

REVISION OF THE GENERA OF THE FAMILY
CAENIDAE (EPHEMEROPTERA)

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The family Caenidae is a group which has grown by addition and subtraction without any kind of review or revision since its inception as "Section 7" in the Revisional Monograph of A. E. Eaton in 1883. The result appears to me to be generic groupings which are both illogical and unnatural and, subsequently, which now block our understanding of the natural processes acting upon and within the populations of these ephemerids. Therefore, as the first step in my work on this group, I have carefully reviewed the species of the world for clues to their true phyletic relations; from this study I envisage a different and, I hope, more natural classification of the caenid mayflies.

The scope of this revision demanded, of course, that a series of specimens from across the continents be obtained. To that end, I am deeply indebted to the many ephemeropterists and institutions who loaned or donated material of this family to me. They are: the Academy of Natural Sciences of Philadelphia; the American Museum of Natural History; Dr. Lewis Berner of the University of Florida; the Canadian National Collection; Dr. Henry Dietrich of Cornell University; Mr. R. S. Crass of the Natal Parks, Game and Fish Preservation Board; Dr. George F. Edmunds, Jr., of the University of Utah; Dr. M. T. Gillies of the East African Malaria Unit; the Illinois Natural History Survey; Dr. Josette F. Lafon of the University of Lyon; the University of Nebraska; the University of Pennsylvania; Dr. J. R. Traver of the University of Massachusetts. Also, I would like to extend special thanks to the following persons: to the Davenport Public Museum, Davenport, Iowa, for support of parts of this project; to Dr. Jay R. Traver, for data on type specimens in her collection and for many other favors which she performed so tirelessly; and last, to the members of the Faunistic Survey Division of the Illinois Natural History Survey, who kindly provided the laboratory facilities used for most of the work and who also gave me many helpful suggestions and much useful advice throughout.

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HISTORICAL AND PRESENT CLASSIFICATION

The family Caenidae as considered here consists of six genera: *Brachycercus* Curtis, *Caenis* Stephens, *Caenodes* Ulmer, *Austrocaenis* Barnard, *Tasmanocoenis* Lestage, and *Caenomedeia*, a new genus described below. It was erected as the tribe Caenini by Banks in 1900 and, according to the Copenhagen decisions of the International Commission on Zoological Nomenclature, Banks should be credited with the authorship of the family. Moreover, until 1942 the various tricorythid genera were considered to be part of this family. At that time, however, Lestage showed convincingly that the caenid and tricorythid genera had evolved separately and so erected the family Tricorythidae for the latter.

Brachycercus was the first genus of the family to be described. It was erected by Curtis in 1834, with *B. harrisellus* Curtis as the type species. Until recently, the synonym *Eurycaenis* Bengtsson (1917) has been used by some workers. Next, the name *Caenis* was proposed by Stephens (1835) for the then newly described species *macrura*, which is its type species. It was unnecessarily renamed *Ordella* by Campion in 1923. In addition, these two genera were lumped and renamed *Oxycypha* by Burmeister in 1839.

In 1924 Ulmer redescribed what he believed to be *Caenis cibaria* Eaton and at once separated it from the remaining species of *Caenis* as the genus *Caenodes* on the basis of the ratios of the foreleg segments. Kimmins (1949) later demonstrated that *cibaria* was entirely different from the species described by Ulmer under that name and so renamed the latter *Caenodes ulmeri*. Then, in 1930, Lestage erected the genus *Tasmanocoenis* for the newly described species *tonnoiri*. *Austrocaenis* was described by Barnard in 1932 for his heretofore unknown species, *capensis*.

The most recent review of the present classification was presented by Demoulin (1955a). The characters he used are as follows:

Prosternum broader than long; fore coxae widely separated.

Brachycercus—antennal pedicel three times the length of the scape.

Austrocaenis—antennal pedicel twice the length of the scape.

Prosternum longer than broad; fore coxae nearly contiguous.

Forelegs of ♂ only slightly longer than the hindlegs.

Caenodes—forefemur of ♂ $4/5-5/6$ the length of the foretibia, which is only slightly longer than the foretarsi.

Forelegs of ♂ at least twice as long as the hindlegs.

Caenis—foretibia of ♂ longer than foretarsi.

Tasmanocoenis—foretibia of ♂ equal to or shorter than the foretarsi.

