

A REVIEW OF THE NEARCTIC *HEPTAGENIA* (HEPTAGENIIDAE, EPHEMEROPTERA)

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ABSTRACT

Nearctic *Heptagenia* is a polygeneric group consisting of true *Heptagenia* and a complex allied to Old World ecdyonurids. Nymphal mouthparts, adult eyes, genitalia and tarsi separate these ecdyonurids from true *Heptagenia*. The ecdyonurid complex is shown to consist of two new genera. One new genus is identical to Traver's *maculipennis* group while the other corresponds to the combined *lucidipennis* and *simplicioides* groups. Since the *lucidipennis* and *simplicioides* groups are distinct only in the adult stage, each should receive subgeneric rank.

REVIEW

The world-wide genus *Heptagenia* Walsh contains 37 Nearctic species (Edmunds *et al.* 1976). Although widespread, often abundant, and familiar to most aquatic entomologists, they present many unresolved problems for the taxonomist, and the non-systematic biologist still cannot reliably identify many species.

The existence of species groups within Nearctic *Heptagenia* has long been known (Traver 1933). Based on the shape of the male genitalia, Traver recognized six groups: *flavescens*, *pulla*, *elegantula*, *lucidipennis*, *simplicioides* and *maculipennis*. She divided the nymphs into two groups; *flavescens-pulla-elegantula* lacking pectinate claws and with filaments on the 7th pair of gills, and *maculipennis-lucidipennis* with pectinate claws but lacking filaments on gill 7. Traver also noted variability in other nymphal characters, notably the mouthparts and abdominal spines. Although these groups have

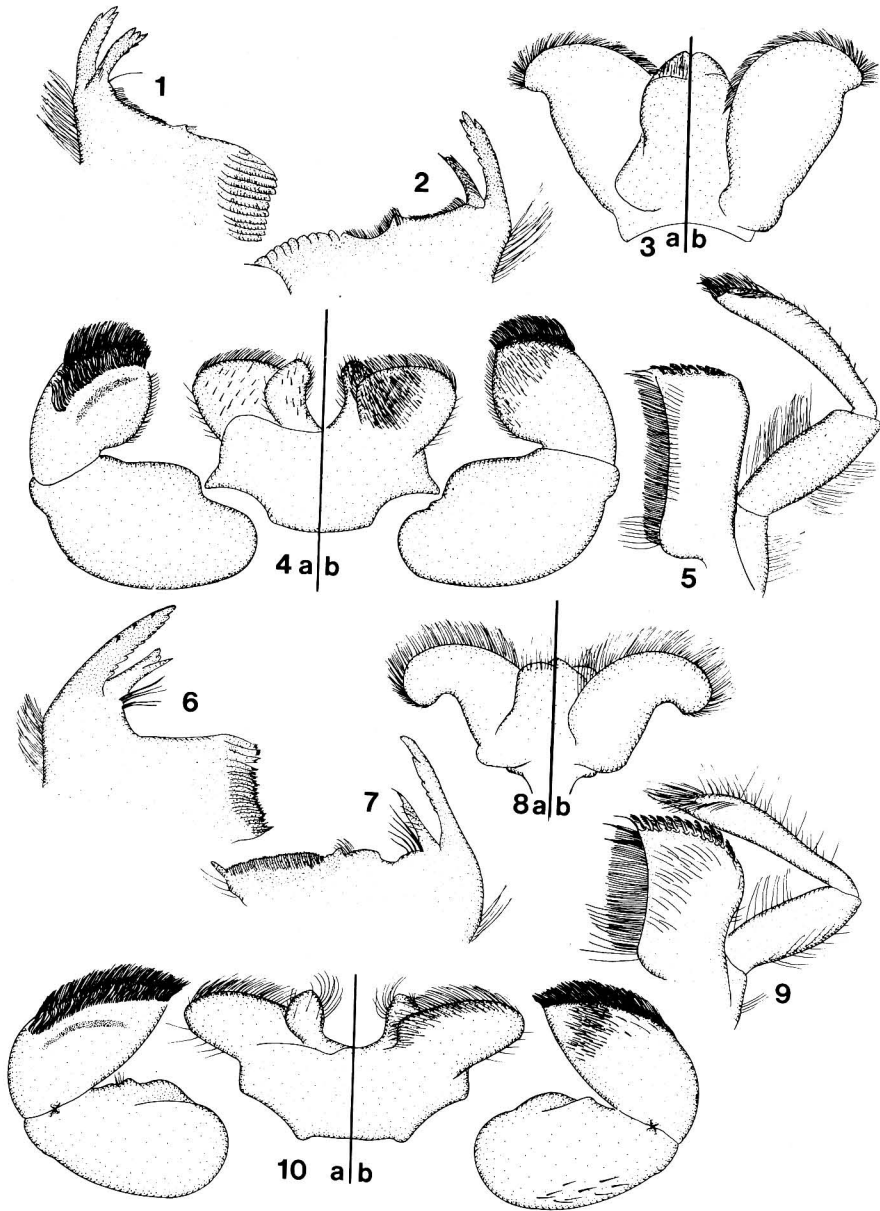
been used in keying out species, their taxonomic significance has not been fully appreciated.

