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Studies in the Comparative Anatomy and Systematic Importance of the Hexapod Tentorium—IV. Ephemeroptera

by

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INTRODUCTION.

From a study of available literature it appears that the tentorium of the Ephemeroptera has received little attention, so that the necessity has arisen for a detailed examination of this skeletal system, in both larval and adult forms.

A brief description of the larval tentorium was given by Hsu (Needham, et. al., 1935), in which he stated that this structure was " composed of three pairs of ingrown arms or apodemes, anterior, dorsal, posterior. The tips of these expand and coalesce to form a platæa, the body. The posterior arms form the anterior boundary of the occipital foramen, through which the alimentary canal passes into the thorax." This description is, however, misleading for the dorsal arms are not invaginated, and are only attached to the head-capsule, and no tentorial pits occur at the points of their attachment to suggest that the dorsal arms are invaginated. Hsu's (t.c.) description of the larval tentorium was accompanied by a small diagram, but no description or figure of the adult Ephemeropteron appeared in his work.

Hansen (1930) stated that in the Ephemeroptera " the tentorium is well developed. Its anterior branches run to the cranium above and somewhat outside the clypeus: at the middle it is an unpaired rather short plate which posteriorly has a pair of strong rami going to the cranium outside the occipital foramen." No mention of the dorsal arms appears in this generalised description.

Thus, the unsatisfactory state of our knowledge of the tentorium in the Ephemeroptera is readily apparent, and the object of this study is a further investigation into this structure in both larval and adult forms.

The writer is indebted to the Council for Scientific and Industrial Research for the award of a Research Grant Bursary.

Special thanks are due to Professor F. Carpentier of Liège University, Belgium, for a valuable gift of larval and adult Ephemeroptera. The kind co-operation in the presentation and identification of material by Dr. K. H. Barnard, Dr. J. Hewitt and Mr. R. Crass is gratefully acknowledged, and appreciation and thanks are again extended to Professor J. Omer-Cooper for consistent interest and encouragement in these studies.

TECHNIQUE.

Hsu (Needham, et. al., 1935) stated that the tentorium in the Ephemeroptera may be studied after the mouthparts of the ventral side of the head have been dissected out and all soft parts removed by boiling a few minutes in 2% K O H, the head being finally rinsed and mounted. The writer, however, finds that in both the larva and the adult the head should be left in cold 10% caustic potash solution from one to three days, after which it may be rinsed and finally preserved in 70% alcohol. It is possible in dealing with larval forms to remove the mouthparts and then mount material thus prepared, but examination of the tentorium in both the larva and the adult under a dissecting microscope is recommended in preference to examination of mounted specimens. In the case of the adult, it is often necessary to execute a very careful dissection of the postero-ventral region of the head, before the structure of the tentorium can be studied. A clear definition of the outline of the tentorium may be obtained by the use of a saturated solution of iodine in 70% alcohol Hudson (1946). The use of Hæmalum and Kernschwarz are also to be recommended for use in this study.

MATERIAL.

The following species were selected and examined:—

Austrocœnis capensis Bnrd., family: Leptophlebiidæ (larva), *Atalophlebia* sp., *Eatonica schoutedeni* (Navas), *Bœtis harrisoni* Bnrd., *Adenophlebia auriculata* Eaton, *Acentrella natalensis* Crass, *Afronurus harrisoni* Bnrd., *Polymitarcys savigni* (Pict.), *Tricorythus discolor* (Burm.), *Aprionyx tricuspidatus* Crass, all from South Africa. *Coloburiscus humeralis* Eaton (New Zealand), *Potamanthus luteus* L. (Belgium), *Ephemera* sp. (Great Britain), *Ephemera* sp. (Belgium), *Ellasoneuria trimeniana* MacLach. (Congo), *Epeorus assimilis* Eaton (Belgium), *Oligoneuriella rhenna* Imh. (Belgium), *Torleya Belgica* Lest. (Belgium).

Larva.

The larval stage of the Ephemeroptera is accomplished in a variety of acquatic conditions, and the wide range of habitat encourages diverse adaptive modifications of a structural and functional nature.

Larvæ of fossorial habit usually occur in slow-flowing waters which are not subject to floods, and which possess suitable banks. They may be taken near the bases of rushes in soft mud overlying a clayey substratum, according to Crass (1947), or they may tunnel through sand or gravel assisted in this task by the possession of mandibular tusks and powerful fossorial forelegs. Their food consists mainly of plant detritus, diatoms and other micro-organisms. Included in this category are *Eatonica schoutedeni* (Navas), *Polymitarcys savigni* (Pict.), and *Austrocœnis capensis* Bnrd.

In contrast to fossorial larvæ are those larvæ which may be free-swimming or found on rocks from which they swim actively when disturbed. Structural modifications may occur in such forms, the body becoming dorso-ventrally flattened and pressed to the substratum, and functioning as a vacuum by retraction of the central portions, e.g. *Tricorythus discolor* (Burm.). Femora may be flattened to aid in adhesion and denticulate claws may occur to enable the larva to cling to rocks and so resist strong currents. Swift-water inhabitants often possess thick-set setæ on the mouth-parts, by means of which they can strain particles from their surroundings. Crass (1947) states that most Leptophlebiids are found in swift-flowing water, but exceptions do occur in slow-flowing rivers and even swamps and still pools in the back waters of mountain streams. Swift-water types are able to inhabit slow-flowing reaches, but still-water forms are unable to resist strong currents. Examples of swift-water larvæ include *Bœtis harrisoni* Bnrd., *Afronurus harrisoni* Bnrd., *Acentrella natalensis* Crass, *Adenophlebia auriculata* Eaton, *Tricorythus discolor* Eaton, *Torleya Belgica* L., *Epeorus assimilis* Eaton, *Coloburiscus humeralis* Eaton.

Larvæ which favour slow-flowing waters and still pools usually occur amongst algæ and herbage. As a rule these larvæ are vegetable feeders with mouth-parts adapted to biting off plant tissues, and representatives of such larvæ are *Aprionyx tricuspidatus* Crass and *Potamanthus luteus* L.

In the Ephemeroptera, the larval stage is campodeiform, cylindrical or flattened. With the exception of the Bætidæ, where hypognathism is encountered, the head of the mayfly larva tends to be prognathous or semi-prognathous.

The head-capsule is usually broad in free-living forms, but in those larvæ of fossorial habit, the head may become wedge-shaped and pointed. The dorsal or dorso-laterally placed compound eyes are well-developed and three ocelli are usually present in the inter-ocular region. The short filiform antennæ are forwardly directed and notably anterior in position. In prognathous forms the mouth-parts occur anteriorly and the occipital foramen has been drawn forwards so that it lies at an angle to the vertical axis of the body. In the hypognathous Bætidæ, the occipital foramen is vertical in position and the ventrally directed mouth-parts have caused a downward depression of the head-capsule in the interocular region.

The tentorium of the ephemeropteron larva was incorrectly described by Hsu (Needham et. al., 1935), who stated that the structure consisted of three pairs of ingrown arms, anterior, dorsal and posterior. The dorsal arms of the tentorium are not ingrowths, however, but arise from the body of the tentorium between the anterior and posterior arms, and extend either to the front or to the margin of the antennal sclerite. (Comstock and Kochi, 1902). Furthermore, in the ephemeropteron larva no tentorial pits occur at the points of attachment of the dorsal arms to the head-capsule to indicate that the dorsal arms have been invaginated. Carpentier (1946), in studying the thoracic pleurites of the Thysanura, clarifies the position with regard to invaginations of the exo-skeleton.