The points of confusion in this present system of classification are two in number. First, as can easily be seen from Table I, considerable gradation of the ratios of the various leg segments is present within the known species; obviously, the characters which have been used in the past are arbitrary, representing the extreme conditions, and so are not valid criteria for genera. As Kimmins (1956) has already pointed out, *Caenis brevipes* fairly well invalidates the genus *Caenodes* as it now stands. Moreover, *Caenis nigropunctata*, *C. cibaria*, and all of the known Nearctic species seem to lie as close to *Tasmanocoenis* as to *Caenis* in regards to the fore leg/hind leg ratio, while *Caenis valentinae* would almost be placed in *Tasmanocoenis* on the tibia/tarsus ratio alone.

Second, there is a wide variety of genitalic types in each of the genera as they now exist. Van Bruggen (1957) has pointed this out for *Tasmanocoenis*. It can be said for the others as correctly. As these structures along with the wings and forelegs are most important in the brief life of the adult mayflies, during which their only activity of consequence is mating, one would assume that the genitalia would be subject to discreet selection. Therefore, one would expect the types of genitalia to be important taxonomically in this group and not randomly distributed under various generic names.

TAXONOMIC CHARACTERS

The caenid mayflies present a combination of structures which are remarkable for their extreme reduction to a simple functional form. These ephemerids have lost their hind wings entirely, reduced and modified their venation to the sculling type of flight, greatly enlarged the thorax while foreshortening the abdomen, and, in part, reduced the genitalia to the bare essentials. All of these modifications may be said to be specializations, for they are found in many other specialized genera to some degree, e.g.

Table I.
Ratios of Leg Segments in Three Genera of Caenidae¹

Genus	Class	Foreleg/Hindleg			Forefemur/Foretibia			Foretibia/Foretarsus					
		Min.	Max.	Mean	Diff.	Min.	Max.	Mean	Diff.	Min.	Max.	Mean	Diff.
<i>Caenodes</i>	old	1.00	1.12	1.06		0.83	1.17	1.00		1.28	1.35	1.32	
	new	1.00	1.41	1.20	0.14	0.47	1.17	0.71	0.29	1.25	1.64	1.23	0.09
<i>Caenis</i>	old	1.27	2.80	1.78		0.33	0.66	0.50		1.09	1.82	1.51	
	new	1.55	2.80	2.03	0.25	0.33	0.65	0.57	0.03	1.09	1.82	1.51	0.00
<i>Caenomedea</i>	new	1.36	2.08	1.98	—	0.48	0.66	0.59	—	1.13	1.75	1.38	—

¹ Data from published sources and from personal observations of the author.

Baetis, *Homoeneuria*, *Isca*, etc. The nymphs, which have ely-troid gill covers, appear to be adapted to inhabit a wide variety of aquatic conditions, especially those of turbid water where the majority of ephemerid groups would fail. The next problem, then, is to determine the taxonomic significance of each of the structures found in this family.

Penis lobes.—Snodgrass (1957) has recently published a revised interpretation of the evolution of the male genitalia of insects. In this hypothesis, the penis lobes arose as two simple out-pocketings from the tenth segment. The penis lobes of the mayflies are cited as examples of this primitive condition. Within the family Caenidae, two extremes with various intergradations can be found. Based on the Snodgrass hypothesis, the primitive extreme (fig. 1, A and B) would be that type which has the lobes

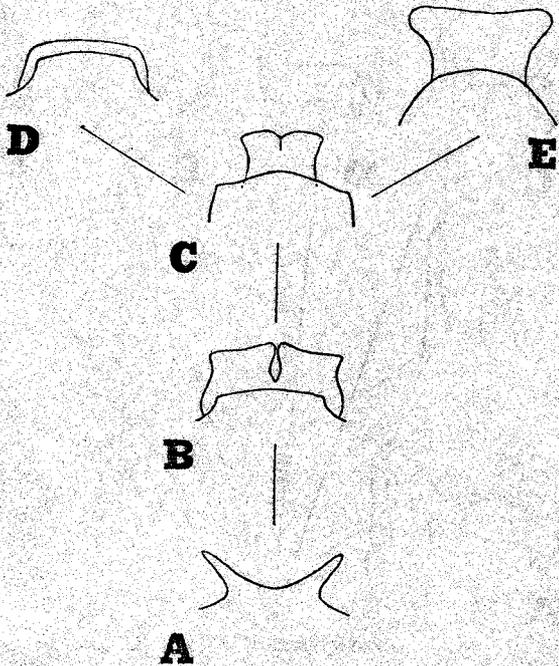


Fig. 1. The basic trend in the evolution of the penis lobes as seen in the genus *Caenis* (revised). The species are: A = *C. scotti*; B = *C. macrura*; C = *C. jocosa*; D = *C. edwardsi*; E = *C. robusta*.