Based on detailed morphological studies, Bogoescu and Tabacaru (1962) concluded that a number of European mayflies then assigned to *Heptagenia* should be placed in *Ecdyonurus*. They did this on the basis of nymphal mouthpart structure and of adult genitalia and tarsal ratios of the middle and hind legs. *Ecdyonurus* nymphs differ from *Heptagenia* nymphs by having the paraglossae of the labium and the superlinguae of the hypopharynx distinctly expanded. Adults of these two genera are distinguished by structure of the male genitalia and by tarsal ratios. Jensen (1972) used mouthpart characters, those listed above and others, to define an Old World phyletic line of five genera: *Afromurus*, *Ecdyonurus*, *Cinygmia*, *Thalerosphyrus*, and *Compso-neuriella*. Adult characters were not used in his phylogenetic analysis.

It is thus apparent that prior to the work of Bogoescu and Tabacaru, European *Heptagenia* was polygeneric. The structural diversity of Nearctic *Heptagenia* also indicates a polygeneric group and the present research is an attempt to clarify the composition of this assemblage. A detailed external morphological study was undertaken on representatives of all Traver's species groups in all life stages. The results show an interesting parallel between New and Old World *Heptagenia*: the same characters that led to the transfer of some European *Heptagenia* species to *Ecdyonurus* are found in many Nearctic *Heptagenia*. This clearly indicates that two distinct phyletic groupings, unnoticed for many years, existed within the taxon *Heptagenia*.

One phyletic grouping is represented by the *flavescens-pulla-elegantula* group which, as it includes the genotype of *Heptagenia* (*H. flavescens* (Walsh)) is *Heptagenia* s.s. As characterized below, *Heptagenia* s.s. agrees well with *Heptagenia* as defined by Bogoescu and Tabacaru (1962). The second phyletic grouping, represented by the *maculipennis*, *lucidipennis* and *simplicioides* groups, differs substantially from *Heptagenia* s.s. in both adult and nymphal characters. This grouping is part of the Old World ecdyonurid complex (*Afromurus*, *Ecdyonurus*, etc.), based on the condition of nymphal mouthparts and claws and the middle and hind tarsi of the adult. There are also striking similarities in nymphal color

Fig. 1-10. Nymphal mouthparts: 1-5, *Heptagenia flavescens*; 6-10, "A" *hebe*. 1,6, tip of left mandible, enlarged; 2,7, tip of right mandible, enlarged; 3,8, hypopharynx (a-ventral, b-dorsal); 5,9, left maxilla; 4,10, labium, palpi detached (a-ventral, b-dorsal).



Figures 1 - 10

patterns between many New and Old World members of this complex.

