

THE CLASSIFICATION OF THE EPHEMEROPTERA ¹

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INTRODUCTION

Although there has been general agreement at the family or subfamily level, there has been little agreement on the higher classification of the Ephemeroptera. EDMUNDS (1962) ably reviewed the earlier schemes (NEEDHAM, TRAVER and HSU 1935; BURKS 1954; EDMUNDS and TRAVER 1954; DEMOULIN 1958), and presented a concise outline of a new classification. EDMUNDS, ALLEN and PETERS (1963) made slight changes to this classification and dealt with it in more detail although the interrelationships between the superfamilies are not adequately discussed. ILLIES (1968) accepted this classification.

Earlier classifications have tended to emphasise the structure, especially wing venation and tarsal segmentation, of the adults, whereas I consider that the nymphs offer a sounder basis for an outline of the higher classification of the order, although supporting evidence of the distinctiveness of some nymphal types is supplied by the adults. I agree with EDMUNDS and ALLEN (1966) that a knowledge of the immature stages is essential to the task of reconstructing the probable phylogeny of the order. LANDA (1959) has shown that the internal anatomy of the nymphs is also significant in this respect.

The proposed classification (Fig. 1) differs from that of EDMUNDS, ALLEN and PETERS (1963) mainly in separation of the Heptageniidae from the Baetoidea and elevation to superfamily status equivalent to the Leptophlebioidae. However, there are apparently greater differences between the two schemes when one considers the presumed interrelationships between the superfamilies.

Although the Prosopistomatidae and Baetiscidae are referred to the same superfamily at present, the differences, both in nymphs and adults are such that a more-detailed study may indicate that they are not as closely related as at present assumed. The Prosopistomatidae, in which the venation is very reduced, are the only Recent mayflies in which there is no evidence of a triadic branching of MA. The Baetiscidae, on the other hand, have the most generalized venation of all Recent species; the venation differs from that of the Lower Permian *Misthodotidae* mainly in the basal alignment of the veins. There is also a slight reduction in the anal field.

The position of the Caenoidea is also somewhat doubtful but, as pointed out by EDMUNDS, ALLEN and PETERS (1963), the evidence seems to indicate that the superfamily is most closely related to the Baetiscidae. There is a distinct similarity between the nymphs, if one makes allowance for the extreme development of the carapace and the correlated changes that have taken place in the Baetiscidae. However, there, is a difference in the caudal filaments. They

¹ Figures 1 and 2 modified after presentation at the conference, and do not correspond to some of the discussion.

are of siphonurid form with lateral hair fringes in Baetiscidae whereas the hairs are in whorls in the Caenoidea, in correlation with the sluggish habits of the nymphs.

There has also been doubt about the relationships of the Ephemerellidae-Tricorythidae complex. The slow-moving nymphs have the hairs on the long caudal filaments in whorls, as in Leptophlebiidae, Caenoidea and Heptagenioidea. The nymphs resemble those of Caenoidea in having a relatively large thorax. They can also be compared with some nymphs of the Leptophlebiidae. The gill structure is unique within the Ephemeroptera. However, it seems most probable that the ephemerellid type gill is a derivative of the type occurring in the Leptophlebiidae. The position of a few poorly-known genera, at present referred to the Tricorythidae, remains in doubt. They may be more closely related to the Leptophlebiidae than to the Ephemerellidae.

I am of the opinion that the Heptagenioidea, Leptophlebioidea and Ephemeroidea are all derivatives of a siphonurid-like ancestor along independent lines, and that there is as much justification for recognizing the superfamily Heptagenioidea as there is for recognizing the Leptophlebioidea and Ephemeroidea.

The nymphs of the Ephemeroidea are, basically, burrowers and the gills are modified accordingly. There can be no confusion between the gills that are developed in Ephemeroidea and those of any other mayfly nymph. A few Ephemeroidea are sprawlers in fast water but, nevertheless, they have the typical ephemeroid-type gills.

The nymphs of both Leptophlebioidea and Heptagenioidea are basically sprawlers although those of *Jappa* (Leptophlebiidae) are semiburrowers. The caudal filaments bear whorls of setae in both superfamilies, which differ in the nymphs mainly in the shape of the head. The labrum is widely exposed in Leptophlebioidea and concealed, or almost so, by the enlarged frons, in Heptagenioidea. There is also a difference in the usual type of abdominal gill. There is usually a fibrillar tuft at the base of the single gill lamella in Heptagenioidea whereas there is never a fibrillar tuft and the gills are usually bilamellate in Leptophlebioidea.

I consider that the shrimp-like, actively swimming type of nymph that is of general occurrence in Siphonuridae and Baetidae (Baetoidea) is the basic form of mayfly nymph and that all other nymphal types have been derived from it. The first recorded mayfly nymphs, from the Lower Permian, are of the generalized siphonurid type with short caudal filaments bearing only lateral hair fringes.

The actively swimming type of nymph would have been better adapted than other types to withstand the rigors of life at the period when insects were making their first appearance. The landscape at the time that the first land plants were becoming established would have been subjected to marked erosion. The upper reaches of the streams would have been very unstable and the stream bed of the larger rivers would have consisted mainly of shifting sand in the lower reaches. It would have been difficult to maintain aquatic life, initially, in the upper reaches of the streams whereas the actively swimming type of nymph would be well adapted to the lower reaches. Primitive nymphs of Siphonuridae and the nymphs of Baetiscidae live under these conditions today. The nymphs of Baetiscidae are basically very primitive; the only specialization is development of a large thoracic carapace and the correlated changes both in internal and external anatomy. Other nymphs that live under the same conditions also combine primitive and specialized attributes. The predaceous nymphs of *Pseudiron* (Siphonuridae) have long thin legs with long tarsal claws, and the nymphs move spider-like on the sandy bottom. *Dolania* (Behningiidae) is a most efficient burrower; the body is covered with stout bristles to reduce abrasion by the sand grains. Behningiidae are the only Ephemeroidea to have the first gill fully developed.