almost entirely separated, while the derived extreme would be the one which has them entirely fused (fig. 1, D and E). The Nearctic species (fig. 1, C) represent an intermediate stage. Also, within the cases of the derived extreme, i.e. the two lobes fused, there are two conditions present—the penis lobes are longer than broad or broader than long. As the lobes of the primitive extreme are longer than broad, I am considering those with this condition to be the primitive ones and the others to be the secondary. The penis lobes, then, appear to reflect stages that existed in the evolution of these structures and therefore are important taxonomically as well.

Forceps.—There are five main forms of forceps in this group: barbed, as in *Caenodes ulmeri* (fig. 2, A); tufted, as in *Austro-*

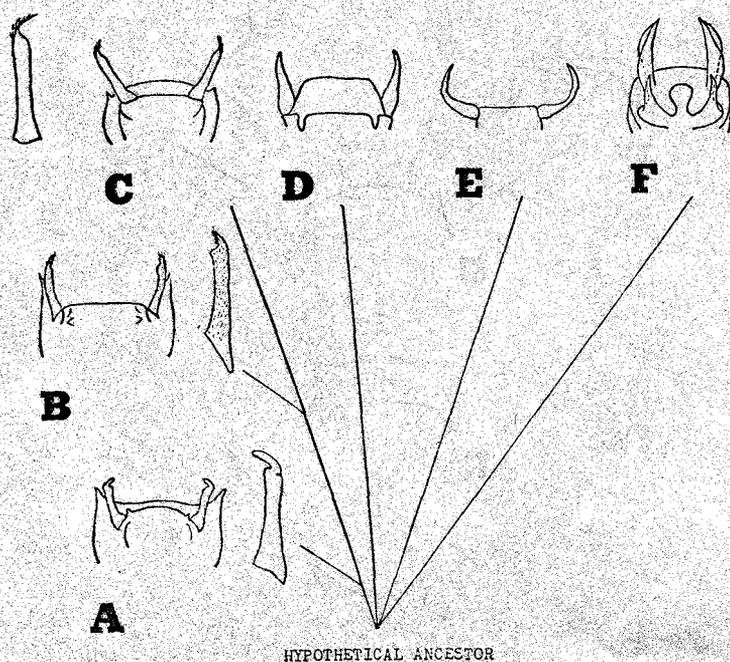


Fig. 2. The basic trends in the evolution of the forceps of caenid mayflies. The species represented are as follows (revised classification): A = *Caenodes hoggariensis*; B = *Caenodes felsinea*; C = *Caenomedea kivensis*; D = *Caenis hilaris*; E = *Tasmanocoenis tonnoiri*; F = *Brachycercus prudens*.

caenis capensis (fig. 2, C); blunt, as in *Caenis macrura* (fig. 2, D); bowed, as in *Tasmanocoenis tonnoiri* (fig. 2, E); and grooved, as in *Brachycercus harrisellus* (fig. 2, F). This variety in the form of the forceps within a single family is almost without parallel in the order, for in most other families the forceps vary but little. Thus, to analyze a situation such as this is difficult, as there is no supporting evidence from the rest of the order.

