

SOME CRITICAL PROBLEMS OF FAMILY RELATIONSHIPS IN THE EPHEMEROPTERA

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The phyletic relationships as hypothesized in this study are based on nymphal and adult characters of a large number of genera. The classification is based principally on the amount of differentiation rather than the sequence of splitting. Hence the Siphonuridae are recognized as a family with possible phyletic relationships to all other families.

Most mayfly workers consider the Siphonuridae to be the most primitive extant group of mayflies. The general affinities of the subfamilies and the families derived from this group are indicated in Figure 1. Probably one of the first branchings in the phylogeny of the Siphonuridae was into the two basic lines, one of which leads to the Siphonurine group, and the other of which leads to *Isonychia* and its relatives. BURKS (1953) first separated *Isonychia* from other American Siphonurinae and others have separated *Isonychia* and other genera from the Siphonuridae. I place the Siphonuridae and Isonychiidae of authors all in a single family, the Siphonuridae, recognizing two basic phyletic lines. No extant mayfly retains what I believe to be the primitive (plesiomorphic) characters of the Ephemeroptera. By combining various characters from the siphonurine, isonychiine and acanthametropodine Siphonuridae, however, one can approach what the ancestral form must have been like.

The Isonychiinae are a primitive group whose nymphs have evolved a highly specialized and successful feeding mechanism. The only groups that share these highly specialized feeding modifications with the isonychiines are the coloburiscines, whose distribution is amphinotic (*Coloburiscus* in New Zealand, *Coloburiscoides* in Australia and *Murphyella* in Chile-Argentina) and the widespread but largely tropical and subtropical Oligoneuriidae (O in Fig. 1). The adults of Oligoneuriidae have an exceedingly large number of apomorphic or derived characters, being remarkably distinct from other adult mayflies. Before the evolution of the specialized feeding in the above lineages, the Heptageniidae (H in Fig. 1) split off. *Arthroplea* may have branched separately, but I am uncertain as yet that it should be removed from the Heptageniidae. However, I do not seriously object to separating it off as a separate family Arthropleidae because of its distinctive characters.

Of the members of the other phyletic line, the Siphonurinae have the largest number of plesiomorphic characters. The subfamily Rallidentinae is recognized for a single New Zealand genus, *Rallidens*, with peculiar mouthparts in the nymph but otherwise not particularly different from the *Metamonius*-group of the siphonurines. DEMOULIN (1969) has recently transferred this subfamily into the isonychiine phyletic line. This change appears to be unwarranted, and I believe that PENNIKET (1966) placed *Rallidens* approximately correctly at the time of the original description. The Siphlaenigmatidae and Baetidae are also closely related, but are considered in detail later. The Ameletopsinae are amphinotic in distribution and the larvae are all carnivorous. The four genera share a large number of morphological and behavioral characters. The genus *Chiloporter* is the most unusual member of the cluster.

The subfamily Acanthametropodinae is poorly understood at the present time. This subfamily has three described genera and one genus not yet named. The genus *Acanthametropus* was described by TSHERNOVA from Siberia and by BURKS from Illinois (as *Metreturus*). An undescribed genus occurs in Utah, Wyoming and also in Saskatchewan where it recently was found by LEHMKUHL (1970). R.W. KOSS has reared this genus in Wyoming and this has allowed us to recognize that the Chinese genus *Siphuriscus* belongs in this subfamily. There is even some suspicion that *Siphuriscus* and *Acanthametropus* are adults and larvae of a single genus. The larvae of this subfamily are carnivores and the adults have very large hind wings. The Lower Jurassic fossil genus *Stackelbergisca* also clearly belongs here.

The two subfamilies formerly recognized in the family Ametropodidae appear to represent two groups of quite separate origin. The genus *Ametropus* is thus the only genus in the Ametropodidae (Am in Fig. 1). It has a Holarctic distribution in large rivers and is a phyletically isolated genus that seems to have originated near the base of the Siphonuridae. As an isolated lineage of early origin, it is difficult to determine its relationships very precisely. The genera *Metretopus* and *Siphloplecton* are now placed as a family Metretopidae and are almost certainly a derivative of the Holarctic Siphonurinae (M in Fig. 1).

