

HEPTAGENINE MAYFLIES OF NORTH AMERICA¹

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The subfamily Heptageninæ, as the term is used in this paper, comprises those mayflies in which two pairs of free intercalaries are present in the cubito-anal region of the forewing. Each tarsus is composed of five freely movable joints. The eyes of the males are more or less remote from one another, and are never divided to form an upper turbinate and a lower portion. Nymphs of this group have more or less flattened bodies and wide flattened heads. The term Heptageninæ as thus used corresponds to Dr. Ulmer's family Ecdyonuridæ. North American genera considered to be of this subfamily are: Heptagenia, Ecdyonurus (perhaps), Epeorus (perhaps), Rhithrogena, Iron, Cinygma, Arthroplea, Anepeorus, Pseudiron, and the new genus Stenonema.

There has been much confusion in the literature dealing with this group, as to the characters on which the genera should be recognized. Unfortunately, all are so closely allied that characters of venation are of little use. I follow Dr. Needham and Dr. McDunnough in the use of the relative lengths of the fore-tarsal joints of the imagoes as primary generic characters, rather than the tarsal joints of the third leg, as used by Eaton. The type of the male genitalia is of great importance in determining the genus. Whether or not the likeness or unlikeness of the fore claws of the male imagoes will prove of generic value in this group is at present doubtful. Anastomosis of cross veins in the pterostigmatic area of the forewing is useful in separating species, but seems to be a constant character only in the one genus Rhithrogena. Characters of the nymphs, correct association of nymphs and imagoes as determined by rearing, and definite correlations between nymphal characters and those of the imago, are essential to a real knowledge of the genera of this group. As regards nymphal characters, the structure of mouthparts, claws, and the presence or absence of lateral abdominal spines, are very important, as well as gill characters. The gills, although

¹ Contribution from the limnological laboratory, Cornell University.

more fragile than chitinized parts and thus more subject to injury, serve as easy recognition marks of the genera, and seem relatively constant for each genus.

The rearing of many species of mayflies from the nymphal stage has convinced me of the great importance of correlating nymphal characters with those of the imago. Whenever it becomes possible, after careful study of any genus in its nymphal and imaginal stages, to predict accurately from the characters of the imago those characters to be expected in the nymph, and *vice versa*, such a genus is well established and has good claim to existence. Lack of evidence upon which to make such predictions leads to doubt as to the validity of the genus under consideration. Much rearing work remains to be done, however, before we will be able to make such predictions in several of the genera concerned. Such predictions can at present be made with apparent certainty and accuracy in the genera *Heptagenia*, *Stenonema* and *Rhithrogena*. While nymphs of *Cinygma* are known, too few species have been reared to make it possible to predict more than the generic characters of the imago from a given nymph. Nymphs of *Anepeorus* and *Pseudiron* are as yet unknown. Although but one species of *Arthroplea* has been reported from North America, the characters of both nymph and imago are so striking as to make it probable that others of this genus could be readily recognized in either stage. In the species of the *Epeorus-Iron* group there is still much confusion as to what characters are of generic value, or even whether two genera are concerned. Even more doubtful is the status of the genus *Ecdyonurus*. These difficulties are discussed at more length in later paragraphs dealing with the groups in question.

My present conceptions of the relations of the genera of the Heptagenine group are presented in the following keys and the discussions of the genera. Further study has led me to believe that my use of the terms *Heptagenia* and *Ecdyonurus* in my previous key to the nymphs of the mayfly genera (*J. Elisha Mitchell Soc.* 47:101) is incorrect. The term *Stenonema* should replace *Heptagenia*, and the term *Heptagenia* should be used in the place of *Ecdyonurus*. In the key to the male imagoes, in that paper, I used primarily the characters of the tarsal joints of

the third legs, in dealing with this group. The present keys, therefore, supplant those I have published previously.

KEY TO MALE IMAGOS²

- 1. First joint of fore tarsus considerably shorter than second joint (not more than $\frac{2}{3}$ of 2nd) 2
 First joint of fore tarsus equal or almost equal to second joint, or slightly exceeding it in length 5
- 2. First joint of fore tarsus very short ($\frac{1}{3}$ to $\frac{1}{2}$ of second) 3
 First joint of fore tarsus longer ($\frac{1}{2}$ to $\frac{2}{3}$ of second) 4
- 3. Lobes of penes separated from one another very near the base, thus appearing as two long narrow projections. Cross veins of pterostigma tend to anastomose *Rhithrogena*
 Lobes of penes joined together except near apex; broad, often somewhat angulate laterally and distally, never as above. Cross veins of pterostigma not anastomosed *Heptagenia*
- 4. First joint of fore tarsus rather more than $\frac{1}{2}$ of second. Claws of fore leg blunt, similar *Anepeorus*
 First joint of fore tarsus varying in length from $\frac{1}{3}$ to $\frac{2}{3}$ of second. Claws of fore leg dissimilar (one blunt, one smaller and pointed). *Stenonema*
- 5. First joint of fore tarsus not quite equal to second. Wings often amber-tinted *Cinygma*
 First joint of fore tarsus as long as or longer than second. Wings not amber-tinted 6
- 6. Forceps five-jointed; basal joint short, second very long, the three terminal joints together not equalling second in length *Arthroplea*
 Forceps four-jointed; basal joint long, second long, the two terminal joints together not quite equalling second 7
- 7. Fore claws dissimilar; one blunt, one sharp *Iron*
 Fore claws similar, blunt *Epeorus*