The New World ecdyonurid complex differs from *Heptagenia* s.s. by the following combination of characters: in the adult, (1) first segment of hind tarsus subequal to second, (2) eyes of male meeting on vertex or separated by 3-5 times the width of median ocellus (Fig. 12,13), (3) male genitalia with large or small dorso-lateral spines, if large, discal spines present (Fig. 17-21); in the nymph, (1) mandible with 4-5 prosthecal setae and lacking small setae between molar and incisor areas (Fig. 6,7) (2) maxilla with ventral setae of galea-lacinia scattered (Fig. 9), (3) superlinguae of hypopharynx laterally elongated and curved (Fig. 8), (4) glossae oval, stalked, not bent in middle, paraglossae strongly expanded laterally, apical segment of labial palp elongated and acutely pointed (Fig. 10), (5) 7th abdominal gill lacking filamentous tuft, (6) tarsal claws pectinate, (7) postero-lateral spines on abdominal segments 3-8. In New World *Heptagenia* s.s., these characters are as follows: in the adult, (1) first segment of hind tarsus usually shorter than second, if subequal, then first segment of middle tarsus shorter than second, (2) eyes of male separated on vertex by 1-1.5 times the width of median ocellus (Fig. 11), (3) male genitalia with large dorso-lateral spines but no discal spines (Fig. 14-16); in the nymph, (1) mandible has one or no prosthecal setae and a row of small setae between incisor and molar areas (Fig. 1,2), (2) maxilla with ventral setae of galea-lacinia in a sub-median row (Fig. 5), (3) superlinguae of hypopharynx short, notched on lateral margin (Fig. 3), (4) glossae curved at middle, not stalked, paraglossae moderately expanded laterally, apical

Table 1. Composition of *Heptagenia* s.s. and the ecdyonurid complex in North America

Heptagenia s.s. - (*flavescens-pulla-elegantula* group)

Ecdyonurid complex

New Genus A. - (*maculipennis* group)

New Genus B. - (*lucidipennis* - *simplicioides* group)

New Subgenus 1. - (*lucidipennis* group)

New Subgenus 2. - (*simplicioides* group)

segment of labial palp not elongated (Fig. 4), (5) 7th abdominal gill with filamentous tuft, (6) tarsal claws lacking pectines, (7) postero-lateral abdominal spines absent or on segment 8 only.

The New World edcyonurid complex divides into two new genera; one (New Genus A) represented by Traver's *maculipennis* group and the other (New Genus B) by her *lucidipennis* and *simplicioides* groups (Table 1). Formal descriptions of these genera are in preparation for publication elsewhere.

New Genus A adults can be recognized by the wide separation of the male eyes (Fig. 12) and the presence of discal and large dorso-lateral spines on the penes (Fig. 17,18). In all species except "A" *umbratica* the costal and sub-costal cross veins are heavily margined with brown. Eggs of this genus are similar to those of *Heptagenia* s.s. (Fig. 22) in having knob-terminated coiled threads (KTC's of Koss and Edmunds 1974) either concentrated at the poles or evenly distributed; the chorion has fine granular sculpture (Fig. 23, 24). Nymphs of New Genus A differ from those of the other New World edcyonurids by the absence of setae of the caudal filaments. The head capsule often has dark granulations on the frontal margin and is slightly wider than the pronotum.

New Genus B can be recognized in the adult stage by the male eyes which meet on the vertex (Fig. 13). The penes have small dorso-lateral spines (Fig. 20,21) and segments 3 and 4 of the forceps are longer than in either New Genus A or *Heptagenia* s.s. (Fig. 19). The eggs of New Genus B (Fig. 25-29) have the KTC's evenly distributed, sometimes densely packed, with the chorion sculptured with ridges or small knobs. Nymphs of this genus have fine setae on the caudal filaments and the head capsule does not exceed the width of the pronotum or have dark granulations on the frontal margin.