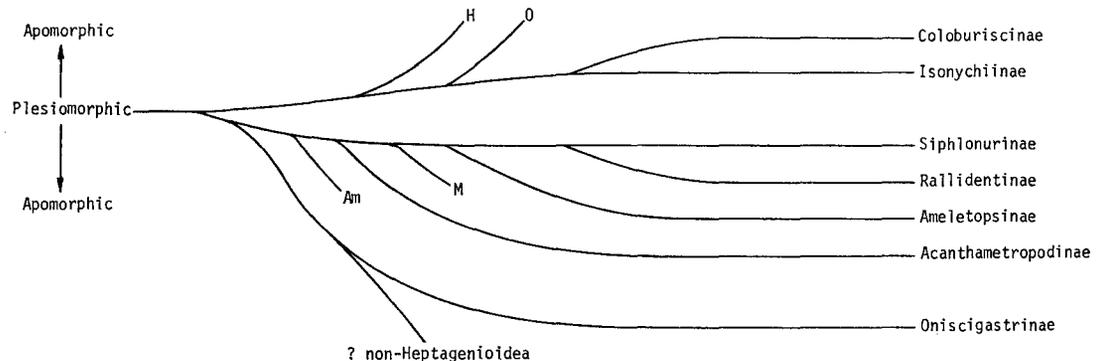


FIGURE 1. Phylogeny diagram of Siphonuridae and some of the derived families.

Some studies indicate that the peculiar amphinotic Oniscigastrinae share a number of characters with the higher, more advanced, groups of mayflies. The subfamily Oniscigastrinae of the Siphonuridae may have originated from the stem which gave rise to all of the non-heptageniod mayflies.

Figure 2 indicates some of the details of phylogeny of some Southern Hemisphere Siphonurinae and their derivatives. The upper line represents the Holarctic Siphonurinae. The *Metamonius* group is somewhat specialized and has an amphinotic distribution. *Rallidens* appears to be the nearest relative of the *Metamonius*-group because living *Rallidens* strongly resembles *Nesameletus* and others of the *Metamonius* complex in behavior and structure. In many detailed characters, other than the mouthparts, it is similar to *Metamonius*. It differs in one important character; *Rallidens* has a fibrilliform tuft on the gill which the *Metamonius* group lacks.

It is uncertain whether the ancestral Siphonuridae had a fibrilliform tuft and a gill plate or just a plate. I am inclined to concur with PENNIKET (1966) who believed that a tuft plus a plate was the primitive form. He said, "It is easier to swallow the gnat of convergent loss (or the fibrilliform tuft in the Siphonuridae) than the camel of convergent acquisition."

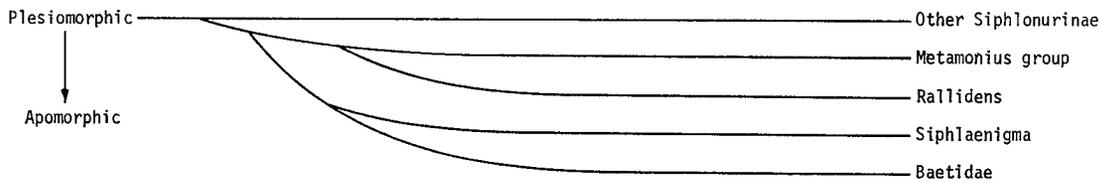


FIGURE 2. Phylogeny diagram of details of some Southern Hemisphere derivatives of the Siphonurinae.

The New Zealand genus *Siphlaenigma* (Siphlaenigmatidae) appears to be completely intermediate between the Siphonuridae and the Baetidae.

This cluster shares the apomorphic character of a ventral nerve cord in the form of a single flat ribbon. This is true in all of the Baetidae, *Siphlaenigma*, *Rallidens*, and the *Metamonius*-complex. The Malpighian tubules of the Baetidae are quite distinct from those of the Siphonurinae. The nerve cord and the Malpighian tubules of *Siphlaenigma* are of the *Rallidens* and *Metamonius* type, not of the baetine type. The Baetidae thus shows some advances in the nerve cord and in the Malpighian tubules in relation to the rest of the cluster.