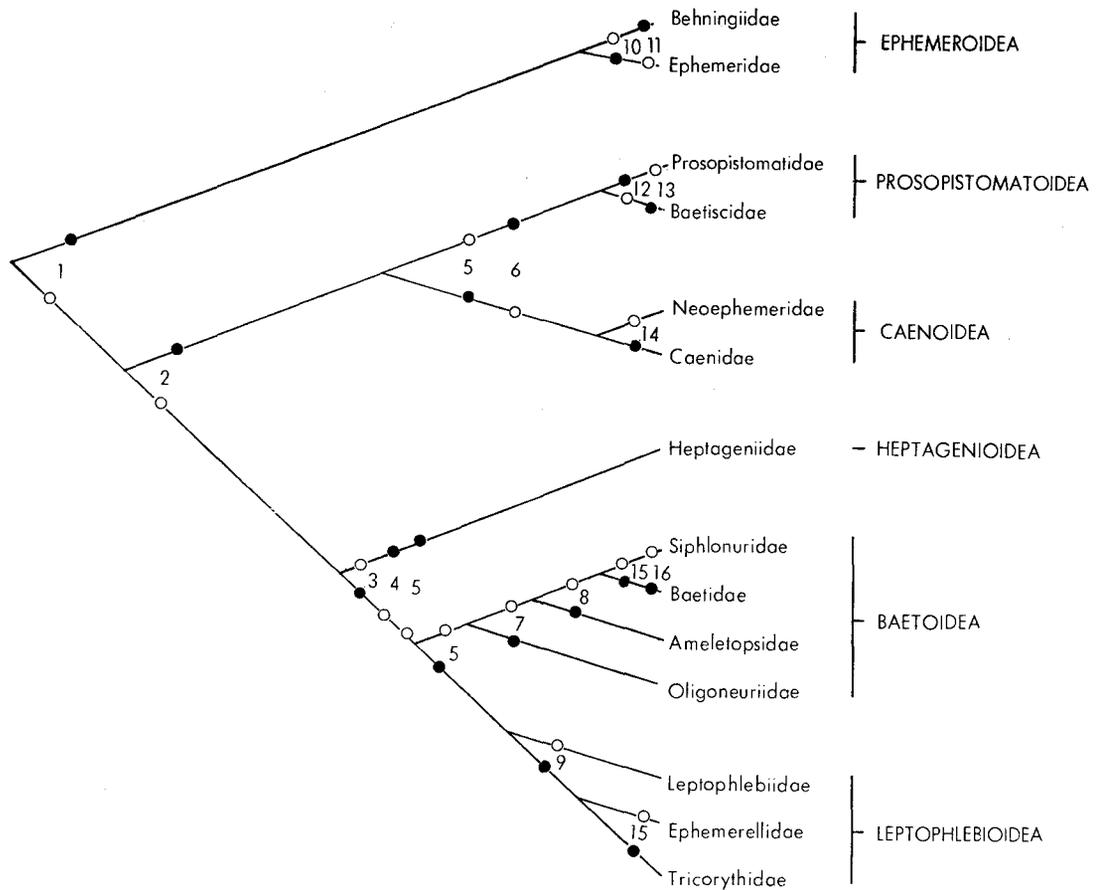


FIGURE 1. Phylogeny of the Ephemeroptera. Apomorphic state, represented by a blackened circle, defined.

1. Gill of specialized type, with very dense margining of long, fine, respiratory filaments. [Fringes, when present in other nymphs, either fine hairs or coarser lobes of the gill.] Nymphs basically burrowers, a few secondarily sprawlers in fast water. [Other nymphs not burrowers, except *Jappa* (Leptophlebiidae) and a very few, very specialized Oligoneuriidae.] Venation with distinctive MP field, with MP2 strongly curved at base towards CuA or fused with it for a short distance. [A similar development also in Neophemeridae but then Rs arises some distance from wing base.] Marginal intercalary area between MP and CuA. [Also present in Neophemeridae and Ephemerellidae.]

2. Second abdominal gill operculate and gills joined or overlapping at meson, except when the thoracic carapace covers the gills. [When operculate or semioperculate gills are present on the second segment in Ephemerellidae and Tricorythidae, they are not joined at meson by interlocking hair-fringes.] Hairs on caudal filaments not forming dense lateral fringes except in Prosopistomatidae, hairs either in whorls or lateral fringes not dense and regular. [The development of the hairs on the caudal filaments is correlated with the habits of the nymphs to a marked extent. The hairs are in whorls in nymphs that are basically sprawlers.]

3. Segmentation of hind tarsi of adult reduced from the basic five segments. [Five segments present only in Heptageniidae.]

4. Abdominal gills with a fibrillar tuft. [A fibrillar tuft that is a functional gill is also developed sometimes on other parts of the body. The tuft on the abdominal gills was apparently developed independently a number of times in the Ephemeroptera. A tuft occurs also in most Oligoneuriidae, in Ameletopsidae, in *Pseudiron* (Siphonuridae), in *Siphlaenigma* (Baetidae), and in Neophemeridae.] Frons produced, usually completely covering clypeus and labrum. [The frons is also somewhat produced in Oligoneuriidae, in at least one baetine genus, and to a slight extent in some Leptophlebiidae. This development is correlated with habitats in swift water.]

5. Hairs on caudal filaments in whorls. [Hairs in whorls are correlated with habits. This condition is present in all

The generalized siphonurid type of nymph swims as actively as do fish of comparable size, and apparently it is the abdominal gills that provide the main propulsive force after the initial flipping of the tail-fan. The so-called abdominal gills are, basically, articulated, muscled, reduced appendages, and only secondarily function as gills in the majority of species. They are not essential to normal respiration in a number of mayfly nymphs (WINGFIELD 1939), especially some Baetidae and Siphonuridae. There are no abdominal "gills" in *Murphyella*, the nymphs of which do not swim but live between rocks in fast water. There are, however, respiratory gills on other parts of the body.

ABDOMINAL GILLS

The abdominal "gill" of a mayfly nymph is basically a single lamella, with strengthened fore and hind margins. It has a relatively fine, median tracheal trunk that is more or less equally branched to both sides. The "gill" does not function as a respiratory structure, and the tracheal trunk and its branches are apparently associated with the respiratory needs of an actively moved organ (a swimming paddle) and not with a general respiratory exchange between the nymph and the water in which it lives. The "gill" articulates by a single condyle in a manner similar to that of a coxa. The basal thickening that forms the condyle is joined to both fore and hind thickened margins, more especially to the fore margin. The gill is moved by a pair of abdominal muscles inserted at its base. This basic type of lamellar swimming paddle occurs almost unaltered in *Ameletus* (Fig. 3).

The plate-like primary processes may be variously modified, and may become functional gills, although in many species a secondary respiratory lobe is added to the primary "gill".

The "gills" sometimes develop a fibrillar tuft that arises, ventrally, from close to the base of the "gill." The fibrillar tuft is thin-walled and abundantly supplied with tracheal branches. It is the functional gill. This type of abdominal gill with a basal fibrillar tuft is present in most Heptageniidae, most Oligoneuriidae, Neophemeridae, in *Pseudiron*, *Isonychia*, *Mirawara*, and a few other Siphonuridae. The fibrillar tuft of the first gill may be very large and the lamellar portion reduced or absent, as in most Oligoneuriidae.

The fibrillar tuft is absent in *Arthroplea* and *Epeorus*, and may be variously modified in other Heptageniidae. The basal portions of each lobe of the tuft may be united into a lamella but the filaments remain free at the apex in all. The plate-like "gills" are sometimes markedly

sprawlers with the exception of the Euthyplociinae (Ephemeridae)]. Nymphs basically sprawlers. (Burrowing nymphs in *Jappa* (Leptophlebiidae).

6. Carapace covering abdominal gills.
7. First maxillae with fibrillar gill tuft. Filter feeders. [Maxillary palps 2-segmented.]
8. Predaceous nymphs in which maxillary and labial palps are multiarticulated.
9. Venation specialized, with distinct marginal intercalaries between MP and CuA, or venation reduced.
10. First abdominal gill reduced, but sometimes with two lobes. Mandibular tusk present. CuA2 strongly divergent from CuA1 in fore wings, and with cubital intercalaries parallel to CuA1.
11. Venation very specialized. Nymphs specialized sand burrowers, the body with tufts of stout bristles for protection against abrasion by sand. Gills directed ventrally.
12. Venation radial, cross veins absent. Body markedly flattened. Mouthparts specialized.
13. Hair fringes on caudal filaments not dense. Gills on sixth abdominal segment forming valves to the gill chamber.
14. Venation almost radial. Cross veins very reduced.
15. Venation reduced.
16. Tarsi 3-segmented. Nymphs without pleural spines or spines very reduced.