This is what I believe has happened. First, one must determine whether the caenid forceps are basically primitive or specialized in form. Spieth (1933) in his study of the phylogeny of some of the mayfly genera concluded that the forceps of mayflies were originally one-segmented. Snodgrass (1957) agrees with this in his reinterpretation of these structures. Since all of the forceps of the caenid genera are one-segmented, one might suspect that this represents a primitive condition. I do not feel that this is the case, however, for the following reasons. Foremost, the evidence of Spieth and Snodgrass consists primarily of ontological and comparative anatomical findings in the orthopteroid insects. It does not take into consideration the limited, but valuable knowledge of fossil forms which is now available. In all fossil species which appear to have been ancestral or close to the ancestors of the true Ephemeroptera, the imagal forceps are multi-segmented. I cite the examples of *Cronicus*, *Electrogenia*, *Protereisma*, *Triplosoba*, and *Hexagenites* (Carpenter 1933, Demoulin 1955*b* and *c*, 1956*a* and *b*). In addition, there are other genera in the order which have one-segmented forceps, e.g. *Homoeneuria*, *Behningia*, etc., and which are certainly specialized, thereby showing that in these cases the one-segmented condition is a derived one. Thus, I believe that the evidence given by earlier workers shows a very early condition commonly ancestral to the orthopteroid orders as a whole and persistent in the mayflies ontologically. I also believe, however, that by the time the mayflies arose as a specific group, the imagal forceps were fully segmented, and that all primitive mayflies have continued to show such a condition. In this manner, the paleontological and anatomical evidence can be made compatible. If this be the case, one must conclude that the one-segmented condition of the caenid forceps is a derived or specialized condition.

none

Second, one must consider the adaptation of the five forms of forceps mentioned above. From available evidence on mayfly reproduction, it appears that the forceps function only to hold the female during copulation. Theoretically, then, the blunt condition as well as the barbed, tufted, grooved, and bowed conditions arose under selective pressure designed to improve the function of this organ. I can offer no proof of this statement, but it is the only explanation that appears likely to me. Since there appears to be a variety of adaptive forms in this structure, the function of which is vital to the existence of the species, one would thus assume that the forceps have been involved in important evolutionary changes in the group and would be important taxonomically, also.

And last, the trend in the evolution of these forms must be determined. The evidence here is scanty. It is possible that the barbed condition represents a reduced two-segmented condition with the long proximal segment being the first and the barb the second. Also, the tufted condition may have arisen from the barbed type, for the forceps of *C. felsinea* are barbed and at the same time bear small spines (fig. 2, B). The foiled, bowed, and blunt conditions probably arose independently, however, as no integrating forms are known or even logically conceivable.

In summary, then, it is considered here that the five forms of forceps are derived or specialized conditions which have largely arisen as separate trends in the process of adaptation to the same function. Such major evolutionary changes invite taxonomic recognition.

Ratios of the leg segments.—As shown above, the ratios exhibit a wide range of variation and therefore are not reliable taxonomic criteria. In regards to the reduction of the length of the forelegs, I believe that this is the derived extreme, as it is found in other specialized genera, e.g. *Binoculus*, while the hypertrophied condition is normal to the order in general, including most primitive genera. As to the other ratios, little can be said as their functional significance is not yet understood.

Prosternum.—The genera *Austrocaenis* and *Brachycercus* both have the prosternum broader than long with the fore coxae widely separated, while the condition basically found in the order

is the opposite one. Thus, the forms of the prosternum in these two genera probably arose in the process of fore-shortening the thorax and is a derived one. I would tend to accept this condition as a rather broad and important one, becoming fixed early in the reduction of a phyletic line.

Venation.—The forewings of the caenid mayflies are obviously specialized by the process of reduction. As it is often the case that where a structure is reduced or somewhat vestigial there is a considerable amount of variation, I have considered it unwise to use the small differences existing between genera and species as reliable characteristics.

Nymphal characters.—Unfortunately, very little work has been done on the nymphs of this family up to this time. The European species are the best known, but still only in part. For the rest of the world fauna, only scattered descriptions, often incomplete, are available. Through the kindness of Dr. R. C. Crass and Dr. L. Berner, I have been able to examine a great number of reared nymphs heretofore unknown. From this material, I have been able to draw a description of the nymph of at least one species for each genus. In this work, the forms of the pronotum, gills, gill covers, and mouthparts have all proved to be useful characters, just as they have in the limited fauna studied by Macan (1955) and Kimmins (1943). Until such a time when more details are known, however, one can only utilize the small knowledge of the nymphal forms now available as a check on the conclusions drawn from the imagoes. This is the procedure used in this work.

PATTERNS OF EVOLUTION

The concept has now been presented that the forms of the penis lobes and forceps are important and specific taxonomic characters; that the form of the prosternum is a broad, but significant character; that the ratios of the leg segments and the venation are less significant ones; and that the nymphal characters are not well enough known to be of immediate use. The task now is to arrange these characters into generic patterns which are at once both natural and practical and which are the results of the evolution of these mayflies.