In the isonychiine lineage (Fig. 3) there is a tendency for the labium and maxillae to be broad and short, and a tendency for the palpi of the labium and maxillae to fuse the last two segments.

The relationships of the Chromarcyinae have been the subject of controversy and the reasons for this are simple. The adults retain a modified derivative of the ancestral isonychiine wing venation pattern, but the nymphs are virtually totally oligoneuriid. They differ from the rest of the Oligoneuriidae in one very minute character only. The first gill in *Chromarcys* is dorsal rather than ventral as in all the rest of the oligoneuriids, but the gill structure is typically oligoneuriid. The mouthparts and all other larval characters are also oligoneuriid. A mayfly such as *Chromarcys* poses some severe problems in classification because the evolutionary grade is not the same in the two stages. Certainly on the basis of phenetic clustering using a large number of larval characters, *Isonychia*, *Chromarcys* and the oligoneuriids would form a tight cluster, with the Coloburiscinae closely clustered nearby. But if you used the adult characters, the subfamily Oligoneuriinae would separate out from all other mayflies as the most strikingly different mayfly subfamily known.

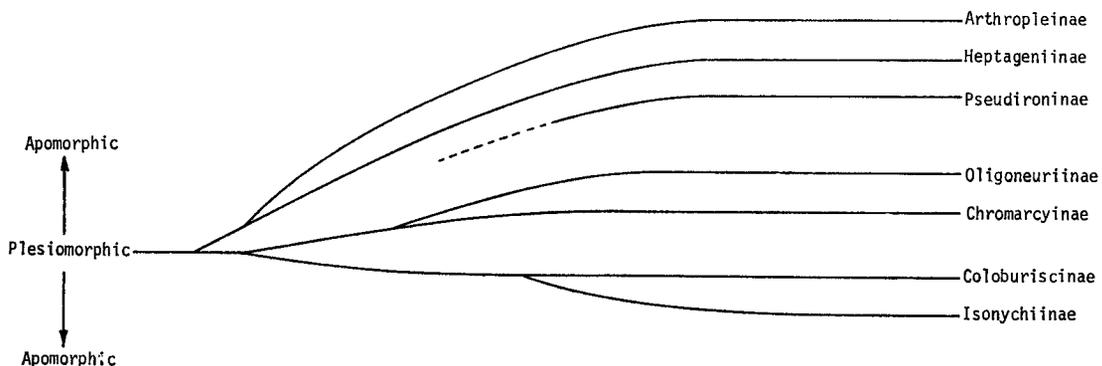


FIGURE 3. Phylogeny diagram of some details of the isonychiine lineages.

At this time the phylogenetic position of Pseudironinae is uncertain, but the genus is currently being worked on. However, it is clearly related to the heptageniid cluster.

In my view of the relationships of the families Neophemeridae, Caenidae, Baetiscidae and Prosopistomatidae, I place the Baetiscidae and Prosopistomatidae as one pair and the Neophemeridae and Caenidae as closely related. The Neophemeridae and the Caenidae share a great many characters and there are only minute differences to tell these two families apart as nymphs. This depends on the presence of developing hind wing pads in the neophemerids and the lack of hind wings in the caenids, but this in turn has led to apomorphic modifications of many kinds in the adult caenids. The relationships among these four families indicated to me by Dr. LANDA are in part based on the arrangement of Malpighian tubules. The Caenidae and the Prosopistomatidae share a greatly reduced Malpighian tubule system. I believe that the explanation as to why the Malpighian tubules are so reduced in these two families relates to the physical law of similar figures — that as you increase the linear dimensions of an object you increase its surface area to the square and its volume to the cube. This means that smaller insects need a relatively much smaller excretory system. In the Baetidae you can get an almost direct correlation between the number of Malpighian tubules and the size of the mature nymph regardless of phyletic relationship. Large mayflies have many Malpighian tubules and small ones relatively few.