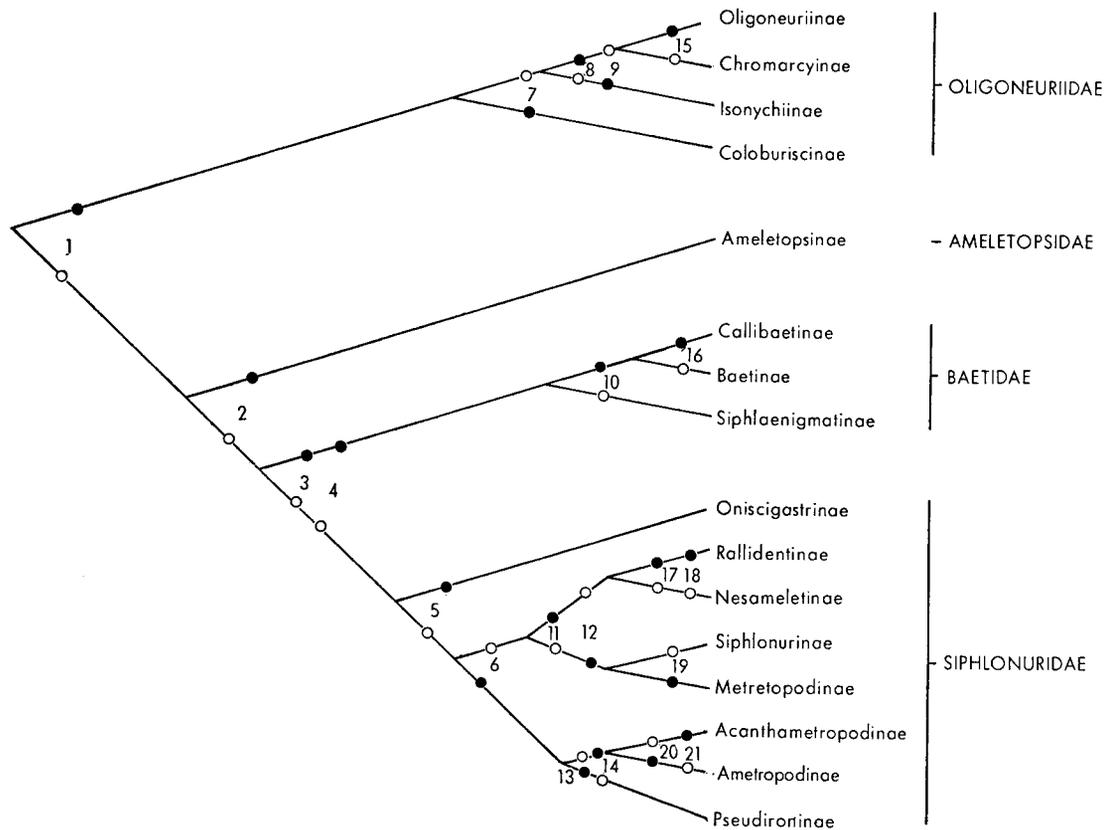


FIGURE 2. Phylogeny of the Baetoidea. Apomorphic state, represented by a blackened circle, defined.

1. First maxillae with a fibrillar gill tuft. Filter feeders. [Maxillary palps 2-segmented.]
2. Predaceous nymphs in which maxillary and labial palps are multiarticulated.
3. Tarsi 3-segmented in adult. Nymphs without pleural spines on abdominal segments 8 and 9 or spines weak.
4. Cross veins reduced, sometimes absent.
5. Thickening of anterior portion of all gills or first gill semioperculate. Head with processes and ridges and basal abdominal tergites each with a median spine. Nymphs settle into sand and silt.
6. Mouthparts of predaceous type. Legs long, with long tarsal claws.
7. Abdominal gills of very modified form, with deeply bifid apex, or absent.
8. Frons produced over clypeus and labrum. Nymphs cling to rocks in swift water or are semiburrowers or burrowers. Sc absent, or present only apically in fore wings.
9. Gill tuft present at base of fore coxae.
10. Cross veins absent (not partially indicated). Nymphs without pleural spines on abdominal segments 8 and 9.
11. Mouthparts modified, for scraping algae from substrate.
12. Gills with at least a distinct posterior widening or with development of an overfolded secondary lobe.
13. Labial palps 2-segmented. Caudal filaments with reduced fringes. Spider-like movements of nymph. Fore legs hypertrophied in female. [Marginal intercalaries in cubital field.]
14. Tibiae shortened, each very much shorter than tarsi. Prosternum and mesosternum with median process.
15. First gill ventral, the fibrillar tuft enlarged. Venation reduced, specialized.
16. Tarsal claws of nymph long, simple, with two long lateral fringes.
17. Fibrillar tuft present and gill single.
18. Mandible with a terminal row of recurved setae.
19. Fore tarsal claws bifid. Maxillary palps 2-segmented [Labial palps 2 or 3-segmented.]

expanded and all combine to form an adhesion disc, as in *Rhithrogena*, and then the basal fibrillar tufts are directed dorsally although, as in other nymphs, they arise from the ventral surface of the gill. The tufts would not be able to perform a respiratory function if they were enclosed within the adhesion disc that enables the nymphs to maintain a hold in swift waters. The single plate-like gill lamella present in Heptageniidae is abundantly supplied with tracheae and apparently it, too, functions as a gill, in addition to the fibrillar tuft.

A similar respiratory fibrillar tuft is sometimes developed on other parts of the body of mayfly nymphs. A tuft is present on the fore coxa, mesally, in *Isonychia*, on the first maxilla, posteriorly, in *Isonychia*, Coloburiscinae (Siphonuridae), Oligoneuridae, and on all coxae, mesally, in *Baetodes* (Baetidae).

The plate-like gills are wider and thinner, and the margins less thickened in *Parameletus* than in the basic type of lamellar swimming paddle that is present in *Ameletus*. The tracheal trunk is relatively large and the process apparently functions as a respiratory structure as well as a swimming paddle, and can correctly be referred to as a gill. The gills in Baetidae are usually broader than in *Ameletus* but the posterior thickening is at the posterior margin, as in *Parameletus*. The size and branching of the tracheal trunk varies within the family. There is a large, well branched tracheal trunk in the *Callibaetis* group that lives in weed-beds in slowly flowing or even standing waters. (The gills are bilamellate in *Cloeon*). However, the trunk is small and the branching incipient in the *Baetis* group that live in swift waters and are very active swimmers. *Ametropus* has gills similar to those of *Parameletus* except that each gill has a margining of long, fine hairs that apparently protect against the fine sand and silt in which the nymphs rest partly buried on the bottoms of large sandy rivers.

Development of a basal lobe on the posterior margin of the gill increases the respiratory surface in *Siphonisca*. Further increase in respiratory surface in this type of gill occurs in a number of ways. Gills 2-5 of *Oniscigaster* have a distinct lobe on the posterior margin of the gill, finer in texture than the main portion of the gill, and the lobe is secondarily fluted. A similar but unfluted posterior lobe is folded up dorsally to overlies the main part of the gill of gills 2-4 of *Tasmanophlebia* and *Siphonella*.

The gill may have a ventral lamellar outgrowth from close to the base of the gill and similar in appearance to the gill, as in the first two gills of *Siphonurus* and all gills of most Leptophlebiidae. These ventral outgrowths are folded longitudinally in the first three gills of *Siphonoplecton*.

The expanded posterior margin of the gill is deeply dissected and has numerous fine processes in *Baetisca* and *Acanthametropus*.

Some gills have a dorsal lamellar outgrowth from the base, posteriorly, of the gill, as in gills 3-7 of some species of *Siphonurus*. (These species have a ventral lamella on gills 1-2 and a dorsal lamella on gills 3-7).

The gills are sometimes markedly expanded so that all gills together form an adhesion disc, comparable with that present in the nymphs of *Rhithrogena* but without a basal fibrillar tuft, as in *Epeorus* and *Arthroplea* (Heptageniidae). The fore margin of the expansion is thickened in *Epeorus* to give better adhesion to the substrate. In *Kirrara* (Leptophlebiidae) only gills 2-7

20. Gills with distinct marginal hair fringe. Nymphs settling into sand and silt. Fore tarsal claws with a few, long, stout, lateral spines. Prosternal process a backwardly-directed median plate. A large endite on fore coxae. [Marginal intercalaries in cubital field.]

21. Gills deeply dissected posteriorly. Maxillae with apex produced to a sharp point. Two caudal filaments in adult. [Three caudal filaments in Ametropodinae.]

