THE PHYLOGENY OF SOME MAYFLY GENERA*

By HERMAN T. SPIETH

ABSTRACT

The phylogenetic relations of twenty-five North American genera have been studied. The data for this study have been derived from the following characters: wings, genitalia, gills, and mouth parts. Intensive study of the wings supports Lameere's view of the primitive insect wing structure. By boiling the wings in KOH, it has proved possible to separate the two surfaces, and thus show that the mayflies possess every major vein that was to be found in the Dictyonuridæ. Apparently the Ephemerida have the most primitive wings of all living insects. The genitalia and mouth parts have been interpreted in accordance with the findings of Crampton and Walker. The gills have been of great value as phylogenetic indicators.

Four distinct lines of development are recognized within the family. Two of these are monotypic and are represented by *Caenis* and *Baetisca*, respectively. The Heptageniidæ, the Baëtidæ, and the genus *Siphlonurus* make up the third branch. The Ephemeridæ, *Blasturus*, *Leptophlebia*, *Choroterpes*, *Tricorythus*, and *Ephemerella* constitute the fourth evolutionary stem.

ticular, has given me considerable aid in methods of collecting and in offering kindly criticism, as well as providing inspiration.

INTRODUCTION

This paper deals with the generic relationships and relative phylogenetic position of some of the genera of Ephemerida found in the United States.   Former workers, including Eaton, have created a linear arrangement for the classification of the Ephemerida, and the workers since Eaton have not differed greatly from the Eatonian classification.   While all of these workers have attempted to show relationships of genera by means of the classification, the result has nevertheless been more or less artificial and incomplete, since obviously the evolution of the group did not take place in such a manner as that indicated by a linear arrangement.

The data presented here have been acquired by the intensive study of four characters, *i.e.,* gills and mouth parts of the nymphs, and wings and genitalia of the adults.   The genera that have been studied are all represented in North America and are as follows: *Siphlonurus, Isonychia, Heptagenia, Ecdyonurus, Epeorus* (in the broad sense, including *Iron*) *Rhithrogena, Baetisca, Caenis, Ephemerella* (including *Chitonophora* and *Drunella*)*, Tricorythus, Blasturus, Choroterpes, Leptophlebia, Potamanthus, Hexagenia, Ephemera, Polymitarcys, Pentagenia, Campsurus, Callibaetis, Baëtis* (including *Acentrella* and *Heterocloëon*)*, Pseudocloëon, Centroptilium,* and *Cloëon.*   Naturally a complete phylogenetic picture can not be drawn until all the species in existence are available for study.   Nevertheless these twenty-five genera are sufficiently representative of the various and diverse lines of evolution that have taken place within the family to create a frame-work around which the complete classification can be built when sufficient material is available.   The present study also opens up several biological problems which need to be solved.

The material for this study has been collected during a period of the past five years in the following states: Indiana, Ohio, Michigan, Illinois, Missouri, Kentucky, Maryland, Virginia. West Virginia, North and South Carolina, Georgia, Florida,

Alabama, and Tennessee.   During this time between 25,000 and
30,000 individuals, both nymphs and adults, have been collected.
In all of the above named genera, both nymphs and adults have
been available for study.   A few of the genera (*i.e., Pentagenia,
Cloëon, Pseudocloëon,* and *Centroptilium*) are represented in my
collection by less than a score of individuals per species.   *Ecdyo-
nurus* and *Hexagenia* are each represented by thousands of
individuals, and the remainder of the genera by at least 100
specimens each.

PHYLOGENETIC DATA

Wings

In these delicate, thinly chitinized insects, the wings are better
and more easily preserved than any other parts of the insect.
They are less subject to distortion and discolorization than other
parts of the body.   In the abundant veins and diverse shapes
and sizes of the wings, they present characters which have under-
gone great modification in several directions during the evolution
of the group, while retaining their primitive basic venation.
Further, the investigation of the wings is not restricted to the
adult but can also be extended to the nymph, for by studying the
tracheation of the wing pads the nymphal stages can be corre-
lated with those of the adults.   Of prime importance also is the
fact that there exists an abundance of fossil wing material of
mayflies, of mayfly ancestors, and of other closely related groups.

In this paper the phylogenetic significance of the wing in the
existing forms will be discussed, and an outline will be given of
the evolution of the wing and a demonstration of certain facts
that help to elucidate the nomenclature and homologies of the
wing veins.

The insects that are generally accepted as the ancestors of the
mayflies, namely, *Triblosoba* and the Protereismidæ, exhibit hind
wings which are similar in size and shape to the fore wings.   The
wings are elongate oval in shape as in the Paleodictyoptera
(Fig. 1), lacking the definite apex and the anal angle of the
present day forms.   From the tip of the wing to the base, the
posterior margin presents a long arc.

In the present day forms, the flight function has undergone a decided cephalization, with a consequent great reduction of the size of the hind wings. In some genera, *Pseudocloëon, Cloëon, Caenis,* and *Tricorythus,* the hind wing has completely disappeared. In the most primitive existing North American genus, *Siphlonurus* (Fig. 4), the hind wings are of moderate size (more nearly the size of the fore wing than in any other living forms) and roughly oval in form. The fore wings (Fig. 3) are roughly triangular in shape and exhibit definite apical and anal angles. The distance from the anal angle to the apex is comparatively great. The Baëtidæ (Figs. 17, 18, 23, 25, 26), which are undoubtedly specialized genera, have either lost or have greatly reduced hind wings, but seem to have somewhat re-assumed the primitive shape of the fore wing. Other genera which are intermediate in respect to wing size show a shortening of the posterior margin (distance between the base of the wing and the anal angle) that parallels the reduction in hind wing size, *e.g., Heptagenia, Leptophlebia, Choroterpes,* and *Ephemerella* (Figs. 13, 21, 29, 55). Consequent with the reduction of the posterior margin in these genera, there is also the re-assumption of the primitive wing shape of the fore wing which reaches completion in genera which entirely lack the hind wing.

This cephalization of flight function and reduction in hind wing size, judging from present fossil evidence, have all occurred since the Paleozoic.

Nomenclature and Homologies. The homologies of the veins of the ephemerid wings have been points of contention for several years. Eaton, in his monograph of the group, employed a notation of his own which did not attempt to homologize the plan of venation found in the mayflies with that found in any other group, but he did, however, correctly homologize the veins of the hind wings with those of the fore wing.

Eaton's system was modified by Redtenbacher in 1886, by Comstock in 1888, and by Kellogg in 1895. In 1898 Comstock and Needham published their *Wings of Insects,* in which they advanced a nomenclature that was founded upon a study of the nymphal tracheæ and the correlation with the conditions found in other insects.

In 1912 Miss Anna Morgan, after making an intensive investigation of the nymphal tracheation of the mayflies and having correlated it with the adult venation, published a paper in which she interpreted the median and radial sector in the same manner as Needham had interpreted them in Odonata.

Tillyard (1922) re-worked the whole subject in correlation with his work on the veins of the Odonata. He employed not only the venation and tracheation of modern mayflies but also the paleontological evidence as presented by Permian fossils.

Lameere (1923) published a paper dealing with the veins of the Paleodictyoptera, Odonata, and mayflies, in which he advanced the hypothesis of a posterior median and cubitus and anterior median and cubitus, in which the posterior member bears the same relationship to the anterior as the radial sector bears to the radius.

Martynov (1922, published 1924) holds a view very similar to that of Lameere but differs slightly from him as to the fate of certain veins. Tillyard (1926), influenced by Lameere's hypothesis, modified his earlier system. Working with the Kansas Permian insects, Tillyard (1931) again made a few changes in the nomenclature. In our own work we find evidence in support of Tillyard's interpretations and in the present paper will employ the nomenclature advanced by Tillyard in 1931.

In determining homologies of the various veins, there are three distinct methods of approach: (1) fossil evidence; (2) distribution of the tracheæ in the wing pads of the nymphs; (3) convexity and concavity of the veins. To this latter method of interpretation the following data are of significance.

