherwise much more apotypic in adult and larval characterization. *Siberionurus* is distinguished from *Leucrocuta* in the male adults by the proximate eyes that are typical of other related genera but not *Leucrocuta*. The eye character will also apply to mature male larvae, and whereas *Leucrocuta* larvae tend to have a head capsule noticeably broader than the pronotum, this is not the case in *Siberionurus*.

Composition.—Species of *Siberionurus* currently include *S. asperus*, n. comb. (the here designated type species of the genus), and *S. inversus* (Kluge), n. comb. These two species were described as *Ecdyonurus* from the Taymyr Peninsula of Siberia by Kluge (1980). *Siberionurus aspersus* was later reported from Mongolia by Braasch (1986), and according to J. Morse (pers. comm.) both species have also recently been taken in the Selenge River Drainage of Mongolia.

Material examined.—All materials listed are deposited in the Purdue Entomological Research Collection, West Lafayette, Indiana.

E. bellus, all larvae: GUATEMALA, Sololá Panajachel, 1550 m, VII-21-1962, GG Musser; MEXICO, Queretaro, Arroyo Jalpan, 1 km S Huasquilco, 725 m + 1 km SSE San Pedro Escanela, Arroyo Real, 1685 m + Chuveje, Río Chuveje, VII-11, 12-2000, WC Shepard; Veracruz, 3 km W Zacualpan, 6000 ft, IV-14-1960, M Raymond.

E. criddlei: larvae, SOUTH DAKOTA, Custer Co, French Cr at Hazelrodt Picnic Grounds, Black Hills Natl For, VI-11-1975, WP McCafferty, AV Provonsha, B Heath.

E. simplicioides: adults, UTAH: Utah Co, Provo River at Vivian Park, VII-2-1954, AR Gaufin.

L. aphrodite: adults, VERMONT, Washington Co, Montpelier, VIII-30-1952.

L. hebe: adults, ARKANSAS, Montgomery Co, Ouachita R at Hwy 270, VI-01-1974, WP McCafferty, AV Provonsha L Dersch; larvae, VERMONT, Windham Co, North Brook at W edge of Wilmington, VI-20-1976, WP McCafferty, AV Provonsha, M Minno; adults, SOUTH CAROLINA, Pickens Co, Wildcat Cr, V-2, 22,-1968, PH Carlson.

L. juno: larvae, INDIANA, Orange Co, Bacon Cr at Valeene, VI-20-1972, WP McCafferty, AV Provonsha, E Levine.

L. maculipennis: larvae, NEW BRUNSWICK, NW Mirimichi R, VII-13-1951, FL Bousefield; adults, NEW HAMPSHIRE, Grafton Co, Lebanon, VI-26-1933.

L. minerva: larvae, KENTUCKY, Knott Co, Carr Fork, 1.1 mi E on Ky 582 from jct Ky 160, VI-27-1978.

N. kennedyi: adults, CALIFORNIA, Napa Co, Capell Cr, VI-07-1952, WC Day.

N. perfida, all adults: NORTH CAROLINA, Swain Co, Confluence of Oconaluftee R and Raven's Frk, VI-18, VII-16, VIII-16-2001 + Oconaluftee R ca 50 m from confluence with Raven's Frk, VI-18-2001 + Oconaluftee R under Blue

Ridge Prkwy Overpass, VI-18-2001, RC Harrington, DR Jones.

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