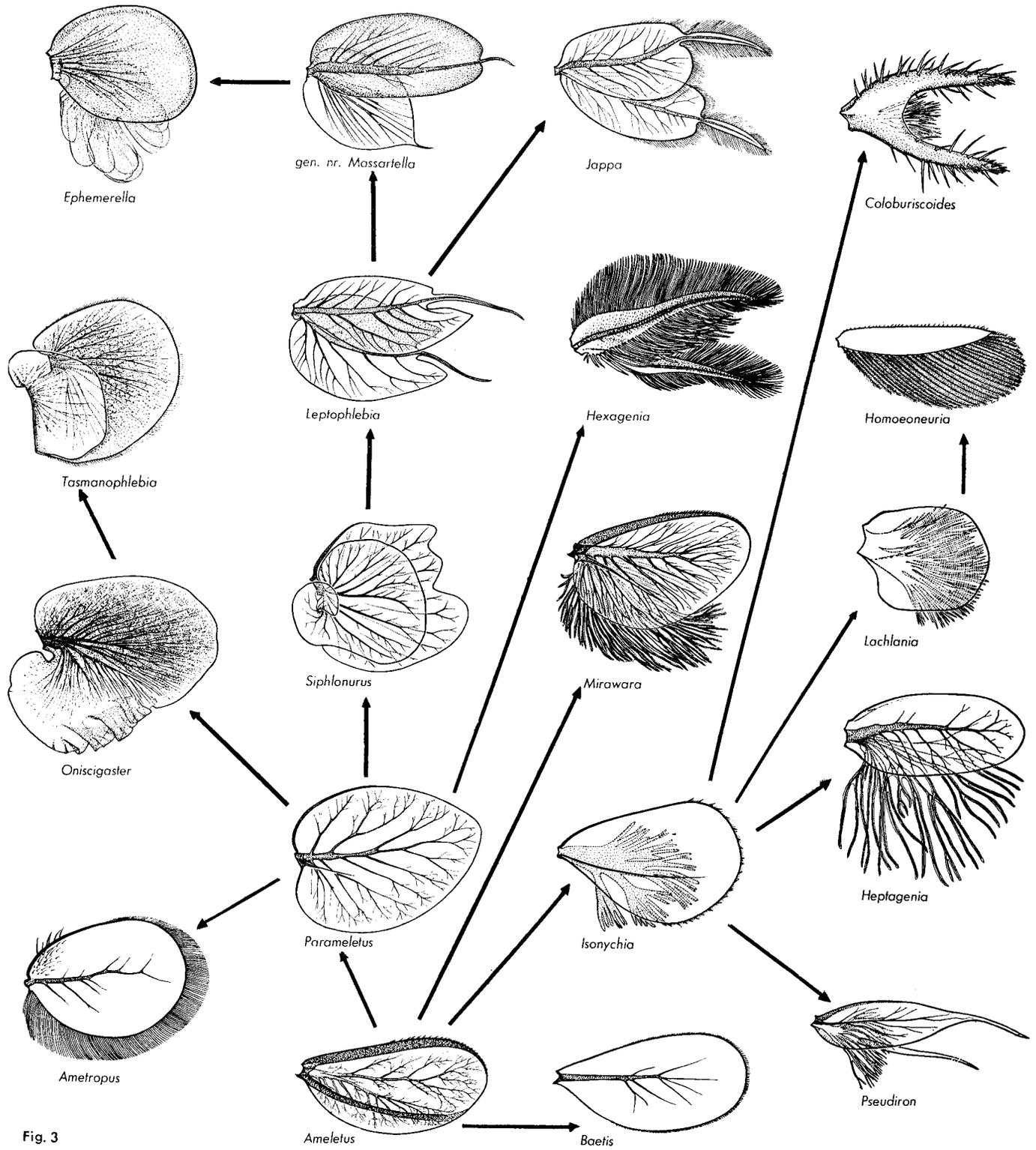


Fig. 3

FIGURE 3. Trends in the development of mayfly gills (gill 3).

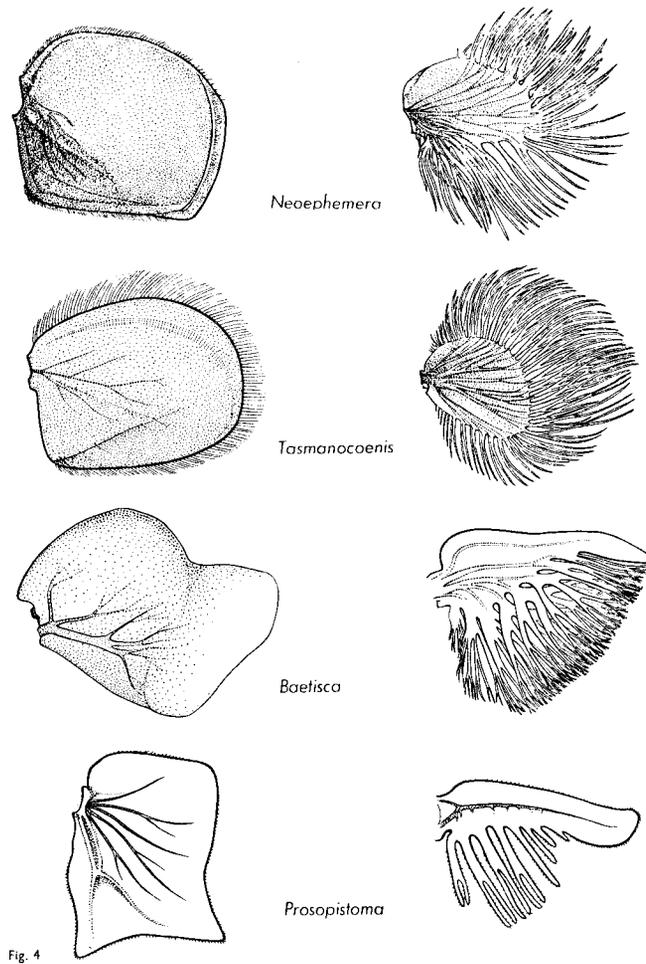


FIGURE 4. Gill structure of Prosopistomatoidea and Caenoidea (gills 2 and 3).

are expanded. These suction type gills are well supplied with tracheal branches but it is not known whether this is correlated with a general respiratory function or with individual respiratory requirements of a very active organ. The nymphs live in very fast-flowing well aerated waters in which large gills are not usually developed. There is sometimes a tendency for the first or second gill or for portions of several gills to be thickened and to act as a protecting cover for the functional respiratory portion of the gills, as in *Oniscigaster*, *Tasmanophlebia* and *Siphonella*. In *Oniscigaster* the first gill and the outer (exposed) portions of the next 3 or 4 gills are thickened. In *Tasmanophlebia* and *Siphonella* the first gill is operculate although the two opercula do not meet at the meson. In Caenidae, Neophemeridae and Baetiscidae (Fig. 4) the second gill is the operculate gill. Gills on different segments are operculate or semioperculate in Ephemerellidae and Tricorythidae.

In *Coloburiscus* and *Coloburiscoides* the anterior and posterior areas of the gills are very heavily sclerotized and bear stout moveable spines whereas the central lamellar portion of the gill is markedly reduced or absent. These stout, spiny gills apparently aid the nymphs in

maintaining a hold between boulders and rubble in very swift waters. They may possibly serve a small respiratory function in *Coloburiscus*, but in *Coloburiscoides* the fibrillar tuft that is present is probably the only functional respiratory part. The closely related *Murhpyella* does not have abdominal gills. However, all three genera have fibrillar gill tufts on anterior parts of the body.