The wing of a mayfly consists essentially of a sacular out-pocketing of the body wall, into which, during the immature stages, tracheæ, blood vessels, and nerves penetrate. In the adult, this sac becomes flattened, greatly extended, and very thin, and veins have been laid down. By soaking an adult wing in a strong caustic soda solution for 24 to 48 hours, the connections between the two sides of the wings are broken and the wing separates into its component dorsal and ventral part. By careful manipulation, the two surfaces can be cut apart and the parts then mounted for study. Hagen (1889) separated the two

surfaces of the wing of an Odonata.   He accomplished this by injecting water between the two surfaces of a teneral wing.   He reported that he had also achieved the same end with other insect wings.

The striking feature to be noted is that all the convex veins belong to the dorsal surface of the wing and the concave veins to the ventral surface of the wing.   The cross veins belong principally to the dorsal surface, *i.e.*, at the base where they join the concave veins a stump of the cross vein is attached to the main vein, while on the dorsal surface the cross veins are always complete and vigorously developed.   The single exception to this condition is in the area between the costal edge of the wing and the sub-costal vein.   Here the cross veins are better developed on the ventral wing surface, or at least developed equally on both surfaces of the wing.   It is important to note that veinlets at the edge of the wings are always restricted to the dorsal surface.   Calvert, working with a mature wing pad of a larva of *Cora* (Odonata), determined that all the concave veins were located on one side of the wing and all the convex veins on the other side, with the exception of the costa which was equally developed on both sides.   Several other veins showed on both sides of the wing pad but always more faintly on one side than on the other.   Thus, if the vein were concave it would be heaviest on the side where the other concave veins were located and faintest on the side where the convex veins were located.

Bearing in mind the distribution of the veins on the two surfaces of the wing, let us turn to a discussion of the nomenclature and homologies of individual veins.

Costa.   In the mayflies known from the Permian (Protereismidæ) (Fig. 2), the costal vein consisted of a very short vein that forked on its distal end, with the two branches running almost at right angles to the parent vein.   The anterior fork met the anterior edge of the wing and the posterior fork went back to the subcostal vein.   In living mayflies (Fig. 3) the costal seems to have migrated to the anterior wing edge with the consequent disappearance of the anterior fork, and the posterior branch of the "Permian" costal has given rise to the humeral brace.   From the humeral brace out to the apex, the

wing edge is strikingly different from that part of the margin
which is thickened by the true costal vein.   This apical section
of the margin consists of a slightly thickened, folded wing mem-
brane, and bears a number of minute spines.   It is to be noted
that the costal trachea arises much later than the other prin-
cipal tracheæ in the ontogeny of the individual (Tillyard, 1922).

Subcosta and Radius.   The subcosta (Sc) is a concave, un-
branched vein that extends from the wing base to the apex, while
the radius (R_1) which runs parallel and close behind it is similar
except that it is a convex vein.

Accompanying the convex and concave system of vein place-
ment is the triadic type of branching found in the mayflies, so
that whenever a vein forks there is interpolated between the fork
a vein of opposite position (Fig. 8).   For example a concave
vein forks into two concave branches, the interpolated vein is
convex, and the regular alternation of convex and concave veins
is preserved.   Thus the radial sector, which is a concave vein
lying between two convex veins, the radius and the anterior
median, may be viewed as the middle concave member of a con-
vex triad.

Radial Sector.—In the paleodictyopteran family Dictyo-
neuridæ (Fig. 1) and the presumed ancestors of the mayflies
(Eubleptidæ, Metropatoridæ), the radial sector (Rs), a concave
vein, arises from the radius about one-third of the distance from
the base to the apex.   In the Permian *Triblosoba* (Fig. 9) the
point of origin has migrated back toward the base of the wing
and in the Protereismidæ (Figs. 2, 3) and present day mayflies,
it has moved still farther toward the base and is no longer at-
tached to the radius, but rather *abuts* against the anterior
median near its base.

Distally the radial sector (Fig. 3) branches into three pri-
mary branches.   Between these, which are concave, there are
two interpolated convex veins which are designated by Tillyard
as IR_2 and IR_3b.   These are the interpolated convex veins which
lie behind the first (R_2) and second (R_3) *primary* branches of
the radial sector. R_1 is the first primary branch of the radius;
and R_2, which is the second branch of the radius but the first
branch of the sector, is an unbranched vein and seems always to

have been so throughout the history of the group. R_3, the second branch of the sector, is unbranched in the Carboniferous families Eubleptidæ, the Metropatoridæ, and *Triblosoba* (Fig. 9), but branched as early as the Permian (Fig. 2) into a simple triad with an interpolated convex vein IR_3a. The last primary branch of the sector is designated as R_{4+5} in order to keep the nomenclature homologous with that of other groups. Judging from fossil evidence, the R_{4+5} has always been an unbranched vein.

Regarding the origin, significance, and interpretation of the so-called interpolated veins IR_2 and IR_3b, a few salient points may now be discussed. Both veins are convex and thus are to be found on the dorsal surface of the wing. Thus they are both in the same position as IR_3a which is a convex vein. IR_3a is, as noted above, the interpolated vein of the triad which was formed by the branching of R_3. In *Triblosoba* (Fig. 9), R_3 is undoubtedly unbranched, but in the Permian mayflies (Fig. 2) it has branched and IR_3a is present. In the present-day species (Fig. 3), IR_2, IR_3a, and IR_3b have lost their basal connections and terminate freely in the wing membrane. In the Permian mayflies (Fig. 2) however, IR_2, IR_3a, and IR_3b were all distinctly joined to concave members of their respective triads. Thus, fundamentally there is no difference between these three interpolated branches, and since in a sense we have a record as to how IR_3a arose, it is perfectly logical to hypothesize that IR_3b and IR_2 both arose in a like manner, viz., as convex members of a concave triad.

Median. The mayflies possess a complete, archaic median with a convex anterior median (MA) and a concave posterior median (MP). Martynov (1922) considered the anterior median of the mayflies to have been lost and Lameere (1923) thought that both the anterior median and anterior cubitus had been lost. Lameere hypothesized that along with the loss of the anterior median the posterior median had shifted from a concave vein to a convex vein. Now, by separating the wing into its two component parts as described above, we find that all the convex veins lie on the dorsal surface and all of the concave veins on the ventral surface. It is very difficult, under these circum-

stances, to conceive of the mechanics by which a "down" vein might become an "up" vein, which perforce would have to happen if the posterior median had shifted from a concave to a convex position. Further, in *Triblosoba*, which possesses an unbranched anterior median, we also find that R_3 is unbranched; but in the Permian Protereismidæ we find both R_3 and MA forming simple triads. Is it any more difficult to conceive of MA branching and forming a simple triad than it would be for R_3 to form a triad (which it undoubtedly did)? Thus, MA which was an unbranched, convex vein in the Paleodictyoptera and *Triblosoba* is to be found in the Permian fossils and in the present-day species as a convex vein which has branched distally and formed a simple triad.

Behind the anterior median lies a concave triad which represents the posterior median. In the primitive paleodictyopterid family, Dictyoneuridæ (Fig. 1), this vein was unbranched. In the ephemerid stock as early as the Upper Carboniferous (*Triblosoba*, Fig. 9), this vein had formed a triad and the same condition presents itself in the Permian fossils (Fig. 2) and the present living members of the group. Apparently there has been a tendency for the point of branching to take place nearer and nearer the base of the wing. *Siphlonurus* (Fig. 4) which is undoubtedly the most primitive genus to be found in America exhibits a condition like that found in the Permian Protereismidæ. However, in some genera, *Hexagenia* and its relatives (Figs. 34, 37, 39, 41, 43), the posterior branch of the triad arises at right angles to the anterior member and after traversing the wing membrane almost (*Hexagenia*, Fig. 41) or all the way (*Ephemera*, Fig. 39) to the anal, it swings outward and runs to the outer wing edge. Since the posterior median is a concave vein and since cross veins are restricted primarily to the dorsal surface, separation of the two sides of the wing shows that in *Hexagenia*, etc., the basal connection of the posterior limb (MP_2) of the triad with the anterior limb (MP_1) is not a true part of the triad, but is a cross vein. Thus the basal part of MP_2 has actually been lost in these genera.