KEY TO NYMPHS³

- 1. Tails two, in mature nymph 2
 Tails three, in mature nymph 3
- 2. Gills rather small, not overlapping; first and last pair smaller than others. No triad of spines at tip of galea-lacinia Nameless genus
 Gills large, tending to overlap; last pair, also first pair usually, as large or larger than others. Triad of stout curved spines at tip of galea-lacinia *Iron*, *Epeorus*
- 3. Gills of seventh pair slender tapered threads or spines; tracheæ, if present, without lateral branches *Stenonema*
 Gills of seventh pair flat and plate-like; tracheæ always present, bearing lateral branches 4

² Does not include the doubtful genus *Ecdyonurus*.

³ No attempt to distinguish between *Iron* and *Epeorus*

4. Head definitely emarginate in front. Gill filaments wanting, or reduced to few tiny threads 5
 Head not emarginate in front. Fibrillar portion of gill present, at least on segments 1-6; well developed 6
5. Second joint of maxillary palp more than four times the length of the lacinia; bears long movable hairs of spines *Arthroplea*
 Second joint of maxillary palp less than twice as long as lacinia; bears only short curved spines *Cinygma*
6. Gills of first and last pairs much enlarged, converging beneath body of nymph *Rhithrogena*
 Gills of first and last pairs not as large as some of the central pairs; directed laterally, not converging beneath body of nymph 7
7. Postero-lateral margins of pronotum prolonged backwards in epaulet-like extension *Eodyonurus*
 Postero-lateral margins of pronotum not prolonged backwards. *Heptagenia*

HEPTAGENIA WALSH 1863

In this paper I follow Dr. McDunnough, as regards the species considered to belong to the genus *Heptagenia*. As I use the term at present, the genus includes those *Heptagenine* species in which the first fore tarsal joint of the male is $\frac{1}{6}$ to $\frac{1}{4}$ the length of the second joint (rarely almost $\frac{1}{3}$), and in which the male genitalia are never of the *Rhithrogena* type. In *Rhithrogena*, the penes are long slender projections united only at the base. In the genitalia of *Heptagenia*, the penes are relatively wide, and separated only near the tips. One to three pairs of spines are present, of which one pair is situated centrally between the two divisions of the penes. Nymphs of this genus do not have the pronotum prolonged backwards at the postero-lateral angles. The seventh pair of gills is similar in form to preceding pairs, slightly smaller than the central pairs but larger than the first pair. In this last pair of gills, the lamellæ or blade-like portion is always present, although the filaments may be wanting. Mouthparts vary somewhat in the different groups of the genus. Those of *marginalis* Bks. are quite similar to Eaton's figures of mouthparts of the nymph from North America which he tentatively referred to *Eodyonurus* (Monograph, Pl. 61).

If the genus *Eodyonurus* proves to be a synonym of *Heptagenia*, as seems at present not unlikely, a modification of the statement of the generic characters may be necessary.

Examination of my reared species of North American Heptagenia nymphs shows clearly that the nymph of *H. gallica* Etn., as figured by Eaton (Monograph, Pl. 60) is not similar to any of these. True Heptagenia nymphs were figured by Eaton, however, on Pl. 61, as Ecdyonurus, and Figs. 24 and 25 of Pl. 62 of the Monograph, as a nameless genus. It is probable that the nymph shown on Pl. 59 is also a true Heptagenia, although I have found none which correspond exactly to it. I doubt that the nymph which Eaton figures on Pl. 60 occurs in North America. I feel sure that rearing will prove it to be of a genus different from the true Heptagenia of Walsh. If the genitalia figured on Pl. 24, Fig. 45a, of the Monograph, are really of the same species as the nymph figured as *H. gallica*, I think there can be no doubt that Eaton's conception of the genus Heptagenia is different from Walsh's conception of that genus, and that *H. gallica* is not a Heptagenia.

The great confusion which has arisen regarding the genera Heptagenia and Ecdyonurus is due in part, I think, to the fact that Eaton did not know Walsh's Heptagenia, at least in the nymphal stages, and hence has used the nymph of a different genus to represent it. It is due also to the fact that European and American workers in this group have seemingly been referring to different genera under the same name, and have tried vainly to make Eaton's figures of nymph fit the corresponding figures and descriptions of the imagoes. Thus the North American genus for which I am proposing the name *Stenonema* has been referred to the genus Ecdyonurus, on the basis of the similarity in the shape of the male genitalia and the relative lengths of the fore tarsal joints, without regard to the discrepancy between the nymphal stages of this genus and Eaton's Ecdyonurus. The same genus had previously been included in Heptagenia. There are still several points to be cleared up. The rearing of many species of nymphs to imagoes, and the definite linking of nymphal and imaginal characters, will in time set the matter straight. It may then develop that Ecdyonurus is a true synonym of Heptagenia, as Dr. McDunnough has suggested, in correspondence with me on this subject.