The gill lamella is reduced in width and the gill has a posterior fringe of long, stiff, fine hairs in some Oligoneuriidae. The tracheal trunk is very fine. The gills apparently protect the body against abrasion by fine sand grains in these burrowing nymphs of *Homoeneuria* and *Oligoneurisca*. These processes may also help to create water currents over the functional respiratory gill on the first maxilla. There is a thin-walled, finger-like, ventral outgrowth arising some distance from the base of the gill in *Pseudiron*. The process has a tracheal branch that arises from the main tracheal trunk. This outgrowth is probably comparable with the secondary lamella of other nymphs and its rather distal origin may be an adaptation in nymphs that move spider-like across the sandy bottoms of fast water.

Each abdominal gill is typically double in Leptophlebiidae, and the two lamellae are usually similar in structure and similarly supplied with tracheae. The gills are apparently functional respiratory structures. They are usually larger in species from slow-flowing waters than in those from fast-flowing waters. In a few genera, the apex of each gill lamella is divided into a few to many lobes (*Habrophlebia* and some species of *Atalophlebia* s.lat.) or the entire margin may be lobed (*Traverella* and some species of *Atalophlebia* s.lat.). Occasionally the lower (posterior) lamella of the gill is reduced or absent, especially, as in *Kirrara*, when most of the gills are modified into a combined adhesion disc. The first gill of *Kirrara*, which does not enter into the suction disc, is reduced in size but it is a double lamella. The margins of the gills are usually bare but there is a margining of long, very fine hairs on the apical portion of each lamella in *Jappa*. These hairs are similar to those on other parts of the body of these burrowing nymphs.

The upper lamella of the gill is thickened in the *Massartella* group. It protects the lower, thinner lamella in these sluggish nymphs which, in many respects, resemble those of the Ephemerellidae.

The nymphs of the Ephemerellidae have very distinctive lamellate gills that consist of a thickened lamella from which arise, ventrally, a number of flattened processes. In some respects these processes resemble flattened fibrillar tufts. Although the gills are very unusual they can be derived more readily from those of the Leptophlebiidae than from any other mayflies.

The gills of the Ephemeroidea are very different from those of all other Ephemeroptera, but they have most probably been derived from a form similar to the bilamellate type that is present in most Leptophlebiidae. Each of the two lobes of the gill consists of a fleshy central stem and a dense series of fine, lateral, respiratory filaments. The gills are important in respiration (MORGAN and GRIERSON 1932). There is a very large, central tracheal trunk but the lateral respiratory filaments are not traversed by obvious secondary tracheal branches and, in this respect, differ noticeably from the markedly dissected gills that are present in a few Leptophlebiidae. However, the anlage of the lateral filaments of the Ephemeroidea may be represented by the fine hairs that are present on the whole surface of the narrow gills of some species of Leptophlebiidae and are well developed on the apical portion of the gills in the burrowing nymphs of *Jappa*.

I am therefore of the opinion that the different types of gills present on the abdomen of mayfly nymphs have all been derived from the siphonurid type which, in the initial stages, was a single, lamellar, non-respiratory appendage used for locomotion. Also, that the basic

mayfly nymph was an active swimmer of siphonurid form. The nymphs of *Ameletus* and *Parameletus* are probably close to the archetype mayfly nymph.

NYMPHAL FORM

The nymphal form of the Prosopistomatoidea is similar in many respects to the siphonurid form, with a more or less shrimp-like body ending in short caudal filaments bearing only lateral hair fringes. *Baetisca* resembles the Siphonuridae in gill structure except that the upper (posterior) margin of each gill, except the enlarged second gill, is deeply dissected and developed into respiratory filaments similar in appearance to the lobes of the fibrillar tufts that are sometimes developed in Baetoidea. A strengthening of the lower (anterior) margin of the gill, comparable with that in Baetoidea, is distinct on the posterior gills.

The nymphs of the Ephemeroidea are mostly burrowers that are also active swimmers. The Euthyplociidae are, secondarily, sprawlers in fast water. The nymphs of Ephemeroidea have short caudal filaments with lateral hair fringes, as in Baetoidea and Prosopistomatoidea. The gills are double and each gill lamella is margined all round with long, finger-like respiratory filaments. Although the filaments are fine they differ in structure from the long hairs present on other parts of the body.

The nymphs of the Caenoidea are semi-burrowers in which the gills on the second abdominal segment are modified into opercula, as in Baetiscidae. The nymphs are slow-moving and inactive on the silty bottoms of slowly-flowing streams. The rather long cerci have hairs in whorls.

The nymphs of the Heptagenioidea and Leptophlebioidea are not active swimmers although they are able to swim feebly through dorso-ventral undulations of the body. The nymphs run on the substrate, sometimes very swiftly, especially nymphs from fast-flowing waters. The long cerci have hairs in whorls. The unilamellate gills of the Heptagenioidea resemble those of the Isonychiinae and Ameletopsidae, whereas those of the Leptophlebioidea are usually bilamellar processes comparable with those in Siphonurinae and both lamellae have a respiratory function.

Thus, the nymphs, especially in the structure of the gills and development of hairs on the caudal filaments, indicate that there have been different lines of development from the actively swimming siphonurid type in which the hairs on the caudal filaments are restricted to the lateral margins. The Prosopistomatoidea developed a large carapace but were otherwise unmodified. The Ephemeroidea became burrowers and changed the type of abdominal gill but retained the swimming type caudal filaments. The Caenoidea developed sluggish habits living on silty surfaces; the functional gills are protected by an operculum and the hairs on the cerci are in whorls. The Heptagenioidea and Leptophlebioidea are independently developed sprawlers, and both have the hairs on the cerci in whorls.

ADULTS

Specializations in the structure of the adults have not paralleled those in the nymphs.

Wing venation and tarsal segmentation are the attributes of the adults used most extensively in definition of the higher categories of the Ephemeroptera, but LANDA (1969) has shown that the internal anatomy is also important. The 5-segmented hind tarsi have been used to define the

Heptageniidae but even this attribute must be used with caution because segmentation is rather indistinct in *Rhithrogena* which, on attributes of the nymph, is unquestionably referred to the Heptageniidae. The hind tarsi are 4-segmented in most other Ephemeroptera but they are only 3-segmented in Baetidae.

The wing venation, also, must be used with caution because within each superfamily there is a comparable range in venation from the fully developed condition with abundant cross veins to one in which cross veins are very reduced or absent. Prosopistomatidae (Prosopistomatoidea), Caenidae (Caenoidea), Baetidae (Baetoidea) and Tricorythidae (Leptophlebioidea) represent comparable end-points in separate trends.

Correlated with a reduction in cross veins there is usually a reduction in the development of the hind wings. The hind wings are always much smaller than the fore wings, and are absent in a number of species. The hind wing venation is much more reduced and the homologies of the veins less readily determined than are those of the fore wings.

The Lower Permian Misthodotidae have the most generalized mayfly venation. The hind wings are fully developed, and similar in venation to the fore wings. I consider that the venation of *Baetisca* is less specialized than that of any other Recent mayfly and that, except for the deeper forking of MP and reduction of the more caudal anal veins, it can be compared closely with the Permian Misthodotidae. The most significant differences between the fore wings of *Baetisca* and those of other Recent mayflies are associated with the cubital and anal fields. CuA and CuP are close and parallel in *Baetisca* and connected by a series of cross veins except that there may be a few short branches at the wing margin or short marginal intercalaries. The anal field is reduced in *Baetisca*, in correlation with reduction in the hind wings, as compared with Misthodotidae. However, the anal field is larger and 1A extends further along the posterior margin of the wings in *Baetisca* than in any other Recent mayfly.

Specializations in the fore wing venation of Recent species are basically the result of reduction in the size of the hind wings, with a correlated shift in the position of the tornus in the fore wings. The tornus is placed towards the middle of the hind margin in primitive Siphonuridae and both CuA and CuP are relatively straight. As the hind wings are reduced, the tornus approaches closer to the base of the wings, and CuP is progressively more curved close to the wing margin.