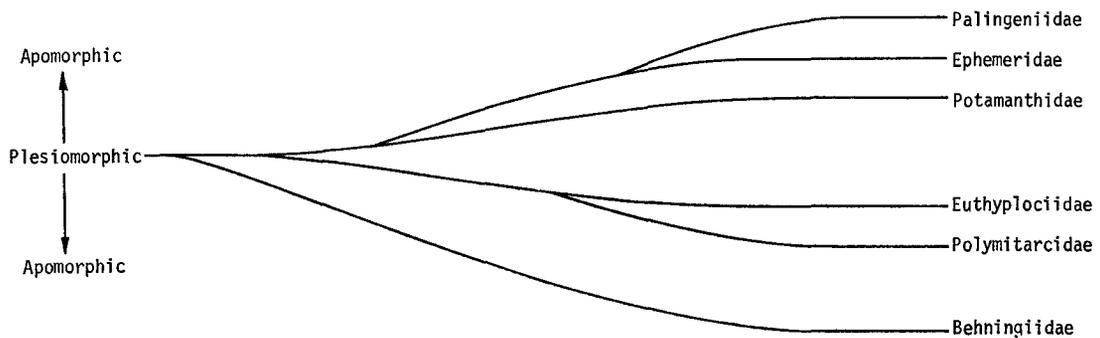


FIGURE 4. Phylogeny diagram of the Ephemeroidea.

Baetisca and *Prosopistoma* have a carapace covering the gills. The point at which that carapace hits the abdominal terga is the same in both of them and there are many other similarities. Both have the last ganglion of the nervous system in the metathorax. There are many other characters that would lead me to group these together in this way, but the argument boils down to which characters you are willing to admit are convergent. That is really the basis of disagreement, I believe. This is unfair to Dr. LANDA who is not here to defend himself.

In the Ephemeroidea there are three groups that either lack mandibular tusks or where most of the larvae do not burrow. These are the Potamanthidae, which generally occur on stones rather than in burrows, the Euthyplociidae which generally do not burrow and are found on stones, and the Behningiidae which burrow in loose sand but have no mandibular tusks. The burrowing habit and its adaptations in this group seem to be a very important character, and I think the relationships are not quite as I thought originally. I have been told that the very early instars of one species of *Potamanthus* do burrow. Perhaps because they do not have the proper gill and burrowing mechanisms, they are forced to the surface as they become larger and

then resume a life on exposed surfaces. I would not be surprised to find the same character discovered in the Euthyplociidae, but we have no evidence for it. The Behningiidae are very peculiar mayflies, as will be seen by those of you who go to the Blackwater River. Most of those who have tried to understand the relationships of this family have agreed that Behningiidae are Ephemeroidea. This is indicated by their internal anatomy and their gills. Their position within the Ephemeroidea is less certain.

The Polymitarciidae are true burrowers apparently derived from the non-burrowing Euthyplociidae and the Ephemeridae are a burrowing family derived from the non-burrowing Potamantidae. The old-world family Palingeniidae seem to be derived directly from the Ephemeridae. There are some plesiomorphic characters that occur in this lineage that show up in the most primitive genera of each of these burrowing families that tend to tie them rather closely to the ancestral family. This concept is quite different from one of my earlier diagrams in which I placed the Potamantidae and the Euthyplociidae as closely related. The Potamantidae and Euthyplociidae seem to represent an adaptive grade rather than a pair of closely related families. In other words, my former grouping of these two families was based on symplesiomorphic characters rather than on synapomorphic characters.

You will notice that as my title indicated I have not tried to review all of the relationships within the Ephemeroptera, but merely a few critical problems on which new data have become available.

RÉSUMÉ

Quelques problèmes critiques à propos des relations entre les familles des Éphéméroptères

Dans cette étude les relations phylogénétiques sont déterminées à partir des caractères larvaires et adultes d'un grand nombre de genres. La classification est basée essentiellement sur le degré de différenciation plutôt que sur la séquence des ramifications. C'est pourquoi les Siphonuridae sont considérés comme une famille ayant des relations phylogénétiques éventuelles avec toutes les autres familles.