Except for color patterns, no reliable characters distinguish the nymphs of the *lucidipennis* and *simplicioides* groups. However, these two groups are differentiated by characters of the eggs and genitalia. The penes of the *lucidipennis* group have non-divergent lobes and thick, spiculate median titilators (Fig. 19,20). The penes of the *simplicioides* group are divergent and the titilators are slender and smooth (Fig. 21). All *lucidipennis* group eggs studied so far are readily distinguished by the large-mesh reticulation of the chorion (Fig. 25-27). This feature has been previously known only from the *Hexagenia* complex in North America (Koss 1968). Unlike *Hexagenia*, however, *lucidipennis* eggs have a KTC in each mesh. The *simplicioides* group eggs lack a reticulated mesh. One species ("B" *simplicioides*) has an irregular system of ridges (Fig. 28), while another species ("B" *criddlei*) has only small knobs between densely packed KTC's (Fig. 29). Based on the criteria of Edmunds (1962) and Peters and Edmunds (1970), the *lucidipennis* and *simplicioides* groups should be considered separate

subgenera of New Genus B (Table 1).

Except for the California "B" *kennedyi* (provisionally included here on the basis of adult male characters), Subgenus 1 occurs east of the Great Plains. Subgenus 2 is found from the Rocky Mountain region westward with one species ("B" *salvini*) in northern Mexico.

New Genus A is distributed throughout North America.

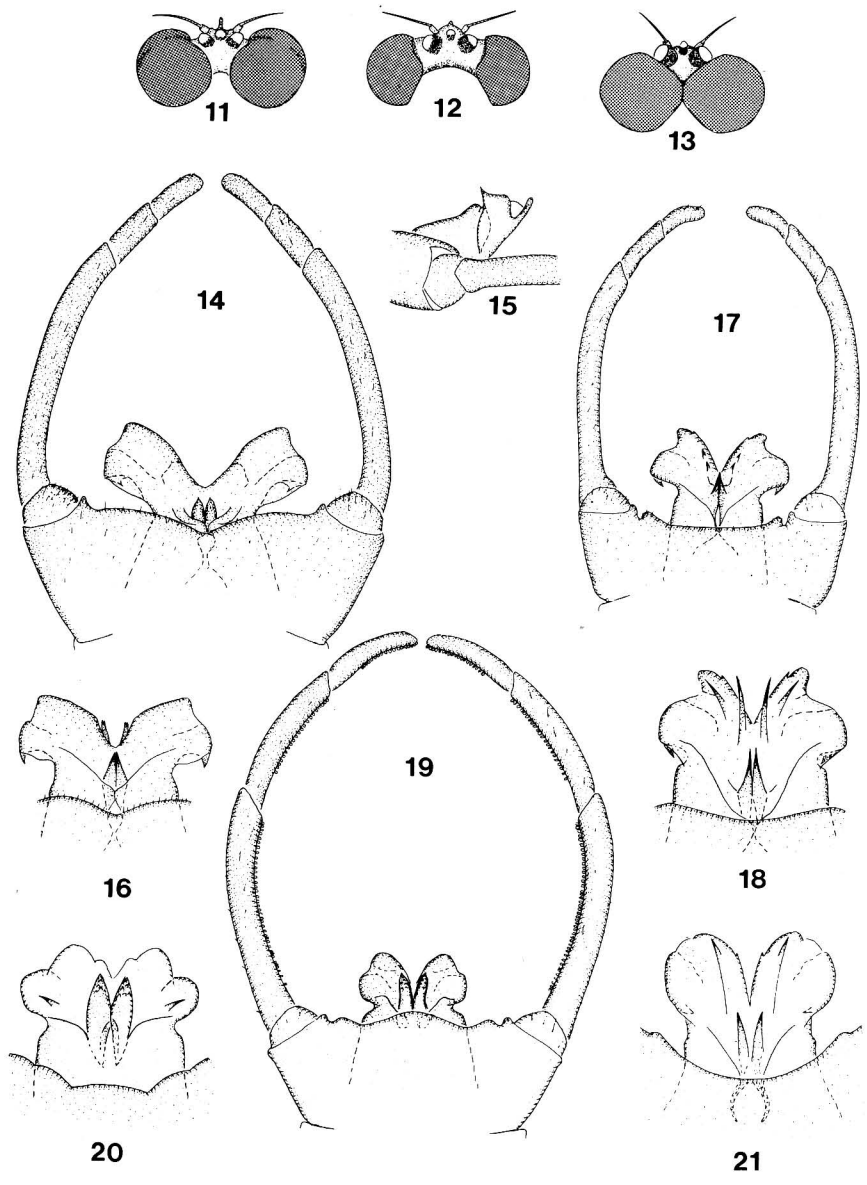
As far as can be determined from available specimens and the literature the genera proposed for the New World edcyonurid complex are endemic to North America. European *Ecdyonurus* have some derived characters in common with New Genus B, and *Afromurus* nymphs (particularly some small Asian species) are strikingly similar to nymphs of New Genus A, a similarity that even extends to color patterns. However, in both these cases the New World genera differ in other important characters and there is at present no reason for classifying New Genus A or B with any currently known Old World genera. A geographic region worthy of particular study is the eastern Siberian and Japanese area. Several *Ecdyonurus* illustrated by Imanishi (1936) could possibly be allied to the New World fauna, and Bajkova (1972), describing an adult Siberian *Rhithrogena*, gave a figure of the male genitalia which suggests that her species may be allied with the *simplicioides* group.