As the penis lobes and forceps appear to have been involved in basic changes in the evolution of the Caenidae, I believe that any classification must take these two structures into consideration above all others. There are two possible patterns that can be formed with the different types of these organs. First, one can group those species with similar penis lobes together. On the other hand, the species may be grouped according to the form of the forceps. I believe that this latter way is correct for the following reasons.

As was pointed out above, the forceps in most ephemerids do not appear to have undergone intense selection. They seem to have evolved in a much broader manner than have the penis lobes, which are usually distinct for each species. If the species are grouped according to the form of the penis lobes, i.e. the first possibility, there will be several different kinds of forceps in each genus. One would hardly expect, however, that the same type of forceps would be evolved randomly among certain species of

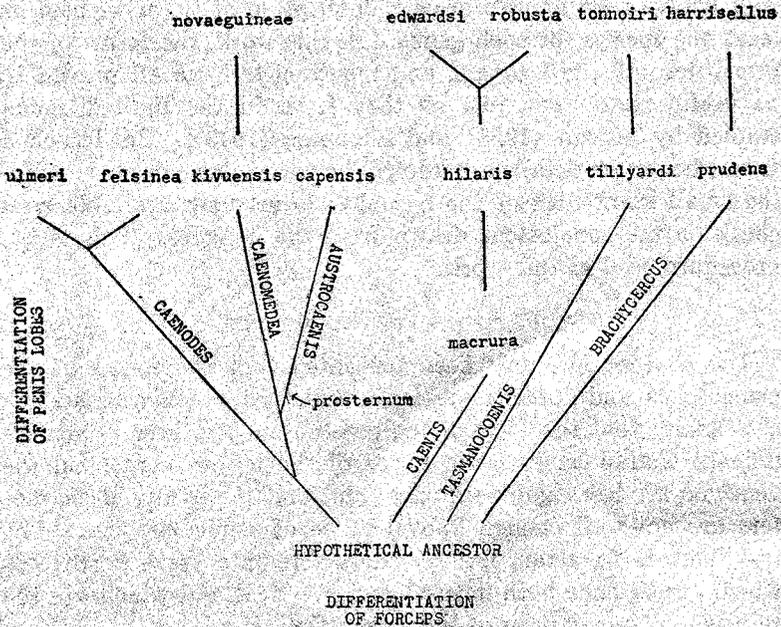


Fig. 3. A phylogenetic diagram of the revised classification of the caenid mayflies as explained in the text.

several genera, if this structure is indeed of such importance to the reproductive functions as is assumed here. Moreover, the groups would not be practical, for the boundaries between the different types of penis lobes are graded and indistinct.

If the species are arranged according to the form of the forceps, however, patterns which are both theoretically probable and also practical are formed (fig. 3). In this manner, the importance of the form of the forceps is given full weight, and the resultant groups are very distinct. Also, the different forms of the penis lobes can be arranged within each group from the primitive extreme to the derived condition. Thus, it appears to me that the caenid mayflies which have a common form of forceps also have had a common ancestry and that this was in the distant past. As a result, the genera now existing have some members with rather primitive penis lobes while others in each group have evolved the more specialized fused condition. In addition, the form of the prosternum and what is now known of the nymphal characters fit well into such a scheme, as is shown below. The ratios of the leg segments are not much affected (Table I), thereby showing the uselessness of this character. These are the reasons on which this new classification of the caenid mayflies is based.

KEY TO THE GENERA

IMAGOS

1. Base of male genitalia with two short spines; forceps foil-like, with median depression (fig. 2, F). Prosternum broader than long
Brachycercus
 - Base of male genitalia without spines; forceps more cylindrical and without median depression. Prosternum longer than broad (except *Austrocaenis*) 2
2. Male forceps with single, stout barb at tip (fig. 2, A and B) *Caenodes*
 Male forceps blunt, tufted, or bowed, without barb at tip 3
3. Male forceps with tuft of spine-like bristles at tip (fig. 2, C) 4
 Male forceps lacking such a tuft of bristles 5
4. Prosternum longer than broad, with the fore coxae nearly contiguous
Caenomedeia
 - Prosternum broader than long, with the fore coxae widely separated
Austrocaenis
5. Male forceps straight and blunt or pointed; not bowed (fig. 2, D)
Caenis
 - Male forceps strongly bowed (fig. 2, E) *Tasmanocoenis*