" La chitine endosquelettique sous-épithéliale (1) des Lépismes et autre Thysanoures représente donc, en elle-même — morphologiquement parlant — autre chose que celle des furcas et des spinas sécretée vers l'extérieur (1) par l'épithélium de la peau des Pterygotes. Il na foudrait cependent pas croire qu'aucune introflexion cuticulaire ne s'associe chez les Lépismes aux endosternites. A un niveau correspondent à certaines au moins de leur attaches, on observe effectivement, en la chitine extérieure, une fosette qui n'est jamais très forte, mais qui, pour deux attaches homologues, peut se presenter comme plus importante en un segment que dans l'autre. A supposer qu'une de ces fosettes, s'accroisse jusqu'à production d'une furca ou d'une spina caractérisées comme celle des insectes ailés et que corrélativement, se réduise l'endosquelette sous épithelial, on ne voit pas que l'orde de succession des strates histologiques en serait bouleversé ni la position relative des muscles sensiblement modifée. Il était donc legitime d'homologuer comme l'a fait Maki, des muscles endosternaux de Thysanoures à ceux des furcas et des spinas de Pterygotes et je me trouvais moimême en droit d'utiliser les attaches endosternites de Ctenolepisma pour caractériser certain constituants essentiels de son mesosternum."

In the tentorium of the ephemeropteron larva, the anterior tentorial arms arise from the anterior tentorial grooves which are located at the edges of the inflected ventral areas of the genæ, and before the bases of the mandibles. According to Snodgrass (1935), these grooves represent the subgenal sutures of higher insects. Snodgrass (1928) also states that this position of the anterior tentorial arms in ephemeropteron larvæ is more primitive than the condition found in orthopteroid insects, where the anterior tentorial pits lie in the fronto-clypeal (=epistomal) suture and have become diagnostic marks of this suture or the fronto-clypeal line when a suture is absent.

The anterior tentorial grooves give rise to the invaginated anterior tentorial arms, which in most ephemeropteron larvæ are well developed, and along their grooves of origin these arms are considerably expanded, but taper as they converge to meet in the medianly placed body of the tentorium. The dorsal arms in the larval tentorium occur as broad plate-like expansions of the anterior tentorial arms, which become attached to the head-capsule in the interocular region. The body of the tentorium displays considerable variation in shape: it may occupy a somewhat posterior position in the head-capsule and occur as a narrow rectangular band, resulting in the considerable elongation of the anterior tentorial arms which tend to brace the greater part of the head-capsule. The body of the tentorium may be square or rectangular in shape, in which case the anterior tentorial arms, though broad and well developed, do not display unusual length. In some cases the anterior region of the body of the tentorium is wider than the posterior, but in most instances the body of the tentorium may be described as a fairly well-developed plate-like structure. The posterior tentorial arms are less well developed than the anterior tentorial arms and very much shorter. They arise as invaginations of the posterior tentorial pits, the latter occurring as deep depressions in the extremities of the post-occipital suture. The posterior tentorial arms unite to form the posterior of the body of the tentorium.

As previously indicated, Hudson (1945), the tentorium braces the walls of the cranium, and also affords attachment for muscles. The principal cephalic muscles include muscles of the antennæ, muscles of the mouth-parts and cervical muscles. As many of these muscles take their origin from the tentorium, a digression at this stage would facilitate a better understanding of the variations in the tentorium which occur amongst the Ephemeroptera.

In general, the levator and depressor muscles of the antennæ take their origin from the anterior and dorsal arms of the tentorium, or the dorsal arms only. The ventral adductor muscles of the mandibles, the maxillæ and the labium originate on the anterior tentorial arms and part of the body of the tentorium. Retractors of the hypopharynx have their origin on the anterior tentorial arms, and lateral dilators of the pharynx on the dorsal arms. Ventral dilators of the buccal cavity and the pharynx usually have their origin on the body of the tentorium, while the posterior tentorial arms may support retractors of the labium, adductors of the mandible, dilators of the pharynx and the crop, and the longitudinal ventral muscle of the prothorax.

Ephemeropteron larvæ of fossorial habit are exemplified by *Eatonica schoutedeni* (Navas), *Polymitarcys savigni* (Pict) and *Ephemera* sp.

In the larva of *Eatonica schoutedeni* (Navas), the anterior tentorial grooves give rise to strong, well-developed anterior tentorial arms which are heavily chitinised at their bases (Fig. I, ata). Arising as outgrowths of the anterior tentorial arms and occurring on their dorsal posterior margins are the dorsal arms (Fig. I, da). The latter are attached to the head-capsule in close proximity to the lateral ocelli. Each dorsal arm is a wide expansion proceeding from each anterior tentorial arm. This plate-like expansion tapers to become triangularly shaped, being slightly expanded at the apex where it is attached to the head-capsule. The anterior tentorial arms are long, bracing the greater part of the head-capsule and converging in a V-shaped manner to meet postero-mesadly in the broad short body of the tentorium (Fig. I, bt.). The body of the tentorium is short, broad and well developed (Fig. I, bt.). The posterior tentorial arms are comparatively broad but short and arise as invaginations of the posterior tentorial pits, the latter occurring as deep depressions in the extremities of the post-occipital suture (Fig. I, pta., ptp.). The posterior tentorial arms unite to form the posterior of the body of the tentorium. In *Eatonica schoutedeni* (Navas) a small tendonous outgrowth occurs on each posterior tentorial arm and this is directed posteriorly into the cavity of the occipital foramen (Fig. I, tp., of.).