Until more is known about Old World *Ecdyonurus* and allied genera, it is premature to speculate further on the generic affinities and phylogeny of the New World edcyonurids.

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- Fig. 11-13. Eyes of male, dorsal view: 11, *Heptagenia flavescens*; "A" *hebe*; "B" *lucidipennis* group.
 Fig. 14-21. Male genitalia and lobes of penes. Fig. 14, 17, 19, ventral view of genitalia: 14, *Heptagenia flavescens*; 17, "A" *thetis*; 19, "B" *lucidipennis* group.
 Fig. 15-16, 18, 20-21, lobes of penes, enlarged: 15-16, *Heptagenia pulla* (lateral and ventral views); 18, "A" *hebe*; 20, "B" *horrida*; 21, "B" *simplicioides* all ventral views).



Figures 11 - 21

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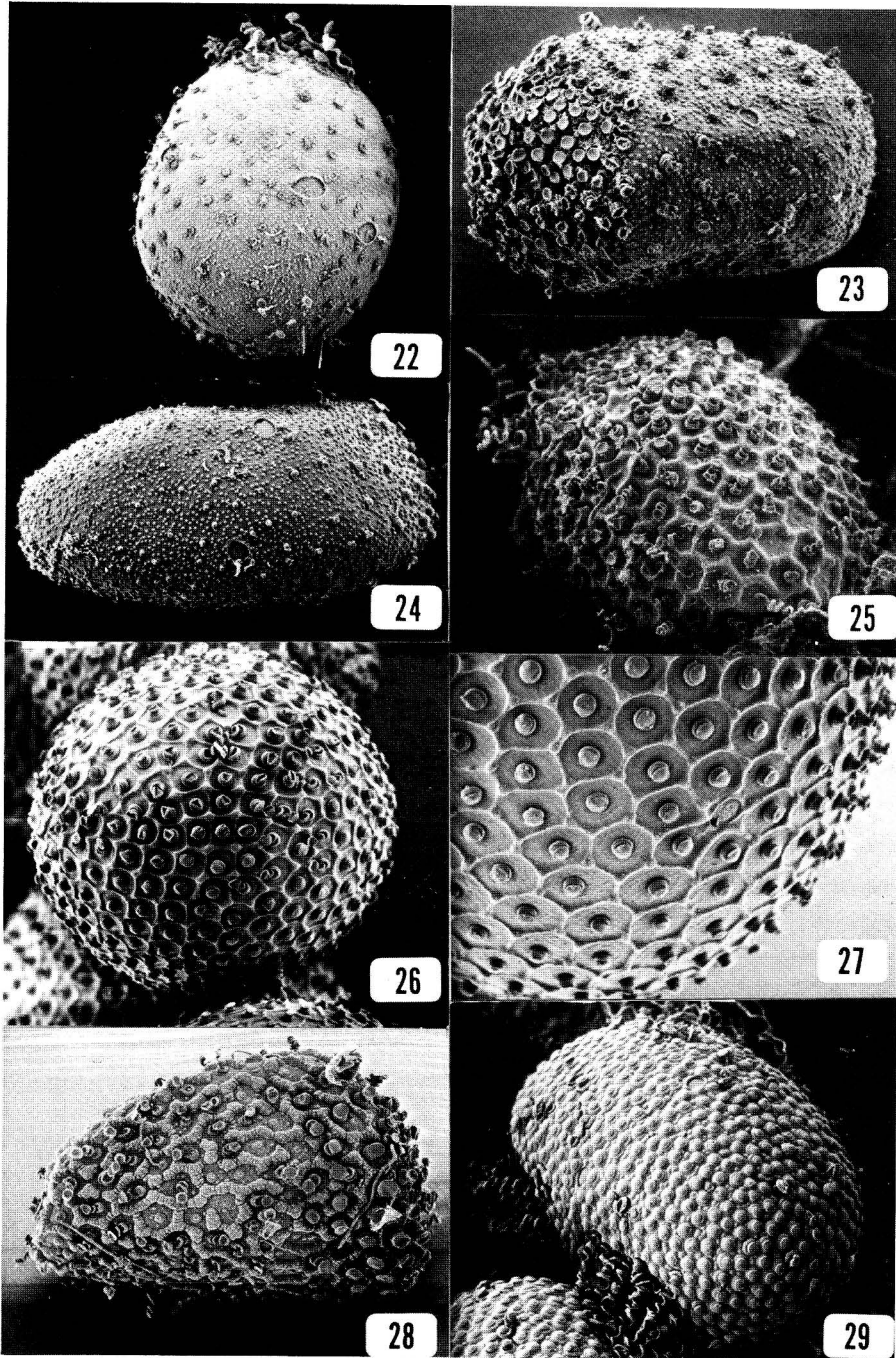
RESUME

L'*Heptagénia* néarctique est un ordre polygénérique comprenant l'*Heptagénia* véritable et d'autres genres associés aux ecdyonurides de l'ancien monde. Les pièces buccales des larves, les yeux des adultes, les organes génitaux et les tarsi distinguent ces ecdyonurides de l'*Heptagénia* véritable. Le complexe ecdyonuride compte deux genres. L'un, récent, est identique au groupe *maculipennis* de Traver, l'autre correspond au tandem de *lucidipennis* et *simplicioides*. Comme ces deux derniers ne se différencient qu'à l'état adulte, ils devraient tous deux être classés dans un sous-genre.

