

STUDIES IN THE COMPARATIVE ANATOMY AND  
SYSTEMATIC IMPORTANCE OF THE  
HEXAPOD TENTORIUM.

A      THESIS  
SUBMITTED IN FULFILMENT OF THE REQUIREMENTS FOR  
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## GENERAL INTRODUCTION.

During a study of the morphology of the orthopteroid Hexapoda between the years 1939-1941, it appeared to the writer that further investigation into the structure of the insect tentorium was necessary.

The early entomologists laid the foundation of our knowledge of the tentorium, but during the latter half of the last century little was added in this particular field. Comstock and Kochi (1902), as far as the writer is aware, are the only workers who have published a paper devoted entirely to the skeleton of the head of insects, and they did much to clarify both nomenclature and existing knowledge of this structure at that time. Berlese (1909) described a typical tentorium as observed in orthopteroid Hexapoda, and then considered the variations of the tentorium, which occur in other groups of insects. Some confusion then appears to have arisen amongst workers, over the origin of the dorsal arms, which were erroneously considered by some to be cuticular invaginations and not secondary outgrowths of the anterior tentorial arms.

Certain morphologists, amongst them, Hoke (1924), Denis (1928), Snodgrass (1928, 1935), Hansen (1930), Walker (1933),

Leas (1934), and Symmons (1952), have done much towards improving our knowledge of the tentorium, but all too frequently workers offer brief and inadequate descriptions of this structure in otherwise comprehensive investigations of the insect head.

The main objects in this study are threefold, viz :-

- (1) The clarification of nomenclature.
- (2) The examination and the interpretation of the tentorium in certain groups of insects.
- (3) The deliberation as to whether the tentorium is of phylogenetic significance, and thus of use in assessing various schemes of insect classification which have been presented.

After 2

## A study of the tentorium in some orthopteroid Hexapoda

by

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### Introduction.

In 1939 studies of the exoskeleton of the Orthopteroid Insects, classified by J. Omer-Cooper (1938) and published in this journal as Phasmida, Dictyophora and Saltatoria, were commenced with the object of testing the validity of his conclusions. The unsatisfactory state of our knowledge of the tentorium soon became apparent. It appeared to the writer that a thorough investigation of this structure would be of service to entomologists and might also prove useful in assessing the various schemes of insect classification which have been put forward.

In 1943, opportunity occurred for the writer to put this project into execution. The present paper is a preliminary study of the three groups originally studied, but it is felt that before any certain conclusions on taxonomic questions can safely be discussed, a much wider survey is essential. That, it is hoped, will form the subject of further communications.

The writer is indebted to Dr. J. Hewitt for the identification of specimens and to Professor J. Omer-Cooper for his encouragement and valuable counsel.

### Material.

From the orthopteroid group, the following species have been selected and examined:

**Phasmidae:** *Diapheromera femorata* Say., *Bactrododema aculiferum* Kirby, *Leptima* Sp.

**Blattidae:** *Aptera fusca* Thunb., *Phyllodromia germanica* L., *Deropeltis erythrocephala* Stal.

**Mantidae:** *Polyspilota pustulata* Stoll., *Polyspilota caffra* Westw., *Popa undata* F., *Harpagomantis tricolor* Lin., *Mantis Sacra* Thunb.

**Gryllotalpidae:** *Gryllotalpa africana* Pal.

**Gryllidae:** *Gryllus capensis* Oliv., [REDACTED]

**Tettigoniidae:** *Homorocoryphus nitidulus* Scop., *Arytropteris* sp., *Eurycorypha prasinata* Stal., *Clonia* sp., *Oecanthus capensis* Saus.]

**Acrididae:** *Acanthacris ruficornis lineata* Stoll, *Acridella nasuta* L., *Zonocerus elegans* Thunb.

### Technique.

Some specimens were treated with a 5% solution of caustic potash. In many cases it was found necessary to leave the speci-

mens in the solution for several days, after which they were rinsed and preserved in 70% alcohol. Other specimens used for dissection purposes were fixed in Bouin's fluid for 24 hours, and then placed in 70% alcohol until used.

It was found that the tentorium was seen to greatest advantage after all the mouth-parts had been removed. From the ventral or ventro-caudad aspect, it was then possible to examine the entire structure of the tentorium. The specimens were examined in 70% alcohol placed in a watch-glass under a Zeiss binocular dissecting microscope. The following stains were successfully used: Eosin, Azo-eosin and Haemalum. Drawings were made with the aid of a camera lucida attached to a Leitz microscope.

#### Nomenclature.

Owing to confusing nomenclatures, it is necessary to define clearly the regions of the endoskeleton, and for this purpose a description of a typical tentorium will be given.

Certain apodemes are developed from the external skeleton of the head which proceed towards the median longitudinal axis of the body. These apodemes are derived from invaginations of the cuticular layer at the edge of a sclerite, or between adjacent sclerites. Constant muscle contraction causes the inward withdrawal of the cuticular layer but a deep furrow or pit is conserved which represents the small crater formed on the outside by the invagination process. It is generally possible to detect four pits where invagination has taken place.

The two anterior tentorial pits (Figs. I, II, *atp*) lie on either side of the epistomal suture, when this suture is present, or just above the condylar articulations of the mandibles, or above the bases of the mandibles. The shape and size of the pits depends on the breadth of the apices of the tentorial apodemes arising from these pits.

The two posterior tentorial pits (Figs. I, II, *ptp*) occur ventrally on either side in the post-occipital suture. In prognathous types the post-occipital suture with the posterior tentorial pits has extended forwards on the head capsule, so that the posterior tentorial pits appear as grooves rather than pits.

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#### Abbreviations used in figures.

a. — antenna; as. — antennal ridge; ass. — position of antennal ridge indicated by dots; ata. — anterior tentorial arm; bt. — body of tentorium; c. — compound eye; da. — dorsal arm; e. — lateral expansion of outer margin of anterior arm; es. — epistomal suture; esf. — external surface; fp. — frontal plate; is. — internal surface; ma. — median aperture; mc. — metopic crest; of. — occipital foramen; ocs. — ocular ridge; ors. — position of ocular ridge indicated by dots; ot. — oeso-tendon; pg. — post-gena; pta. — posterior tentorial arm; ptp. — posterior tentorial pit; to. — tendinous outgrowth.

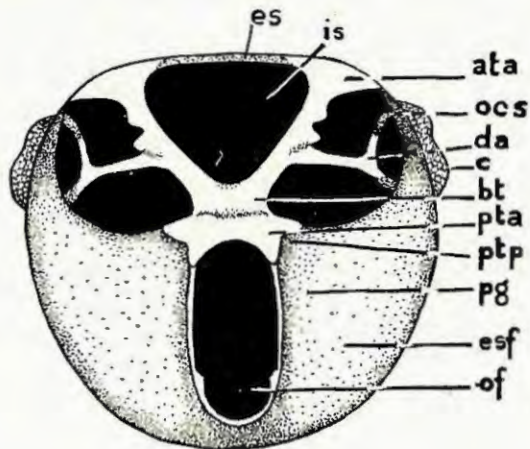


FIG. I.

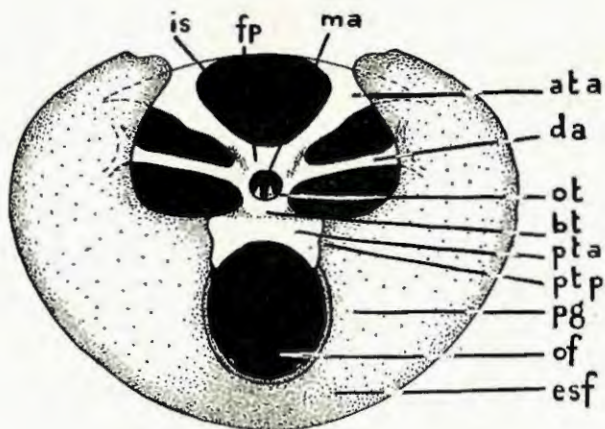


FIG. II.

- Fig. I. Diagrammatic representation of a prognathous type of Orthopteroidean tentorium, illustrating terminology used in the text. Ventro-caudal aspect, mouth-parts removed.
- Fig. II. Diagrammatic representation of a hypognathous type of Orthopteroidean tentorium, illustrating terminology used in the text. Posterior aspect, mouth-parts removed.

The two anterior apodemes arising from the anterior tentorial pits are called the anterior arms of the tentorium (Figs. I, II, *ata*) while the two apodemes arising from the posterior tentorial pits are known as the posterior arms of the tentorium (Figs. I, II, *pta*). The anterior arms of the tentorium may be fused at their bases forming a broad plate which is called the frontal plate of the tentorium.

In addition to the anterior and posterior arms, there occurs a pair of dorsal arms (Figs. I, II, *da*) extending from the anterior tentorial arms to the region of the antennal or ocular ridges. As there is no evidence that they originate as invaginations from the cuticular layer, the dorsal arms are not true tentorial arms but are considered to be secondary outgrowths of the anterior tentorial arms.

Snodgrass (1935) mentions that depressions or dark spots occur where the dorsal arms unite with the epicranial wall, and these he terms "tentorial maculae."

The apodemes arising from the anterior and posterior tentorial pits coalesce internally at their bases and form a somewhat solid, chitinous supporting structure known as the tentorium or endoskeleton of the head. (Figs. I, II *bt*). This traverses the whole head longitudinally and proceeds from the occipital region of the head to the anterior face. In orthopteroid insects the tentorium is an X-shaped structure, with the mid-region expanded. This median plate is often large, but its shape varies in conformity with the general shape of the head. It is conveniently termed the "body of the tentorium" and may, in some cases, contain an aperture through which the circum-oesophageal connectives pass (Fig. II, *ma*).

TABLE I.  
*Comparison of nomenclatures.*

Snodgrass, Imms.	MacGillivray, Crampton.	Berlese.
Anterior Arms	Pretentoria.	Internal lateral branch and external branch.
Dorsal arms.	Supratentoria.	Superior branch.
Posterior arms.	Metatentoria.	Fourth branch.
Body of tentorium.	Corpotentorium.	Fifth branch.
Frontal plate.	Laminitentorium.	
Anterior tentorial arms	Pretentorina.	
Posterior tentorial pits.	Metatentorina.	

### Functions.

The tentorium as a general supporting structure has several well-defined functions. Where large mandibles are present, strong support is required for the attachment of muscles moving these

mandibles, so that the tentorium may be regarded primarily as a structure for the attachment of gnathal muscles.

The tentorium also affords support to the fore-intestine and the brain. The brain or supra-oesophageal ganglion, or cerebral ganglion, lies just above the oesophagus between the supporting anterior apodemes of the tentorium. The tritocerebral portion of the brain gives origin to the circum-oesophageal connectives, or crura ceribri, which proceed posteriorly and eventually unite the brain with the sub-oesophageal ganglion. In some orthopteroid insects a pair of median processes arises at the bases of the anterior tentorial arms and these processes become united into an anterior bridge before the circum-oesophageal connectives which pass through the aperture formed in the body of the tentorium. Thus support is given to the fore-intestine and the brain, so that the tentorium may be described as a general brace lending support to the whole epicranium.

#### **Prognathism and hypognathism.**

The insect head may be either prognathous or hypognathous, depending upon the actual position of the mouth-parts. In the forward or prognathous type, the longitudinal axis of the head is horizontal, while the mouth-parts are anteriorly directed. In the hypognathous type, the longitudinal axis of the head is vertical, while the mouth-parts are directed ventrad.

In the orthopteroid insects studied, it has become evident that secondary prognathism may occur; in which case, from a study of the tentorium, it may be readily distinguished from primary prognathism. The Phasmidae are completely separated from the other orthopteroid types studied in their retention of the primitive prognathous type of head, and it is shown that the tentorium likewise exhibits the characters of primary prognathism. In the prognathous Tettigoniid and the *Gryllotalpa* species studied, the tentorium shows secondary modification of a return to prognathism.

According to Walker (1932), prognathism is common among carnivorous insects; those that chase and capture their prey with their mandibles; larval forms which burrow in hard substances by means of their mandibles; and in forms that rest on broad surfaces and hide in crevices. The Phasmidae fall into the last category. They are all vegetable-feeders and have adapted themselves to their environment in such a way as to become completely inconspicuous. The leaf-insects have suffered depression of head and body, a character often associated with prognathism; whereas the general elongation of stick-insects has encouraged the persistence of primary prognathism.

Hypognathism, according to Walker, is found in carnivorous types which await their prey, e.g., mantid and dragonfly nymphs. Also, it is common among phytophagous insects with perching habits, e.g., Tettigoniidae, Acrididae. However, change of habit

may produce change of head-form, showing that prognathism and hypognathism can be adaptive, e.g., *Gryllotalpa* has become specially modified for a burrowing existence.

Walker states that hypognathous types developed among the earliest groups of winged insects as soon as the insect had acquired the habit of capturing its prey during flight and of using its legs mainly for perching. The examples he refers to, of present isolated orders, are the Odonata and Ephemeroptera. In this connection it is interesting to note that the nymphs of Odonata are predaceous and possess hypognathous heads; whereas the nymphs of Ephemeroptera are herbivorous and possess prognathous heads. Thus the form of the head is adaptive and may change during metamorphosis from one type to another in accordance with change of habit.