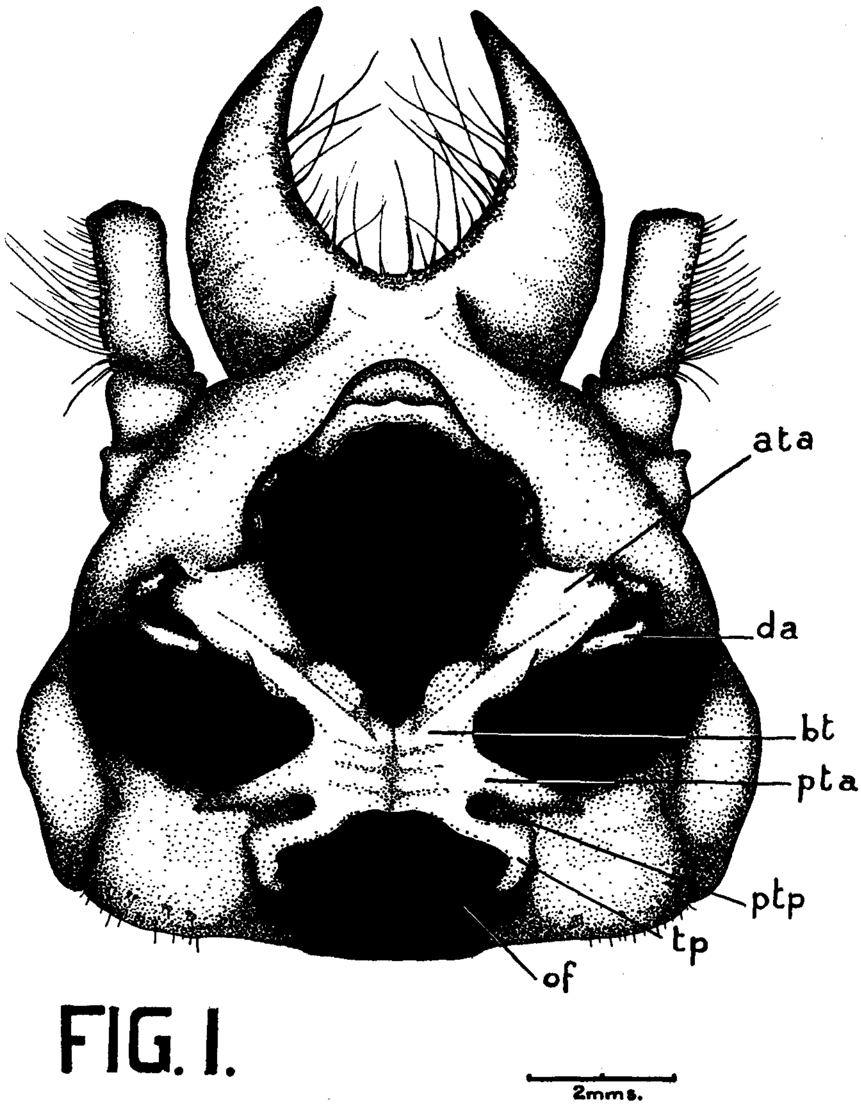


Fig. I. — Ephemeroptera. *Eatonica schoutedeni* (Navas). Larva. Postero-ventral aspect.

ABBREVIATIONS USED IN FIGURES.

ata — anterior tentorial arm.
atp — anterior tentorial pit or groove.
bt — body of the tentorium.
da — dorsal arm.
of — occipital foramen.
pta — posterior tentorial arm.
ptp — posterior tentorial pit.
tp — tendonous outgrowth.

In comparing the larval tentorium of *Polymitarcys savigni* (Pict) with that of *Eatonica schoutedeni* (Navas), a general similarity between the two may be discerned. However, in the tentorium of *Polymitarcys savigni* (Pict), the body of the tentorium occupies a more central position in the head-capsule. The posterior tentorial arms are thinner than in *Eatonica schoutedeni* (Navas), and converge to unite in a V shape, rather than in a broad band, to form the posterior of the body of the tentorium. In the *Ephemera* sp., the tentorium is similar to that of *Eatonica schoutedeni* (Navas) and the anterior tentorial arms are again remarkably strong and well developed.

Variations in the tentorium as exhibited by *Afronurus harrisoni* Bnrd., *Adenophlebia auriculata* Eaton, *Acentrella natalensis* Crass, *Tricorythus discolor* (Burm.), *Torleya Belgica* L., *Coloburiscus humeralis* Eaton, and *Bœtis harrisoni* Bnrd., have been studied. The larvæ in all cases inhabit swift-flowing waters.

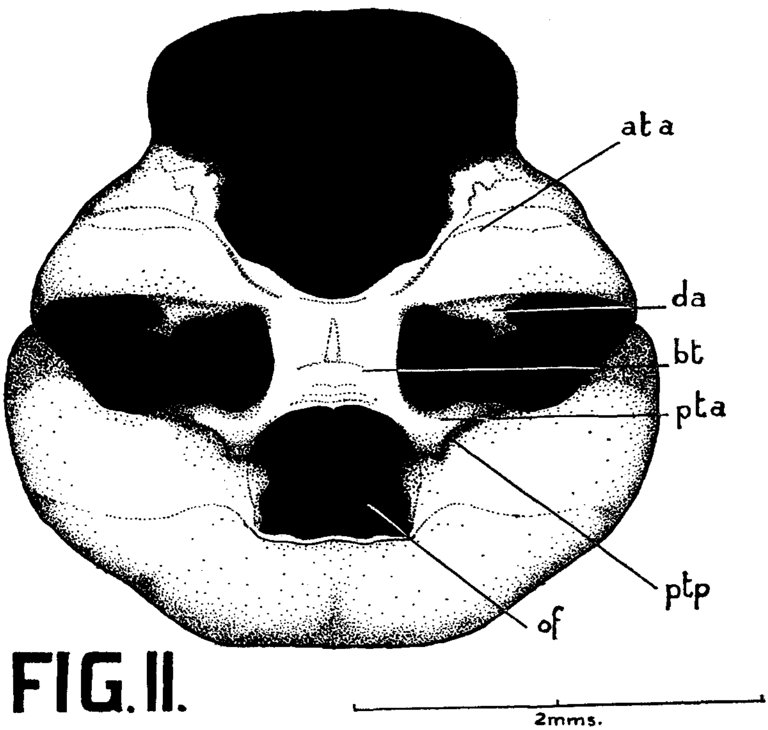


FIG. II.

Fig. II. — Ephemeroptera. *Adenophlebia auriculata* Eaton. Larva. Postero-ventral aspect.

In *Afronurus harrisoni* Bnrd., the anterior tentorial arms are very well developed (Fig. II, ata.), and they converge to meet in the short, broad body of the tentorium (Fig. II, bt.). The posterior tentorial arms are short and meet in the band-shaped posteriorly placed body of the tentorium (Fig. II, pta.). There are two tendonous outgrowths occurring on the median ventral posterior surface of the body of the tentorium and these are backwardly directed (Fig. II, tp.). The dorsal arms in *Afronurus harrisoni* Bnrd., are larger than in *Eatonica schoutedeni* (Navas). They are broad, plate-like expansions attached to the head-capsule close to the lateral ocelli (Fig. II, da.). Thus in structure the tentorium of the fossorial larva of *Eatonica schoutedeni* (Navas) does not show significant variation from that of the swift-water inhabitant *Afronurus harrisoni* Bnrd.,

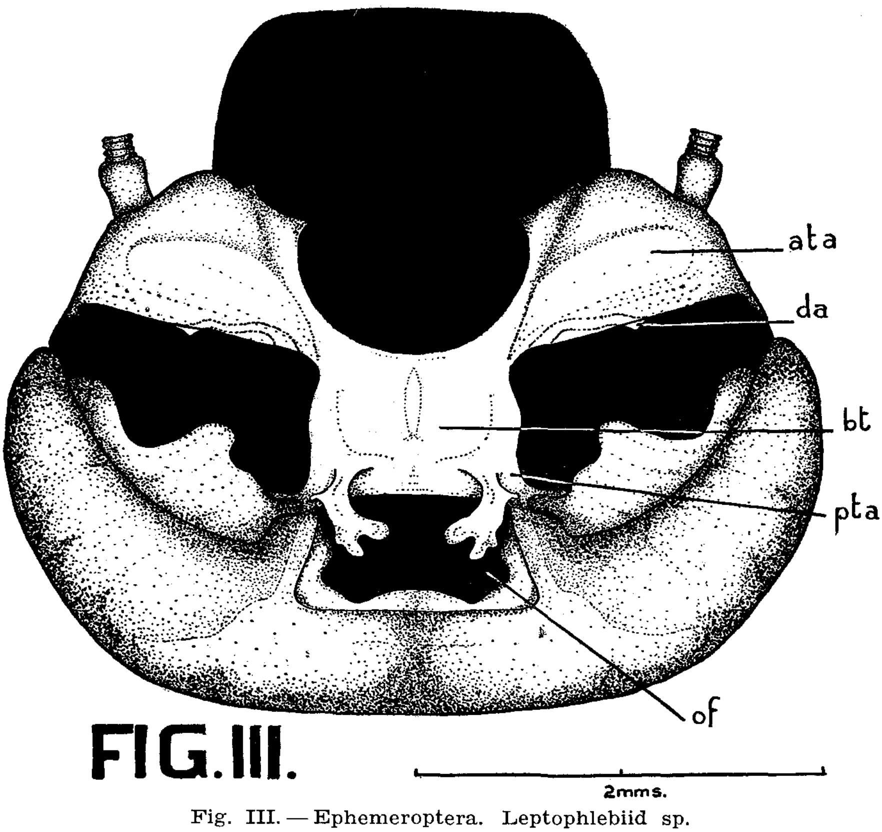


FIG. III.