Les Siphonurinae primitifs conservent beaucoup de caractères plésiomorphiques de même que les Isonychiinae qui ont un système trachéal plésiomorphique. On suppose que ces deux lignées se sont séparées très tôt. Apparemment un pré-Isonychiinae a donné naissance aux Heptageniidae (comprenant les Arthropleinae) et un proto-Isonychiinae a donné naissance aux Oligoneuriidae et en conséquence aux Coloburiscinae. La place des Pseudironinae n'est pas certaine.

Les pré-Siphonurinae ont donné tôt naissance aux Oniscigastrinae. Les Ametropodinae et les Acanthametropodinae ont très tôt formé des groupes distincts à partir des pré-Siphonurinae. Les Metretopodidae semblent être une ramification précoce d'un proto-Siphonurinae. Apparemment un proto-Siphonurinae a donné naissance aux Ameletopsinae carnivores. Les Rallidentinae d'une part et les Siphlaenigmatidae plus les Baetidae d'autre part proviennent d'un Siphonurinae de type proto-*Metamonius*.

Chez les Oniscigastrinae on trouve un mélange de caractères plésiomorphiques et apomorphiques suggérant un origine possible à partir d'un pré-Siphonurinae et que l'ancêtre de tous les non-Heptagenioidea pourrait être un pré-Oniscigastrinae.

Il y a trois lignées phylogénétiques d'Ephemeroidea chez lesquelles manquent soit les prolongements mandibulaires, soit les membres antérieurs utilisés pour le fouissage. Les Pota-

manthidae présentent les caractères les plus plésiomorphiques et les proto-Potamanthidae ont donné naissance aux Ephemeroidea fouisseurs dont une des branches a donné naissance à son tour aux Palingeniidae. Les Euthyplociidae ont de grands prolongements mandibulaires mais leurs membres ne sont pas fouisseurs. Les Polymitarciidae dérivent apparemment des proto-Euthyplociidae. Les Behningiidae sont si uniques par tant d'aspects qu'ils doivent s'être individualisés très tôt à partir des pré-Potamanthidae. Les larves sont fouisseuses des sables mouvants. Elles n'ont pas de prolongements mandibulaires et les membres sont grandement modifiés. Les familles d'Ephemeroidea Potamanthidae et Euthyplociidae semblent être ainsi des lignées paraphylétiques plutôt que des familles ayant en commun des caractères synapomorphiques.

Les Neoephemeridae semblent occuper une place centrale dans la séquence évolutive de quatre petites familles. Une première cassure semble séparer les Neoephemeridae, Caenidae et les Baetiscidae-Protopistomatidae. La réduction des tubes de Malpighi des Caenidae et Protopistomatidae sont des caractères convergents accompagnant la réduction de taille de ces insectes. L'ancêtre de ces quatre familles doit avoir été une ramification précoce de la lignée non-Heptagenioidea.

ZUSAMMENFASSUNG

Einige kritische Probleme der Familienverwandtschaften von Ephemeroptera

Die phyletischen Verwandtschaften wie in dieser Studie hypothesiert, sind auf Charakteren von Nymphen und Erwachsenen von einer grossen Zahl der Gattungen basiert. Die Klassifikation ist im Prinzip eher auf die Menge der Verschiedenheit als auf die Folge der Aufspaltung aufgebaut. Darum sind Siphonuridae als eine Familie mit möglicher phyletischer Verwandtschaft zu allen anderen Familien anerkannt.

Die primitiven Siphonurinae behalten viele plesiomorphischen Charaktere wie auch die Isonychiinae, welche ein plesiomorphisches Tracheensystem haben. Hypothetisch haben sich diese zwei Linien abgezweigt. Eine pre-Isonychiinae Form hat scheinbar den Heptageniidae (einschliesslich Arthropleinae) Ursprung gegeben, und eine Proto-Isonychiinae gab den Oligoneuriidae und folgend den Coloburiscinae Ursprung. Die Position der Pseudironinae ist ungewiss.