NYMPHS

1. Head with prominent median and smaller lateral tubercles bearing ocelli. Maxillary and labial palpi 2-segmented *Brachycercus*
Head lacking such tubercles. Maxillary and labial palpi 3-segmented .. 2
2. Gill covers with triangular ridge on dorsum and with marginal fringe of hairs. First gill 2-segmented; lamellate gills with fringe multi-fid 3
Gill covers without triangular ridge and without marginal fringe of hairs. First gill 3- or 4-segmented; lamellate gills with fringe single or bifid. Mandible without marginal tufts of hairs; labrum narrowly emarginate and without marginal fringe of hairs *Tasmanocoenis*
3. Mandibles with marginal hairs on one or both sides 4
Mandibles without marginal hairs or at most with few apical hairs on lateral side 5
4. Labrum usually narrowly, sometimes broadly, emarginate. Gill covers with large spines on mesal fork of triangular ridge; without row of submarginal spines. Tarsal claws usually with 4-5 minute spines basally *Caenodes*
Labrum broadly emarginate. Gill covers lacking such spines on ridge, but with row of minute submarginal spines. Tarsal claws without basal spines *Caenis*
5. Distal segment of labial palpi much smaller than second. Gill covers without row of minute submarginal spines. Tarsal claws broad and hooked. Prosternum broader than long, with fore coxae widely separated *Austrocaenis*
Distal segment of labial palpi smaller than second. Gill covers with row of submarginal minute spines. Tarsal claws long and slender, not hooked. Prosternum longer than broad, with fore coxae nearly contiguous *Caenomedeia*

In the following sections, it will be noted that each genus is generally divided into several complexes. Keys to these complexes have not been included, but they conform to the form of the penis lobes as shown in fig. 1 and diagrammed in fig. 3. I intend to treat them more specifically in subsequent papers.

Genus CAENODES Ulmer

Caenodes Ulmer 1924: 7.

Type species.—*C. ulmeri* Kimmins.

Imago.—Male forceps with terminal barb, without tuft of spines, though it may be finely hirsute (*C. felsinea*); not bowed or grooved. Penis lobes fused basally, but with median indentation apically, as in the *hilaris* section of *Caenis*. Prosternum longer than broad with fore coxae nearly contiguous.

Nymph.—Head without tubercles. Mandibles with lateral margins fringed with long hairs; lateral canine with 3-5 teeth, mesal one with 2-3. Maxillary palpi 3-segmented, hirsute. Labium hirsute, with palpi 3-segmented; distal segment small, about one-fourth length of second. Labrum hirsute, either narrowly or broadly emarginate medially. Gill covers with triangular ridge, the mesal fork of which bears long spines; marginal fringe of hairs present, but not submarginal spines. Lamellate gills with fringe multifid. Tarsal claws small, broad, and hooked and with 4-6 minute basal spines.

Components.—*C. felsinea* (Grandi), comb. nov.; *C. hoggariensis* (Grandi), comb. nov.; *C. jinjana* Kimmins; *C. kungu* (Eaton), comb. nov.; *C. nigropunctata* (Ulmer), comb. nov.; *C. ulmeri* Kimmins.

Distribution.—Primarily African; also from Italy, China, Java, Sumatra, and Bali.

Discussion.—The single form of the penis lobes present in the genus, which is intermediate on the evolutionary scale, as well as the distinct type of forceps, make this genus a well defined unit.

Genus **CAENOMEDEA** gen. nov.

Type species.—*C. kivuensis* (Demoulin), comb. nov.

Imago.—Male forceps with terminal tuft of spines, without terminal barb; not bowed or grooved. Penis lobes either fused basally and with apical indentation or completely fused. Prosternum longer than broad, with fore coxae nearly contiguous.

Nymph.—Head without tubercles. Mandibles lacking marginal fringe of hairs except for a few bristles on the lateral apical angle; right lateral canine with 3 teeth, mesal one with 2; left lateral canine with 4-5 teeth, mesal one with 3. Labium hirsute, palpi 3-segmented; distal segment small, about one-fourth of second. Labrum hirsute, broadly emarginate medially. Gill covers with triangular ridge, which bears long spines; marginal fringe of hairs and submarginal spines present; margins per se hyaline. First gill 2-3 segmented; lamellate gills with fringe multifid. Tarsal claws long, slender, and straight. Posternum longer than broad, with fore coxae nearly contiguous.