Fig. III. — Ephemeroptera. Leptophlebiid sp. Larva. Postero-ventral aspect.

Some variation in general structure of the tentorium does occur, however, amongst swift-water species. In the leptophlebiid species (Fig. III) it will be observed that the anterior tentorial arms are remarkably strong and broad, but shorter than in either *Afronurus harrisoni* Bnrd., or *Eatonica schoutedeni* (Navas) (Fig. III, ata.). The posterior tentorial arms are also comparatively short (Fig. III, pta.), but the body of the tentorium is a large, square, centrally placed plate (Fig III, bt.), and an inverted T-shaped tendonous outgrowth occurs on the median ventral surface, and there is an outgrowth on either side of the posterior ventral margin of the body of the tentorium (Fig. III,tp.). The dorsal arms arise as marginal outgrowths on the anterior tentorial arms, and may be located on the posterior margin of the anterior tentorial arms, before the latter coalesce to form the body of the tentorium (Fig. III, da.). The dorsal arms are attached to the head-capsule adjacent to the lateral ocelli, and they are less plate-like and more tendonous than in *Eatonica schoutedeni* (Navas) or *Afronurus harrisoni* Bnrd.

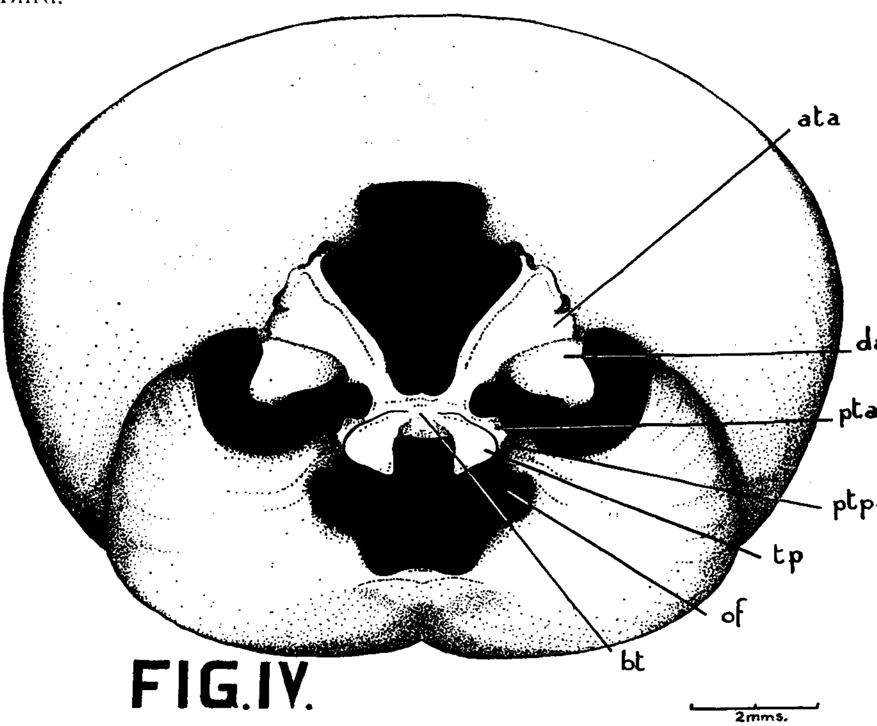


Fig. IV. — Ephemeroptera. *Afronurus harrisoni* Bnrd. Larva. Postero-ventral aspect.

The tentorium of *Adenophlebia auriculata* Eaton shows pronounced similarity to that of the leptophlebiid species examined. In *Adenophlebia auriculata* Eaton, the broad, well-developed and expanded anterior tentorial arms coalesce to form the anterior of the body of the tentorium (Fig. IV, ata.). The posterior tentorial arms are longer than those of the leptophlebiid species and meet arcuately in the posterior of the body of the tentorium (Fig. IV, pta.). The body of the tentorium in *Adenophlebia auriculata* Eaton occupies a central position in the head-capsule and is of square proportions, thus resembling that of the leptophlebiid species (Fig. IV, bt.). An inverted

T-shaped tendon is also present on the median-ventral surface of the body of the tentorium (Fig. IV, tp.). The dorsal arms of *Adenophlebia auriculata* Eaton are better developed and more plate-like than those of the leptophlebiid species.

In *Acentrella natalensis* Crass, a crawling inhabitant of rocky sections in flowing waters, the anterior tentorial arms are well developed, broad, and meet in an arc to fuse in the body of the tentorium. The posterior tentorial arms are also well developed and broad, uniting in the strong band-shaped posterior of the body of the tentorium. The latter is of rectangular shape. The dorsal arms are well-developed marginal expansions of the anterior tentorial arms and taper to their point of attachment to the head-capsule in the interocular region.

The anterior and dorsal tentorial arms of *Tricorythus discolor* (Burm.) are notably well developed. The latter are broadly expanded and attached to the head-capsule close to the inner median margins of the lateral ocelli. The body of the tentorium is somewhat elongated antero-posteriorly, and the anterior of the body of the tentorium is slightly wider than the posterior. The posterior tentorial arms are broad and strong and meet to form a curvate posterior margin to the body of the tentorium. A tendonous outgrowth occurs on either side of this margin, and is posteriorly directed into the occipital foramen. The larva of *Tricorythus discolor* (Burm.) clings to rock surfaces and is an inhabitant of swiftly flowing waters.

Torleya Belgica L., produces a larva which has also become modified to a swift-water existence, usually occurring on the undersides of stones, and using the venter of the abdomen as a sucking disc. In *Torleya Belgica* L., the anterior tentorial arms are very wide and well developed, but the posterior tentorial arms are short and incline slightly to meet in the squarely-proportioned plate-like body of the tentorium. The dorsal arms are well developed.

The larva of *Epeorus assimilis* Eaton has also adapted itself to clinging to stones in rapidly-flowing water. The anterior tentorial arms in this species are very widely extended across the breadth of the head-capsule. The dorsal arms, arising as marginal expansions of the anterior tentorial arms, proceed dorsally and taper to their point of attachment to the head-capsule below and mesad of the ocular ridge. The posterior tentorial arms are less well developed than the anterior tentorial arms, being short and narrow in comparison with the latter. They unite in the posterior body of the tentorium whose posterior margin is slightly curvate. The anterior of the body of the tentorium is broader than the posterior, the anterior width of the body of the tentorium being approximately the same as the length.

In *Coloburiscus humeralis* Eaton the larval stage is passed in swiftly running water, and they may often be taken in cataracts and waterfalls. The anterior tentorial arms are broadly extended and well developed, with their marginal outgrowths, the dorsal arms attached to the head-capsule in the interocular region below and mesad of the compound eyes, and above the antennæ. The posterior tentorial arms are well developed and coalesce to form a curved posterior margin to the body of the tentorium. The proportions of the latter are somewhat square.