A word needs be said here about the relation of the median of the mayflies to its homolog in other groups of insects. As Tillyard has pointed out, the posterior median is Comstock's median.

Cubitus. The cubitus in the Dictyonuridæ (Fig. 1) gives rise to two unbranched veins, an anterior CuA and a posterior CuP, in which the forking takes place at about one-third the way out from the base of the wing. There is a tendency for the point of branching to take place closer and closer to the wing base so that in the Carboniferous genus *Triblosoba* (Fig. 9) the branching takes place almost at the very base. In this extraordinary insect, the two branches are simple and run parallel from the base to the edge of the wing. The Protereismidæ (Fig. 2) exhibit a posterior cubitus similar to that found in *Triblosoba* but the CuA, or the anterior cubitus, has formed a simple triad. In the present-day forms (Fig. 3), along with the formation of the anal angle the two veins have been pulled apart at the wing edge. CuA ends in the distal wing edge while CuP ends in the anal or posterior edge of the wing (except in Baetisca). Among different genera CuA meets the wing edge at various distances from the base of the wing.

The Permian Protereismidæ (Fig. 2) have the anterior cubitus divided into a triad, and this same triad can be identified in the existent genus *Siphlonurus* (Fig. 3). In other genera it has been obscured by various modifications, usually consisting of a series of pectinated veins running posteriorly from the anterior member of the cubitus. These were barely indicated in the Protereismidæ. By separating the two surfaces of the wing with KOH, in *Hexagenia* (Fig. 41) where a series of pectinated veins runs posteriorly from CuA_1, the vein nearest the root of the wing can be recognized as the original fork of the triad or CuA_2. In other more specialized genera, various modifications have taken place until the triad has been obscured.

In the fossil *Triblosoba* (Fig. 9) and Protereismidæ (Fig. 2), it is impossible to tell exactly what is the fate of the medial and cubital veins at the wing base. According to Lameere's hypothesis of the origin of the veins, the anterior median should join the posterior median and likewise with the cubitals. In present-day mayflies of more specialized genera, the course of the veins has been so shifted that it is impossible to tell their exact position. Turning, however, to the primitive genus *Siphlonurus* (Fig. 3) we find the very condition which Lameere hypothesized. The

anterior median distinctly joins the posterior median and it is clear that the posterior cubitus meets the anterior branch.

Anals. As pointed out by Martynov, in the Dictyoneuridæ, the anals consist of 3–4 fairly homologous veins, each shorter than the preceding, but in more specialized members of the family A_1 begins to assume dominance and the remaining veins become less distinct. In *Triblosoba* (Fig. 9) A_1 and A_2 stand out, as long veins with numerous branches. Whether one of the veins which appears as a branch of A_2 is in actuality A_3, it is impossible to determine. If the base of the wing were present we might find the posterior branch of A_1 is in reality IA_1. The Protereismidæ (Fig. 2) are much like *Triblosoba* with a tendency for A_1 to stand out, and A_2 and A_3 to become less distinct. Present-day forms show a highly variable state of affairs. In all genera A_1 is present, but further than that the distribution varies with the genus under consideration. Thus, in *Siphlonurus* (Fig. 3), three anal veins and two interpolated veins can be distinguished, while in the Baëtidæ (Fig. 23) only A_1 is present. It is needless to say that along with cephalization of flight, and the triangularization of the anterior wings the anal area has been gradually reduced. Thus, in the living examples, *Siphlonurus* possesses the largest anal area and the most primitive distribution of the veins.

Hind Wings. In the above discussion only the anterior wings have been taken into consideration. The reduction in size of the hind wings of the mayflies took place during the Jurassic. Some of the fossils from that period had both pairs of wings equal (*Mesephemera*), while members of the genus *Paedephemera* exhibited hind wings about two-thirds or three-fourths as large as the front wings. The reduction has resulted in the hind wings assuming, in the more generalized forms, a somewhat oval shape. In the reduced hind wings the cubital and anal veins are distributed somewhat as in the primitive ancestors, the reduction of the wing having been accomplished by the loss of the distal portion of the wing. Of course, in some specialized forms (*Baëtis*) where the hind wing is minute, the entire wing has been greatly modified. However, in most of the genera the anterior part of the wing has undergone a change in shape, especially near the

base where it has been extended to enlarge the costal and sub-costal areas. The costal spur is a remnant of this in the greatly reduced wings of *Baëtis*.

Thus, since hind wing reduction did not appear until late, the above wing discussion covers both fore and hind wings of the Paleodictyoptera, *Triblosoba*, and Protereismidæ. The hind wings of present-day forms need to be discussed here in a brief manner.

The costa, subcosta, and radius in the hind wings are similar to these veins in the fore wings, except that the costa and sub-costa in the hind wings are strongly arched forward at a short distance from their base (Fig. 11). With the shortening of the wing, the area served by the Rs has become smaller so that the sector consists of a simple triad, R_3 having disappeared and only R_2, R_{4+5} and the long interpolated vein IR_2 being present (Figs. 4, 7, 11). Basally, Rs in some genera is connected to MA, but in others it ends on a Ma–R_1 cross vein (Figs. 7, 14). In *Ecdyo-nurus* (Fig. 7), *Heptagenia* (Fig. 14), *Isonychia* (Fig. 11), and *Siphlonurus* (Fig. 4), MA forms a simple triad, while in *Hexa-genia* (Fig. 40), *Ephemera* (Fig. 33), *Pentagenia* (Fig. 36), *Polymitarcys* (Fig. 42), *Campsurus* (Fig. 44), *Baetisca*, *Blas-turus* (Fig. 32), *Choroterpes* (Fig. 30), *Ephemerella* (Fig. 47), and *Leptophlebia* (Fig. 22), it is a simple unbranched vein, re-minding one of the same vein in the hind wing of *Triblosoba* (Fig. 9). MP, as in the fore wing, is a simple triad (Figs. 4, 7, 16, 47). CuA and CuP are much like the same veins in *Triblosoba* (Fig. 9), *i.e.*, simple veins, running nearly parallel, with or without interpolated veins, depending upon the genus under consideration. As in the fore wings, so in the hind, the first anal stands out clearly while the other anals and the inter-polated veins exhibit extremely variable conditions (Figs. 4, 16, 35, 47).

Significance of Veins. Concerning the importance of the vari-ous veins in demonstrating relationships between the diverse genera and their evolutionary significance, a few words may be said.

In the fore wing the costa, subcosta, and radius are of no value in showing relationships, since they are homogeneous throughout

all genera. As for the radial sector and its branches, the most primitive existing type is that found in *Siphlonurus* (Fig. 3) and *Baetisca* (Fig. 54), where R_2 and R_3 still retain their primitive connection, and the R_3 triad has not been greatly modified even though R_{3a} has been disconnected at its base. Specialization in this group of veins consists in the basal disjunction of R_3 and the modification of the R_3 triad. The anterior median is uniform throughout the family except in *Baëtis* (Fig. 17) and its allies where the posterior fork of the triad has been detached from its anterior member.

The posterior median forms a triad, members of which are designated as MP_1 and MP_2, which displays a tendency for the forking of the main vein to take place closer and closer to the wing base while MP_2 seems to have a tendency to pull away posteriorly from its anterior member. Naturally the most primitive type most closely approaches a typical triad, a condition to be found in the genus *Siphlonurus*.