The external characters of the head-capsule form a basis for the differentiation of primary from secondary prognathism. In this and following papers the writer proposes to show that, from a study of the tentorium, primary and secondary prognathism may be readily discerned and differentiated, so that in this study it will be possible to distinguish originally primitive groups from those that have become secondarily adapted. It should be understood that, in regarding prognathism as primitive in orthopteroid insects, this is not applicable to the Arthropoda as a phylum.

#### PHASMIDAE.

In this primitive prognathous group, considerable elongation of the post-ocular region of the head-capsule has taken place and this has been followed by a slight elongation of the ventral region so that the occipital region has changed its plane from perpendicular to oblique.

The Phasmidae possess a simple tentorium (Fig. III). The body is very short and almost vertical in position. The anterior arms of the tentorium arise from the anterior tentorial pits, which are distinct and definite in their location, lying beneath and laterad of the bases of the antennae. The anterior arms arise as strong, triangular, integumental invaginations. Just before the anterior arms coalesce to form the body of the tentorium, from their outer lateral edges, thin flat triangular expansions are produced. (Fig. III, e) Walker (1933) makes no mention of these, nor are they figured in his diagram (Plate III, Fig. 4c), although they are distinct and well developed in *Diapheromera femorata* Say. There is a slight sug-

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#### Prognathous types of Orthopteroid hexapoda.

Ventro-caudal aspect of head-capsule, mouth-parts removed.

Fig. III. Phasmidae: *Diapheromera femorata* Say.

Fig. IV. Tettigoniidae: *Oecanthus capensis* Saus.

Fig. V. Gryllidae: *Gryllotalpa africana* Pal.

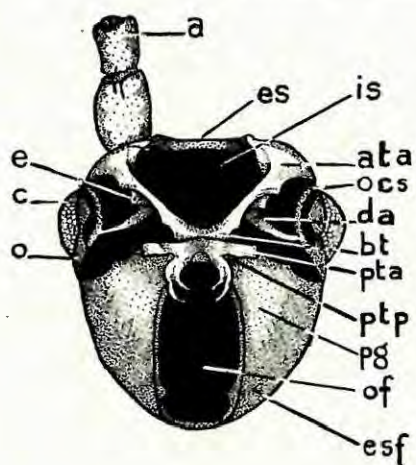


FIG. III.

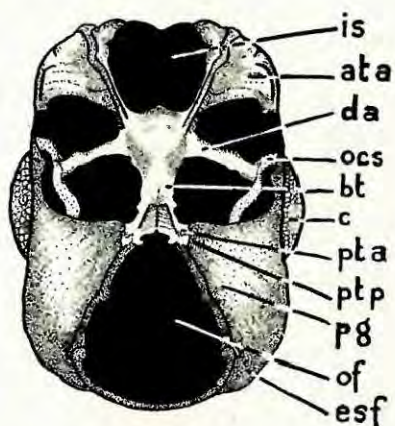


FIG. IV.

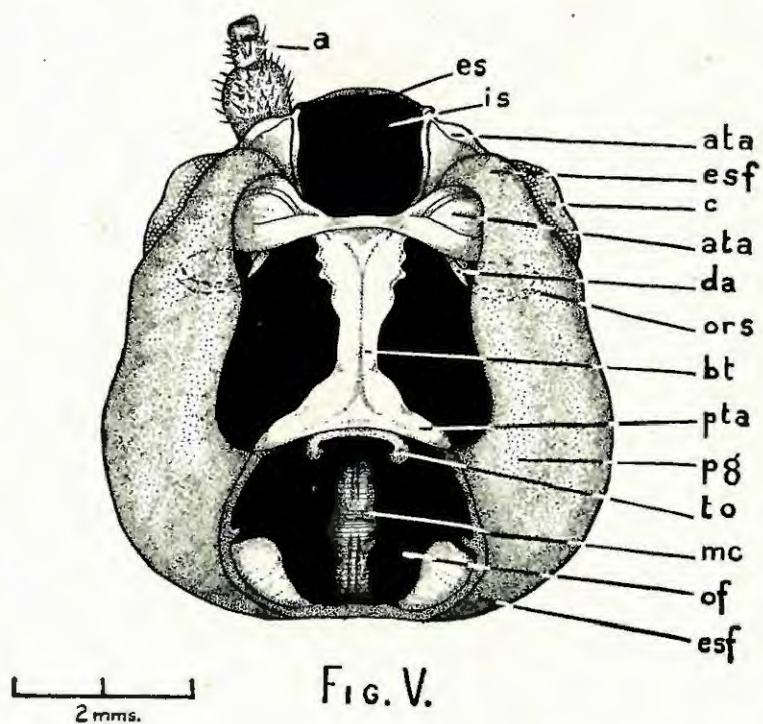


FIG. V.

gestion of their presence in Yuasa's diagram (Plate II, Fig. 38) but they are very indistinctly figured. The anterior arms narrow and unite to form the body of the tentorium. The anterior arms are long, a feature which may be associated with the deepening of the anterior region of the head as a result of the presence of large powerful biting mandibles.

The dorsal arms of the tentorium are comparatively thin and delicate. Walker figures them in his diagram (Plate II, Fig. 4c) as being of the same width and apparent thickness as the anterior arms. In all specimens of *Diapheromera femorata* Say., studied, the dorsal arms were found to be much thinner and flatter than the anterior arms. The dorsal arms originate as outgrowths of the cephalic part of the dorso-lateral margins of the anterior arms of the tentorium. They pass upwards and outwards to become attached to the head-capsule on the fronto-lateral margin of the ocular ridge.

The posterior tentorial arms are short, broad and well-developed, and they fuse with the maxillae ventrally, and with the postgenae laterally, so that the occipital foramen is bounded on its caudal and lateral margins by a thick band, from the inner margins of which thin, tendonlike structures are produced.

#### BLATTIDAE.

The Blattidae possess a hypognathous head. The cephalic region has become depressed but, instead of this being associated with prognathism, it has resulted in the general downward curvature of the head in the inter-ocular region, so that the mouth parts are directed ventro-caudad and the facial region ventrad. This curvature has resulted in the migration of the two reniform eyes from their primitive position close to the mouthparts to one distinctly latero-dorsad. The eyes are large and flat and their hinder margins abut on the occipital ridge, so that the post-ocular region is reduced. The antennae lie just below and slightly laterad of the ocelli and are removed from their primitive position far forward near the articulation of the mandibles.

The Blattidae possess an X-shaped tentorium (Fig. VI). The anterior tentorial pits occur immediately above the bases of the mandibles and laterad of the point where the fronto-genal suture meets the sub-genal suture, anteriorly, on either side. As in the Phasmidae, the general shape of the anterior tentorial arms is triangular, the margins being thickly sclerotized. The anterior arms extend upwards and outwards and are united by a transverse band at their bases, which is known as the anterior base or frontal plate of the tentorium (Fig. VI, fp.).

There is a large median aperture in the body of the tentorium through which circum-oesophageal connectives pass (Fig. VI, ma). The aperture is bounded anteriorly by the frontal plate and posteriorly by the ridge formed by the coalescing of the posterior tentorial arms. From the mid-region of the inner margin of the

posterior tentorial arms, two thin tendon-like structures extend cephalad from the tentorial foramen. These are sometimes known as oesotendons.

The dorsal arms are not integumental invaginations. In *Aptera fusca* Thunb., they arise as thin wing-like expansions of the lateral margins of the body of the tentorium and become drawn out into thin tendon-like structures which are attached to the fronto-lateral margin of the antennal ridge. Gladys Hoke (1923-24) stated that the morphology of the Blattidae had been based on closely-related domestic species and suggested that a study of generalized species might show that the Blattidae possess large dorsal tentorial arms such as are found in *Melanoplus*, *Gryllus* or some of the generalized Plecoptera. It was also suggested that such a study might show the dorsal arms to occur as invaginations of the head-capsule of the Blattidae. A detailed study of the species, *Aptera fusca* Thunb., *Deropeltis erythrocephala* Stal., and *Deropeltis wahlbergi* Stal., and superficial studies of numerous unidentified woodland species have given the same results. In all the species studied, the dorsal tentorial arms arise from the lateral margins of the body of the tentorium and are attached to the head-capsule in the region of the antennal ridge. There is no indication to show that they have arisen as invaginations of the head-capsule. In some species of Blattidae, dorsal arms are reported to be absent. Although this may be the case, the dorsal arms are often extremely delicate processes which are easily destroyed by careless handling.

Riley (1904) has shown that embryological studies of *Blatta* reveal the fact that the posterior tentorial pits are not as well marked as the anterior tentorial pits, due to an apparent retardation in their embryonic development, which shows the anterior tentorial invaginations in the mandibular segment; whereas those of the posterior tentorial arms could not be identified. In the adult, the posterior tentorial pits occur at the extremities of the post-occipital suture. From these pits, rod-like invaginations project into the cavity of the head on each side, and are known as the posterior arms of the tentorium. They are united by the posterior bridge of the tentorium.

#### MANTIDAE.

The head of the Mantidae is considerably modified. The members of this group are carnivorous and await the approach of their prey which is seized by the raptorial front pair of legs. This feeding habit has called for the greater development of the compound eyes; these occur as large antero-dorso-lateral prominences of the head.

The prognathous head does not allow for constant alertness, for the eyes are usually small and placed far forward on the head. In the Mantidae the eyes have moved backwards in the head and have come to occupy the greater part of it. This move has caused

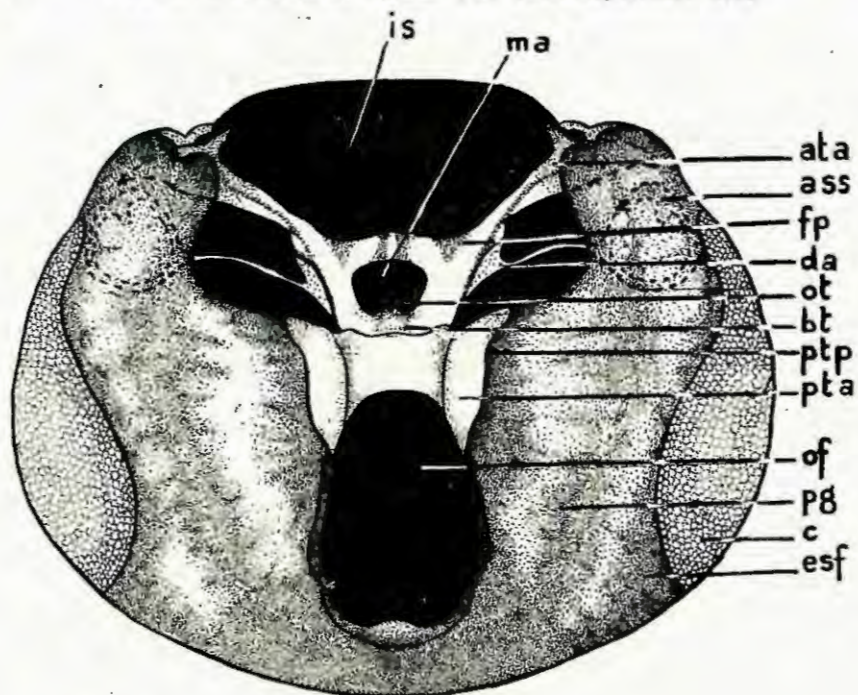


FIG. VI.

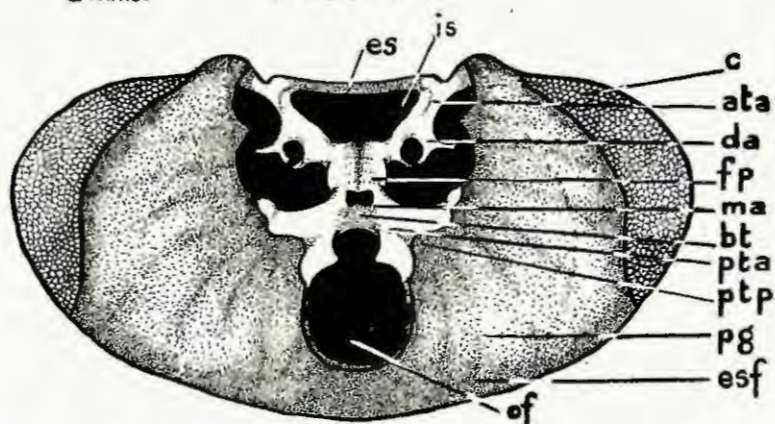


FIG. VII.

considerable expansion of the inter-ocular region and slight expansion of the frontal area, but the genal area is little changed from its primitive condition.

The prey is caught in the fore-legs and held thus while the insect feeds upon it. This habit has resulted in the downward curvature of the head in the inter-ocular region, so that the mouth-parts have become ventrally directed and therefore lie immediately above the raptorial front legs. They are thus in the best position for seizing and sucking the juices of their food immediately after capture.

The tentorium in the Mantidae has consequently undergone considerable modification (Fig. VII). As in the Blattidae, the anterior tentorial arms are strong and heavily sclerotized, to give ample support to the powerful biting mandibles. In *Polyspilota pustulata* Stoll., the anterior tentorial pits occur on each side of the epistomal suture. The anterior tentorial arms are broad, and chitinized on their inner lateral margins. Anteriorly they are without a twist and abut on the border of the circum-ocular ridge. The outer margin of the anterior tentorial arms, near its origin, is semi-curved, widening out to meet a wing-like expansion of the lower margin from which the thin tendon-like dorsal arms originate. In all species studied, the dorsal arms are small, linear, delicate structures which are attached to the head-capsule on the fronto-lateral margin of the antennal socket.