A swift-water inhabitant, the larva of *Bætis harrisoni* Bnrd., differs from those species already examined, for this larva exhibits a hypognathous head-capsule as opposed to the prognathous condition encountered in the other species. The anterior tentorial arms are well developed and in arcuate fashion unite to form the anterior of the body of the tentorium. The dorsal arms arise as wide expansions of the anterior tentorial arms, but narrow to become slightly expanded at their point of attachment to the head-capsule in the interocular area. The body of the tentorium is broad anteriorly, but narrows very considerably before the union of the short, well-developed posterior tentorial arms, in the posterior of the body of the tentorium. It would appear that the body of the tentorium of *Bætis harrisoni* Bnrd., has experienced considerable elongation during the alteration from prognathous to hypognathous condition of the head-capsule. Nevertheless, in general structure this tentorium does not vary extensively from those of prognathous ephemeropteron larvæ.

Aprionyx tricuspidatus Crass, and *Potamanthus luteus* L., are included amongst those larvæ which favour an existence in slow-flowing waters. *Aprionyx tricuspidatus* Crass, is usually located in mountain streams under stones in the stiller pools and backwaters. The tentorium in this species displays no significant variations to differentiate it from the tentoria of species adapted to existence in other acquatic situations. The anterior tentorial arms in *Aprionyx tricuspidatus* Crass are broad, well-developed and medianly inclined to meet in the anterior of the body of the tentorium (Fig. V, ata.). The dorsal arms are plate-like expansions of the anterior tentorial arms which narrow towards their points of attachment to the head-capsule below and mesad of the compound eyes, but above the antennæ (Fg. V, da.). The body of the tentorium is a square plate, posteriorly formed by the union of the short posterior tentorial arms which provide a straight margin to the posterior of the body of the tentorium (Fig. V, bt., pta.).

The larvæ of *Potamanthus luteus* L., live upon silt-covered stones in slow-moving waters, especially those which have much slime and mud in suspension, for these larvæ have a habit of covering themselves with this mud and so remaining concealed. The tentorium in *Potamanthus luteus* L., displays anterior tentorial arms which are wide and converge to meet in the broad anterior of the body of the tentorium (Fig. VI, ata.). The posterior tentorial arms are also well developed and comparatively long (Fig. VI, pta.). They meet to provide an arcuate posterior margin of the body of the tentorium (Fig. VI, bt.), and there are two small lateral tendonous outgrowths of this margin which project into the occipital foramen (Fig. VI, tp.). The anterior of the body of the tentorium is broader than the posterior, and the length is greater than the breadth (Fig. VI, bt.). The dorsal arms are well developed and attached to the head-capsule near the ocular ridge (Fig. VI, da.).

Adult.

The short, transverse head in the adult mayfly is usually hypognathous. The mouth-parts, which are ventrally directed, exist in a weak or atrophied condition and do not function in the capturing and intake of food. The

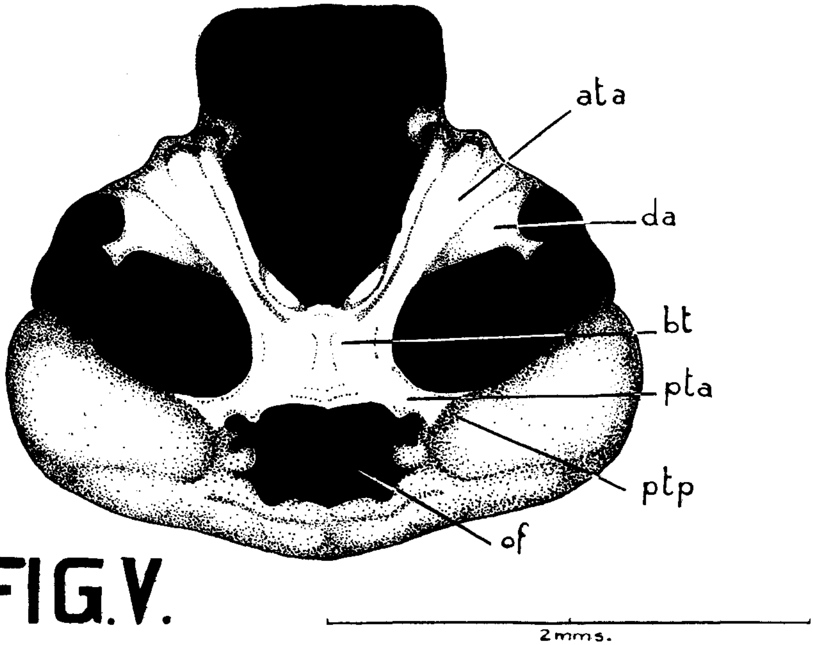
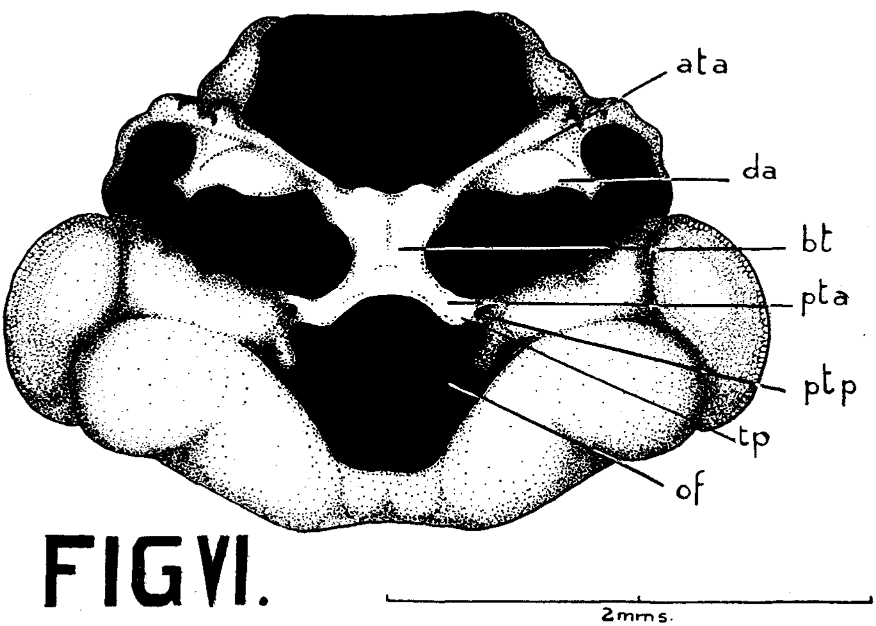


FIG.V.

Fig. V. — Ephemeroptera. ***Aprionyx tricuspidatus*** **Crass.**
Larva. Postero-ventral aspect.



FIGVI.

Fig. VI. — Ephemeroptera. ***Potamanthus luteus*** **L.**
Larva. Postero-ventral aspect.

frontal area of the head-capsule may be triangular or rounded, and the large dorso-laterally placed compound eyes often occupy the greater part of the head-capsule, especially in the male Ephemeroptera. Three ocelli usually occur in the interocular region. The short antennæ are subulicorn, with two basal segments and an indistinctly segmented flagellum: the antennæ occur below the lateral ocelli.