The cubital veins, anterior and posterior, which have been designated in this paper as CuA and CuP, respectively, are perhaps the most variable and important set of veins in the wing, so far as phylogenetic value is concerned. Judging from the fossil evidence and from the hypothetical ancestral wing of insects, these two veins should meet at the base, CuP should be simple and CuA should form a triad at its distal end. Such a condition is actually found in *Siphlonurus* (Fig. 3) and without a doubt represents the most primitive condition in the extant forms. Specialization within the group has involved the obscuring and even complete obliteration of the CuA triad, and the shifting of the roots of the cubitals within the wing base so that they have completely lost their primitive aspect in many forms.

The anals have always been a variable group, but apparently the mayfly ancestors had three convex anal veins with at least two interpolated veins. Such a condition is now present in *Siphlonurus*. Various modifications exist in the group, the extreme condition being the reduction to a single anal vein which is simple.

The hind wings have undergone greater modification than the fore wings. Here the subcosta becomes significant, for the strong

forward arching and consequent enlargement of the Sc–R area is a specialization, while the condition found in *Siphlonurus* (Fig. 4), where the Sc runs more nearly parallel to the radius, is primitive. The radius, as in the fore wing, presents a homogeneous condition throughout the group. While the Rs was important in the anterior wings, it fails to display phylogenetic significance in the hind wings. As remarked before, Rs has been reduced to a triad which is uniform throughout the group, except in cases of excessive wing reduction. The anterior median is found in two conditions, either simple or forked as a triad, of which the unbranched form probably represents the specialized condition. The behavior of MA and R at the base of the wing gives us some clue as to relationships. In *Siphlonurus* (Fig. 4) and *Isonychia* (Fig. 11), these two run into the base without fusing, while in some other forms, *Ecdyonurus* (Fig. 7), *Hexagenia* (Fig. 40), etc., they fuse into a common trunk before reaching the base. Throughout the entire group, except in some genera where the hind wing is greatly reduced or even lacking, the posterior median forms a typical triad. CuA and CuP are unbranched veins, whenever present. Judging from fossil evidence, those forms such as *Siphlonurus*, etc., which possess no interpolated veins in the Cu area, are more primitive than those that do.

As in the fore wing, the anals in the hind wings present a highly variable condition; but forms in which there are three anals and two interpolated veins with a network of cross veins behind the true anal veins have been considered most primitive.

This discussion of the hind wing veins assumes that the hind wings possess vein for vein those that are found in the fore wing. Needless to say, those forms which lack some of the veins are specialized and those possessing a full complement of veins in the hind wings are primitive so far as wings are concerned. More will be said about the loss of veins in the hind wings in our section on Shape of Wings, and in the discussions of the various genera which follow.

Tracheation. Miss Morgan (1913) made an extensive study of the tracheae of mayflies and their relation to the veins of the adults. She utilized nymphs that were well developed, but did

little work with younger stages, and thus fell into the error of incorrectly homologizing in some genera the Cu tracheae with the subsequent veins. She also stated that the alar loop consisted of only a single straight trachea entering the wing pad. Tillyard (1924) pointed out her error and also showed that in the younger stages some genera, at least *Ameletus, Coloburiscus,* and *Oniscigaster* (occasionally), possess a complete, looped alar trachea as in other insects. Martynov (1924) gave an excellent critique of Miss Morgan's work and reinterpreted her data.

It suffices to say here that there is an enormous amount of individual, specific, and generic variation in the tracheation and that a detailed study of many species, employing various nymphs of various ages, is greatly needed.

Cross Veins. A word needs to be said about the cross veins and veinlets, and their phylogenetic significance.

The amount of cross venation, except in *Polymitarcys,* has constantly decreased since the Pennsylvanian. The extent and abundance of the venation, so far as can be determined at present, offers little help in the solution of generic relationships. *Siphlonurus* (Fig. 3), *Baetisca* (Fig. 54), *Hexagenia* (Fig. 41), *Pentagenia* (Fig. 37), *Potamanthus* (Fig. 34), *Ephemera* (Fig. 39), *Campsurus* (Fig. 38), all the Heptageniidæ (Figs. 6, 12, 13, 15), *Blasturus* (Fig. 31), *Leptophlebia* (Fig. 21), *Choroterpes* (Fig. 29), and *Ephemerella* (Fig. 55) all possess an abundant cross venation. *Tricorythus* (Fig. 46) has the cross venation restricted to the inner part of the wing disk. *Caenis* (Fig. 45) and the Baëtidæ (Figs. 17, 18, 23, 25, 26) have the amount reduced greatly, while *Polymitarcys* (Fig. 43) possesses almost a superabundance of cross veins.

The arrangement of the cross veins is, however, of considerable phylogenetic significance. The mayfly wing on the anterior edge is slightly concave, with the deepest part of this concavity coming about mid-way between the apex and the base or in the region known as the bulla. Sometimes there is an accumulation —a sort of piling together—of the cross veins in this area. This accumulation at the bulla has not entailed the addition of more cross veins, but is due entirely to cross veins having migrated into the vicinity of the bulla. Naturally, since no veins

have been added, the area between the veins of such a group and the veins outside of the group is larger than any to be found in a wing where the cross veins are evenly distributed. Thus, within the *tripunctata* complex of the genus *Ecdyonurus*, we find species (Fig. 6) with accumulations of veins that extend from the costa to the anterior median.   Each accumulation consists of three or four cross veins in each of the anterior vein areas (costal, subcostal, radial$_1$, and radial$_2$).   Each accumulation of veins, within a primary vein area, lies directly behind the same group in the preceding vein area.   In one specific complex in *Ecdyonurus* (Fig. 12) there is no sign of such a vein aggregation.   All of the members of the *Heptagenia maculipennis* complex (Fig. 13), with the exception of one species, show similar aggregations.   In this *maculipennis* complex, however, the cross veins posterior to R$_2$ are not pulled together, but are distributed exactly as in the rest of the wing.   Members of the *Ecdyonurus interpunctata* complex (Fig. 5) present a condition exactly similar to that found within *maculipennis* except that a longitudinal black streak is to be seen intersecting these cross veins in the area between R$_1$ and R$_2$.   This congregating of cross veins in the bulla area seems to be restricted, in American genera, to the Heptageniidæ, and even then only to certain species.   Thus, within the single genus *Ecdyonurus*, there are, as far as wings are concerned at least, three lines of evolution.   In the *Heptagenia maculipennis* complex, there are two lines of development.

A peculiar arrangement of the cross veins within the genus *Baëtis* (Fig. 17) and its allies indicates that these several genera are very closely related, but these characters in these genera offer no bases for distinguishing the lines of evolution in this group.

The veinlets, however, indicate something more than do the cross veins.   Between the primary veins these short veinlets run inward from the margin.   In *Baëtis* and *Pseudocloëon* (Figs. 17, 18) these veinlets are paired; in *Centroptilium* and *Cloëon* (Figs. 25, 26), they are single.

Wing Shape.   As stated before, the wings of the Protereismidæ (Fig. 2) lacked both a definite apex and the anal angle which are to be found in all present-day forms with the exception of

Baëtis (Fig. 17) and its allies.   Accompanying the reduction of
the hind wing there has been a modification of the fore wing,
until now the edge of the wing between the anal angle and the
base of the wing follows a comparative straight line.   It should
be expected that the most primitive extant genus would show
some relationship in form to the ancestral type or at least should
be nearer the ancestral type than the more highly specialized
types.   This we find to be so, and the genus *Siphlonurus* (Fig.
3) exhibits a wing which is elongate and triangulate.   The outer
edge has undergone practically no modification, and if the edge
of the wing from the base to the anal angle were *arched,* instead
of straight as it is, the wing would approach the Protereismidæ
wing in shape.   The important fact to note is that the propor-
tions of the wing have not changed, as demonstrated by actual
measurements, with the result that while the wing of *Siphlonurus*
is triangulate it is elongated and narrow.

   Isonychia (Fig. 10) is like *Siphlonurus* except that the wing
is broader and thus more broadly triangulate.

   All other genera of the family Heptageniidæ (Figs. 5, 6, 12,
13, 15) have wings that are similar in shape to those of the genus
Isonychia, except that the distance between the anal angle and
the wing root has been reduced, thus shifting the anal angle
toward the wing base and making the distance between the apex
and the anal angle comparatively greater.