Components.—This new genus may be divided into two sections: *kivuensis* complex: *C. brevipes* (Kimmins), comb. nov.; *C. cibaria* (Eaton), comb. nov.; *C. kivuensis* (Demoulin). *novae-guineae* complex: *C. novae-guineae* (van Bruggen), comb. nov.

Distribution.—Africa; New Guinea.

Discussion.—I am erecting this new genus to account for what I believe has been one of the major phyletic lines in the family.

On the basis of forceps form alone, this group would be included within the genus *Austrocaenis*. However, the condition of the prosternum in the latter points to an early and separate origin. Indeed, *Caenomedeia* and *Austrocaenis* may have had a common origin, being separated by "splitting", or they may have had separate origins and then evolved convergently in regards to the forceps type. No matter, they are separate and distinct units which merit generic rank. The nymphal characters support this conclusion.

Genus **AUSTROCAENIS** Barnard

Austrocaenis Barnard 1932: 227.

Type species.—*A. capensis* Barnard.

Imago.—Male forceps with terminal tuft of spines, without terminal barb; not bowed or grooved. Penis lobes fused basally, but separate apically. Prosternum broader than long, with fore coxae widely separated.

Nymph.—Head without tubercles. Mandibles lacking marginal fringe on both sides; lateral canine with 3 teeth, mesal one with 2. Maxillary palpi 3-segmented. Labium hirsute, with palpi 3-segmented; distal segment large, about one-half of second. Labrum hirsute, broadly emarginate medially. Gill covers with triangular ridge, which bears spines; marginal fringe of hairs present, but lacking submarginal spines and hyaline margin. Lamellate gills with fringe multifid. Tarsal claws small, broad, and hooked. Prosternum broader than long, with fore coxae widely separated.

Compenent.—*A. capensis* Barnard.

Distribution.—Entirely African.

Genus **CAENIS** Stephens

Caenis Stephens 1835: 61.

Oxycypha Burmeister 1839: 796, in part.

Ordella Campion 1923: 518, new name unnecessarily proposed.

Type species.—*C. macrura* Stephens.

Imago.—Male forceps pointed or blunt, without terminal barb or tuft of spines; not bowed or grooved; longer or shorter than penis lobes. Penis lobes variable, from totally separate to completely fused. Prosternum longer than broad (though it may be almost as broad as long in some of the larger species, e.g. *C. simulans*), with fore coxae nearly contiguous.

Nymph.—Head without tubercles. Mandibles with lateral margins fringed with long hairs; lateral canine with 3 teeth, mesal one with 2. Maxillary palpi 3-segmented. Labium hirsute, with palpi 3-segmented; distal segment small, about one-fourth of second. Labrum hirsute, broadly

emarginate medially. Gill covers with triangular ridge, which lacks spines; marginal fringe and submarginal spines present. Lamellate gills with fringe multifid. Tarsal claws small, broad, and hooked and without minute basal spines.

Components.—This large genus may be divided into four sections based on the penis lobes (figs. 1 and 3): *macrura* complex: *C. bernerii* Kimmins; *C. macrura* Stephens; *C. moesta* Bengtsson; *C. rivulorum* Eaton; *C. scotti* Ulmer. *hilaris* complex: *C. amica* Hagen; *C. anceps* Traver; *C. delicata* Traver; *C. diminuta* Walker; *C. forcipata* McD.; *C. gigas* Burks; *C. hilaris* (Say); *C. jocosa* McD.; *C. latipennis* Banks; *C. nivea* Bengtsson; *C. punctata* McD.; *C. ridens* McD.; *C. simulans* McD.; *C. tardata* Traver; *C. undosa* Tiensuu. *robusta* complex: *C. horaria* (Linn.); *C. lactea* Pictet; *C. robusta* Eaton. *edwardsi* complex: *C. edwardsi* Kimmins; *C. fennica* Aro; *C. picea* Kimmins; *C. srinagari* Traver; *C. ulmeri* Brodsky; *C. valentinae* Grandi.

Distribution.—Worldwide.