On the basis of the male genitalia, the twenty-seven species of the genus *Heptagenia* which have thus far been described may be separated into at least five groups or subdivisions. These I term the *maculipennis* group, the *flavescens* group, the *elegantula* group, the *inconspicua* group and the *persimplex* group. The genitalia of *H. kennedyi* McD. are rather different from any other species in the genus, and may well represent a sixth group. An undescribed species which I have from North Carolina evidently represents a seventh group. Figures of the genitalia of the species mentioned above, as representatives of different groups, have been published in connection with the descriptions or notes on the species, by Dr. McDunnough, with the exception *H. elegantula* Etn.

As might be expected from the different types of genitalia found in this genus, the nymphs likewise show structural differences separating them into groups corresponding somewhat to the grouping given for the imagoes. Unfortunately the nymph of *H. flavescens* Walsh, the genotype, is as yet unknown. Judging by the similarity in genitalia, *H. marginalis* Bks. is closely allied to *flavescens*, and as the nymph of this species is definitely known, I use it as a representative of the *flavescens* group. A large nymph from the Mississippi River, which has many of the same characters as *marginalis*, appears to belong also in this group. It may be the true *flavescens*, but this can be determined only by rearing. No nymphal material of the *persimplex* group, of *kennedyi* nor of the North Carolina species which represents the seventh group, is available for study. However, I have made a comparative study of nymphs of three species of the *maculipeennis* group, three of the *elegantula* group, two of the *inconspicua* group and the two of the *flavescens* group mentioned. The structural characters observed in each species studied, as well as the type of genitalia of the imagoes, are presented in the following table.

The pronotum of the nymphs in the *maculipennis* and *inconspicua* groups is widest near or at the center, while in the *elegantula* and *flavescens* groups it is definitely widest at the anterior margin. A difference in claws occurs between these same two groups, the *masculipennis* and *inconspicua* groups

NYMPHS OF HEPTAGENIA

Species	Abd. spines on 8	Claw with on 6-7 spines	Filaments on 7 gill	Pronotum widest	Genitalia type	
<i>marginalis</i>	No	Yes	No	Yes	Front	Flaves.
Sp? from Fair- port, Ia.	No	No	No	Yes	Front	?
<i>elegantula</i>	No	No	No	Yes	Front	Elegant.
Sp? from North Carolina	No	No	No	Yes	Front	Elegant.
<i>pulla</i>	No	No	No	Yes	Front	Elegant.
<i>maculipennis</i>	Yes	Yes	Yes	No	Middle	Maculip.
<i>aphrodite</i>	Yes	Yes	Yes	No	Middle	Maculip.
<i>juno</i>	Yes	Yes	Yes	No	Middle	Maculip.
<i>lucidipennis</i>	Yes	Yes	Yes	No	Middle	Inconsp.
Sp? from Calif.	Yes	Yes	Yes	No	Middle	Inconsp.

possessing teeth or spines near the tip of the claw, while such spines are not present in members of the *flavescens* and *elegantula* groups. In all species observed, one large spinous projection is present on the claw, about the center of the inner margin. The presence or absence of gill filaments on the seventh pair of gills follows the same grouping. Abdominal spines on the sixth to seventh segments are present in the *maculipennis* and *inconspicua* groups, and in *marginalis* of the *flavescens* group, but absent in the *elegantula* group and the nymph from the Mississippi River. Until more nymphs of each of these groups have been studied, as well as nymphs of the groups not here represented, it will be impossible to draw definite conclusions as to how far the species of nymphs follow the groups of the species of imagoes, as based on genitalic differences.

Eaton's figures 24 and 25 of Pl. 62, in the Monograph, seem to represent a nymph of the *elegantula* type, a species close to *pulla* Clem. Clemens has figured *lucidipennis* Clem. and a species of the *maculipennis* group (not the true *maculipennis*, however) under *Ecdyonurus* (Canad. Ent. 45; Pl. 6, Figs. 4 and 5). In the same paper he figures *pulla* (Pl. 5, Fig. 10) also in *Ecdyonurus*.

ECDYONURUS EAT. 1868

It is quite possible that this genus may fall as a synonym of *Heptagenia*. I am considering the two genera distinct, however,

until I have been able to study specimens of *E. venosus* Etn., the genotype, which is a European species, and to rear a species of nymphs I took in North Carolina. These latter nymphs correspond very closely to the figures of Eaton, Pl. 62, Figs. 1-23, and Figs. 2-3, in the Monograph, of nymphs of *Ecdyonurus*. There are many points of similarity, however, between these nymphs from North Carolina and nymphs of the *maculipennis* and *inconspicua* groups of *Heptagenia*. The principal distinguishing feature is the presence, in the North Carolina nymphs, of the peculiar epaulat-like backward extension of the pronotum,—a character which Eaton mentioned as distinctive of *Ecdyonurus*. Dr. Schoenemund has used this character as the primary distinguishing feature between nymphs of *Ecdyonurus* and *Heptagenia*. (*Zool. Anz.* 90: 45. 1930.) It is of course quite possible that his reference to *Heptagenia* is to a nymph of the type figured by Eaton as *H. gallica*, which is most certainly not a true *Heptagenia*. Eaton mentions the fact (Monograph, pg. 277) that North American nymphs he has seen, and considered to be *Ecdyonurus*, lacked this extension of the pronotum.