The anterior arms narrow considerably before converging to form the broad anterior bridge of the body of the tentorium. This bridge is mesally constricted, giving it a somewhat carinate appearance from the ventral aspect. It borders the median aperture of the tentorium, through which circum-oesophageal connectives pass. Oeso-tendons are absent. The posterior tentorial arms are apodemes arising from the posterior tentorial pits. The latter are located in the extremities of the post-occipital suture. In *Polyspilota pustulata* Stoll., the posterior arms of the tentorium are thick and heavily chitinized. They are presumably the supports for the muscles of the cervical region, which are used to greater extent in the predaceous Mantidae than in other types studied. The small occipital foramen is a feature of the modification which has occurred as a result of the predaceous habits, for it allows greater freedom of movement for the cervical region.

The posterior bridge of the tentorium is broad and strong and unites the posterior tentorial arms at their bases. From the extremi-

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#### Hypognathous Types of Orthopteroid hexapoda.

Posterior aspect of head-capsule, mouth-parts removed.

Fig. VI. Blattidae: *Aptera jussiaei* Thunb.

Fig. VII. Mantidae: *Polyspilota pustulata* Stoll.

ties of the inner margins of the posterior tentorial arms thick tendon-like processes are produced.

#### GRYLLIDAE.

##### Family: Gryllotalpidae.

In this family, there are definite indications of a change from hypognathism, to a secondary form of prognathism. In most Gryllidae, the head is semi- or completely hypognathous, but in the Gryllotalpidae a fossorial habit has favoured prognathism, so that the head-capsule has become secondarily modified. In *Gryllotalpa africana* Pal., the head is shielded posteriorly by the large velutinous pro-thorax. The post-ocular region of the head is elongated; the occipital foramen is oval and lies at an inclined plane to the body-axis. The mouth-parts are antero-ventrally directed. The eyes are reduced and, with the antennae, have moved from a dorso-lateral position to one far forward and in close proximity to the mandibular articulations. In consequence of the reduction and forward movement of the eyes, the genal area is poorly developed.

The tentorium of the Gryllotalpidae readily discloses the secondary modifications of a return to prognathism (Fig. V). The most striking feature is the greatly elongated body of the tentorium, which has become drawn out in the process of change and shows a completely different structure from that of the aberrant Phasmidae (Fig. III).

The anterior tentorial pits arise immediately below the antennal socket and dorsad of the mandibular articulations. The anterior tentorial arms are very short and much flattened. They form a triangular heavily-chitinized platform which extends from their point of origin below the antennal socket, along the circum-ocular ridge.

The dorsal arms of the tentorium occur as outgrowths of the outer lateral margins of the anterior tentorial arms at their bases. The dorsal arms are comparatively well-developed and are firmly connected to the head-capsule on the median fronto-lateral margin of the circum-ocular ridge. Although the dorsal arms are very well developed in this group and securely attached to the cephalic region, there is no indication, whatsoever, of pits, grooves or similar structures which could suggest that the dorsal arms arose as ectodermal invaginations.

The short broad anterior arms unite to form the greatly elongated "X-shaped" body of the tentorium. This elongation of the body of the tentorium has probably arisen with the return to prognathism. With the forward movement of eyes, antennae, mouth-parts, and the muscles which control them would have followed the anterior tentorial arms which, together, would have exerted considerable pulling force on the body of the tentorium which has gradually become more and more elongated.

The posterior tentorial pits lie in the lower ends of the post-occipital suture. The posterior tentorial arms are very short and soon coalesce with the body of the tentorium. The inner margin of each converging posterior tentorial arm is curvate and from its outer extremities tendinous processes project inwards. The occipital foramen is comparatively large.

Mention may be made here of the metopic crest (Fig. V, *mc.*) which is in reality an independent apodeme of the dorsal region of the head, since it proceeds like a knife-edge from the vertex into the cephalic cavity.

#### GRYLLIDAE.

The Gryllidae have a hypognathous head. It has become considerably depressed so that the mouth-parts are ventrally directed and the head lies in a vertical position. The original ventral area of the head becomes posterior, so that it lies in the same plane as does the occipital region. The change in position of the mouth-parts has caused a downgrowth of the head-capsule in the interocular region and this has been followed by a backward movement of the eyes and antennae.

The tentorium of the Gryllidae is X-shaped (Fig. VIII). It is thick, expanded and heavily chitinized. The anterior arms of the tentorium have their origin in the anterior tentorial pits which are elongate slits lying in the sub-genal and epistomal sutures, above the mandibular articulations. The anterior arms are wide and fan-shaped with heavy marginal chitinization. The two arms converge to meet in the wide anterior end of the body of the tentorium. The dorsal arms are well-developed; they arise as outgrowths of the anterior part of the body of the tentorium immediately below the region which receives the anterior arms. The dorsal arms of the tentorium are attached to the head-capsule in the caudo-lateral angles of the antennae. Again, in this group with well-developed dorsal arms there is no indication to show that they arose as invaginations. The body of the tentorium is broad anteriorly but narrows towards the posterior bridge, in front of which it becomes considerably constricted. Just before this constriction, there may be a thin small curvate expansion of the margin, after which the body of the tentorium narrows before diverging where the posterior tentorial arms coalesce. In the Gryllidae there is no elongated body of the tentorium as found in the prognathous Gryllotalpidae.

The posterior tentorial pits in the lower depths of the post-occipital suture give rise to the posterior tentorial arms which form a strong transverse bar and coalesce with the body of the tentorium.

Thus in the gryllid tentorium no striking modifications are encountered.

## TETTIGONIIDAE.

The Tettigoniidae are usually hypognathous, but [*Oecanthus capensis* Saus. is an interesting species which shows a secondary return to the semi-prognathous condition. The head-capsule has become anteriorly elongated as the mouth-parts have become forwardly directed. This change has effected certain regions of the head-capsule. The eyes have moved forward, and the antennae have come to lie slightly below and laterad of the eyes and immediately above the mandibles, so that the genal area is considerably reduced. With the dorso-anterior elongation of the head-capsule, the post-ocular region has become better developed. The occipital foramen is large and lies at an oblique plane to the longitudinal axis of the body. The change from hypognathous to semi-prognathous position has caused an elongation of the body of the tentorium, which shows great similarity to that of the Gryllotalpidae (Fig. IV).

The points of origin of the anterior tentorial arms are located on either side of the epistomal suture where the invaginations leave the anterior tentorial pits in the head-capsule. From these pits, the broadly expanded anterior arms project into the cephalic cavity. The anterior tentorial arms, with their heavy marginal chitinization, have become considerably twisted, so that the outer expansion of the arm which follows the sub-ocular ridge is at right angles to the expansion of the dorsal arm which proceeds directly into the cephalic cavity. The two anterior tentorial arms converge widely to meet in the body of the tentorium, the anterior margin of which forms a considerable bridge between the two anterior arms. The dorsal arms arise as lateral expansions of the outer margins of the anterior arms, slightly anterior to the body of the tentorium. The dorsal arms are firmly attached to the head-capsule on the fronto-lateral area of the ocular ridge but, here again, they leave no trace to suggest their origin as invaginations of the body-wall. After giving rise to the dorsal arms, the lateral margins of the body of the tentorium become inwardly curvate and narrow considerably behind.

The posterior tentorial pits arise in the extremities of the post-occipital region. They give rise to the posterior tentorial arms which are elongated and bridged by a posterior bar, which is slightly constricted mesally and appears carinate on the ventral surface.

Thus, the most striking modification of this tentorium is the greatly elongated body, not encountered in the hypognathous Tettigoniidae, which suggests that prognathism in this group is a secondary modification arising out of change of feeding mechanism.]

Amongst hypognathous Tettigoniidae considerable modification of the head-capsule has taken place. In many species the facial region is caudo-ventrally inclined at angles of 45° or more, so that the mouth-parts are backwardly directed. The facial and genal regions have become greatly elongated and elevation of the compound eyes and antennae has brought them from positions near the

\* See page 87.

#### ERRATA.

Geometridae Saus. was erroneously placed in the Family Tettigoniidae. It is generally regarded as a member of the Acrididae. This displacement does not affect the conclusions reached on the tentorium in the two groups concerned, more especially as the Tettigoniidae and Acrididae share many similarities of feature in the structure of the tentorium.

epistomal and sub-genal sutures to dorso- and antero-lateral positions on the head-capsule.

The tentorium of hypognathous types (Fig. IX) shows great shortening of the body of the tentorium due to dorso-ventral elongation of the head-capsule, which tends to cramp the tentorial apodemes, for the elongation of the head-capsule has caused a decrease in its width.

The anterior arms of the tentorium arise from the groove-like anterior tentorial pits in the sub-genal sutures, above the mandibular articulations. Before meeting in the body of the tentorium, the inner margins of the anterior tentorial arms, half-way down their length, become slightly dorsally twisted and a triangular expansion of this marginal area gives rise to the tendonous dorsal arms, which extend upwards and become attached to the outer lateral margin of the antennal ridge. When disrupted these dorsal arms appear to be formed of three separate tendons each, which are coalesced at either end.

The anterior tentorial arms unite to form the anterior part of the body of the tentorium, which has become medially constricted. The body of the tentorium is anteriorly pierced by a small median aperture through which pass circum-oesophageal connectives. The body of the tentorium is broadest posteriorly, where the heavily chitinized posterior tentorial arms unite with it and a strong posterior bar bounding the comparatively small occipital foramen bridges the posterior tentorial arms, which have their origin in pits in the lower extremities of the post-occipital suture.

#### ACRIDIDAE.

The Acrididae are the best developed of all saltatorial orthopteroïd insects. They may be considered to preserve the generalized orientation of the more highly developed groups in having the facial area anteriorly directed and the mouth-parts ventrally suspended.

The tentorium in this group is typically X-shaped and not unlike that of similarly hypognathous Tettigoniidae (Fig. X). The anterior tentorial pits occurring laterad of the epistomal sutures give origin to well-expanded and heavily chitinized anterior tentorial arms. These converge in a curvate manner to meet in the body of the tentorium. The dorsal arms arise as outgrowths of the anterior margin of the body of the tentorium. They are very delicate tendon-like structures, which usually proceed dorsad to become attached to the head-capsule cephalo-laterad of the antennal ridge. In *Acridella nasuta* L. and other species studied, the dorsal arms are considerably elongated and, in addition, there are two similar tendonous outgrowths which may be located on the anterior meso-ventral area of the body of the tentorium (Fig. X, to), which proceed to become attached to the margin of the maxillary pleurites, (Maxillariae, MacGillivray) i.e., the paired narrow ribbon-like

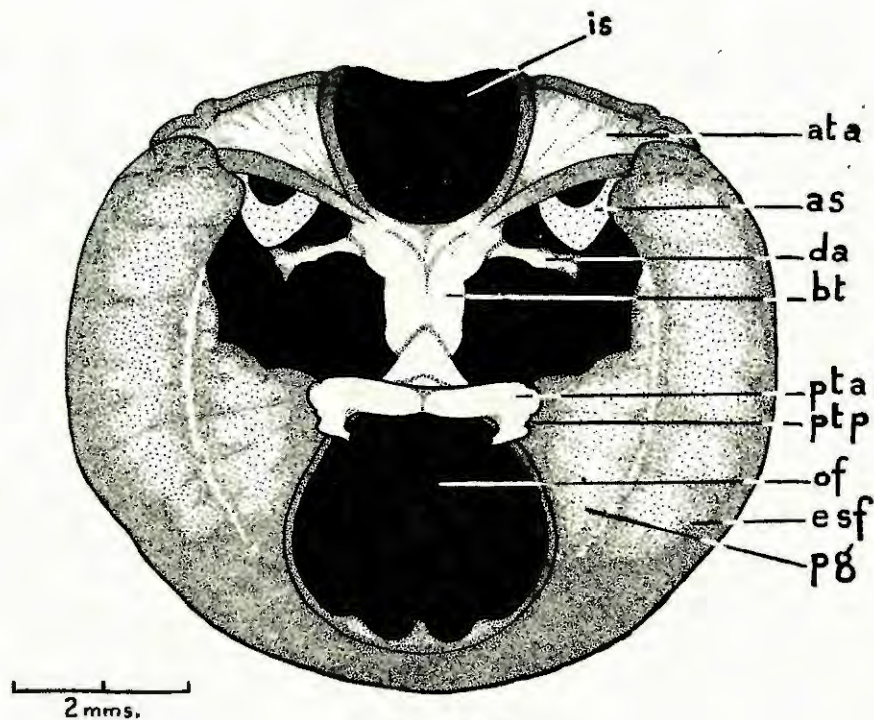


FIG. VIII.