Von einer Pre-Siphonurinae sind die Oniscigastrinae früh abgestammt. Die Ametropodinae und Acanthametropodinae haben auch einen frühen isolierten und separaten Ursprung von den Pre-Siphonurinae. Die Metretopodidae scheinen ein früherer Abzweig von den Proto-Siphonurinae zu sein. Ein Proto-Siphonurinae gab scheinbar dem karnivoren Ameletopsinae Ursprung. Die Rallidentinae und Siphlaenigmatidae plus Baetidae stammten von einem Proto-*Metamonius* Type Siphonurinae ab.

Die Oniscigastrinae haben ein Gemisch von plesiomorphischen und apomorphischen Merkmalen, was nahelegt, dass sie von einen Pre-Siphonurinae abstammten und dass der Vorfahre von all den Non-Heptagenioidea auch ein Pre-Oniscigastrinae war.

Es sind drei phyletische Linien von Ephemeroidea, die entweder mandibulare Fangzähne oder bohrende Vorfüsse mangeln. Die Potamanthidae haben die meisten plesiomorphischen Charaktere, und Proto-Potamanthidae gaben den bohrenden Ephemeroidea Ursprung, wovon eine Linie den Palingeniidae den Ursprung gab. Die Euthyplociidae haben grosse Fangzähne, aber die Beine sind nicht fossorial. Die Polymitarciidae scheinen von den Proto-Euthyplociidae abgestammt zu sein. Die Behningiidae sind in vieler Hinsicht so eigenartig, dass

sie früh von Pre-Potamanthidae abstammend sein müssen. Die Nymphen sind im lockeren gleitenden Sand bohrend. Sie haben keine Fangzähne, und die Beine sind hoch modifiziert. Die Ephemeroidea Familien Potamanthidae und Euthyplociidae scheinen darum eher paraphyletisch zu sein als andere Familien mit denen sie synapomorphische Charaktere teilen.

Die Neoephemeridae scheinen zentral in der evolutionären Sequenz von vier kleinen Familien zu sein. Die basische Spaltung scheint die Neoephemeridae-Caenidae und Baetiscidae-Prosopistomatidae zu sein. Die reduzierten malpighischen Schläuche der Caenidae und Prosopistomatidae sind zusammenlaufende Merkmale, in Beziehung zu der kleineren Grösse dieser Insekten. Der Ahne von den vier Familien muss eine frühe Abzweigung von der non-Heptagenioidea Linie sein.

DISCUSSION

E. RIEK : How do you account for the very marked difference in venation between *Baetisca* and *Prosopistoma*? I'm referring to the absence of any evidence of a triad development on MA in the illustrations of *Prosopistoma*. Every other mayfly has evidence of a triad.

G. EDMUNDS : *Prosopistoma* has a very peculiar and greatly reduced venation as do many very small mayflies that fly rapidly.

E. RIEK : It is very different from Caenidae in the basal region of the wing.

G. EDMUNDS : Yes, and I am aware of the fact that the mouthparts of these two families are strikingly different also.

E. RIEK : I don't place much weight on mouthparts.

G. EDMUNDS : You also could have asked me about the extremely small and remote eyes in *Prosopistoma* but this always occurs in exceedingly tiny mayflies. It probably has to do with depth of perception.

B. RUSSEV : Vor 5 oder 6 Jahren haben sie eine Arbeit über die Klassifizierung der Eintagsfliegen publiziert. Ich möchte hier im Sinne dieses Berichtes fragen, ob gewisse Veränderungen in der systematischen Stellung der verschiedenen Familiengattungen jetzt im Verhältnis zu diesen Arten von Publikationen sind.

G. EDMUNDS : The classification for the Ephemeroidea is quite different. I cannot recall many other changes.

V. PUTHZ : As I understood you, the four branches below Siphonurinae (in Fig. 2) had synapomorphy because of the nervous system but the Baetidae are different from the middle three because of their Malpighian tubules. Why do you place the *Siphlaenigma* together with the Baetidae and not with *Metamonius*?