As regards the genitalia of *Ecdyonurus*, I have not seen, in any of the North American species of the entire subfamily *Heptageninae*, any forms which are similar to Eaton's figures (Pl. 24, Figs. 46 a to e, of the Monograph). Species of the genus *Stenonema* possess boot-shaped or L-shaped penes, it is true, which superficially resemble Eaton's figures. But in none of them are there any small spines or teeth on the *inner margin* of the penes, such as are present in all of Eaton's figures. Further, the nymphs of *Stenonema* are entirely different from Eaton's *Ecdyonurus* and also from Walsh's *Heptagenia*. They are, in fact, the nymphs which Eaton figured on Pls. 57 and 58 of the Monograph, as nameless genera from North America.

Until I have more evidence, in the form of reared material in which nymph and imago are correctly associated, I hold the matter in abeyance, tentatively considering *Ecdyonurus* as a valid genus. It seems to be very sparingly represented in North America, if indeed it is represented here at all. It must not be confused with *Stenonema*, which is abundantly represented in the eastern and central portions of Canada and the United

States. No species of *Ecdyonurus* (as considered above) has been described from North America, and it is solely because of the nymphs from North Carolina that I consider it here at all.

STENONEMA⁴ TRAYER, 1933

This is a new name for those species of Heptagenine mayflies of North America, some of which have been included in *Heptagenia* (by Drs. Banks, Needham and Clemens) and by Dr. McDunnough and others in the genus *Ecdyonurus*. I designate *tripunctatum* Bks. as the genotype. To this genus belong the following twenty species:—*tripunctatum* Bks., *femoratum* Say, *pubicum* Hag., *vicarium* Wlk., *ithaca* Clem., *fuscum* Clem., *subaequalis* Bks., *rubromaculatum* Clem., *luteum* Clem., *pulchellum* Wlsh., *placitum* Bks., *ruber* McD., *mediopunctatum* McD., *bipunctatum* McD., *terminatum* Wlsh., *integer* McD., *interpunctatum* Say, *canadensis* Wlk., *carolina* Bks., and *frontalis* Bks.

To this genus I assign those species, so abundant in the United States and Canada, in which the nymphs bear on the seventh segment a single spine-like or thread-like filament, with or without a tracheal branch. This single gill is always much smaller than the gills of the first pair. Male imagoes have the first fore tarsal joint $\frac{1}{3}$ to $\frac{2}{3}$ the length of the second, and penes which are L-shaped or boot-shaped, without spines on the inner margin. A pair of stout spines is present near the median line of the penes, between the two divisions. The subanal plate of the female imago is truncate at the tip, usually very slightly retuse.

At least three groups of nymphs may be recognized in this genus, and corresponding differences in the penes of the males are observable. In the first group, which I term the *interpunctatum* group, the first six pairs of gills of the nymphs are pointed distally. The seventh gill is not fringed laterally, and possesses a single unbranched tracheal trunk. Male imagoes have boot-shaped penes bearing bristles or spines on the lower lateral margins, below the boot-shaped portion. Mouthparts and gills are figured by Eaton on Pl. 57 of the Monograph, as a nameless genus from North America. These have also been figured by

⁴ The name is given in allusion to the slender and thread-like character of the seventh gill. It is neuter gender.

Clemens in *Heptagenia* (*Canad. Ent.* 45: Pl. 7). To this group belong *interpunctatum* Say, *canadensis* Wlk., *frontalis* Bks., and several undescribed species.

Mr. Y. C. Hsü, who has studied this genus intensively, has found that the two species *tripunctatum* Bks. and *femoratum* Say belong to a second group, which he terms the *tripunctatum* group. The first six pairs of gills of the nymphs are rather rounded at the tip. The seventh gill is fringed laterally, and has a forked tracheal branch. The penes of the imago show some slight variation from those of the third or *vicarium* group, to which they are more similar than to the *interpunctatum* group.

All other described species of the genus except *carolina* Bks. belong in the third or *vicarium* group. The first six pairs of gills are square or truncate at the tips. The seventh gill is fringed laterally, and lacks tracheae. Imago males have L-shaped penes entirely lacking the lateral spines of the *interpunctatum* group. Nymphs of this group have been figured by Eaton on Pl. 58, as nameless nymphs from North America. Clemens figured the structures of the nymphs and genitalia of the imago on the same plate referred to above.

The male of *carolina* Bks. has penes which are allied to the *interpunctatum* type, but differ in that the lateral spines are very minute. The outer margin below the boot-shaped portion thus appears to be merely slightly roughened. This is the only described species which possesses these features, but two undescribed forms from North Carolina are similar in structure. As

NYMPHS OF STENONEMA

Species	Gills 1-6	Gill on 7 Fringed	Trachea	Claw with spines	Genitalia type
<i>tripunctatum</i>	Rounded	Yes	Yes	Yes	Tripunct.
<i>femoratum</i>	Rounded	Yes	Yes	Yes	Tripunct.
<i>interpunctatum</i> ...	Pointed	No	Yes	No	Interpunct.
<i>frontalis</i>	Pointed	No	Yes	No	Interpunct.
Sp? from Kirt- land, Ohio	Pointed	No	Yes	No	Interpunct.
<i>ithaca</i>	Truncate	Yes	No	No	Vicarium
<i>vicarium</i>	Truncate	Yes	No	No	Vicarium
<i>fuscum</i>	Truncate	Yes	No	No	Vicarium
<i>pudicum</i>	Truncate	Yes	No	No	Vicarium

the nymph of none of these three species is known, it is not possible to be certain whether or not a fourth group is here represented.