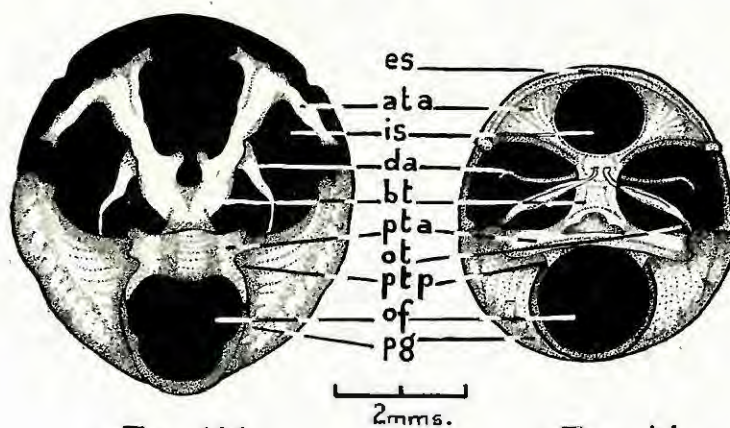


FIG. IX.

FIG. X.

sclerites along the mesal margin in the post-gena.

The body of the tentorium is comparatively small and devoid of apertures. It is distinctly X-shaped and there is heavy marginal chitinization. The posterior portion of the body of the tentorium is often slightly larger than the anterior.

The posterior tentorial pits in the extremities of the post-occipital suture gives rise to strongly chitinized and broadly expanded posterior tentorial arms. These arms enter into the cephalic cavity to unite in the body of the tentorium and are bounded posteriorly by a thickened marginal bridge. There is a large occipital foramen.

\* [.....]  
^ **Conclusion.**

A study of the tentorium of orthopteroid insects clearly indicates that they may be divided in the following manner:

Group 1.— Phasmidae.

Group 2.— Blattidae and Mantidae.

Group 3.— Saltatoria.

(a) Gryllidae.

(b) Tettigoniidae and Acrididae.

The Phasmidae possess a tentorium which differs fundamentally from that of any of the other orthopteroid groups studied. This is not surprising, considering that the Phasmidae are the only members studied which have retained a primitive prognathous type of head. They may be separated from all other Orthoptera by the possession of a very small posteriorly-placed body of the tentorium and considerably elongated anterior arms. The triangular outer marginal expansions of the anterior arms are absent in all the other groups studied. In the Phasmidae there is no median aperture in the tentorium, which separates them from the other cursorial groups, the Mantidae and Blattidae, with which they are usually associated.

The Blattidae and Mantidae show considerable similarities in the general structure of the tentorium. Both possess exceptionally strong, heavily-chitinized and well-twisted anterior tentorial arms which, before converging to unite at their bases, are crossed by the thick anterior tentorial bridge or frontal plate. In both groups a large median aperture is present in the body of the tentorium, but

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**Hypognathous Types of Orthopteroid hexapoda.**

Fig. VIII. Gryllidae: *Gryllus capensis* Oliv. Posterior aspect, mouth-parts removed.

Fig. IX. Tettigoniidae: *Clonia* sp. Caudo-ventral aspect, mouth-parts removed.

Fig. X. Acrididae: *Acridella nasuta* (L.). Caudo-ventral aspect, mouth-parts removed.

only in the Blattidae are oeso-tendons found projecting into this aperture. In both the Mantidae and Blattidae the dorsal arms are comparatively well-developed and are attached to the epicranium in the region of the antennal ridge and not on the ocular ridge as in the case of the Phasmidae. In both Blattidae and Mantidae there is considerable similarity in the broad, well-developed posterior arms, so that from a study of the tentorium, these two groups may be considered to be very closely allied and well separated from the Phasmidae.

In the saltatorial Orthoptera, the tentorium displays the generalized structure of the Orthoptera as a whole. Gryllidae, Tettigoniidae and Acrididae all possess an X-shaped tentorium, but the Tettigoniidae and Acrididae show closer relationship to each other than do the Gryllidae to either of the other two groups.

In all three, the anterior arms of the tentorium are broadly expanded and heavily sclerotized. They converge in a curvate manner and the body of the tentorium is comparatively short, though well-developed. In the Tettigoniidae and Acrididae there tends to be a shortening of the body of the tentorium. This is the result of dorso-ventral elongation of the head-capsule, which has caused a decrease in width and thus confined the tentorium to a smaller space. In some species of Tettigoniidae the possession of a small median aperture in the body of the tentorium may readily distinguish them from the Acrididae. In the Gryllidae, the body of the tentorium is widest anteriorly; whereas, in the Tettigoniidae and Acrididae the reverse holds true and, posteriorly, the body of the tentorium is often better developed, or as well developed, as it is anteriorly. In all three the dorsal arms of the tentorium arise independently from the body of the tentorium. In the Gryllidae they are strong, well-formed marginal expansions of the body of the tentorium and are firmly attached to the head-capsule in the caudo-lateral angles of the antennae. In the Acrididae and Tettigoniidae, however, the dorsal arms, though also arising from the body of the tentorium, are very delicate tendonous structures attached to the caudo-lateral margins of the antennal ridges. In the Acrididae there may be two additional tendonous outgrowths of the body of the tentorium which become attached to the head-capsule in the mesal margin of the post-genae. Thus, superficially, there is distinct similarity between the saltatorial types, but the Gryllidae are not as closely related to the Tettigoniidae and Acrididae as the latter are to each other.

In the saltatorial Orthoptera, two very interesting semi-prognathous species have been studied, *Gryllotalpa africana* Pal., and *Oecanthus capensis* Saus., the former a gryllid and the latter a ~~tettigoniid~~ <sup>acridid</sup>. That the prognathism which these two species exhibit is probably secondary, may readily be seen when a comparison of their tentoria is made with that of the primitive, prognathous phasmid. In both species, the most striking feature of the tentorium

is the greatly elongated body of the tentorium, which has not been encountered in any of the hypognathous or primitively prognathous groups studied. This suggests that secondary modification has occurred as a result of change of habit or habitat.

The structure of the tentorium is influenced by the structure and position of the mouth-parts. As these have gradually become anteriorly directed, the head-capsule has been drawn out and, with it, the body of the tentorium, which has become considerably elongated. In both species the anterior tentorial arms are broad, tortilis, heavily chitinized and their inner margins are slightly curvate, as they converge to meet in the body of the tentorium. In both species it is interesting to note that the dorsal arms are very well developed and firmly attached to the head-capsule on the fronto-lateral margin of the circum-ocular ridge, as in the primitively prognathous Phasmidae; whereas, in hypognathous Gryllidae and Tettigoniidae studied, the dorsal arms are found to be attached to the epicranium in the region of the antennae. It is difficult to account for this change, but it seems to indicate quite clearly that the dorsal arms are not integumental invaginations. It is unlikely that their position as invaginations could be so readily changed when a secondary return to prognathism was established; for, in both species, though the posterior tentorial pits have become drawn out slightly to form grooves rather than pits, they have not changed their position in any other way. The same is true for the anterior tentorial pits. If the dorsal arms were merely attached to the head-capsule, it would be far more likely that their position could thus be changed if support was needed in some other more medially placed region of the head-capsule, as the antennae are placed very far forward in prognathous types.

A further consideration of the posterior arms of the tentorium in the two species, shows them to be similar and they retain, in general, the structure of the two groups they represent, namely, the Gryllidae and the Tettigoniidae.

Thus it is seen that, in orthopteroid insects, primitive and secondary prognathism of the head-capsule may be present. From a study of the tentorium, these may be readily distinguished from each other.

These conclusions from a general study of the tentorium in the orthopteroid group are in agreement with those reached after a comparative study of the external morphology of the group. Similar results were achieved by Yuasa (1920) whose work on "The comparative anatomy of the head and mouth-parts of Orthoptera and Euplexoptera" showed anatomical evidence that the Blattidae and Mantidae are closely related and that the Gryllidae followed the Mantidae, though they did not develop directly through the latter. He also places the Locustidae (Tettigoniidae) and Acrididae together, but considers the Phasmidae as a remote group, of which the exact phylogenetic position cannot be determined.

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## Studies in the comparative anatomy and systematic importance of the hexapod tentorium.

### II. Dermaptera, Embioptera and Isoptera\*

by

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#### Material

The following species were selected and examined:—

*Dermaptera*: *Picrania liturata* Stal. *Forficula senegalensis* Serv.  
*Mesochelidura peringuei* Burr. *Hemimerus hanseni* Sharp (slide only).

*Isoptera*: *Hodotermes mossambicus* subsp. *Havilandi* Sharp.  
*Termes* sp. *Termes incertus* Hav. *Termes trinervius* Hav. *Mastotermes darwiniensis* Frogg.

*Embioptera*: *Haplocambia capensis* Esb. Pet. *Oligotoma* sp.

#### Acknowledgments

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#### Technique

Specimens were placed overnight in a warm 5% caustic potash solution. They were then rinsed and preserved in 70% alcohol. Specimens were examined under a Zeiss binocular dissecting microscope. Mouth-parts were removed, thus facilitating the examination of the tentorium, which is seen to the greatest advantage from the posterior or postero-caudad aspect. The specimens were examined in 70% alcohol, cedarwood oil, or glycerine. The following stains were used: Alcoholic Eosin, Azo-eosin, dilute Azo-black, Haemalum and Kernschwarz. Of these, Haemalum and Kernschwarz were the most satisfactory. Experiments with a saturated iodine solution in 70% alcohol gave excellent results and greatly improved definition of outline of parts under examination. Specimens can be examined in this solution, or the solution may be further diluted by 70% alcohol. Specimens used for dissection were fixed for six hours in

\* For Paper I see Journ. Ent. Soc. S. Africa. Vol. VIII.

warm Diedrich's solution (Formula: 40% Formalin, 12 ccs., 95% Alcohol, 30 ccs., Glacial Acetic Acid, 2 ccs., Distilled water, 60 ccs.) and then transferred to 70% Alcohol. Drawings were made with the aid of a camera-lucida attached to a Leitz microscope.

### DERMAPTERA

In the Dermaptera, the head is prognathous and an additional selerite or gula is developed behind the submentum. The head is depressed: the antennal sockets are placed far forwards on the head, above the bases of the mandibles. The compound eyes are antero-laterally placed, so that there is a small genal area, but the post-ocular region of the head is well developed. The mouth-parts are forwardly directed and the long axis of the head is slightly inclined ventrally, so that the occipital foramen lies in a postero-ventral position. The dorsal elongation of the post-ocular region of the head has been accompanied by a corresponding elongation of the ventral region, so that the base of the labium has elongated between the post-genae and an additional plate called the gula or guliform selerite (Hansen, 1930 = praementum) has been formed immediately behind the submentum and the posterior tentorial pits. As this plate lies behind the posterior tentorial pits in the Dermaptera, it cannot be considered a part of the submentum but, as suggested by Walker (1933, p. 313), it should be regarded as a secondary sclerotization of the anterior part of the cervical membrane which has become stretched owing to the anterior position of the mouth-parts.

The tentorium in the Dermaptera is X-shaped, and the cephalic portion may be elongated and enlarged (Yuasa, 1920). The anterior tentorial arms arise from the anterior tentorial pits, which are located immediately below the antennal sockets on either side in the epistomal suture. The apices of the anterior tentorial arms are broad and well developed and outer marginal curvate expansions at the apices of the anterior tentorial arms produce wedge-shaped platforms which are firmly connected on either side to the head capsule along the ventral rim of the antennal ridge. (See Figs. I, II, ata.) The two anterior tentorial arms converge gradually and then unite to form a broad anterior portion to the body of the tentorium.

The body of the tentorium is elongated and the broad anterior portion becomes slightly constricted behind the dorsal arms and tapers to the narrow posterior of the body of the tentorium. (See Figs. I, II, bt.)

From the anterior dorso-lateral margins of the body of the tentorium and immediately behind the union of the anterior tentorial arms, plate-like expansions of the body of the tentorium occur. These are the dorsal arms which taper as they pass upwards and outwards to broaden at their points of attachment to the head-capsule in the inter-ocular region, a little removed from the inner median border of the circum-ocular ridge.

*Hudson: Hexapod tentorium.*

Externally, the two places of attachment of the dorsal arms to the epicranial walls are located by two dark semi-circular markings on the head-capsule. These are termed the tentorial maculae by Snodgrass (1935, p. 110).

The posterior tentorial arms originate from the posterior tentorial pits, which lie in the extremities of the post-occipital suture. These pits are rounded and not elongated. The posterior tentorial arms are short, meeting almost transversely to form the posterior body of the tentorium. (See Figs. I, II, pta.)

It was not possible to obtain material of the families Arexeniidae and Apachydae and only a slide-specimen of *Hemimerus hanseni* Sharp was available. Jordan [1909 (a), p. 321] states that the tentorium of *Arixenia* is similar to that of *Forficula*, except that its anterior half is much shorter. In the same paper, he states that *Hemimerus* also has a tentorium of the same type. Hansen (1894) does not give any details of the tentorium of *Hemimerus talpoides* Walk., and Jordan [1909 (b), p. 329] in his paper on the anatomy of this insect merely repeats his former statement that the tentorium of *Hemimerus talpoides* resembles the tentorium of earwigs and *Arixenia*.

## EMBIOPTERA

The Embioptera have an oval prognathous head. The eyes are placed far forward and, according to Walker (1933, p. 313), they are very like those of *Grylloblatta* in form, size and position. The antennae are likewise antero-lateral in position. The post-ocular region of the head is markedly developed, while the genal area is reduced. An additional sclerite has developed in the cervical membrane posterior to the base of the labium, and has become completely fused with the margins of the post-genae. This sclerite or plate cuts off the occipital foramen from the posterior tentorial arms and has been termed the gula plate but, although it performs the same function, it cannot be regarded as a true gula.