G. EDMUNDS : I am willing to defend the phylogenetic diagrams. Now we come to the arguments concerning the relationships between phylogeny and a classification system. When PENNIKET first sent *Siphlaenigma* to me I told him it was intermediate between Siphonuridae and Baetidae. As most workers know, the Baetidae in most of the world are a very well defined and distinctive family. They are quite easy to key. They share many synapomorphic characters, and therefore they make a nice family unit. *Siphlaenigma* tends to destroy that unity to some extent. When PENNIKET asked me what he should do in the classification with *Siphlaenigma*, my answer was that he could place it in the Baetidae, or in the Siphonurinae, or propose a new family, which is what he chose to do. I am willing to follow that decision. What I am saying is that I feel much more certain about treating the phylogeny in this case than I do the classification. The Baetidae are a very convenient family to define and therefore it should not

matter to most people what we do with *Siphlaenigma* as long as we understand its phylogeny which matters a great deal in the zoogeography of the group. From the standpoint of classification each group is still monophyletic. If I follow a purely HENNIG system, I will raise group after group to family level, but I will be unable to write a key that anyone who needs it can use.

V. PUTHZ : You suppose one ancestor for *Siphlaenigma* and Baetidae. Then there should be apomorphic characters to separate these two groups from the other three (other Siphonurinae, *Metamonius* group, and *Rallidens* in Fig. 2).

G. EDMUNDS : The genitalia of *Siphlaenigma* are intermediate. The venation is intermediate, having some of the venational characters of the Baetidae, but not all of them. Externally the nymph is baetid, totally. It is very easy to key to the Baetidae, but internally it has the Malpighian tubules of the Siphonurinae and the nervous system of most of the Siphonurinae. We are dealing with a continuity. Dr. Koss, what is the egg like?

R. KOSS : It is siphonurine.

E. RIEK : In both lines, the Baetidae and *Siphlaenigma*, you have reduction, whereas in the rest of the Siphonuridae you have total characterization. You have reduced gills. You have reduced spines on the abdomen. You have reduction in the Malpighian tubules, but not as much in *Siphlaenigma* as in the Baetidae. Everything is on a reduction in both the nymphs and adult, and it is a toss-up as to where you draw the family line. I put *Siphlaenigma* into Baetidae, myself, and draw the point of furcation further back, because there is no definite character, but everything is being reduced in both stages.

G. EDMUNDS : I couldn't argue with this because I don't feel that there is any real solution to this. It is a solution of convenience for classification and I don't want to get into an argument of the relationship of classification to phylogeny. But you cannot do historical zoogeography from anything but a phylogenetic diagram. Every classification system available obscures phylogeny. There is no system of classification that will not obscure phylogeny because classification cannot be all things to all kinds of biologists.

L. BRUNDIN : What did you say about the connections between classification and a phylogenetic system — that it is impossible to combine them? I think you must be wrong there because it is quite easy to explain all known phylogenetic relationships in a group classification.

G. EDMUNDS : You have said that you can explain relationship by a linear system and on another page of your same book you say it can only be done by means of a phylogenetic schedule. I agree with you totally only on the phylogenetic schedule.

L. BRUNDIN : But you have four groups here and they are related to one another (Fig. 2). You can express exactly that in a linear system in a book, in print, in a classification. You are treating first these two groups and then all of them together, or you can start from the other end. You have a classification here actually.

G. EDMUNDS : If you can start from either end, can that explain the same thing?

L. BRUNDIN : No, but in your diagram there you showed Baetidae as a sister group for one New Zealand genus, *Siphlaenigma*. You then have only two possibilities. You can put this New Zealand genus into Baetidae and make a subfamily or you raise this New Zealand group to a family.

G. EDMUNDS : It is now a family. Do I then have to raise the *Metamonius*-group to a family?

L. BRUNDIN : Only such an arrangement can give a sound classification.

G. EDMUNDS : Can I call Siphlaenigmatidae one family and *Metamonius*-group one family without calling *Rallidens* one family?

L. BRUNDIN : No, but do the "other Siphonurinae, *Metamonius*-group and *Rallidens*" (Fig. 2) now belong to the Siphonuridae ?

G. EDMUNDS : Yes.

L. BRUNDIN : Then your diagram must be wrong, because you have Baetidae as a sister group of this New Zealand genus only.