The tentorium in the adult mayfly provides considerable interest, for it differs somewhat from this structure as previously described, Hudson (1945, 1946, 1948). The anterior tentorial arms in the ephemeropteran adult arise as invaginations of the anterior tentorial pits, which are groove-like in structure and occur above and somewhat outside of the clypeus. The anterior tentorial arms are remarkable, for they are very long and tend to brace the greater part of the head-capsule, inclining medianly and tapering to meet in the body of the tentorium. The dorsal arms in the adult tentorium usually arise as plate-like expansions of the anterior tentorial arms. Often broad and triangular in shape, the dorsal arms may be produced along the entire posterior margin of the anterior tentorial arms and at right angles to the latter, so that the dorsal arms of the tentorium may be confused with and identified as incorporations of the anterior tentorial arms, dorsal arms under these circumstances being regarded as absent. The dorsal arms are usually attached to the head-capsule near the antennal ridge. The posterior tentorial arms are exceedingly short and arise as apodemes from the posterior tentorial pits which are located in the lower extremities of the post-occipital suture. The body of the tentorium occupies a postero-median position in the head-capsule, and is a somewhat delicate, plate-like structure of rectangular shape, the width being usually greater than the length. The general structure of the tentorium is thus seen to differ significantly from the X-shaped tentorium of the orthopteroid insects, the tentorium of the Dermaptera, Embioptera and Isoptera, and from the tentorium as observed in the Odonata and Plecoptera. Of these insects studied, the ephemeropteron tentorium may be most readily compared with that of the Odonata, where the anterior tentorial arms are again long and well developed, and the body of the tentorium posteriorly placed in the head capsule. The dorsal arms in the Odonata, however, are readily recognisable as such, and occur as secondary outgrowths of the anterior tentorial arms, extending towards the head-capsule, where they become attached on or near the antennal ridge.

The tentorium in the Ephemeropteron adult *Eatonica schoutedeni* (Navas) whose larva is of fossorial habit, is fairly well developed (Fig. VII). The anterior tentorial arms arise as apodemes of the groove-like anterior tentorial pits, located above and outside of the clypeus (Fig. VII, ata.). The anterior tentorial arms are fairly broad, and each anterior tentorial arm gives rise to a wide plate-like expansion, which develops at right angles to the posterior margin of the anterior tentorial arm and becomes attached to the head-capsule near the antennal ridge. This is the dorsal arm (Fig. VII, da.). The anterior tentorial arms are remarkably long supporting the greater part of the head-capsule and converging medianly to meet in the posteriorly placed body of the tentorium (Fig. VII, bt.). The latter consists of very delicate plate-like anterior and posterior margins, which are fused into the stronger band-shaped median area. The body of the tentorium thus assumes a somewhat rectangular shape. The posterior tentorial arms are very short (Fig. VII, pta.).

In *Polymitarcys savigni* (Pict.) the tentorium is comparable with that of *Eatonica schoutedeni* (Navas). The anterior tentorial arms are better

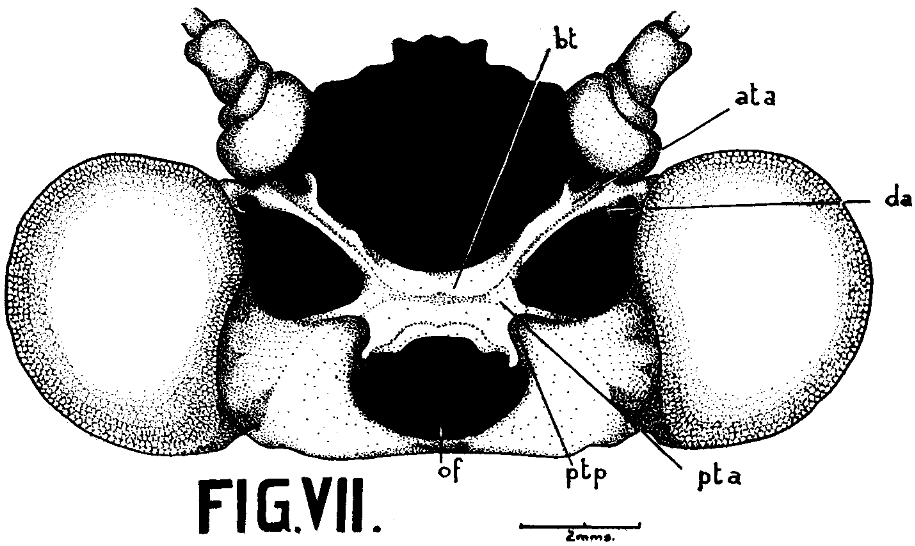


FIG.VII.

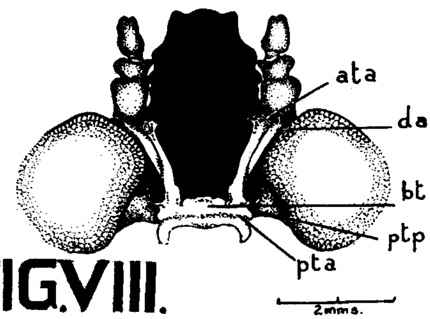


FIG.VIII.

Fig. VII. — Ephemeroptera. *Eatonica schoutedeni* (Navas). Adult. Postero-ventral aspect.

Fig. VIII. — Ephemeroptera. *Ephemera sp.* (Great Britain). Adult. Postero-ventral aspect.

developed and possibly broader in the former species and they converge sharply to form the body of the tentorium. The dorsal arms occur as marginal expansions along the greater length of the anterior tentorial arms, becoming attached to the head-capsule near the antennal ridge.

In the *Ephemera* sp. (Fig. VIII), the tentorium does not appear to be as well developed as in either *Eatonica schoutedeni* (Navas) or *Polymitarcys savigni* (Pict.). The anterior tentorial arms are fairly long, but narrower than in *Polymitarcys savigni* (Pict.) (Fig. VIII, ata.) and they incline medianly to meet in the body of the tentorium which again occupies a posterior position in the head-capsule (Fig. VIII, bt.). The dorsal arms occur as well-developed marginal outgrowths of the anterior tentorial arms (Fig. VIII, da.). The posterior tentorial arms are short (Fig. VIII, pta.). The body of the tentorium is narrow and transverse, and posteriorly placed in the head-capsule (Fig. VIII, bt.).

In *Afronurus harrisoni* Bnrd., the anterior tentorial arms are short, but well developed (Fig. IX, ata.) and the dorsal arms arise as expansions of the posterior margins of the anterior tentorial arms. The dorsal arms become attached to the head-capsule in the interocular area, below the compound eye and slightly dorsad of the antennal ridge (Fig. IX, da.). The posterior tentorial arms are short and broad (Fig. IX., pta.), and meet in the body of the tentorium, which is broad and short and plate-like (Fig IX, bt.).

The tentorium in *Acentrella natalensis* Crass, exhibits anterior tentorial arms which are less widely splayed than in those adults already studied. At their points of origin in the anterior tentorial grooves, these arms are broad, but they taper medianly and coalesce to meet in the body of the tentorium, whose anterior margin is curvate. The dorsal arms are wide expansions of the anterior tentorial arms, and they are attached to the head-capsule below the compound eyes and adjacent to the antennal ridge. The posterior tentorial arms are short and unite in the body of the tentorium, whose posterior margin is arcuate. The body of the tentorium is a well-developed supporting plate, fairly broad and of rectangular proportions.

Ellassoneuria trimeniana M., offers a variation of form as compared with those adult tentoria already described. In this species, the anterior tentorial arms lie almost parallel to each other with a very much slighter degree of median inclination to their union in the body of the tentorium. The dorsal arms are comparatively poorly developed and thin, somewhat triangular outgrowths of the anterior tentorial arms. The body of the tentorium occupies a posterior position in the head-capsule, and is a rectangular plate. The posterior tentorial arms are short, but well developed.

In *Bætis harrisoni* Bnrd., the anterior tentorial arms arise from the elongated anterior tentorial grooves above and outside of the clypeus (Fig. X, ata.). They are broad and expanded at their grooves of invagination and converge medianly to meet in the body of the tentorium (Fig. X, bt.). The dorsal arms occur as marginal outgrowths of the anterior tentorial arms (Fig. X, da.). The posterior of the body of the tentorium is formed by the coalescence of the posterior tentorial arms which are broad, but short (Fig X, pta.).