ZUSSAMENFASSUNG

Die nearktische *Heptagenia* ist eine polygenerische Gruppe, die aus echten *Heptagenia* und einem weiteren Komplex besteht, der verwandt ist mit Ekdylonuriden der alten Welt. Mundteile, der Nymphen, Augen der reifen Tiere, Genitalien und Fußwurzeln unterscheiden diese Ekdylonuriden von den echten *Heptagenia*. An Hand dieser Arbeit wird gezeigt, daß der Ekdylonuriden Komplex aus zwei neuen Gattungen besteht. Eine dieser neuen Gattungen ist identisch mit Travers *maculipennis* Gruppe, während die andere mit den kombinierten *lucidipennis* und *simplicioides* Gruppen übereinstimmt. Da die *lucidipennis* und *simplicioides* Gruppen nur im ausgewachsenen Stadium verschieden sind, sollte jede von ihnen den Rang einer Untergattung erhalten.

Fig. 22-29. Eggs: 22, *Heptagenia flavescens* (425X); 23, *aphrodite* (550X); 24, "A" *juno* (525X); 25, "B" *inconspicua* (475X); 26-27 "B" *lucidipennis* group (450 and 800X); 28, "B" *simplicioides*; 29; "B" *criddlei*.



Figures 22 - 29

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