The anterior arms of the tentorium arise from the anterior tentorial pits, which occur slightly mesad and below the antennae, on either side, in the epistomal suture. The anterior tentorial arms are fan-shaped or expanded at their points of origin and the broad anterior elongately triangular platform is curvately attached to the outer lateral rim of the antennal ridge. (See Figs. III, IV, ata.) Each anterior tentorial arm is directed caudo-mesad, then extends to the meson to unite with the other anterior tentorial arm in the anterior body of the tentorium. The body of the tentorium is short and rectangular, while the lateral margins are inwardly curvate. There is no median aperture in the body of the tentorium. The dorsal arms arise as marginal outgrowths of the body of the tentorium and occur at the bases of the anterior tentorial arms. They are tendonous processes, which expand and flatten before becoming

attached to the head-capsule on the anterior aspect of the antennal ridge. (Figs. III, IV, da.)

The posterior tentorial arms are very well developed; they arise from the posterior tentorial pits and proceed inwards for some distance before coalescing mesally to form the posterior of the body of the tentorium. Thus the posterior arms are arcuate and not transverse. The ventral aspect of the head-capsule is modified here; the occipital suture divides the gena from the post-gena and extends on either side to end between the points of articulation of the mandibles. The post-genal area is a slightly concave depression and it is in this area that the two posterior tentorial pits occur, i.e., behind the submentum, where the post-genae abut on the anterior border of the gula region. The two posterior tentorial pits occur as transverse pits and not as longitudinal slits, clearly indicating that the elongation of the head capsule in the Embioptera has taken place behind the region of the posterior tentorial pits.

### ISOPTERA

The Isoptera possess a prognathous head. In the worker and reproductive castes the head is ovoid or rounded. In the soldier caste it is oblong or pyriform in shape and may be larger than the thorax and abdomen together.

The mouth-parts are forwardly directed and the occipital foramen has become postero-ventrally inclined to a small degree. In the soldier caste, however, the vertical position of the occipital foramen has been retained, the ventral and dorsal regions of the head-capsule having elongated equally, thus obviating the necessity for a change in position of the occipital foramen. The elongation of the ventral surface of the head has resulted in a considerable stretching of the submentum in the region of the posterior tentorial pits. These pits have consequently lost the form of rounded depressions and have become drawn out into slits. As indicated by Walker (1932, p. 317), the prolongation of the submentum has not resulted in the separation of a true gula region, for the submentum remains undivided by any suture. Snodgrass (1935, p. 126) also shows that, though the structure of this part of the termite head is similar to that in the Coleoptera, it is not identical with the usual gular structure in this order. Macropterous forms possess compound eyes which are antero-laterally placed, but in the reproductive castes eyes may be greatly reduced. The antennae are widely separated and arise from shallow fossae situated immediately above the articulation of the mandibles. The genal area of the head has suffered reduction, but the post-genae are elongated.

The anterior tentorial pits are located on either side of the epistomal suture, below and laterad of the bases of the mandibles. From these pits, the anterior tentorial arms arise. Each arm is widely expanded anteriorly, forming a wedge-shaped platform which is firmly attached to the head-

*Hudson: Hexapod tentorium.*

capsule along the antero-lateral margin and which extends in a curvate manner to the rim of the antennal ridge. (See Figs. V, VI, VII, ata.) The anterior tentorial arms are posteriorly directed towards the median plane of the head. Each arm is triangular in shape and becomes slightly twisted, before it fuses with the other anterior tentorial arm, to form the distinct anterior bridge or frontal plate of the tentorium. Walker (1933, p. 317) states that the basal portions of the anterior tentorial arms are united by a thin anterior bridge. This doubtless refers to the thin plate-like structure, for the width of the bridge is considerable. The ventral surface of the frontal plate is medianly carinate.

The dorsal arms of the tentorium in the Isoptera are often difficult to locate. These arms arise as triangular expansions of the dorso-lateral margins of the frontal plate, at the bases of the anterior tentorial arms. (See Figs. V, VI, VII, da.) The dorsal arms are thin, transparent, linear processes, which become attached to the head-capsule on the margin of the antennal ridge or in the inter-ocular region. For examination and location of the dorsal arms, especially in the worker caste, the writer recommends examination of specimens in a saturated iodine solution in 70% alcohol, this medium improving definition of outline.

The body of the tentorium is rectangular in shape and is medianly perforated by an aperture through which circum-oesophageal connectives pass. This aperture is bounded anteriorly by the frontal plate and behind by the posterior bridge of the body of the tentorium. (See Figs. V, VI, VII, ma.) In the soldier caste the posterior tentorial pits occur as grooves at the sides of the "gular" region of the labium (Snodgrass, 1935, p. 126). In the other castes the posterior tentorial pits are located in the extremities of the post-occiput.

From the posterior tentorial pits the broad posterior arms of the tentorium arise and meet transversely to form the posterior bridge of the tentorium which, in soldier termites, is well developed. (Figs. V, VI, VII, pta.)

The posterior bridge of the tentorium, as pointed out by Snodgrass (1935, p. 116), forms a long roof-like structure over the basal part of the labium.

#### **Conclusions.**

From a study of the tentorium in the Dermaptera, there is little to commend any association of the Dermaptera with the Embioptera or the Isoptera. The body of the tentorium of the Dermaptera lacks the median aperture which is a characteristic feature of the Isoptera. The tentorium of the Dermaptera is considerably longer than that of the Embioptera and the posterior tentorial arms of the Dermaptera meet transversely, whereas in the Embioptera the posterior tentorial arms proceed inwards for some distance before uniting mesally to form the posterior body of the tentorium. There have been speculations as to

the affinities of the Dermaptera and the Dictyophora, but a study of the tentorium shows no striking features which would recommend such an assumption. Walker (1933, p. 313) states that in the general form of the head-capsule, including the tentorium, *Grylloblatta* is distinctly dermapteroid, or at least forficuloid. Unfortunately, the writer has no material of *Grylloblatta* for confirmation of this statement, but from a study of Walker's diagram (1931, Plate I, p. 533) it appears that the tentorium of *Grylloblatta* is strikingly similar to that of the Dermaptera and in both the dorsal arms are attached to the head-capsule in the interocular regions.

The tentorium of the Embioptera bears no striking resemblance to that of the Dermaptera or the Isoptera. The anterior tentorial arms are expanded apically at their points of origin, but narrow considerably before coalescing to form the anterior body of the tentorium. The dorsal arms are poorly developed tendonous outgrowths fused with the anterior tentorial arms. The dorsal arms are anteriorly attached to the antennal ridge. The body of the tentorium, as pointed out by Walker (1933, p. 314), is more nearly rectangular than in *Grylloblatta* and Dermaptera. The body of the tentorium further lacks the conspicuous median aperture of the Isoptera. The posterior tentorial arms are well developed and differ from those of the Dermaptera and Isoptera, for they proceed inwards for some distance before uniting mesally to form the posterior body of the tentorium. In this feature, the Embioptera differ widely from the Dermaptera and Isoptera where the posterior tentorial arms are almost transverse. There is no strong evidence to support an association of the Embioptera with the Phasmida, Dictyophora or Saltatoria previously studied. Furthermore, the Embiopteran tentorium leaves nothing to suggest a relationship with the Dermaptera or Isoptera. From a preliminary study of the Plecoptera, it is evident that the Embiopteran and Plecopteran tentoria show distinct similarities, but these will be considered in a future communication.

The tentorium of the Isoptera is very striking in that it closely resembles the tentorium of the Dictyophora previously studied. In both the Blattidae and Isoptera, the anterior tentorial arms are widely expanded and are united by a transverse band forming the frontal plate of the tentorium. The dorsal arms are difficult to locate, being delicate tendonous strands which arise as thin triangular expansions of the body of the tentorium, immediately posterior to the bases of the anterior tentorial arms. In some Isoptera and in Dictyophora, the dorsal arms are attached to the margin of the antennal ridge. The tentorium of the Isoptera further resembles that of the Dictyophora in the presence of a median aperture in the body of the tentorium. This aperture is bounded anteriorly by the frontal plate and posteriorly by the bridge formed by the union of the well-developed, somewhat transverse, posterior tentorial arms. The median aperture is a pronounced feature of the Isopteran tentorium, which is shared with the Dictyophora previously studied and therefore provides

*Hudson: Hexapod tentorium.*

substantial morphological evidence for linking the Isoptera with the Dictyophora — an association which has been much speculated upon by previous authors, Wheeler (1931), Walker (1933), Crampton (1932), Scott (1929), Imms (1934) amongst various others.

The tentorium in the Dermaptera, Embioptera and Isoptera reveals that the three groups show no immediate relationship to each other, but the tentorium of the Isoptera provides further important evidence for associating the Isoptera with the Dictyophora. In a former paper on a study of the tentorium in orthopteroid hexapoda (Hudson, 1945), the writer indicated that the orthopteroid hexapoda could be divided into:—

- Group 1. Phasmidae.
- Group 2. Blattidae and Mantidae.
- Group 3. Saltatoria.

From a study of the tentorium in Dermaptera, Embioptera and Isoptera, it is therefore suggested that these insects be grouped in the following manner:—

- Group 1. Phasmidae.
- Group 2. (a) Blattidae and Mantidae.  
(b) Isoptera.
- Group 3. Saltatoria.
- Group 4. Dermaptera.
- Group 5. Embioptera.

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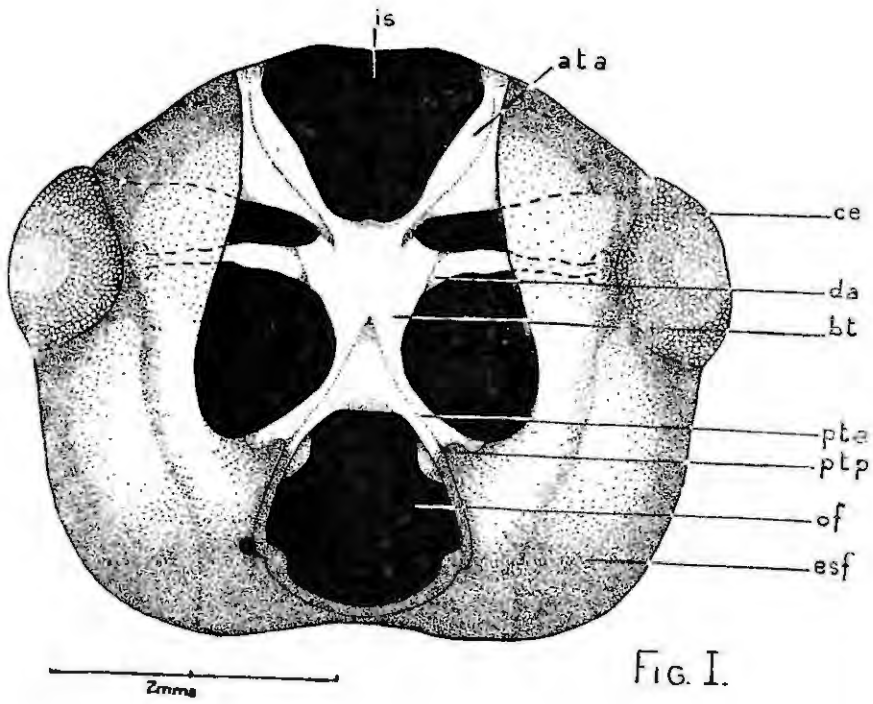


FIG. I.

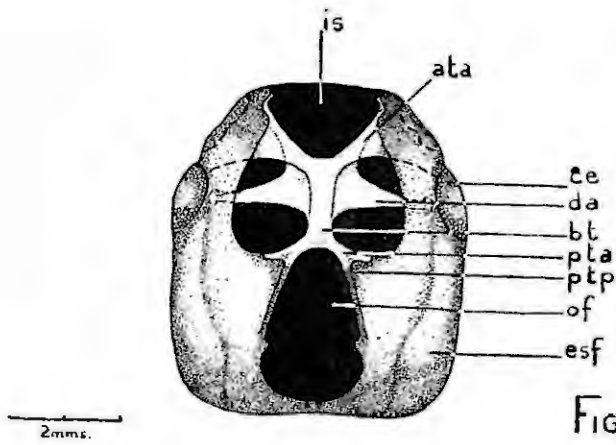


FIG. II.

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Figs. 1 and 2. — Dermaptera: ventro-caudad aspect of head-capsule with mouthparts removed. Fig. 1: *Forficula senegalensis* Serv. Fig. 2: *Picrania liturata* St. a: antenna; ass: position of antennal ridge; ata: anterior tentorial arm; bt: body of tentorium; ce: compound eye; da: dorsal arm; es: epistomal suture; esf: external surface; is: internal surface; ma: median aperture; of: occipital foramen; o: ocellus; pta: posterior tentorial arm; ptp: posterior tentorial pit.

Figs. 3 and 4. — Embioptera: ventro-caudad aspect of head-capsule with mouthparts removed. Fig. 3: *Haploembia capensis* Esb. Pet. Fig. 4: *Oligotoma* sp. Abbreviations as in previous figures.