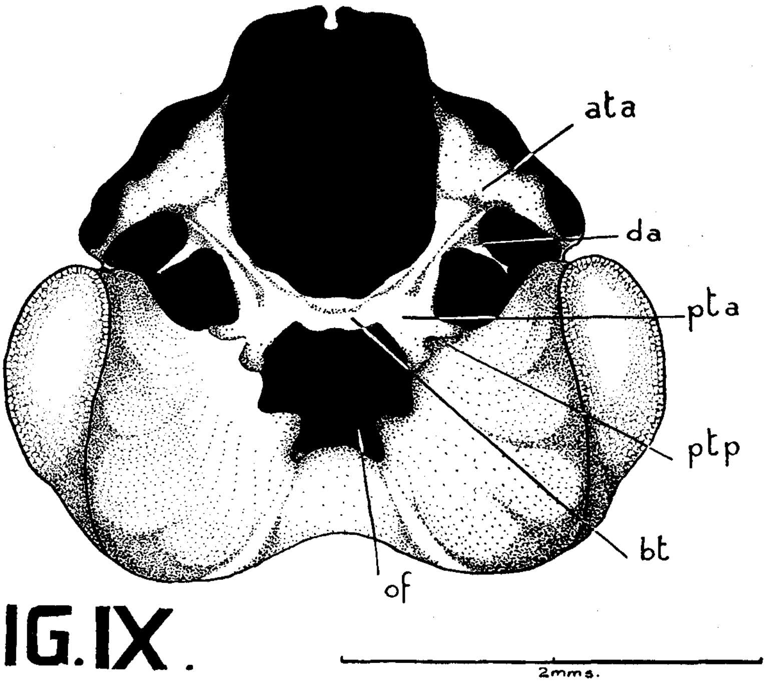


FIG. IX.

Fig. IX. — Ephemeroptera. *Adenophlebia auriculata* Eaton. Adult. Postero-ventral aspect.

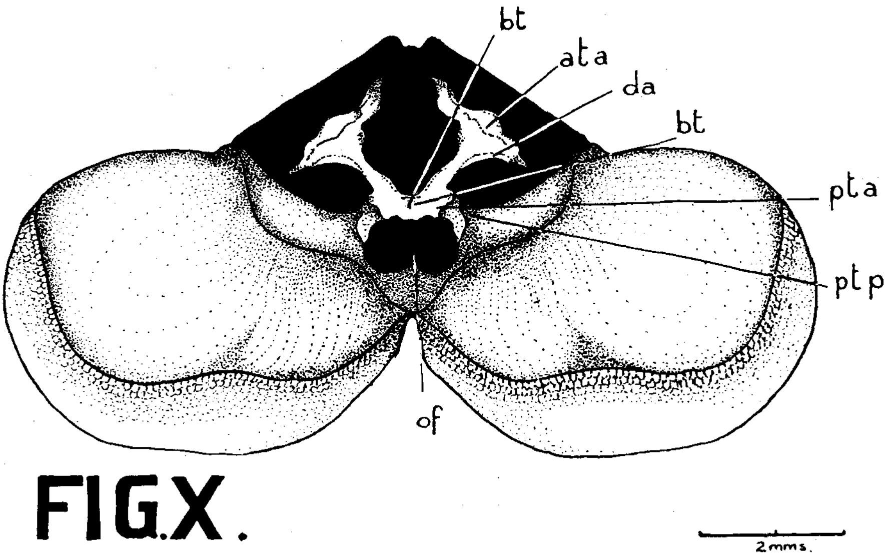


FIG. X.

Fig. X. — Ephemeroptera. *Afronurus harrisoni* Bnrd. Adult. Postero-ventral aspect.

The wedge-shaped head-capsule of *Adenophlebia auriculata* Eaton exhibits anterior tentorial arms which are broad basally, but taper inwards. These arms are long (Fig. XI, ata.), and converge sharply to meet in a wide-armed V, in the band-shaped body of the tentorium (Fig. XI, bt.). Secondary outgrowths arise on the posterior margin of each anterior tentorial arm. These are the dorsal arms (Fig. XI, da.), which become attached to the head-capsule on the antennal ridge. The body of the tentorium is band-shaped. The posterior tentorial arms are short and stout, uniting to form the posterior of the body of the tentorium (Fig. XI, pta.).

In *Aprionyx tricuspidatus* Crass, the anterior tentorial arms are well developed and widely splayed (Fig. XII, ata.), meeting in the body of the tentorium, which is wide and transverse (Fig. XII, bt.). The dorsal arms are well developed, while the posterior tentorial arms are short, uniting in the posterior of the body of the tentorium (Fig. XII, da., pta.).

CONCLUSIONS.

Larva.

In a comparative study of the tentorium within those groups of ephemeropteran larvæ favouring a variety of acquatic habits, certain features are encountered relating to the tentorium as a whole, and also to the phylogenetic significance of this structure amongst the hexapod insects.

In considering the tentorium in fossorial species, e.g. *Eatonica schoutedeni* (Navas), *Polymitarcys savigni* (Pict.) and the *Ephemera* sp., it will be observed that this structure is not markedly similar in all fossorial larvæ. It would appear that although in some cases close structural similarity may be noted, e.g. *Ephemera* sp. and *Eatonica schoutedeni* (Navas), in others, the tentorium of a fossorial larva may be more favourably compared with that of a species inhabiting an entirely different type of environment. Species of ephemeropteron larvæ inhabiting swift-flowing waters may possess tentoria which resemble those of fossorial types; e.g. the tentorium of *Afronurus harrisoni* may be seen to resemble that of the fossorial larva *Eatonica schoutedeni* (Navas), while similarities in tentorial structure may also be observed between two or more species favouring the same swift-water habitat. For example, the larva of the leptophlebiid species studied possesses a tentorium comparable with that of *Adenophlebia auriculata* Eaton, and both may be compared with the tentorium of *Torleya Belgica* L.

Of the slow-water inhabitants, *Aprionyx tricuspidatus* Crass, displays a tentorium with features resembling those of the swift-water leptophlebiid species studied, while *Potamanthus luteus* L., another species favouring a slow-water environment, shows greater similarity of tentorial structure to the larva of *Epeorus assimilis* Eaton, located in swift-waters, than to that of a fellow slow-water inhabitant, i.e. *Aprionyx tricuspidatus* Crass.