In the initial stages of shortening of CuP, the distal cross veins that originally joined CuA and CuP extend from CuA to the wing margin as a series of short pectinate branches of CuA, as in most Siphonuridae. With an increase in reduction of CuP the number of branches is reduced to 4 and these branches become detached from CuA in various ways to produce the distinctive venations of the Heptageniidae, Ametropodidae, Metretopodinae, Pseudironinae, Ephemerellidae and Leptophlebiidae. The intercalaries are not fully detached in a number of Heptageniidae but the number of branches from CuA is smaller than in Siphonuridae. There are usually less than four intercalaries in Leptophlebiidae but, when there are four (in *Habrophlebia*), as in Ephemerellidae, two are very short.

Both CuA and CuP shorten slightly in Ephemeroidea and this results in the development of intercalary veins between MP₂ and CuA. Similar intercalaries are developed in the more reduced venations of the Ephemerellidae. The most significant specialization in the venation of the Ephemeroidea has been a widening of the MP field and a forking of the vein very close to the wing base. A similar development has taken place in the Neophemeridae.

There is considerable variation in the cubital field in Ephemeroidea. There are numerous, sigmoidally curved, pectinate branches from CuA to the wing margin in Euthyplociinae. The stems of these branches are sometimes joined to form a secondary vein parallel to CuA. There

are fewer, less regular branches in Ephemerinae. (This subfamily is also distinguished by the numerous pectinate branches from 1A to the wing margin.). CuA is distinctly forked in Palingeriinae, with one or more secondary branches within the fork; these branches are parallel to CuA₁. There are free marginal intercalaries in the cubital field in Potamanthinae.

I consider that the Baetiscidae have retained the greatest number of generalized attributes in fore wing venation, in the absence of cubital intercalaries or distinct branches of CuA, and in the long 1A that extends to a point on the wing margin that is occupied by CuA in other species. As the anal field becomes reduced in other species, the cubital field, initially, increases in size. The cubital field is well developed in Heptagenioidea, Ephemeroidea and generalized Baetoidea. Expansion of the cubital field is restricted to the distal area in Ephemeroidea whereas the expansion extends more towards the base in Baetoidea and Heptagenioidea. The cubital field, as well as the anal field, is reduced in most Leptophlebioidea.

Superfamily PROSOPISTOMATOIDEA

The Prosopistomatidae and Baetiscidae are united in the same superfamily mainly on the structure of the nymphs in which the first abdominal segment is almost completely fused with the thorax and the dorsum of the thorax is fused into a carapace that covers the basal segments of the abdomen. In most other respects the nymphs are very different, and there are also marked differences in the adults. The two families differ markedly in the structure of the mouthparts of the nymphs and in the relationship between head and thorax. The wing venations of the adults are totally unlike, although this difference is due in part to the very reduced venation in Prosopistomatidae. However, the apparent absence of any indication of branching of MA in Prosopistomatidae is a unique attribute in the Ephemeroptera, unless the Upper Carboniferous *Triplosoba* is referred to the order. The Baetiscidae are the only Recent mayflies in which CuA and CuP are connected by cross veins for the greater part of their length.

However, until a detailed comparative study of these two families has been completed it is deemed preferable to refer them to the same superfamily.

Superfamily CAENOIDEA

The Caenoidea (Caenidae and Neoephemeridae) have very distinctive nymphs that are semiburrowers that move slowly on the surface of fine silt or lie partly buried in it. For this reason, the functional abdominal gills are protected by an operculate gill cover developed from the second abdominal gill. The first gill is reduced to a very small finger-like lobe that bears long hairs. The short cerci have the hairs in whorls.

There is a distinct similarity in basic structure between these nymphs and those of *Baetisca*. The main differences are those correlated with the development of a large carapace in *Baetisca* and the development of the hairs on the caudal filaments of the Caenoidea in whorls, in correlation with their sluggish habits. However, the first gill is large in *Baetisca* whereas it is very reduced in Caenoidea.

There is a marked difference in venation between the Caenidae and the Neoephemeridae. Cross veins are almost absent in the radial venation of the Caenidae. The cross veins are only slightly reduced, and there are marginal intercalaries in the Neoephemeridae. In most other res-

pects the venation of the Neophemeridae can be compared closely with that of the Potamanthinae (Ephemeroidea), especially in the marked deflection of MP_2 towards CuA close to its base and the development of intercalary veins between MP and CuA. The rather distal origin of Rs and its origin on R are distinctive attributes of the venation of the Neophemeridae.

Thus, there is a conflict between the nymphs and the adults in arriving at an understanding of the probable affinities of the Caenoidea. However, I am of the opinion that the structure of the nymphs is more significant than that of the adults in deducing affinities within the Ephemeroptera. Close relationship between the Caenoidea and the Prosopistomatoidea is supported by studies on the internal anatomy of the nymphs (LANDA 1959).

Superfamily BAETOIDEA

The nymphs are, basically, active swimmers of shrimp-like form. The Coloburiscinae (Siphonuridae), even though of typical body form, do not swim actively but cling between rocks and rubble in fast-flowing waters. When forced to swim they do so by dorso-ventral undulations of the body, as in the Leptophlebiidae. A number of species settle on fine sand or silt into which they partly sink; these nymphs are usually more flattened than is general and the gills are modified into semioperculate or operculate gill-covers (Oniscigastrinae : Siphonuridae). The nymphs of the Oligoneuridae are very specialized and some are burrowers and semi-burrowers. Most of the abdominal gills are very reduced in this family but the gill on the first segment is greatly enlarged in many, and usually directed ventrally.

Although there are modifications in body form from the typical shrimp-like nymph, all Baetoidea have short caudal filaments in which the hair fringes are restricted to the lateral margins. The hair fringe is on both sides of the median filament, when this is present, but the fringe is only well developed on the median side of the cerci except in a few primitive genera in which it is developed, distally, in addition, on the lateral side, as in *Baetisca*.

The venation of the adults varies from the complete venation of the Siphonuridae to the very modified venation of most Oligoneuriidae and the very reduced venation of the Baetidae but in all species MP branches some distance from the wing base and the posterior branch diverges only slightly.

The venation of the Ametropodinae, Pseudironinae and Metretopodinae resembles that in Heptageniidae but, on the reduced segmentation of the hind tarsi and attributes of the nymphs, especially in the development of hair fringes only laterally on the caudal filaments, I consider that these subfamilies are more closely related to the Siphonuridae than to the Heptageniidae. EDMUNDS, ALLEN and PETERS (1963) referred *Pseudiron* to the Heptageniidae but I agree with BURKS (1953) in referring the genus to the Ametropodinae [s.lat.] because of hair fringes only laterally on the caudal filaments and because the frons is not produced over the labrum in the nymph.

Superfamily HEPTAGENIOIDEA

The family Heptageniidae has usually been defined on the distinctly 5-segmented hind tarsi of the adult. The venation resembles that of the Ametropodinae, Pseudironinae and Metretopodinae and is only slightly reduced as compared with most Siphonuridae. On this similarity in venation, the family has usually been included in the same superfamily as the Siphonuridae.

However, the nymphs of the Heptageniidae are very different from the shrimp-like nymphs of most Siphonuridae.

The flattened nymphs of the Heptageniidae are of the running type with long caudal filaments that bear the short hairs in whorls. These nymphs resemble those of the Leptophlebiidae in body form and in caudal filaments but are distinguished from them on the forward extension of the frons to cover the labrum and on the uni-lamellar abdominal gills that usually have a basal fibrillar tuft.