Figs. 5-7. — Isoptera: ventro-caudad aspect of head-capsule with mouthparts removed. Fig. 5: *Termes* sp., winged form. Fig. 6: *Termes incertus* Hav., worker. Fig. 7: *Hodotermes mossambicus* sub-sp. *Havilandi* Sharp, soldier. Abbreviations as in Fig. 1.

Hudson: *Herapod tentorium*.

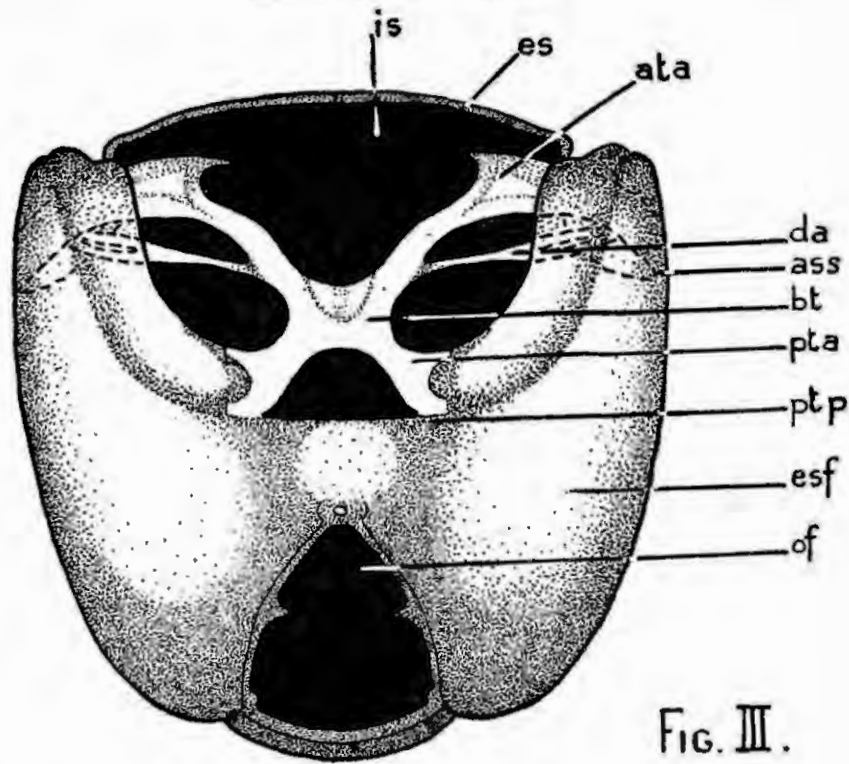


FIG. III.

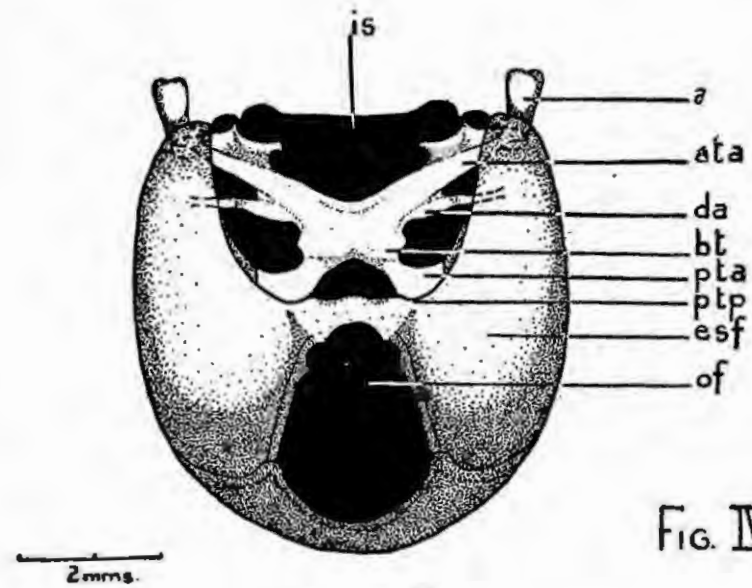


FIG. IV.

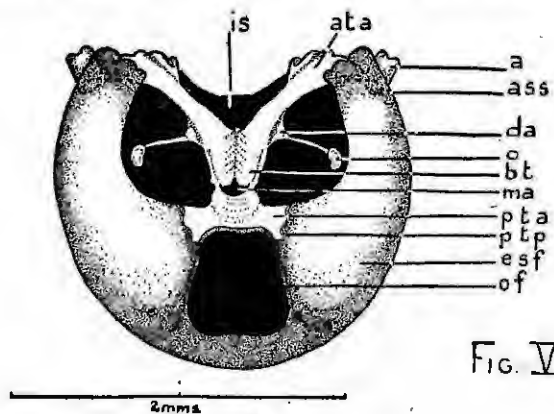


FIG. V.

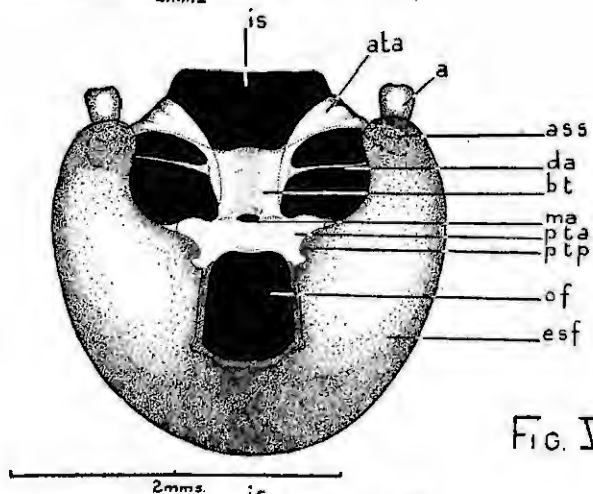


FIG. VI.

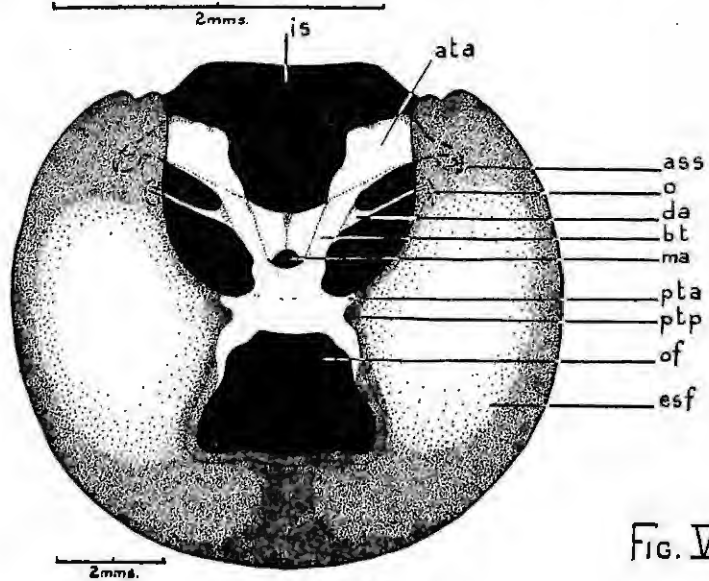


FIG. VII.

# Studies in the comparative anatomy and systematic importance of the hexapod tentorium

## III. Odonata and Plecoptera

by

GERDA BLAND HUDSON, M.Sc., F.R.E.S.

### ODONATA.

#### Material:

The following species were selected and examined:

*Aeschna* sp. (larva). *Anax* sp. (larva). *Orthetrum* sp. *Helothemis dorsalis* Rambur. *Chlorolestes fasciata* Burm. (adult and larva). *Crocothemis sanguinolenta* Burm. *Sympetrum fonscolombei* Selys. *Aeschna minuscula* MacLach. *Rhyothemis semi hyalina*. *Ceriagrion glabrum* Burm. *Pantala flavescens* Fabr. *Crocothemis erythraea* Brulle. *Allocnemis leucosticta* Selys. Gen. *Pseudagrion* Selys.

#### Acknowledgments:

The writer gratefully acknowledges the gift of material and assistance in identification of specimens given by Dr. K. H. Barnard and Dr. J. Hewitt. Special thanks are tended to Mr. Drummond and Mr. O. B. Swallow of Grootvlei Prop. Mines, Ltd. for the loan of a microscope. The writer also wishes to extend appreciation and thanks to Professor J. Omer-Cooper for his unfailing interest and encouragement throughout these researches.

#### Larva:

Dragon-fly larvae are exclusively aquatic and inhabit a variety of fresh-water situations. Some remain concealed in mud, others live among weeds or hide under stones. These larvae are predaceous and feed upon various forms of life encountered in the water.

The larvae of the Odonata are campodeiform and the head is hypognathous, the latter condition being common, according to Walker (1932) among such carnivorous insects as await the approach of their prey, and seize it with prehensile structures. In the Odonata, the larva possesses a remarkable structure called the mask, which is exclusively used for the capture of prey. The mask is a modification of the labium, for prementum and postmentum are elongated and freedom of movement allowed between the two parts. The

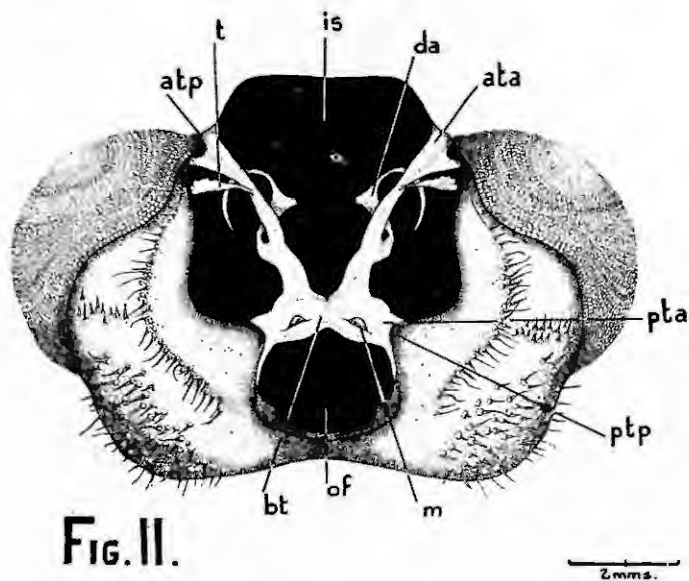
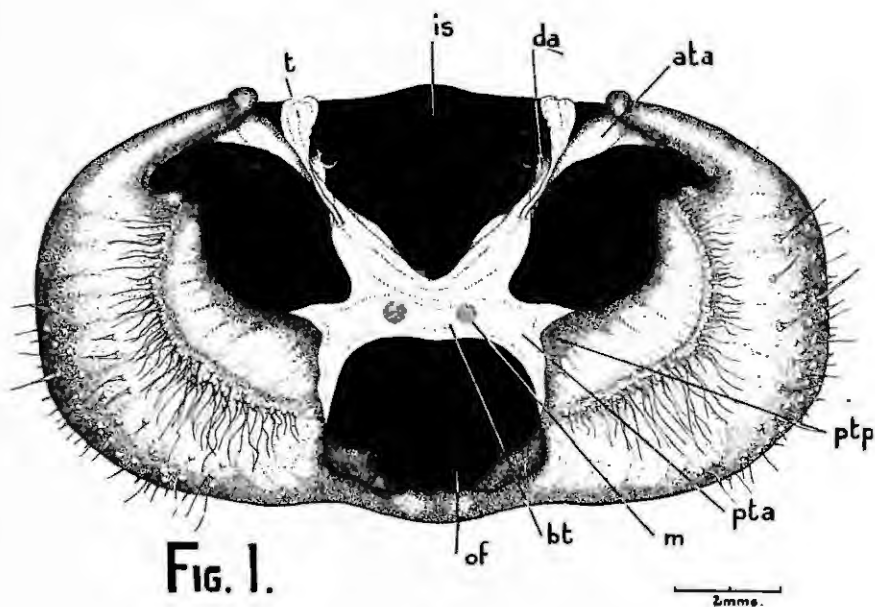


Fig. I. Odonata, Anisoptera: *Pantala flavescens* Fabr. Larva. Ventral aspect, mouthparts removed.

Fig. II. Odonata, Anisoptera: *Aeschna* sp. Larva. Ventral aspect, mouthparts removed.

ligula, occurring as a median lobe, is fused with the mentum, and the labial palps form lateral lobes, each bearing a movable hook on the outer margin. This mask is a powerful weapon for the predaceous larva, for it can be extended at high speed, and the prey captured on the movable hooks.

The hypognathous head of the larva is broad and short. The eyes occurring dorso-laterally, occupy the greater portion of the head-capsule and during metamorphosis they increase in size and the three ocelli developing gradually. The antennae are short and anteriorly directed. The mouth-parts are ventrally placed, though concealed by the mask, the latter being forwardly extended when in action. The longitudinal axis of the head is vertical.