Discussion.—The fact that this genus is distributed over the entire world shows that it is a highly successful competitive group. Within it are preserved species which, I think, show the evolution of the penis lobes quite clearly. The species *C. scotti* Ulmer has the lobes widely separated and therefore appears to be the most primitive member of the genus. All of the other species which are included with it in the *macrura* complex have the same basic form of penis, although several specializations are apparent. For example, *C. moesta* has developed simple ridges on each lobe, while *C. macrura* represents a condition which was probably ancestral to the first fusion of these structures.

The *hilaris* complex represents a condition in which the two lobes have fused basally, but still have an apical indentation to show their separate origin. It is interesting to note that this section includes all of the North American species.

Within the *robusta* and *edwardsi* complexes are found the specialized species of this genus. Here the penis lobes have completely fused, leaving no trace of their separate origins. The two conditions represented by these groups have been discussed above.

Genus **TASMANOCOENIS** Lestage

Tasmanocoenis Lestage 1930: 49.

Type species.—*T. tonnoiri* Lestage.

Imago.—Male forceps blunt and strongly bowed without terminal barb or tuft of spines. Penis lobes either fused basally and with apical indentation or completely fused. Prosternum longer than broad, with fore coxae nearly contiguous.

Nymph.—Head without tubercles. Mandibles lacking marginal fringe on both sides; canines with variable number of teeth (from 1-4). Maxilla with only a few hairs, no thick spines; palpi 3-segmented. Labium with few hairs; palpi 3-segmented, with distal segment small. Labrum lacking marginal fringe of hairs; narrowly emarginate. Gill covers lacking triangular ridge and marginal fringe and with only a few dorsal hairs. First gill 3-4 segmented; lamellate gills with fringe single or bifid.

Components.—*T. tillyardi* Lestage; *T. tonnoiri* Lestage.

Distribution.—Australia and Tasmania.

Discussion.—This group appears to be a highly specialized one restricted to the Australian region. The type species has been admirably reviewed by Demoulin (1955a).

Genus **BRACHYCERCUS** Curtis

Brachycercus Curtis 1834: 122.

Oxycypha Burmeister 1839: 796, in part.

Eurycaenis Bengtsson 1917: 186, new name unnecessarily proposed.

Type species.—*B. harrisellus* Curtis.

Imago.—Male forceps foil-like, with median depression; without terminal barb or tuft of spines; not bowed. Base of genitalia with two short spines (fig. 2, F). Penis lobes either fused basally and with apical indentation or completely fused. Prosternum broader than long, with fore coxae widely separated.

Nymph.—Head with prominent median tubercle and with lateral tubercles bearing ocelli. Maxillary and labial palpi 2-segmented. Prosternum broader than long, with fore coxae widely separated. Tarsal claws long and slender, not toothed.

Components.—*B. flavus* Traver; *B. harrisellus* Curtis; *B. lacustris* (Needham); *B. maculatus* Berner; *B. magnus* Tshernova; *B. minutus* Tshernova; *B. nitidus* (Traver); *B. prudens* (McD.); *B. tenella* (Navas); *B. tubulatus* Tshernova.

Distribution.—Europe and North America; very questionably Argentina.

Discussion.—This genus seems to be quite far removed from the other caenid mayflies, both by the peculiar type of genitalia and also the two-segmented condition of the palpi. Although the species could be broken down into complexes, I have refrained from doing so, as the genus is very poorly known. The species *B. tenella* (Navas), on which the record in Argentina is based, may not belong here. Its generic placement awaits confirmation after examination of the type.

CONCLUSION

It will be noted by anyone familiar with this family that many described species have been neglected in this paper. This is because the genitalia of these species have never been figured in the literature, thereby making them impossible to place in the new classification. They are best kept in their original genera until they can be accurately placed.

Moreover, I have in preparation several papers treating these same species and others in a more detailed fashion. Here will be discussed problems encountered on the species level, as well as those derived from the ecological data of the group.

The new classification which has just been described appears to fit the criteria set forth earlier—it appears to be both meaningful and practical. Whether it shall stand up to future examination is a most intriguing question, which can only be answered in due time. I can only point out that the imagoes have been thoroughly examined, so that new data from this stage is likely to come only from new forms which one always hopes may be discovered, or from studies on the internal anatomy. The nymphs present a different and more promising picture. Here numerous facts on which this classification or any other must be based lay buried. It is hoped that the present work will kindle the interest and enthusiasm of workers for these problems.

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