There seems little doubt that the Heptageniidae evolved from a primitive siphonurid ancestor in which the hind tarsi were 5-segmented in the adult, but I consider that the differences between the nymphs of the Heptageniidae and those of the Siphonuridae are of the same order as the differences between the Leptophlebiidae and the Siphonuridae and that, therefore, the Heptageniidae should be referred to a separate superfamily with status equal to that of the Leptophlebioidea.

Superfamily LEPTOPHLEBIOIDEA

The Leptophlebioidea is a specialized group in which the running type nymph has long caudal filaments bearing short hairs in whorls. The nymphs are slightly to distinctly flattened; the amount of flattening is dependent on the rate of flow of the water in which they live. The nymphs of *Jappa* have developed a burrowing habit. There is considerable variation in gill structure, and a marked difference between the gills of Ephemerellidae and other Leptophlebioidea. The plate-like gills of the Ephemerellidae have irregular flattened lobes on the lower surface. The gills of Leptophlebiidae are usually bilamellate, and each lamella may be produced or variously cleft at apex. There are long fine hair fringes on the gills of burrowing species, but the fringes differ in structure from the marginal fringes on the gills of the burrowing Ephemeroidea. A few leptophlebiid nymphs have deeply dissected gills.

The anal field of the fore wing venation of the adults is more reduced than in Heptagenioidea, and CuP is strongly curved posteriorly at its apex. However, there is only a slight difference in venation, except for the MP field, between *Leptophlebia* and the Potamanthidae (Ephemeroidea).

Superfamily EPHEMEROIDEA

The nymphs are basically burrowers although those of the Euthyplociinae are sprawlers in fast water. The gills have a dense margining of fine finger-like respiratory lobes. The adults have a complete but specialized venation. The MP field is large, the vein branches close to the wing base and the posterior branch is deflected towards CuA or fused with it for a short distance. There is considerable variation in the development of the cubital field which, however, is always large. Because of the distal shortening of CuA there are marginal intercalaries between MP and CuA.

Although the venation is specialized it is not easy to distinguish between the Ephemeroidea and the most primitive Leptophlebiidae (e.g. *Leptophlebia*). There is also a marked similarity in venation between the Ephemeroidea and the Neophemeridae. However, the nymphs of the Ephemeroidea cannot be confused with those of any other mayflies because of the type of abdominal gill.

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RÉSUMÉ

La classification des Éphéméroptères

La nouvelle classification proposée pour les Éphéméroptères insiste sur l'importance de la structure des branchies abdominales et des cerques chez les larves. La nervation des ailes des adultes doit être utilisée avec précaution pour l'étude de la phylogénie parce que des réductions semblables de la nervation se rencontrent dans plusieurs lignées indépendantes. L'ordre est divisé en six superfamilles. Les Heptageniidae sont considérés comme une superfamille séparée dérivant du stock des Siphonuridae distinct mais comparable aux Leptophlebioidea. Les Baetiscidae constituent les Éphéméroptères les plus primitifs : la nervation des ailes antérieures est comparable à celle des Mithodotidae du Permien et les adaptations que l'on trouve chez les larves effectivement nageuses sont toutes associées avec le développement d'une large carence thoracique. La figure 1 représente la phylogénie des familles d'Éphéméroptères, tandis que la figure 2 représente la phylogénie des sous-familles des Baetidae.

ZUSAMMENFASSUNG

Die Klassifikation der Ephemeroptera

Die vorgeschlagene neue Klassifikation der Ephemeroptera hebt die Struktur der abdominalen Kiemen und Cerci von den Nymphen hervor. Die Flügelnervatur von den Erwachsenen muss mit Vorsicht in der Ableitung der Phylogenie gebraucht werden, weil gleichartige Verkleinerungen in Nervatur scheinbar in einigen unabhängigen Abstammungslinien vorgekommen sind. Die Ordnung ist in sechs Superfamilien eingeteilt. Die Heptageniidae sind zu einer separaten Superfamilie hingewiesen, als eine Abstammung des Siphonurid Stocks, vergleichbar mit, aber unabhängig von Leptophlebioidea. Die Baetiscidae sind möglicherweise die am meisten verallgemeinerten Ephemeroptera : Die Nervatur des Vorflügels ist mit den Permischen Mithodotidae vergleichbar, und Spezialisierungen der aktiv schwimmenden Nymphen sind alle mit der Entwicklung von dem grossen Thorax-Carapax verbunden. Figur 1 präsentiert die Phylogenie der Familien von Ephemeroptera, während Figur 2 die Phylogenie der Subfamilie von Baetoidea zeigt.

DISCUSSION AND GENERAL DISCUSSION OF PHYLOGENY

G. EDMUNDS : Mr. RIEK. I believe you indicated that the acquisition of the gill tuft takes place quite easily a number of time. It would be lacking or secondarily lost in *Arthroplea*. The Heptageniidae and Oligoneuriidae have tufts ; in the one case where they are lost, they are still present on the first gill in *Homoeoneuria*. In Coloburiscinae they are present in one genus of three. They are present in *Isonychia*. They show up in Rallidentidae. They are present in

part of the Ameletopsinae. This would require the appearance of the gill tufts several times. Do you maintain that it is easy to acquire these tufts?

E. RIEK : Tufts are developed not only in mayflies, but in stoneflies, caddisflies, and several other aquatic groups. The abdominal gills occur in some of the Megaloptera, but not all of them. So tufts seem to be generally developed and I think they open up niches in the aquatic habitat that previously were unavailable through respiratory limitations. Yes, I do see them easily gained. When you look at the mayflies, I don't think that the tufts have been developed too many times. There seem to be only two major lines in which tufts have developed, three with *Rallidens*.

G. EDMUNDS : Yes, *Rallidens* would call for one additional origin.

L. BERNER : Mr. RIEK. You indicated that *Baetisca* is a primitive genus, but Dr. LANDA indicated that it was highly specialized because of the concentrated nervous tissue at the anterior end. How do you reconcile the two viewpoints?

E. RIEK : Dr. LANDA indicated only specialization in the nervous system. In the tracheal system he showed how simple it was, but he considered this as a secondary reduction. It is very difficult to decide primary and secondary development, and it is the summation of characters that I am using. Every primitive animal has a terrific apomorphic component; there are many specializations. So, to me, the aggregation of the nervous system is correlated with the carapace and nothing further. Concerning my chart — in my mind I tend to feel that some of the families that are indicated on it would be better considered as subfamilies within the Baetidae rather than families, such as the Metretopodidae and the Ametropodidae. I don't see them as being quite as distinct as say the Oligoneuriidae from the rest of the Siphonuridae. But I am following convention to some extent in keeping these as families.

G. EDMUNDS : I would like to compare my phylogenetic diagrams with that of Dr. LANDA. The upper nine families in Dr. LANDA's Figure I are grouped in a manner similar to their grouping in my diagrams. Basically, we place these families in similar clusters, but Dr. LANDA has recognized more families than I. Then he has separated Oniscigastrinae, which I call a subfamily, to make a separate family. He has done this for two or three reasons : the ventral trachealis fuse at the mid-line (this strong fusion also occurs in higher families in this direction), and there are similarities in the digestive tract which suggest that to some extent Oniscigastrinae can be a pre-group to the rest of the phylogeny. I disagree totally with the separation of *Chiloporter* from the other genera of the Ameletopsinae into a separate family. *Chiloporter* is an Ameletopsinae, and there are many characters which group the four genera (*Ameletopsis*, *Chaquihua*, *Chiloporter* and *Mirawara*). They are active carnivores with fantastically modified mouthparts. These forms grab insects half their size and swallow them whole; they have a fantastically wide digestive tube. The four genera also have a common distributional pattern. I think Dr. LANDA has included *Chiloporter* at this point in his phylogeny because of tracheal fusion across the bottom. There is also some question about the accuracy of his grouping of LeptoHyphidae-Ephemerellidae-Tricorythidae. However, the study of this cluster has been hampered because the principal, important part of this cluster is African, and we have not had good preserved material necessary for the study of the internal anatomy. I have no disagreement in the grouping of the Ephemeroidea. In spite of the fact that the diagram (Fig. I) of LANDA looks different from mine, it is not greatly different except for the subdivision of the siphonurid group into a number of families and a few other points.