The roots of the anterior tentorial arms are laterally placed in the subgenal sutures, above the bases of the mandibles (Figs. 1—3, atp.). The anterior tentorial arms of the larva are well developed and they may be widely expanded in a wedge-shaped manner near their roots (Figs. 1—3 ata.). Each anterior tentorial arm extends in

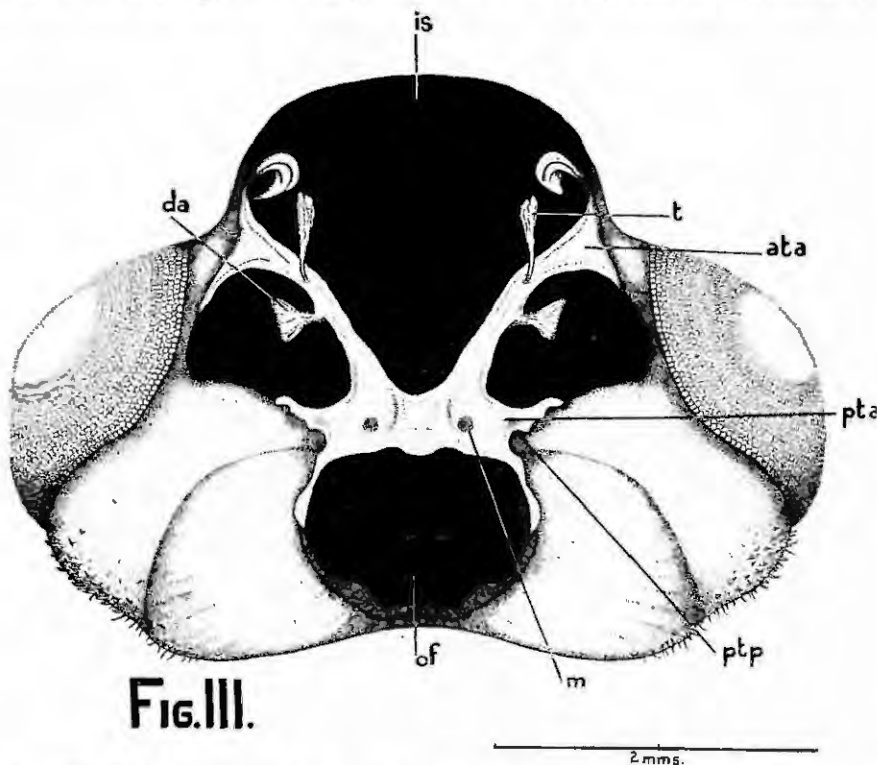


Fig. III. Odonata, Zygoptera: *Chlorolestes fasciata* Burm. Larva, Ventral aspect, mouthparts removed.

a caudomesal direction narrowing slightly, and then expanding along the mesal margin until the two anterior tentorial arms fuse in the body of the tentorium. About mid-length on the ventral surface of the anterior tentorial arms, tendonous outgrowths occur (Figs. 1—3, t.). There is usually one outgrowth on each arm and the shape of this outgrowth varies considerably; it may be linear, or spatulate or irregular in shape, and is usually a very delicate structure.

A short distance before their union in the body of the tentorium, dorsal projections arise from the lateral margins of the anterior tentorial arms; these projections are the dorsal arms, and they may be considerably expanded at their peripheral ends (Figs. 1—3, da.). They extend forward and usually become attached to the dorsal surface of the head on the antennal ridge, e.g. *Aeschna* sp. However, the point of attachment of the dorsal arms to the head-capsule, is variable in the larval forms of the Odonata, for in some cases, attachment of the dorsal arms may occur on or close to the ocular ridge, e.g. *Anax* sp.

The short body of the tentorium is posteriorly placed and borders the occipital foramen (Figs. 1—3, bt.). Ventrally on either side of the median line of the body of the tentorium, circular or semi-circular markings occur. These markings may also occur as small rounded chitinous projections of the body of the tentorium and are somewhat characteristic of the tentorium of the larva (Figs. 1—3, m.).

The posterior tentorial pits are deep depressions occurring in the extremities of the post-occipital sutures (Figs. 1—3, ptp.) and these pits give rise to the posterior tentorial arms (Figs. 1—3, pta.). The latter are stout, transverse bars, which lend firm support to the occipital region of the head and meet in the body of the tentorium.

#### Adult:

In the adult Odonata, the head has become highly modified in correlation with the great development of the compound eyes. In the Anisoptera the compound eyes meet mid-dorsally and occupy the greater part of the dorso-lateral region of the head-capsule. In the Zygoptera the eyes are smaller, rounded, and occur laterally on the transversely elongated head. There are three ocelli in the inter-ocular area which is large in the Zygoptera, but considerably reduced in the Anisoptera. The short antennae are forwardly extended.

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#### Abbreviations used in figures:

ata.—anterior tentorial arm; atp.—anterior tentorial pit; bt.—body of tentorium; c.—cut; da.—dorsal arm; is.—internal surface; m.—marking; of.—occipital foramen; pta.—posterior tentorial arm; ptp.—posterior tentorial pit; scp.—semi-circular projection; t.—tendonous outgrowths (anterior tentorial arm); tp.—tendonous outgrowth (body of the tentorium).

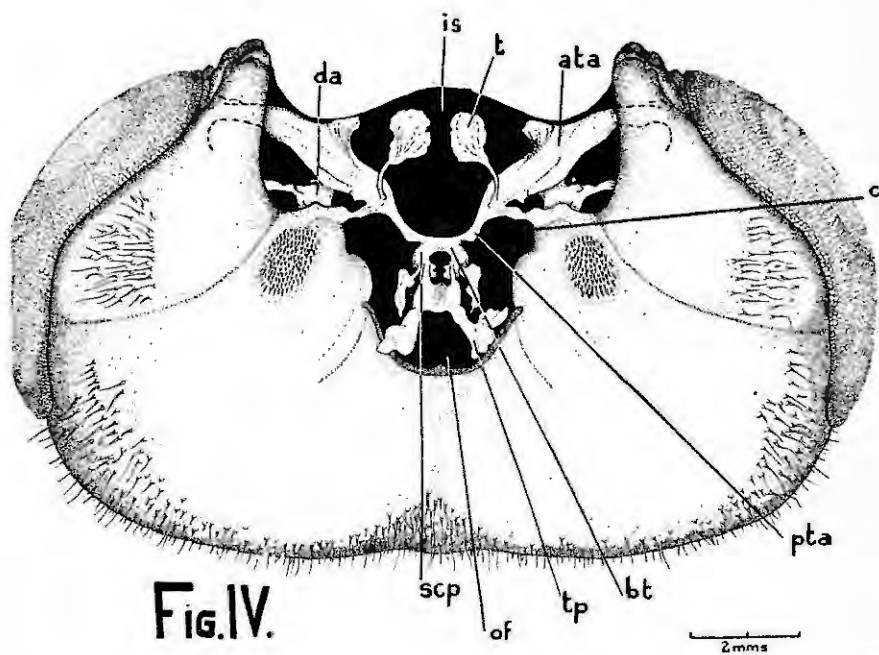


FIG. IV.

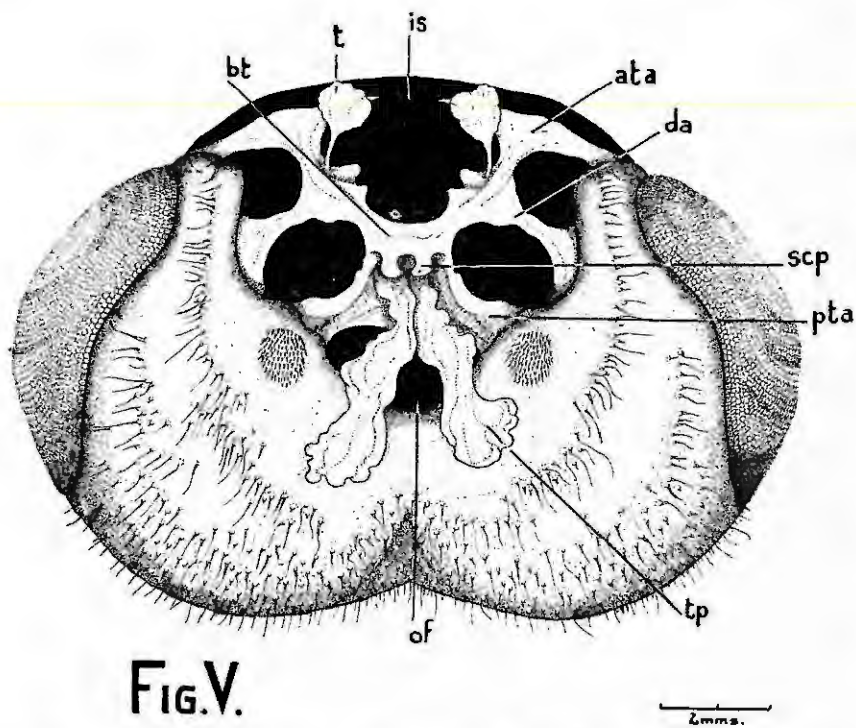


FIG. V.

Fig. IV. Odonata, Anisoptera: *Orthetrum* sp. Adult. Ventro-caudal aspect, mouthparts removed.

Fig. V. Odonata, Anisoptera: *Aeschna minuscula* MacLach. Adult. Ventro-caudal aspect, mouthparts removed.

The biting mouthparts are ventral in position and the head represents the hypognathous condition. Walker (1932) states that hypognathism developed as the insect acquired the habit of seizing its prey during flight and of using its legs for perching. He notes that this is seen among Carboniferous insects in the Megasecoptera and even among the Palaeodictyoptera, and he refers to its presence in the extremely isolated but still existing orders, Odonata and Ephemeroptera.

The tentorium in the adult Odonata is well-developed and somewhat pi-shaped. The anterior tentorial arms are apodemes arising as invaginations from the anterior tentorial pits, the latter being located in the subgenal sutures above the bases of the mandibles. (Figs. IV—VII, atp.). Tillyard (1917) describes the position of the anterior tentorial pits as occurring in the two ends of the frontal furrow.

The anterior tentorial arms are well-developed (Figs. IV—VII, ata.). At their roots they are expanded to form a wedge-shaped supporting platform for the head-capsule. From their points of origin on the head-capsule, the anterior tentorial arms proceed inwards, tapering and converging to meet posteriorly in the body of the tentorium. As in the larva, the ventral surface of each anterior tentorial arm carries one or more pairs of tendonous outgrowths of variable shape (Figs. IV—VII, t.). In some cases the mesal or lateral margins of the anterior tentorial arms may develop slight expansions or projections (Figs. IV—VII, pr.). About mid-length, the lateral margins of the anterior tentorial arms develop secondary outgrowths, the dorsal arms which extend towards the head-capsule, where they become attached on or near the antennal ridge (Figs. IV—VII, da.).

In a description of the tentorium, Tillyard (1917) considers the endoskeleton to be formed of four pieces of endosternites, but he does not mention the presence of dorsal arms. It is possible, however, that owing to the great development of the dorsal arms in some genera, these structures may have been regarded by Tillyard, as the expanded bases of the anterior tentorial arms, encircling the antennal ridge. The body of the tentorium is short and narrow (Figs. IV—VII, bt.). The anterior margin may vary in shape. It may be concave, straight or slightly indented. The posterior margin of the body of the tentorium borders the small occipital foramen and is characterised by two semi-circular projections, whose proximal ends may be widely separated (Fig. VII, scp.) or they may meet but not unite (Figs. IV—VI, scp.). From the ventral surface of these projections of the body of the tentorium there arise two or more irregularly shaped tendonous outgrowths. These may possibly be regarded as the tendons of the flexors of the head, which Comstock and Kochi (1902) describe as arising from the lower surface of the body of the tentorium and extending caudad. The median pair of the tendonous outgrowths may unite as in *Orthetrum* sp., or they may

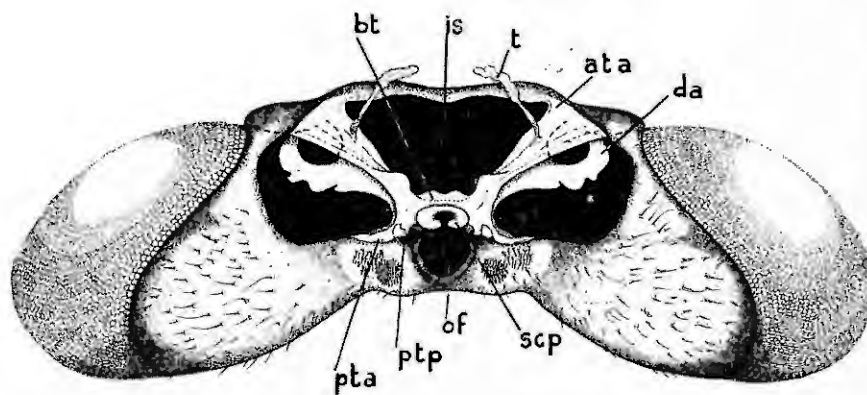


FIG. VI.