Twenty species of this genus have thus far been described, and there are in the Cornell University collection several others as yet undescribed. I have studied several reared species in both nymphal and imaginal stages, as well as species of unreared nymphs and imagoes of which the nymphs are not known. The preceding table, of species known in both stages, summarizes the differences between the first three groups.

RHITHROGENA ETN. 1881

The genus *Rhithrogena*, as here used, contains those Heptagenine mayflies in which (1) the first fore tarsal joint of the male imago is $\frac{1}{4}$ to $\frac{1}{2}$ the length of the second joint; (2) the cross veins of the pterostigma show definite and constant anastomosis; and (3) the male genitalia consist of two long narrow projections separated from one another near the base. The length of the first fore tarsal joint is similar to that of *Heptagenia*, but the structure of the penes, and the seemingly constant presence of anastomosed cross veins in the pterostigma serve to separate the two genera. It is interesting to note that species of this genus other than those found in North America show no such anastomosis of cross veins. The genotype, *R. semicolorata* Curtis, is a European species.

Nymphs of the North American species of this genus accord well with Eaton's figures and descriptions of the European forms. On Pl. 54 of Eaton's Monograph these structures are excellently portrayed. Mouthparts are sufficiently different from those of other genera to serve as good generic characters. The enormous numbers of "diatom rakers" on the maxillary palp, and the very short incurved inner canine of the mandible, are distinctive of this genus. The first pair of gills is always greatly enlarged in the anterior portion, the forward edges of this pair meeting beneath the body of the nymph. Similarly, gills of the last pair meet beneath the body. In the other pairs of gills, each gill touches the one before and the one behind, so that there is formed a complete oval "adhesive disc" beneath

the abdomen of the nymph. A slight variation in gill structure is found in the red-gilled nymph described and figured by Dr. Needham from the Logan River, Utah, as *R. mimus* Etn. (probably a new species). See Utah Agri. Exp. Sta. Bull. 210: 13. In nymphs of this species, each gill on segments 2-6 has a secondary lobe-like projection not observed in any other species of this genus which I have studied.

Genitalia of the male imagoes of this genus, as represented in North America, seem to be of three types. To the *brunnea* group belong the species *brunnea* Hag.; *flavianula* McD.; *morrisoni* Bks.; and *doddsi* McD. In each of these a large lateral spine is present at the base of each division of the penes. Smaller spines may be present near the middle of each penial lobe, usually nearer the inner than the outer margin. Species of the second or *jejuna* group lack the large lateral spine characteristic of the first group. To this group belong *jejuna* Etn.; *undulata* Bks.; and *impersonata* McD. The third type is represented by *robusta* Dodds, and in somewhat modified form by *anomala* McD. In *robusta* the lateral spines are present, but are situated higher up on each lobe of the penes than in the *brunnea* type. Each is blunt at the apex, and indistinctly serrate. The inner apical margin of each lobe of the penes bears one long inwardly directed spine, and a much more slender short spine directed upward, lying almost parallel to the lobe of the penes. The lobes of the penes customarily diverge widely from one another, instead of turning inward, as shown in Dr. Dodds' figure (Trans. Amer. Ent. Soc. 49: Pl. 8, Fig. 12). In *anomala* McD. the blunt lateral process is distinctly serrate at the apex, and borne halfway between the base and the apex of each lobe of the penes. The inner apical margin of each lobe bears three or four short spines directed inward and downward.

Sufficient nymphal material is not available for a comparative study of nymphal characters. Nor is it possible to determine whether or not there are structural differences in the nymphs which correspond to the differences in male genitalia.

EPEORUS ETN. 1861; IRON ETN. 1883

These two genera are quite distinct from others of the Heptagenine group thus far recorded from North America. Nymphs

of these genera have but two tails. Mouthparts of nymphs of the two genera are strikingly similar to one another, and differ from those of all other genera, in the peculiar triad of large curved spines at the tip of the galea-lacinia of the maxilla. Nymphal differences between the two genera were based by Eaton primarily on the shape and size of the first and last pairs of gills. In *Iron*, the first and last pairs are much enlarged, as in *Rhithrogena*, and members of each pair approach one another closely beneath the body of the nymph. In *Epeorus*, the gills of the first and last pairs are not greatly enlarged, and members of these pairs do not approach one another closely.