   The tendency toward a broadly triangular wing reaches its
extreme development in the family Ephemeridæ (Figs. 34, 37, 38,
39, 41, 43), in which all the genera possess wings that are broad;
as an accompanying result the outer margin is long, and the
angle formed at the base of the wing by the anal and anterior
margins is greater than that in *Siphlonurus,* while the anal angle
is more acute.

   As mentioned before, the Baëtidæ have somewhat the shape of
the ancestral wing, but the venation is highly specialized and
different from the primitive venation.   Apparently the primitive
shape has been secondarily acquired, accompanying the extreme
reduction of hind wing.   This is indicated by the fact that in
other genera that have an anal angle and hind wing the smaller
the hind wing the more nearly the fore wing approaches the

shape found in the genera of the Baëtidæ, for example *Choroterpes* (Figs. 21, 22), *Ephemerella* (Figs. 55, 47), and *Heptagenia maculipennis* (Figs. 13, 14).

Caenis and *Tricorythus* have lost their hind wings, and while they have lost all indication of an anal angle the wing has not assumed the primitive shape due to the fact that at the base of the wing the posterior part has developed the so-called recurrent membrane, by which the wing is broadly attached to the body of the insect. This reaches its maximum development in *Caenis* (Fig. 45).

Blasturus (Fig. 31) is much like *Isonychia* as far as wing shape is concerned but is not as wide. The outer margin is comparatively long and the anal margin short. In *Choroterpes* (Fig. 29), *Leptophlebia* (Fig. 21), and *Ephemerella* (Fig. 55) where the hind wings have been greatly reduced, the anal margin is distinctly shorter than in *Blasturus,* the anal angle is no longer distinct, and the wing approaches that of the Baëtidæ in shape.

Baetisca (Fig. 54) stands alone and distinct in wing shape. The outer margin is exceptionally long, the anal margin short, but the anal angle is distinct, while the width of the wing is not excessive.

Genitalia

The genitalia of the male mayfly consist of (1) the styliger plate, which is borne on the terminal end of the ninth sternum; (2) the forceps, which arise from the posterior edge of the styliger plate; and (3) the paired penes, which are commonly considered to arise from the ninth segment and which protrude between the ninth and tenth segments. In the female there are no external organs and the oviducts simply open to the outside between segments 7 and 8.

The phylogenetic history of the insect genitalia and of their homologies between the various insect groups is difficult of interpretation and at present far from complete. The findings and interpretations given here for the mayflies will need modification as still further studies are made. In the mayflies the styliger plate has been interpreted as the tenth sternite by former workers. Evidence advanced by Crampton (1919 and

1920) and Walker (1919) indicates that this structure is in reality a process of the ninth sternum.

In such primitive insects as Thysanura, each sternum consists of a small basal piece or sternite to which are attached posteriorly two plates which are commonly accepted as representing coxites of abdominal legs. From these coxites arise posteriorly directed, unsegmented styli. These styli may represent exopodites of abdominal limbs. *Grylloblatta* presents a similar condition, which is especially evident in the immature stages. In many groups, however, the ninth sternite consists of a single plate which often is expanded posteriorly. This plate has been termed the hypandrium. It may or may not bear styli. Thus, Walker states that in the orthopteroid insects unjointed styli occur in the Blattoidea, Mantoidea, Isoptera, Grylloblattidæ, and Tettigoniidæ. Crampton believes that "in the higher insects a pair of styli form the outer ventral pair of claspers between which the penes valves are located."

The styliger plate of the mayflies is interpreted by Crampton and Walker as representing coxites, which have fused together to form a single structure. This structure, however, is separate from the ninth sternite. A parallel condition is to be found, according to Walker, in the Phasmoidea and Acridoidea, except that in these groups the styli are lacking.

The mayflies of the family Baëtidæ, i.e., *Baëtis* (Fig. 65), *Callibaëtis, Centroptilium, Cloëon,* and *Pseudocloëon,* and the genus *Isonychia* (Fig. 59) all have divided styliger plates. This condition appears to be of secondary origin and will be discussed later.

From the postero-lateral corners of the styliger plate arise the styli or forceps. These are 2–4 jointed in all the mayflies with the exception of the aberrant genus *Caenis.* Thus, while the styli of Thysanura and the orthopteroids consist of a single segment, the styli of the mayflies are jointed.

Since the mayflies belong to the heterometabola, it should be expected that the nymphs of different ages would display the styliger plate and forceps in their various stages of development. In a general way this is true, but there exist some striking differences between the appearance of the genitalia in the nymphs

and adults. The styliger plate, as found in the nymphs, appears as a prolongation of the ninth sternum. Both males and females possess such a structure. More striking than this is the fact that the styliger plate during the nymphal period is shaped much like the ventral prolongation of the ninth sternite of the adult female. The styliger plate of the male, however, undergoes modification during the last instar and the adult state is quite different from the nymphal condition. In most genera the styliger plate is, during nymphal life, roughly cone shaped, with the forceps arising from the sloping sides. In the Baëtidæ (Fig. 73), however, it is completely lacking while in *Hexagenia* (Fig. 85), *Ephemera* (Fig. 81), *Potamanthus* (Fig. 79), and *Polymitarcys* (Fig. 86), it is reduced to a narrow band-like structure.

The forceps, as externally visible organs, do not appear until rather late in the nymphal life of the individual. Their earliest indications are small papillæ borne on the posterior edge of the styliger plate. They are unsegmented when they first appear. In some species they subsequently segment; in others they remain unsegmented throughout nymphal life.

In mature nymphs of all species, the forceps consist of finger-like processes. They may or may not be segmented. Thus in *Blasturus* (Fig. 74), *Leptophlebia* (Fig. 80), *Choroterpes* (Fig. 78), *Ephemerella* (Figs. 92, 93), *Tricorythus* (Fig. 94), they are unsegmented. In *Potamanthus* (Fig. 79), *Heptagenia* (Fig. 50), *Ecdyonurus* (Fig. 51), *Epeorus* (Fig. 66), and *Isonychia* (Fig. 57), they are two-jointed, consisting of a long basal segment and a short terminal segment. This terminal joint of the nymphs corresponds to the two short terminal joints of the adult. In *Siphlonurus* (Fig. 58), *Hexagenia* (Fig. 85), *Ephemera* (Fig. 81), and *Polymitarcys* (Fig. 86), the nymphal forceps are three jointed, with a short basal joint (corresponding to the basal joint of the adult), a long second joint and a short terminal joint.

The members of the family Baëtidæ during the nymphal state lack the styliger plate, and either lack or have greatly reduced the forceps. The nymphs of *Callibaëtis* (Fig. 56) are exceptional and exhibit a tiny, cone-shaped forceps which is borne on a slight, posteriorly directed out-pocketing on the ninth sternite. In the remaining genera, the only visible indication of genital

organs in the nymphs consist of slight out-pocketings of the ninth sternum (Fig. 73). In mature mymphs which are just ready to emerge, the adult forceps and coxites can be seen through the thin chitin of the sternum. The forceps, due to the restricted amount of space in which they lie, are folded back against the coxites. The point where the forceps are folded is located a short distance from the base of the forceps, and this place in the adult forceps superficially appears as an articulation. It has been interpreted thus by former workers, but careful study will show that this is not a true articulation and is in reality due to the effects of the nymphal development. The genus *Caenis* has genitalia so different both in the nymphal and adult stages as to demand separate consideration. I do not have male nymphs of *Baetisca, Campsurus,* and *Pentagenia.*

The number of segments of the forceps during nymphal life is always less than during the adult state. Thus, in the Heptageniidæ (Fig. 53), *Tricorythus* (Fig. 87), and *Ephemerella* (Fig. 88), the adult forceps are articulated near the base but there is no indication of this in the nymphal forceps. The nymphal forceps, however, of *Siphlonurus* (Fig. 58), *Polymitarcys* (Fig. 86), *Hexagenia* (Fig. 85) and *Ephemera* (Fig. 81) have short basal segments that correspond to the short basal segments of the adult forceps. Of these four genera, the nymphs of the latter three, which belong to the family Ephemeridæ, display relationships not only in the segmentation of the nymphal forceps, but also in their method of attachment to the styliger plate, and in the shape of the nymphal styliger plate. In regard to the forceps and styliger plate, both during the adult and nymphal stages, *Siphlonurus* differs so much from the three other genera as to warrant the belief that its type of forceps segmentation has arisen independently.