Thus it would appear that larvæ inhabiting a variety of acquatic conditions do not exhibit diagnostic features of the tentorium which could be used as a means of separating larvæ living in one type of environment from larvæ showing a preference for an entirely different type of environment. For example, the tentorium of a fossorial larva does not exhibit

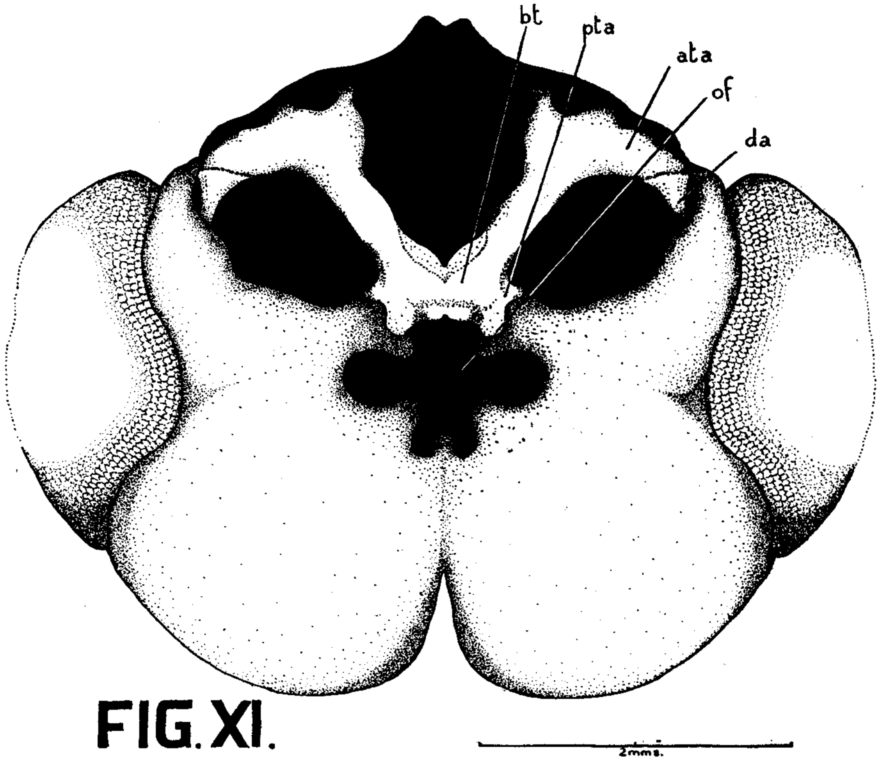


FIG. XI.

Fig. XI. — Ephemeroptera. *Bœtis harrisoni* Bnrd.
Adult. Postero-ventral aspect.

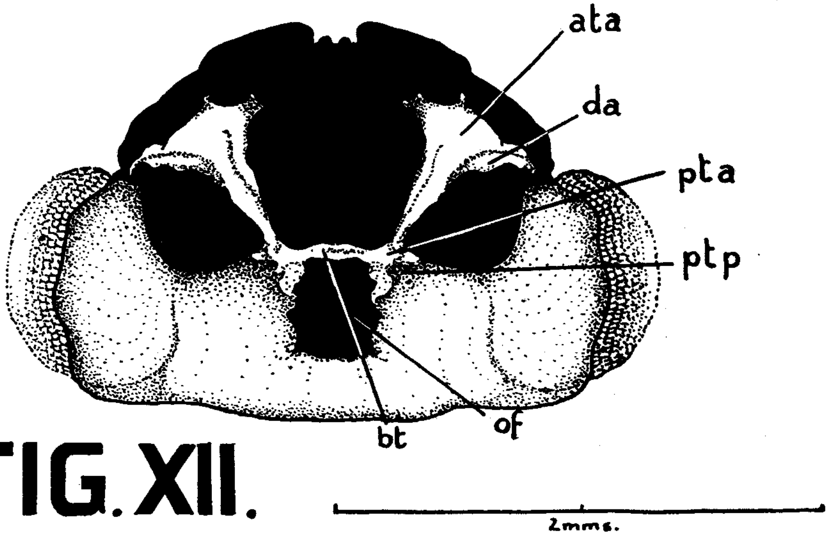


FIG. XII.

Fig. XII. — Ephemeroptera. *Aprionyx tricuspidatus* Crass.
Adult. Postero-ventral aspect.

features which are exclusive to fossorial larvæ only. On the contrary, it has been shown that similarities in tentorial structure may be observed in larvæ inhabiting widely differing types of environment.

Adult.

A comparison of the adult tentorium as observed amongst species whose larvæ show preference for the varying conditions of fossorial, swift-water and slow-water existence, indicates that the adult tentorium does not display a typical structure in relation to its larval habitat-group, i.e. the adult tentorium does not exhibit structural modifications or features which could be of diagnostic importance in separating those adults with fossorial larvæ from others whose larvæ inhabit swift or slow-water environments.

In the adult tentorium, the anterior tentorial arms are expanded at their grooves of invagination as is readily observed in *Afronurus harrisoni* Bnrd., *Adenophlebia ariculata* Eaton, and *Bætis harrisoni* Bnrd. The anterior tentorial arms are usually long, and incline at varying degrees medianly, to coalesce in the posteriorly placed body of the tentorium, which, though generally band-shaped, may be rectangular in proportion, e.g. *Eatonica schoutedeni* (Navas) and *Acentrella natalensis* Crass. The posterior tentorial arms are usually short and broad. The dorsal arms are well-developed expansions of the anterior tentorial arms, expanding as platform-like structures at right angles from the posterior margins of the anterior tentorial arms. The attachment of the dorsal arms to the head-capsule usually occurs on or adjacent to the antennal ridge.

The larvæ of the Ephemeroptera studied are all prognathous, with the exception of *Bætis harrisoni* Bnrd., which is hypognathous. A comparison between the tentorium of the hypognathous adult and the prognathous larva does not provide striking dissimilarities of structure. E.g., in *Eatonica schoutedeni* (Navas) the anterior tentorial arms in both larva and adult are basally broad, tapering somewhat to converge postero-medianly where they unite to form the body of the tentorium. In the larva the anterior tentorial arms are possibly broader and more heavily sclerotized than in the case of the adult. The posterior tentorial arms are short in both the larva and adult, and the body of the tentorium, though narrower and more delicate in the adult, does not display any variation in general structure. The dorsal arms in the adult are better developed than in the larva. In the adult the dorsal arms are fairly wide expansions of the anterior tentorial arms, whereas in the larva the dorsal arms are more delicate and taper to their points of attachment to the head-capsule. This difference in structure of the dorsal arms may be accounted for in the change from the larval prognathous condition to the hypognathous condition in the adult. Both anterior tentorial and dorsal arms are drawn in a ventral direction in the change from the prognathous to hypognathous condition. In this downward movement, additional support in the form of well-developed platform-like dorsal arms assists the anterior tentorial arms in their bracing of the major portion of the head-capsule. In the hypognathous larva of *Bætis harrisoni* Bnrd., it will be observed that this hypognathous condition is secondary, and the body of the tentorium has become greatly elongated during the change from the more primitive prognathous condition to the hypognathous condition. Apart from this secondary development in the body of the larval tentorium, a comparison of the general structure of the larval and adult tentorium indicates no significant variations.

Arising out of the data accumulated on the structure of the tentorium in larval and adult Ephemeroptera it would appear that the tentorium is of significance in establishing relationships, being a structure which is not chiefly functional by nature. If the tentorium was largely functional, greater differences in its structure would be apparent between the different species of Ephemeroptera studied.

A comparison of the tentorium in the Ephemeroptera with this skeletal structure as observed in the orthopteroid Hexapoda (1945), Dermaptera, Embioptera and Isoptera (Hudson, 1946) and the Odonata and Plecoptera (Hudson, 1948) indicates that the Ephemeroptera differ widely from all these groups in the structure of the tentorium. The tentorium in the Odonata does, however, bear some resemblance to the ephemeropteron tentorium, but this similarity is not striking, and the Odonata themselves differ in tentorial structure from the remaining groups studied. Omer-Cooper (1939) stated that " the mayflies and dragonflies are ancient form which appear to be related to the Thysanura Ectotrophi, and differ from all other Pterygota in the muscalature and venation of the wing, the structure of the tentorium and in possessing both an elongation of the eleventh abdominal segment and cerci ".

It would appear that the tentorium in the Ephemeroptera is possibly more primitive than those of the previously studied groups, but a further discussion on the phylogeny of the Ephemeroptera must be postponed until data on the apterygotan tentorium has been accumulated.