According to Eaton, the first fore tarsal joint of the male imago of *Epeorus* equals the second joint in length, while in *Iron* the first fore tarsal joint is slightly longer than the second. It would seem from Eaton's descriptions that he did not consider the two genera similar as regards the structure and appearance of the male genitalia, since he compares the genitalia of *Iron* to those of *Thalerosphyrus*, *Bleptus* and *Rhithrogena*, but does not mention their similarity to *Epeorus*. So also he speaks of a "gibbous enlargement" at the base of each forceps lobe, in *Epeorus*, not mentioned in *Iron*. Nor do the accounts of the so-called forceps-bases agree, for the two genera. In *Epeorus*, the fore claws of the male are similar and blunt, while in *Iron* they are dissimilar. In females of both genera, all claws are dissimilar.

On the basis of the descriptions and figures of the nymphs of the two genera, as given by Eaton, students of this group in many parts of the world have selected two types of nymphs, one to represent *Epeorus*, the other *Iron*. In North American nymphs at least, of the so-called *Iron* type, the head of the nymph is widest near the anterior margin, while in nymphs of the *Epeorus* type the head is widest at or near the middle. Besides this head character, differences have been noted in the structure of those margins of the gills which are appressed to the surface on which the nymph clings. Likewise, the amount of development of the lateral abdominal spines has been noted, these spines being very long and sharp in members of the *Epeorus* group, and much less developed in *Iron*. Femoral flanges of the second and third pairs of legs are sharp and spine-like at the tip in *Epeorus*, but blunt and rounded in *Iron*.

Known species of North American nymphs which exhibit the characters indicated for the Epeorus group are *humeralis* Morgan; *modestus* Bks.; and a new species from North Carolina which I designate as Sp? No. 1. The nymph of *albertæ* McD. has not been reared, but is tentatively associated with the imago of that species by Dr. McDunnough. The other species have been reared. To the so-called Iron group belong *longimanus* Etn.; *fragilis* Morgan; and *pleuralis* Bks. Many other species of nymphs, unreared, are present in the Cornell University collection. Examination of these nymphs, including seven species I took in North Carolina, shows that it is not always possible to assign a definite nymph to either of the above types, on the characters stated. Thus, four of the North Carolina species, as well as two others from the Rocky Mts., have gills of the so-called Epeorus type, but heads, lateral abdominal spines and femoral flanges are of the Iron type. Should these be considered an intermediate group?

A study of the genitalia of known North American species of this group shows that there are at least three, and perhaps four or five, types. Most of the species are similar in form either to *nitidus* Etn. or *longimanus* Etn. However, *deceptiva* McD. (Canad. Ent. 56: 132) has genitalia of a third type. *I. grandis*, McD., while similar in a general way to the *nitidus* type, shows some variations. *E. albertæ* McD. has penes of the *longimanus* type, but differs from all others of this type in the shape of the distal margin of the subanal plate, which in *albertæ* does not project forward in the typical high rounded process found in other species. The species described as *petulans* Seemann evidently does not belong in the Epeorus-Iron group. In none of the above types do we find anything exactly similar to the figures given by Eaton for the genitalia of *torrentium* Etn., the genotype of Epeorus, nor for *E. psi* Etn. (Monograph, Pls. 24, Fig. 44a, and 65, Fig. 7).

Seven species of the Epeorus-Iron group of which the life history is fully known, have been studied in both nymphal and imaginal stages. Results of this study are presented in the following table. In all seven of these species, the fore claws of the males are dissimilar.

NYMPHS OF EPEORUS-IRON

Species	Gills meet	Abd. spines	Head widest	Femor. flange	Genitalia type
longimanus	Yes	Short	Front	Blunt	Longim.
pleuralis	Yes	Short	Front	Blunt	Longim.
fragilis	Yes	Short	Front	Blunt	Longim.
humeralis	No	Long	Middle	Sharp	Nitidus
modestus	No	Long	Middle	Sharp	Nitidus
N. C. Sp? No. 1	No	Long	Middle	Sharp	Nitidus
N. C. Sp? No. 2	No	Short	Front	Blunt	Nitidus

From this tabulation it would appear that the structures of the nymphs can be correlated with the types of male genitalia only on the character of the first and last pairs of gills. This is the character Eaton used to separate the genera *Epeorus* and *Iron*. Yet these species would seem all to be *Iron*. The N. C. Sp? No. 2, alone of the species here listed, has the *Epeorus*-type of gills correlated with other features usually found in the *Iron* type. As mentioned before, other species of nymphs have been found which show this same condition. This species has genitalia of the *nitidus* type. Unfortunately, nymphs of those species which show marked variation from the two types here studied, as to genitalia, are not available for study.

Tentatively I regard all North American species of this group except *alberta* McD. as belonging to the genus *Iron*. The latter I consider, on the basis of the differences in genitalia, and the similar blunt claws of the male, as the only possible North American representative of the genus *Epeorus*. It is quite possible that the genus *Iron* may prove not worthy of generic rank, in which case the likeness of fore claws of the male would not be a character of generic value. The great similarity in the structures of the nymphs of the two genera would seem to indicate that they are in reality but one. However, since nymphs with the characters given by Eaton for both genera occur in North America, along with some intermediate forms, and yet no single species of these agree entirely with Eaton's figures for the genitalia of *Epeorus*, there remains the possibility that Eaton's *Epeorus* is really quite different from *Iron*. It may even not be represented in North America. I leave this question likewise in abeyance, until type material from Europe can be examined.