In *Blasturus* (Fig. 74), *Choroterpes* (Fig. 78), and *Leptophlebia* (Figs. 80), during the nymphal life the forceps consist of a single segment, but the adult forceps are three-jointed, having two short distal segments and a long basal segment. *Ephemerella* (Fig. 93) and *Tricorythus* (Fig. 94) have unjointed nymphal forceps but the adult forceps have a short distal joint. The nymphal forceps of *Siphlonurus* (Fig. 58), the Hepta-

geniidæ (Figs. 50, 51, 52, 57, 66, 67), and the Ephemeridæ (Figs. 81, 85, 86) all have short distal segments which correspond to the two small distal segments of the adult forceps. It should be noted that *Potamanthus* (Figs. 79, 77) stands intermediate between *Blasturus* (Figs. 74, 72), *Choroterpes* (Figs. 78, 63), *Leptophlebia* (Figs. 80, 68), and the remainder of the Ephemeridæ (Figs. 85, 76, 81, 71, 86, 83), in the shape of the forceps, the number of forceps segments, their points of attachment to the styliger plate, and the shape of the styliger plate. This holds for both adults and nymphs.

The peculiar *Caenis* has the adult styliger plate (?) arising from the anterior end of the ninth segment (Fig. 89). It is a narrow, band-like structure with two slender arms arising from the postero-lateral corners. These arms bear unjointed, blade-like forceps (?). In the mature nymph these structures can be seen through the thin chitin of the ninth sternum (Fig. 90). The sternum is produced posteriorly and into this extend the forceps.

What is the phylogenetic history of the styliger plate and forceps? In the Thysanura the styliger plate is represented by two coxites. According to Walker, in all the orthopteroids, with the exception of *Grylloblatta,* these coxites have fused either together or with the ninth sternite. Similarly in all the ephemerid genera under consideration, with the exception of the Baëtidæ and *Isonychia,* the coxites have fused together to form the styliger plate, and this was apparently the primitive condition among mayflies. The divided condition of the styliger plate in the Baëtidæ has been secondarily derived. The lack of a styliger plate and forceps during nymphal life seems also to be a specialization in the Baëtidæ that has been derived from the condition found in more generalized forms. This is substantiated by the fact that the most primitive genus of this family, *Callibaëtis* (Fig. 56), still retains a tiny nymphal forceps. In a mature *Baëtis* nymph, the members of the adult styliger plate can be seen through the thin chitin of the ninth sternite. They are compressed and even the ninth sternite of the adult is reduced almost to one-half the length of the nymphal sternite. It is probable that the divided styliger plate of the adult of *Isonychia,*

a genus not closely related to the Baëtidæ, also represents a secondary condition. This plate is undivided in the nymphs of *Isonychia* (Fig. 57). This genus belongs to the Heptageniidæ and none of the other genera which are included in this family has a divided styliger plate in either the nymphal or adult stages.

Turning to the forceps, we find that their homologues, the styli, are unsegmented in the Thysanura and in all the orthopteroid insects where they are present. In the mayfly nymphs the forceps are 1- to 3-jointed, depending on the genus. The adult forceps are 1- to 4-jointed. It seems feasible to believe that in the primitive mayflies the forceps were unjointed. As shown above, the amount of segmentation of the adult forceps exceeds that of the nymphal forceps. Also, segmentation of the forceps has taken place separately and independently in various stocks of the family. For instance, the short basal segment has been developed four different times: (1) in *Siphlonurus,* in which it appears during nymphal life; (2) in the Heptageniidæ, and in this case it does not appear until the adult state is reached; (3) in the *Ephemerella-Tricorythus* stock, in which the basal segment similarly does not differentiate until the adult stage is reached, but the forceps and styliger plate in this group differ so much from the parts in the Heptageniidæ as to warrant the belief in the separate origin of the basal segmentation in the two groups; (4) in all genera of the Ephemeridæ, except in *Potamanthus,* the most primitive genus of this family. In at least three genera of the Ephemeridæ, namely, *Hexagenia, Ephemera,* and *Polymitarcys,* the segmentation appears during the nymphal stage.

The ædeagus, as stated above, arises from the ninth segment on the ventral surface of the abdomen. In the adult it lies just dorsal to the styliger plate and extends posteriorly between the forceps. The nymphal penes of *Blasturus* (Fig. 74), *Leptophlebia* (Fig. 80), *Choroterpes* (Fig. 78), *Ephemerella* (Figs. 92, 93), *Tricorythus* (Fig. 94), *Ecdyonurus* (Fig. 52), *Heptagenia* (Fig. 50), *Epeorus* (Fig. 66), *Isonychia* (Fig. 57), and *Siphlonurus* (Fig. 58) appear as two posteriorly directed, finger-like processes that lie close together and parallel to each other. In the mature nymph of the Ephemeridæ, the penes approach

in shape the structures found in the adult. The nymphs of the Baëtidæ lack all indications of penes. In mature nymphs of the aberrant *Caenis* the penes can be discerned through the thin chitin of the ninth sternite as a rectangular organ. It seems probable that the primitive mayfly penes consisted of two, finger-like protuberances. Palmen (1888) states that the penes arise as two protuberances of the hypodermis at the points where the vasa differentia are inserted into the hypodermis. Further, the nymphal penes of all the more primitive genera consist of two, finger-like processes. In the nymph there are no external signs of parameres and spurs which are to be found in the adults of some species.

In the adult the ædeagus consists of the paired penes and accessory organs. The penes have undergone considerable modification during the history of the group so that the various genera now show a great diversity of forms and shapes. Basally the penes are more or less united on their inner surfaces. In *Ephemerella* (Fig. 88), *Tricorythus* (Fig. 87), and *Baetisca* (Fig. 75), the penes form a tubular organ. That this condition has been secondarily derived is evident at least in the case of *Ephemerella* and *Tricorythus* in which, during the nymphal stage, the penes are clearly separate (Figs. 92, 93, 94). In the specialized family Baëtidæ, the genera *Baëtis* (Fig. 65), *Callibaëtis* (Fig. 48), and *Pseudocloëon* (Fig. 70) have internal penes, while *Cloëon* (Fig. 64) and *Centroptilium* (Fig. 69) have small, humped organs representing the penes. In the family Ephemeridæ the penes have run rampant. Accessory organs are present in some and absent in others. If present, they consist of lateral parameres, and of heavily chitinized spurs which are on the inner surfaces of the penes. Parameres or spurs, or both structures, may be present or absent. Thus, in *Siphlonurus* (Fig. 61) both the parameres and spurs are present. In the Heptageniidæ (Figs. 49, 53, 60, 62) and *Ephemera* (Fig. 71), the spurs alone are to thus (Fig. 137), *Caënis* (Fig. 141), *Baëtisca* (Fig. 144), and *Leptophlebia* (Fig. 68) may represent parameres. In the remaining genera considered in this paper, all traces of parameres and spurs are lacking.

Mouth Parts

The mouth parts of the mayfly nymphs consist of labrum, hypopharynx, mandibles, maxillæ, and labium. Of these five parts the following three will be discussed in this paper: the maxillæ, the labium, and the mandibles. As is commonly known, the mayfly mouth parts degenerate just before the emergence of the adult, and the resultant imago possesses mere rudiments of the formerly vigorously developed mouth parts. According to Miss Murphy (1922), there is also a progressive degeneracy of the remnant adult mouth parts. The rudimentary mouth parts of the adult are of no value for the interpretation of generic relationships.