G. EDMUNDS : *Rallidens* is a sister group of the *Metamonius*-group. The *Metamonius*-group is a sister group of the other Siphonurinae.

L. BRUNDIN : Yes, but the whole thing is impossible according to your diagram.

G. EDMUNDS : Yes, it is impossible in the HENNIG-BRUNDIN system according to my diagram.

L. BRUNDIN : Your phylogenetic diagram says one thing and your classification says another.

G. EDMUNDS : I agree.

L. BRUNDIN : Your diagram and classification ought to fit together some place.

R. KOSS : Is everything in Figure 2 except the Baetidae in one family ?

G. EDMUNDS : No, not *Siphlaenigma*. The others are in one family. What I call the Siphonuridae, Dr. LANDA has split into several families, and I think as more studies are made, the family Siphonuridae will eventually be split into a number of separate families. This family is the base group of all living mayflies.

L. BRUNDIN : According to your diagram the family Baetidae is a subgroup within the family Siphonuridae.

G. EDMUNDS : Phylogenetically, that is true. I think that the problem of applying classification to phylogenetic data systems is the reason some people want to abandon classification systems or to abandon phylogenetic data for classification, which I think is a hopeless outlook.

E. RIEK : I would disagree with Dr. EDMUNDS only in the basal fork in Figure 2. To me the *Metamonius*-group is the stem of the siphonurids, but I have accepted the current system of a family, Baetidae, as an easily defined group within the Siphonuridae, although it is to my way of thinking only a subfamily of Siphonuridae. For convenience, I am using Baetidae.

G. EDMUNDS : My arguments are the same using the family level for convenience, but I can answer you in one case. The ventral nerve cord in these groups seems to be a very poor ancestral model for divided nerve cords in other groups.

R. KOSS : I agree with Dr. EDMUNDS on the family arrangement. I think the diagram is confusing because Dr. EDMUNDS has *Siphlaenigma* listed as a genus and it should have a family ending. We consider Baetidae as a separate family, Siphlaenigmatidae as a separate family, and the top three groups in Figure 2 as a third family. My only point of disagreement is that I feel that Siphlaenigmatidae probably had a common stem with the Siphonurinae, rather than the Baetidae. They seem to be more siphonurine-like.

G. EDMUNDS : The Siphonurinae are a pre-group of *Siphlaenigma* and the Baetidae a post-group of *Siphlaenigma*. When you talk pre-group, group, postgroup, then you are fine. We can ask, is a man more closely related to his father or his son ?

R. KOSS : Yes. You could apply that to the whole order, except that then you wouldn't have any dividing lines that make any sense. What I'm saying is that I do not think that Siphlaenigmatidae is necessarily the intermediate group between Siphonurinae and Baetidae. I do not think there is common ancestry between Siphlaenigmatidae and Baetidae, because there is nothing I see on eggs of Baetidae which shows that they have any derivation from Siphlaenigmatidae.

G. EDMUNDS : One of the very important things that must be done is to find out if the Australian and Chilean *Baetis* are a sister group of *Siphlaenigma*. Some of these forms are very similar to *Siphlaenigma*.

R. Koss : Can I go to a different diagram (Fig. 1)? Can I ask you why you chose to consider the Isonychiinae lineage as more primitive than the Oniscigastrinae? Your line going to Oniscigastrinae indicates it to be much more apomorphic than the Isonychiinae. By putting Oniscigastrinae where you have, it looks like the egg types of Coloburiscinae and Isonychiinae have evolved independently from the rest of the family.

G. EDMUNDS : I think we are talking about the fact that the more primitive phyletic lines on this diagram have symplesiomorphic characters in the eggs.

R. Koss : I feel that Oniscigastrinae has the most plesiomorphic egg type which gave rise to the rest.

G. EDMUNDS : All stages and all parts of the organism evolved at different rates. That is the only answer I can give you.

R. Koss : I am just asking why you have Isonychiinae where you do. What are the reasons for making it more primitive than Oniscigastrinae?

G. EDMUNDS : *Isonychia* has a primitive tracheal system and other primitive characters, but no one organism on the phylogenetic diagram has all the plesiomorphic characters.

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