CINYGMA ETN. 1885

In this genus, the first fore tarsal joint of the male imago is slightly shorter than the second joint. In some species, the lobes of the penes are separated from one another almost from the base, much as in *Rhithrogena*, each division tending to turn outward from the median line. At least one pair of spines is usually present, sometimes located on the outer margin, but in other species on the inner margin of the penial lobes. In two other species of this genus, the penes are roughly lyre-shaped.

As far as I have been able to determine, *ramaleyi* Dodds is the only species reported as having been reared from the nymph. I have recently reared *atlantica* McD., in the vicinity of Ithaca, N. Y. Several other species of nymphs are known, however, but are not yet definitely associated with known species of imagoes. All of these nymphs have definite structural characters in common, which separate them from nymphs of all other North American genera. The expanded margins of the head fail to cover the mouthparts completely, so that portions of the maxillary palps usually protrude on each side, and all but the extreme basal portion of the labrum protrudes in front. This protrusion of the labrum is due to a distinct emargination of the front border of the head at the median line. This is a character by which nymphs of *Cinygma* may be readily separated from all of the other Heptagenine group except *Arthroplea*. The gills are relatively large and conspicuous, consisting almost entirely of the upper plate-like portion. The filaments may be entirely wanting, or reduced to two or three inconspicuous threads. Gills of the first pair are about as wide as long, the lobes on each side about equally produced on each side of the base. Other gills are longer than wide, and pointed at the tip. Each extends backward almost as far as the center of the third segment behind.

Three tails are present, about equal in size and length. Claws, in those species available for study, bear one large spine toward the base and two or three shorter spines or teeth near the tip on the inner margin. They are very similar in this respect to claws of *Rhithrogena* and *Iron*. The maxillæ are rather similar to *Rhithrogena*, but the "diatom rakers" do not cover so large an area of the palps. Each individual hair or spine composing the

raker is simple instead of pectinate. The outer canine of the mandible is likewise much as in *Rhithrogena*. But the inner canine is much longer than in that genus, being at least one-half the length of the outer. It is not strongly recurved as in *Rhithrogena*, and is stouter than in *Heptagenia*. The hypopharynx is very like that of the *Epeorus*-Iron group. Labrum and labium resemble those of *Rhithrogena*.

Nymphs of this genus are more cylindric in body form than others of the *Heptagenine* group, and are relatively slender. The nymph of *ramaleyi* Dodds is figured by Dodds and Hisaw (*Ecology* 5: Pl. 2, Fig. 10).

On the basis of the male genitalia, at least two groups or subdivisions are recognizable in this genus. To the *integrum* group belong *integrum* Etn. the genotype, and *lyriformis* McD. The fore claws of the males are dissimilar, the wings are not distinctly amber-tinted, and the costal cross veins are "divided by a fine line running just below the costa" (McDunnough). Genitalia, as figured by Dr. McDunnough (*Canad. Ent.* 58: Pl. 3, Fig. 10; *op. cit.* 56, Pl. 5, Fig. 1) are quite distinctive, and differ markedly from others of the group, being somewhat lyre-shaped.

To the second or *mimus-par* group belong the other known North American species of *Cinygma*. Genitalia of these have the lobes of the penes separated near the base and divergent distally. Costal cross veins are usually anastomosed. The wing membrane is often distinctly amber-tinted. Dr. McDunnough writes me that the fore claws of *par* Etn. and *hyalina* McD. are dissimilar, but that *mimus* Etn., *confusa* McD., *ramaleyi* Dodds, *tarda* McD., and *atlantica* McD. all have similar blunt fore claws in the male imago. This character I had observed in *mimus* Etn., but did not have specimens of all of the other species for examination.

As the genus was characterized by Eaton, the fore claws of the male were dissimilar. It is conceivable that some of the species now listed under *Cinygma* may, as Dr. McDunnough has suggested (*Canad. Ent.* 58: 302), fall into another genus. If, however, the character of likeness of fore claws is specific only and not of use in separating genera, perhaps all the species now placed in *Cinygma* rightfully belong there. Only rearing of all

known species from the nymphal stage will determine this point.

It should be noted that the nymph figured by Dr. Needham (Utah Agri. Exp. Sta. Bull. 201: 13) as *Rhithrogena mimus* is a true *Rhithrogena*, probably of a new species, and not *Cinygma mimus* Etn. with the imagoes of which it was erroneously associated.

ARTHROPLEA BGTN. 1909

This genus is represented in North America by the single species *bipunctata* McD. The first four joints of the fore tarsus of the male imago are approximately equal in length. The forceps are five-jointed,—a character unique in the subfamily Heptageninæ. The penes are separated from one another near the base, but often lie closely appressed, in which case they present the appearance of an hour-glass, of which the base is much wider than the apex. Slender lateral spines are situated about midway between the base and apex.