Mandibles. The generalized mandible of a mayfly consists of a strong, sturdy organ which distally bears a dentation that is divisible into two distinct and diverse parts: (1) an outer or ventral incisor area, and (2) an inner or dorsal molar surface (Fig. 95). The molar surface serves as a grinding organ and is made up of a series of ridges and troughs which alternate with each other. The incisors, or canines as they have been called, probably serve as cutting and grasping organs. There are two incisors on each mandible, an outer incisor and an inner incisor. Between the incisors and the molars is a small body known as the lacinia mobilis. It lies close to the inner incisor and is partly surrounded by the latter in some genera. The mandibles of any individual are always asymmetric, both in shape and in regard to the construction of the molars, lacinia, and incisors.

The mandibles are so placed that the long axes of the organs are directed ventrally and inwardly. The incisors are thus located ventral to the molars. In the primitive mayflies the axes of the mandibles are vertical. In the genera *Hexagenia* (Fig. 105), *Ephemera* (Fig. 109), *Polymitarcys* (Fig. 106), and *Pentagenia* (Fig. 110), the axes have become horizontal, but the molars and incisors in these latter genera have so shifted their positions on the mandibles that they are in the same vertical position as in the primitive groups. This warping of the mandibles has been necessitated by the development of a long tusk on each mandible. In *Potamanthus* (Fig. 104) the tusks are short, and the warping of the mandibles is slight.

As stated above, the incisors are bipartite, consisting of two prongs. Terminally each prong gives rise to a number of teeth, the number differing in different genera. In *Baëtis* and *Cloëon* (Figs. 103, 107), the prongs of the incisor have more or less fused to give rise to a single sturdy organ.

The lacinia mobilis assumes a variety of shapes. Among species of the same genus the general pattern seems to be very constant. The exact function of this organ has never been definitely determined and I have no information to add to this phase of the subject. It has been interpreted by Eaton (1883) and Heymons (1896) as a mandibular palp, but as a prostheca by Lestage (1917). According to Crampton (1921) this can not represent a true palp on the mandible, comparable with a palp found on the maxillæ; but it must correspond to the fusion of the hairs making up the gnatho-fimbrium.

In the Ephemeridæ (Figs. 186, 187, 189, 190, 191) the lacinia mobilis consists of a sturdy, trunk-shaped organ of variable size, wholly or partially covered with short or long hairs. Distally it terminates either bluntly or with a tapered point. Sometimes it bears a number of tooth-like structures at the distal end. In the case of the Heptageniidæ (Fig. 174), if present it is slender, resembling a gigantic seta. Some genera of this family completely lack a lacinia mobilis, while in others the organ consists of a number of seta-like processes (Fig. 185). The main body of the lacinia is invariably more or less arched, sometimes near the base, sometimes distally, and the curve may be sharp or gradual.

The studies of Crampton (N. Y. ENT. SOC. 29 : 63–97) indicate that the entire mandible represents a single endite or gnatho-base, the mandible itself being equal to the maxillary lacinia which also is a complete endite, while the stipes is another complete endite. Thus the various parts of the mandible can not be homologized with parts of the maxillæ. Crampton points out that the mayfly nymphs have very primitive mandibles, which, in some respects, approach those found in the crustacea.

On such a basis the type of mandible that is to be found in *Siphlonurus* seems to be primitive. The incisor region of this sort of mandible is divided into two distinct parts, with the molar

areas moderate in size while the laciniæ mobiles are both similar.

Several distinct lines of specialization can be distinguished within the order: (1) the Ephemeridæ with their long anteriorly directed tusks; (2) the Baëtidæ with the more or less fused incisors; (3) the Heptageniidæ lacking the lacinia mobilis or having it reduced to a seta-like structures. The remaining genera present more or less generalized conditions, although each genus displays distinctive shape and structure.

The Maxillæ. The galea, lacinia, stipes, and palpifer are fused in all existing mayflies and form a lacinia-galea. The line of fusion of the galea and lacinia has been completely obliterated in almost all cases. Miss Murphy (1922) reports that it can be identified in *Hagenulus,* and some specimens of *Siphlonurus* show slight indications of the suture. The lacinia-galea bears several heavily chitinized pointed processes on its distal termination which are known as the dentes of the lacinia (Fig. 118), while the inner edge may bear numerous setæ (Fig. 118) which vary in number, length, arrangement, and structure according to the genus under consideration. As a general rule, however, the greatest number is to be found near the terminal end in the vicinity of the lacinial dentes, while a sparse group of long slender hairs is often to be found in the proximal region just opposite the base of the palp. Near the distal end, on the inner edge, amongst the hairs is to be found a number of strong, long, sharply pointed spines. As with the setæ, they vary according to the genus considered.

On the terminal edge of the lacinia-galea, on the part contributed by the galea, there is a patch of setæ which vary greatly in size, length, number, and distribution in the various genera (Figs. 118, 119, 124, 131, 135).

The shape of the lacinia-galea, the number of maxillary palpal segments, and the arrangement, etc., of the various hairs and spines are the structures that will be employed to demonstrate relationship in the following section.

In attempting to determine what is the most primitive maxilla it must be remembered that even the most primitive maxilla of the mayflies (as is patent from the nature of the lacinia-galea) is specialized as compared with more generalized insect types.

Further, some parts of the maxillæ may have undergone specialization while other parts may have remained primitive.

The 3-jointed palp has been considered more primitive than the 2-jointed. There is no definite evidence to support this view or the opposite view. The mayfly genera, however, that are most specialized in other respects have a 2-jointed palp. Further, in *Machilis* the maxillary palp is 4-jointed, while in the crustacea the generalized types possess more than three segments to the endopodite, so that it seems feasible that the reduction is a specialization. Thus, the 3-jointed maxillary palps as found in *Siphlonurus* (Fig. 118), the Ephemeridæ (Figs. 133, 138, 139, 140), *Blasturus* (Fig. 129), *Leptophlebia* (Fig. 132), *Choroterpes* (Fig. 131), *Ephemerella* (Fig. 135), *Tricorythus* (Fig. 137), *Caenis* (Fig. 141), and *Baetisca* (Fig. 144) would be more primitive than the 2-jointed type of the Heptageniidæ (Figs. 120, 121, 124, 125, 128, 130) and the Baëtidæ (Figs. 122, 123, 126, 127). Besides the number of maxillary palp segments, the shape and size indicate relationships.

The ancestral mayfly nymphs crawled around on the bottoms of pools and other relatively still bodies of water, living in habitats similar to those in which *Blasturus* and *Siphlonurus* now dwell. Two distinct lines of evidence support this view: (1) although only few fossil mayfly nymphs are known, judging on the basis of the shape of their bodies, the unprotected gills, and the caudal filaments possessing setæ on both the inner and outer sides, these individuals doubtlessly lived in such a habitat; (2) the mayfly ancestors were terrestrial insects and have secondarily adapted themselves to the water. It appears logical that they made this transition gradually, and that the ancestral nymphs which possessed unprotected gills, and thus were unable to live in swiftly running water or to burrow, or even crawl under flat objects which were closely adhering to the bottom, must have lived in clear, well aerated, still or slowly flowing waters. On these bases, and at the same time keeping in mind the origin of the lacinia-galea, a maxilla which appears more nearly like the ancestral type than any other to be found within the family is possessed by *Siphlonurus*. The body of the organ in this genus (Fig. 118) is more or less straight, unexpanded,

and somewhat cylindrical, with a row of well developed setæ on the terminal edge of the part of the structure contributed by the galea. The lacinia dentes in *Siphlonurus* are moderately developed, the lacinial spurs and setæ evenly distributed along the lacinal portion of the fused structure, and finally there is a slight indication of the suture between the two elements in the structure.