H. ROSS : Mr. RIEK. A good number of us, contrary to your opinion, believe that winged insects arose from a terrestrial planing type ancestor. If this were true, what difference would

it make to your idea of what is a primitive gill and what difference might this make to your thinking about the family tree of mayflies?

E. RIEK : If the gill is not an appendage, it is strange that it should be muscled and articulated to the body. There would be no need to develop any other type of gill than the fibrillar tuft. Again, if you have a terrestrial insect that develops a wing, you must have some functional reason for the initiation of that development. If the animal is in the water, any lateral process on the body is going to have a function in maneuverability of the organism in swimming. To me, the paranotal processes were functional in water and as the animal came out of water, they changed their function to become wings. If you look at some of the mayfly nymphs you find that the pronotum has large paranotal processes separated from the tergum by a very deep groove. It is this sort of structure that I feel became more flexible as the animal came out of water. But I feel that the muscled, articulated gill is more important. It's very hard to visualize an abdominal style of the Machilidae expanding out if such an animal went back into water. The appendage has been reduced down to practically nothing. Then you must redevelop it, and this isn't always easy.

L. BERNER : Do you derive the insects from a Crustacean ancestor?

E. RIEK : No. To me, the insects were derived from a Trilobitomorpha-like ancestor. I don't mean the HANDLIRSCH idea of direct descent from trilobites, but from the actively swimming ancestral form of the trilobites. The Trilobitomorpha had a long caudal style. In other words they were a bit like the Eurypterida in this respect. From that swimming type developed the sedentary trilobite that everyone thinks of. The caudal style that's so well developed in the most primitive insects is, I think, fundamental. You have it in mayflies and in reduced form in Odonata, but you don't have it in any neopterous insect. The caudal style is present in the eurypterids, the arachnid-group, the Trilobitomorpha, and in the insects. I can't see how you could redevelop a caudal style from a myriapod-like ancestor so, to me, the insect arose as a less dominant group in competition with the Crustacea. Even the Crustacea, when you look at it, really divide into two major groups : the free swimming Branchiopoda and the sedentary remaining typical Crustacea. The main things distinguishing the insect from all other groups are the single pair of antennae and the one-segmented mandible. The origin of that one-segmented mandible is crucial in the origin of insects, but at this point it remains unknown. There is no embryological evidence and no fossil evidence to indicate whether it represents the coxal region of an appendage or whether it is a reduced whole limb, as in the myriapods. MANTON'S work is very inconclusive in this regard, I feel. The labium of the insect is not an insectine character, but a character of a terrestrial arthropod. It occurs not only in insects, but in all but one myriapod, the chilopods, and it occurs in the truly terrestrial Crustacea. In the Crustacea it's not on an homologous segment, but yet it is indistinguishable from that of the insects. Again, tracheation has developed independently in a number of different Arthropod lines, a primitive type occurring in the Onychophora, but this is parallel development within different groups. Wings are not an insectine character. They are only developed in the Pterygota. I think there is general agreement on this, that wings have never been present in the Apterygota. You are left with very few characters on which to define an insect, but it is not a trilobite. It is developed from an ancestral form that led to the trilobites. In fact, I think the Trilobitomorpha are possibly ancestral to other groups within the Arthropoda.

R. KOSS : Wing pads are not articulated through all the instars. How do you evolve an aquatic ancestor with the gills articulated but not the wing pads?

E. RIEK : You are comparing paranotal processes above the legs with an articulated abdo-

minal appendage. If you have an aquatic animal swimming in water, contraction of the muscles will vary the angle of the paranotal process. So it is moveable, as it would be on land. As soon as you lift the legs of an insect off the substrate, you are able to use the musculature to change the shape of that segment. By changing the inclination of this lateral flange along the body you are able to get greater precision of movement in the water. The caudal style acts as a rudder, but you have this other process to help.

R. KOSS : What suddenly caused this structure to develop into a functional wing? The small paranotal expansion is not going to help the insect move until it starts to function for flight.

E. RIEK : No, that is not true. The insect coming out from the water has a caudal style. It would probably be able to spring, just like a machilid. When you have an animal that jumps like a machilid, the paranotal processes are of use, keeping the animal righted while it is in the air. It also is able to keep orientated because the legs are no longer on the substrate. So you have flexibility in the process well before it is hinged, and with the process functional there is every reason for its development.

R. ALLEN : The gills of mayflies are articulated for water circulation also. Many species use the gills in this manner.

E. RIEK : Yes. I hadn't given much thought to that point, but I will agree. Having watched siphonurid mayfly nymphs swim and trying to catch them, I was most impressed with their swimming ability. You will notice that they will take one flip and swim across a pool as fast as any fish of comparable size. I don't think they are moving the tails, but that it is the gills that move them. Usually, before they begin to swim, the gills start to move. Under very wet, rainy forest conditions, I have seen mature siphonurid nymphs sitting on wet rocks ready to emerge, and they are still able to flip back into the water when I approach them. I have only observed it once, but I think Dr. EDMUNDS has evidence that this happens in South American species also.

W. PETERS : For the record, I would like to explain the behavior of the baetinae which I collected some years ago in South America. It appears to be semi-terrestrial. The species occurs near Tingo Maria, Peru, in streams where rocks are above the water. This baetinae is about an inch long and can be found on top of the rocks instead of in the water. When bothered by something, it will flip a good 2 1/2 to 3 feet in the air and into the water. I found the best method to collect this species was to poke the rock with a stick and to catch the nymphs in a cup. Dr. EDMUNDS told me that Mrs. MAYO saw the same thing in South America also. While on the subject of Baetidae, I would like Mr. RIEK to explain more about his dual origin of the Baetidae. It seems to me that the Baetidae are of one origin.

E. RIEK : Now I am on very shaky ground. If you take a typical *Baetis* or *Callibaetis*, you will find that they occupy very different habitats and many of the differences one sees in the nymphs may be correlated with these habitats. *Baetis* usually lives in fast water on rocks and it has a very specialized feeding mechanism. The mouthparts are very similar to those of *Ameletus*. *Rallidens*, to me, is just a specialized development from this type of mouthparts. Low in the siphonurine lines occurred this specialized feeding mechanism of scraping algae from rocks, and it has occurred right on up to give a form with reduced wing venation. These nymphs also have very stout tarsal claws with well developed teeth on the underside of the claws. Usually this is correlated with habitat. The more I learn about Baetidae from Dr. MÜLLER-LIEBENAU, the less definite are some of these characters. Nevertheless, there seem to be Baetidae with very reduced teeth or no teeth on the claws. If you look at the other line, *Callibaetis*, *Cloeon* and *Centroptilum*, they live in weeds and often in quiet, standing waters. I know again that some of

these are also found in swift water. The mouthparts of this group are more like those of *Siphonurus* and not adapted for the marked scraping of the substrate. The tarsal claws are long and thin and, as far as I am aware, none of them have teeth. It was on these sorts of differences that I felt one had an endpoint that was similar and an origin that was dissimilar. The marginal intercalaries seem to vary so much in *Centroptilum* that one doubts whether in all cases the distinction here is of any significance in generic definitions.

L. BERNER : You have referred to the gills as swimming organs. Have you ever done any experimental work with *Siphonurus*, which has very large gills, and removed the gills to determine how effective the swimming of the nymphs would be? It seems to me that this would be a good confirmation or denial of one of your points, at least in part.

E. RIEK : No.

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