The nymph differs from all others of this subfamily (1) in the very greatly elongated second joint of the maxillary palp, and (2) in the appearance of the labium. The mandible also is not typical, bearing a closer resemblance to the Baetinæ than to the Heptageninæ. Gills are simple, consisting of the upper blade-like portion only. Each gill is pointed at the apex, and more or less cordate at the base, where its margin is produced into an anterior lobe. The nymph somewhat resembles *Cinygma* in that some of the mouthparts protrude from beneath the margins of the head, which is likewise emarginate in front. The very long maxillary palp should serve as an easy recognition mark for the nymph of this genus.

ANEPEORUS MCD. 1925

Two species of this genus are known, *rusticus* McD. the genotype, and *simplex* Wlsh (in Heptagenia). Male imagoes have similar blunt fore claws, as in *Epeorus* and some species of *Cinygma*. The first fore tarsal joint of the male is rather more than one-half the length of the second, which is longer than the third. Forceps are four-jointed, as is usual in the Heptageninæ. Penes are "united and broadly triangularly expanded at the base, apically forming two simple cylindrical lobes, separated by

a V-shaped incision" (McDunnough—Canad. Ent. 57: 190). The apical portion consists of three superimposed projections. The basal plate of the forceps is unlike all others of the Heptagenine group in North America, in being deeply carved out at the apical margin. Nymphs of this genus are unknown.

PSEUDIRON MCD. 1931

This genus, represented by the single species *centralis* McD., is known in the female sex only. In the female imago, the tarsi of the hind legs are fully as long as the tibia. The first tarsal joint of all the legs is slightly longer than the second, and all femora exceed the tibiae in length. Dr. McDunnough states that this genus "is probably best placed close to *Siphloplecton*" (Canad. Ent. 63: 91). However, the wings have "typical Heptagenine venation." As I am considering *Siphloplecton* and its allies as members of the subfamily Baetinae rather than of the Heptageninae, it is possible that the genus *Pseudiron* may properly belong to the Baetine group. The nymph is unknown.

NAMELESS GENUS

In 1927, Mrs. Seemann described and figured a two-tailed Heptagenine nymph from California as *Iron petulans* Seemann (J. Ent. and Zool. 19: 42—Pl. 4). Similar nymphs are in the Cornell collection. An examination of the figures and the nymphs shows that this species is not an *Iron* and presumably not an *Epeorus*. Nor is it the nymph of any known Heptagenine genus, unless it be *Pseudiron* or *Anepeorus*, the nymphs of which are not known. Characters of the nymph which distinguish it from the *Iron-Epeorus* group are:—(1) the double row of dorsal abdominal spines; (2) the absence of the characteristic triad of stout curved spines at the tip of the galea-lacinia; (3) the shape of the pronotum, which in this nymph is much widened at the anterior margin; (4) the shape and appearance of the gills, of which the first and last pairs are smaller than any of the central pairs; (5) the shape of the hypopharynx; (6) the shape of the labrum; and (7) the appearance of the mandible.

Fortunately one male nymph of this species in the Cornell collection was killed as it was transforming to the subimago stage.

It was possible to remove the subimago carefully from its nymphal skin, and mount the genitalia. The penes consist of two long slender processes, united only at the base, much as in *Rhithrogena*. These processes diverge at the tip. There is no slightest evidence of lateral or other spines, which are always visible in subimagoes of those species of *Rhithrogena* which bear spines. The first fore tarsal joint is slightly longer than the second. The second and third joints are subequal, the fourth slightly shorter, the fifth about equal to the fourth. Claws of all legs are dissimilar. Femur and tibia of the third leg are subequal, the tarsus shorter than the tibia. The wings are so crumpled that it is impossible to determine the character of the costal cross veins of the stigmatic region. In lengths of tarsal and other joints, this species does not agree with *Anepeorus* nor *Pseudiron*. Further, the genitalia are of a different type than those of *Anepeorus*.

Several male imagoes taken at Cucumonga Canyon the same spring that some of Mrs. Seemann's specimens were collected are also in the Cornell collection. These are definitely *Rhithrogenas*. The first fore tarsal joint is about one-sixth of the second; the cross veins of the stigmatic area anastomose; the penes are typical long slender processes, divergent at the tips and bearing rather prominent lateral spines. These male imagoes agree well with the description of the male imago of *I. petulans* Seemann. Further, the genitalia are similar to the published figure of that species.

Since the male genitalia of the male subimago taken from the nymphal skin bears no lateral spines, it seems doubtful if the genitalia figured on Pl. 4 (*J. Ent. and Zool.* 19) really belong with the nymph figured there. While there is no direct nor conclusive evidence, it seems not impossible that the nymph and imago of *petulans* have been erroneously associated. Although Mrs. Seemann reports rearing this species from San Dimas Canyon, she found others of the same species at Evey's Canyon (the male subimago in its nymph skin was of her collection) and at Cucumonga. Imagoes of this entire group look much alike until examined critically. If the reared specimen had been defective, it is possible that others which looked superficially

like it might have been used as the basis for the description and figures. Until other nymphs of this species have been reared, and associations clearly established between nymph and imago, I consider the species *petulans*, based on the description of the male imago, as a *Rhithrogena*. I think it is a valid species of that genus, and not synonymous with any previously described species. The nymph, however, I remove both from the genus *Iron*, and from all connection with the imago of *petulans*, and consider it a representative of a new genus. No name is given to this genus, until more evidence regarding its life history can be obtained.