Several definite and distinct lines of development of the lacinia-galea can be distinguished within the family: (1) a broadly flattened type, with the characteristic curve to the galea, as found in the Heptageniidæ (Figs. 120, 124, 130); (2) a type in which the structure is heavy and massive, with the lacinial dentes strongly developed and the setæ and lacinial spurs restricted to the terminal end, as found in *Ephemerella* (Fig. 136), *Tricorythus* (Fig. 137), *Caënis* (Fig. 141), *Baëtisca* (Fig. 144), and the Baëtidæ (Figs. 122, 127); and (3) a type in which the structure is more or less flattened, roughly rectangular, with the lacinial dentes reduced, with heavy, dense setæ on the galeal portion as well as on the lacinial portion, a condition which is characteristic of *Blasturus* (Fig. 129), *Leptophlebia* (Fig. 132), *Choroterpes* (Fig. 131); and all the Ephemeridæ except *Ephemera* (Fig. 138) and *Hexagenia* (Fig. 139). These latter genera have a slender, curved lacinia-galea which is very distinctive.

Labium. The insect labium, as is commonly known, consists of the fused second maxillæ, and the various parts of each half can be identified as homologous to the corresponding parts of the first maxillæ. In the Ephemerida the glossæ and paraglossæ, unlike their first maxillary homologues, have not fused but are separate and distinct organs. In this paper the mentum, palpiger, and the ligula (which have fused to form a single structure) will be termed the internal lobe.

The labial palp, with few exceptions, parallels the maxillary palp in the number, shape, and relative proportions of its segments. The exceptions occur in highly specialized genera, such as *Hexagenia* (Fig. 161) which has only two segments to the labial palp, although it has a 3-jointed maxillary palp. *Tricorythus* (Fig. 158) and *Ephemerella* (Fig. 164) have labial palps which are much more generalized than the maxillary palps. In the more primitive genera (especially *Siphlonurus*

(Figs. 118, 143) the maxillary and labial segments correspond closely.

The internal lobe with its appendages, the glossæ and paraglossæ, assumes a diversity of shapes and arrangements. It may be greatly expanded as in *Ephemerella* and *Tricorythus* (Figs. 164, 158), or small as in *Siphlonurus* (Fig. 143). The paraglossæ may be finger-like as in *Siphlonurus* (Fig. 143), and the Baëtidæ (Figs. 150, 154, 157), or broadly expanded as in *Blasturus* (Fig. 151), *Choroterpes* (Fig. 155), *Leptophlebia* (Fig. 159). In the Ephemeridæ (Figs. 152, 153, 156, 160, 161) they are expanded and postero-laterally produced, or they may be small and reduced as in *Tricorythus* (Fig. 158) and *Ephemerella* (Fig. 165), or characteristically flattened as in the Heptageniidæ. The glossæ never exceed the paraglossæ and are usually much smaller, especially in the case of the Heptageniidæ (Figs. 142, 145, 146, 147, 148, 149), Ephemeridæ (Figs. 152, 153, 156, 161), *Blasturus* (Fig. 151), *Choroterpes* (Fig. 155), and *Leptophlebia* (Fig. 160).

Since the various modifications that the labium has undergone parallel those of the maxillæ, *Siphlonurus* appears to have the most primitive mayfly labium in existence.

Gills

The gills of present-day mayflies are highly diverse and present many adaptations to the environmental conditions in which the nymphs live. The two mayfly species known from the lower Permian (belonging to the genus *Phthartus*) had nine pairs of slender, unbranched, finger-like gills. *Mesobaëtis sibricia* Brauer of the lower Jurassic (Dogger series) is very similar to *Phthartus*, while *Mesobaëtis antiqua* Brauer, Redtenb., Ganglb. possesses seven pairs of small, leaf-like gills. *Ephemeropsis orientalis* Eichwald of the Malm series of the Jurassic has eight pairs of simple gills like those found in *Phthartus*. *Phacelobranchus*, also of the Malm, has only eight pairs of gills, but they are compound. There are never more than seven pairs of gills in any present-day species, and these are located on the first seven abdominal segments. This is generally the number in present-day forms. In a few genera, such as *Ephemerella*, *Baetisca*, and *Caenis*, there are less than seven pairs. These exceptions would,

however, appear to have been derived from an ancestral stock that possessed at least seven gills.

Drucken (1907) advanced the view that the gills were serially homologous with the wings, but works by Heymons (1896) and Borner (1908) have led to the general acceptance that the gills are homologous with the legs. Thus, the gills are ambulatory appendages that have been modified for respiration. Recent work by Snodgrass (1927) has added support to this theory. In this connection it is interesting to note that gills have been developed upon the maxillæ of *Isonychia* (Fig. 119) in the region of the union of the cardo and stipes. In the genus *Oligoneuria* gills are also developed on the maxillæ.

From the paleontological evidence, plus the facts demonstrated by the rearing of various species, it would appear that the primitive gills of the ancestral mayflies were simply slender tubular structures, into which the tracheæ enter, and that the compound structures of the present-day forms have arisen as modifications of this primitive type. The two principal ends attained by these modifications are a superior respiratory organ and protection for the gills. In some cases, as in *Caenis* (Fig. 250), *Tricorythus* (Fig. 249), and *Ephemerella* (Fig. 245), whole gills or parts of gills are given over in the main to protection.

The modifications that the gills have undergone include the flattening of the gill into a foliaceous organ and the changing of the gill from a simple, finger-like out-pocketing into a double organ consisting of two leaves lying against each other. This doubling seems to have been accomplished by the gill developing a small lobe at the base which develops into the posterior or inferior lamella. The two leaves may be similar [as in *Leptophlebia* (Fig. 228), *Hexagenia* (Fig. 230), *Blasturus* (Figs. 225, 226), *Choroterpes* (Figs. 222, 223), etc.], or they may be very different [as in *Heptagenia* and *Isonychia* (Figs. 200, 205)].

It will be helpful in determining the mutual relationships between genera to follow the fate of the gills in the younger post-embryonic stages. Work of this type in every instance (Vayssiere, 1882; Lubbock, 1863–66; Gros, 1923; Murphy, 1921, and Wiebe, 1926) shows that the newly born larvæ do not display any indications of gills but that these arise later as simple out-pushings of the dorso-lateral abdominal wall. These later dif-

ferentiate into the various shapes characteristic of the several species. Although only a few species have been studied, it seems likely that the gills of all mayflies arise as simple out-pushings. To learn just how these simple gills develop into the highly complex gills of such forms as *Caenis, Tricorythus, Ephemerella,* etc., would be of enormous value in determining relationships between various genera.

I have incubated the eggs of *Hexagenia limbata* Guerin and reared the nymphs until they were half grown. Due to diffi-culties resultant from the method of handling the nymphs, I was not able to preserve specimens of every instar, but a complete enough series was taken to enable me (with the aid of Wiebe's findings) to demonstrate how the gills grew into the highly com-pound structure of the adult nymph. The gills arose as de-scribed above during the second instar. The gill analogues increased in length and in diameter. In a nymph eleven days old (Fig. 236) filaments, irregularly placed and spaced, extend laterally from the body of the gill. The main trunk is still cylindrical. Near the base on the posterior side there arises a short finger-like projection that extends caudally. This is slightly larger than any of the other filaments. As the nymph grows older (Fig. 235) this projection, which becomes the pos-terior gill lamella, grows much faster than the main trunk so that by the time the insect is twenty-five days old the two la-mellæ are of equal size, just as in the adults. Meanwhile these two lamellæ have become flattened laterally and the filaments have become localized along the edge with a regular arrange-ment. When the nymph is about twenty-two days old, the gills are very similar in appearance to those found in *Potamanthus* (Fig. 229), and by the time the nymph is thirty days old the gills are identical in shape, proportions, and arrangement of the filaments with those found in the adult *Hexagenia* nymphs (Figs. 231, 232).

From Gros and Vayssiere's descriptions of species of *Hepta-genia,* it is evident that the history of the compound gills in these species is parallel to that in *Hexagenia,* although the resultant gill is quite different in shape.