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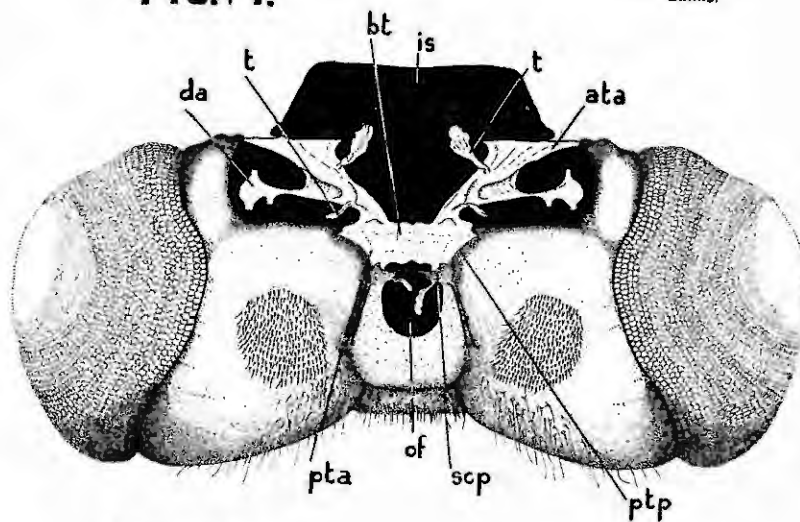


FIG. VII.

2mm.

Fig. VI. Odonata, Zygoptera: *Chlorolestes fasciata* Burm. Adult. Ventro-caudal aspect, mouthparts removed.

Fig VII. Odonata, Zygoptera: *Ceriagrion glabrum* (Burm). Adult. Ventro-caudal aspect, mouthparts removed.

remain separate as in *Aeschna* sp. (Figs. IV, V, tp.). In the Zygoptera these outgrowths when present are developed to a lesser degree than those of the Anisoptera (Fig. VII, tp.).

The posterior arms of the tentorium are short and well-formed. They originate as invaginations of the posterior tentorial pits, located in the depths of the post-occipital region (Figs. IV—VII, pta.). The posterior tentorial arms meet transversely in the body of the tentorium.

#### PLECOPTERA.

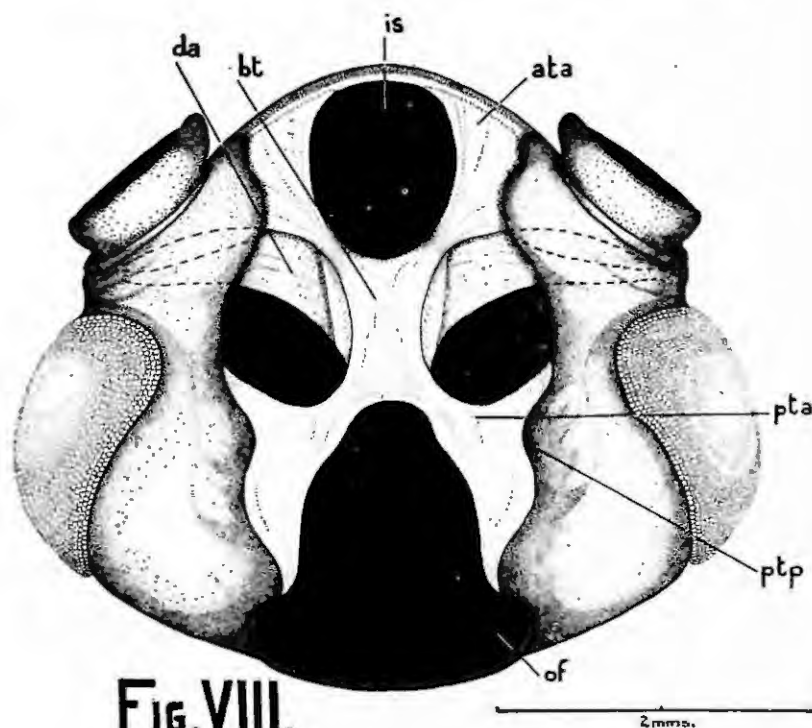
A comprehensive study of the anatomy of the head and mouthparts of the Plecoptera was undertaken by Hoke (1923) in which the tentorium of a representative series of genera was described and figured. The writer has therefore considered it unnecessary to duplicate this work by a further detailed study of the tentorium in a variety of genera, so that in describing this structure, account will be taken of those tentoria studied and figured by Hoke (1923) as well as the two species investigated by the writer. Species of *Acroneuria* were obtained from U.S.A. and specimens of *Nemouridae* were collected at Hogsback, Cape Province.

The campodeiform larvae of the Plecoptera are exclusively aquatic, inhabiting clear streams and well-aerated waters where they pursue a predaceous existence. In general form the larvae resemble the adults, those features in which they differ being mainly adaptive.

The head in both larva and adult is prognathous or semi-prognathous, and is considerably depressed. The posterior region of the head-capsule has been shortened and the genal area reduced. The many-jointed antennae are long and setaceous and arise far forward, their bases being set widely apart. The compound eyes are dorso-laterally placed and two or three ocelli occur in the wide inter-ocular area; the ocelli of the larva are smaller than those of the adult. The plane of the occipital foramen varies, and in specialised types tends to acquire a posterior, instead of a postero-ventral position, which is the more primitive position in prognathous insects. Hoke (1923), Walker (1933). The mouthparts are anteriorly directed but although completely formed in the adult, they are usually weakly developed.

When Comstock and Kochi (1902) investigated the skeleton of the head of insects, their study was mainly based on the Plecoptera, the Orthoptera and the Neuroptera, though other orders of insects were also considered.

The tentorium in the Plecoptera is of the same general type as that of orthopteroid insects. The anterior tentorial arms (Fig. VIII, ata.) originate from the anterior tentorial pits, the latter occurring near the extremities of the epicranial arms, and when present, in the lateral limits of the epistomal suture. The anterior tentorial arms



**FIG. VIII.**

Fig. VIII. Plecoptera: Family Nemouridae. Species collected from Hogsback, Alice, C.P. Diagram of head of adult, mouthparts removed, ventro-caudal aspect. (To avoid confusion, the glabrous condition of the headcapsule has not been represented).

may or may not become expanded at their roots. In the South African species of the Nemouridae family, studied by the writer, each anterior tentorial arm forms a stout platform, encircling and attached to the meso-lateral margin of each antennal ridge. The anterior tentorial arms converge and narrow slightly before uniting in the body of the tentorium. In the *Acroneuria* sp. examined the form of the tentorium diverges considerably from that of the above named species, and also from the more primitive species studied by Hoke (1923) and Walker (1933). Hoke has shown, however, that such divergences are only specialisations of the generalised types of tentoria occurring in the Plecoptera. In the *Acroneuria* sp. studied, the anterior tentorial arms are very long and narrow and coalesce in the broad posteriorly placed transverse body of the tentorium. This type of tentorium is frequently encountered in the larval forms.

The dorsal arms of the tentorium in the Plecoptera are developed as outgrowths of the body of the tentorium, or they are developed in common with the distal ends of the invaginated anterior tentorial arms, from which they are produced as secondary outgrowths. In some genera, these arms diverge from the anterior tentorial arms very near to the junction of the latter with the body of the tentorium (Fig. VIII, da.) while in others the dorsal arms are far removed from the body of the tentorium, e.g. *Acroneuria* sp. The dorsal arms are either attached to the head-capsule laterad of each lateral ocellus, or they may be attached to the head-capsule on the antennal ridge. "In the Plecoptera, it appears to be merely a chitinized tendon, the peripheral end of which is less chitinized than the base, and is only loosely attached to the skull. Here the point of attachment is on the front some distance from the antennal sclerite, beneath a spot in the cuticle which is marked by numerous polygonal areas. This spot is very distinct and bears some resemblance to an ocellus" . . . . Comstock and Kochi (1902). The polygonal areas described above have since been termed tentorial maculae by Snodgrass (1935) and are not invagination pits. Comstock and Kochi (1902) were uncertain as to whether or not the dorsal arms in the Plecoptera were homologous with the apodeme-like dorsal arms of other insects. The homology has since been accepted by most entomologists.

Wu (1923) erroneously describes the dorsal arms as invaginated from the front, at the frontal sutures. The dorsal arms are not invaginated. They may arise as outgrowths from the sides of the body of the tentorium between the anterior and posterior arms of the tentorium, e.g. Gryllidae, or the dorsal arms may arise in common with the anterior tentorial arms, and then, as secondary outgrowths of the latter, they may diverge and become attached to the roof of the head-capsule.

The imperforate body of the tentorium in the Plecoptera, varies considerably in shape (Fig. VIII, bt.). The anterior margin may be curved, straight or indented or produced to form an oesotendon. The posterior tentorial arms arise as apodemes from the posterior tentorial pits, these prominent pits occurring in the extremities of the post-occipital suture (Fig. VIII, pta., ptp.). The posterior tentorial arms are often as great in length as the anterior tentorial arms, and they extend into the head-cavity as unfused rod-like invaginations, which converge to meet in the posterior of the body of the tentorium. In the more specialised Plecoptera, the body of the tentorium may be posteriorly rather than medianly placed in the head-capsule, so that the posterior tentorial arms are no longer separate rod-like apodemes, but instead, these arms coalesce with the somewhat short, transverse body of the tentorium which bounds the occipital foramen.

**Conclusions:**

A study of the tentorium in the Odonata and the Plecoptera reveals that these two groups of insects differ widely in the shape and characteristics of the head skeleton.

In the Odonata, the tentorium is pi-shaped in both larva and the adult. This feature distinguishes the Odonata from the orthopteroid insects (Hudson, 1945) and the Dermaptera, Embioptera and Isoptera (Hudson, 1946) previously studied. In the Odonata, the anterior tentorial pits are somewhat laterally placed and lie in the subgenal sutures. This position of the anterior tentorial pits is an important feature, for it denotes a more primitive condition than that found amongst the orthopteroid insects where the anterior tentorial pits occur in the fronto-clypeal suture. In larva and adult, the anterior tentorial arms are well developed, and usually bear tendonous outgrowths on the ventral surface. The dorsal arms are better developed in the adult than in the larva, but they are conspicuous structures in both cases. These arms occur as secondary outgrowths of the anterior tentorial arms and are attached to the head-capsule on the mesal margin of the antennal ridge, or in close proximity to this ridge.

The posterior tentorial arms occurring as apodemes of the posterior tentorial pits, are transverse and soon unite in the broad body of the tentorium. A comparison of the tentorium in both larval and adult Odonata seems to indicate that there is no initial difference between the two, and that the adult tentorium is merely a better-developed and more compact structure than that of the larva. It is tentatively suggested that the circular markings or chitinous projections on the ventral surface of the body of the tentorium of the larva, may later develop into the semi-circular chitinous projections of the body of the tentorium in the adult.

There is little to suggest that the tentorium in the Odonata resembles the X-shaped tentorium of the orthopteroid insects. The tentorium of the Odonata also differs widely from that of the Plecoptera, though the tentorium of the more generalised Plecoptera may be favourably compared with that of the orthopteroid insects. In all but the highly specialised Plecoptera, the X-shaped tentorium occurs. As in the orthopteroid insects, the anterior tentorial pits in the Plecoptera lie near the extremities of the epicranial arms and in the lateral limits of the fronto-clypeal suture, when this suture is present.

The anterior tentorial arms are well developed, and the posterior tentorial arms occurring as rod-like invaginations of the posterior tentorial pits, project into the head cavity, where they converge to meet in the body of the tentorium. The dorsal arms occur as outgrowths of the lateral margins of the body of the tentorium and they are attached to the head-capsule on or near the antennal ridge or between the antennal ridge and the lateral ocellus. In the more

generalised Plecoptera studied by Hoke (1923) the tentorium bears some resemblance to that of the Embioptera. The anterior tentorial arms in the latter, have their roots in the fronto-clypeal suture, and from their expanded bases the anterior arms converge to unite in the body of the tentorium. In the Embioptera the body of the tentorium is rectangular and the dorsal arms arise as marginal outgrowths of the body of the tentorium. They are dorsally attached to the head-capsule on the anterior aspect of the antennal ridge. The arcuate posterior tentorial arms of the Embioptera are very similar to the posterior tentorial arms of the generalised Plecoptera. Thus certain similarity may be found in a comparison of the tentorium in the Plecoptera and Embioptera, but there is nothing to suggest a close similarity between the Plecoptera and the Odonata.

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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 plate, 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.

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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% KOH, 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:—

*Austrocænis capensis* Brnd., family: Leptophlebiidæ (larva), *Atalophlebia* sp., *Eatonica schoutedeni* (Navas), *Batis harrisoni* Brnd., *Adenophlebia auriculata* Eaton, *Acentrella natalensis* Crass, *Afronurus harrisoni* Brnd., *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), *Ellasoncuria trimeniana* MacLach. (Congo), *Epcorus assimilis* Eaton (Belgium), *Oligoneuriella rhenna* Imh. (Belgium), *Torleya Belgica* Lest. (Belgium).

#### Larva.

The larval stage of the Ephemeroptera is accomplished in a variety of aquatic 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 *Austrocænis capensis* Brnd.

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 *Batis harrisoni* Burd., *Afronurus harrisoni* Burd., *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 sécrétée vers l'extérieur (1) par l'épithélium de la peau des Pterygotes. Il ne faudrait cependant pas croire qu'aucune introflexion cuticulaire ne s'associe chez les Lépismes aux endosternites. A un niveau correspondant à certaines au moins de leur attaches, on observe effectivement, en la chitine extérieure, une fossette qui n'est jamais très forte, mais qui, pour deux attaches homologues, peut se présenter comme plus importante en un segment que dans l'autre. A supposer qu'une de ces fossettes, 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'ordre de succession des strates histologiques en serait bouleversé ni la position relative des muscles sensiblement modifiée. Il était donc légitime 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 moi-même 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

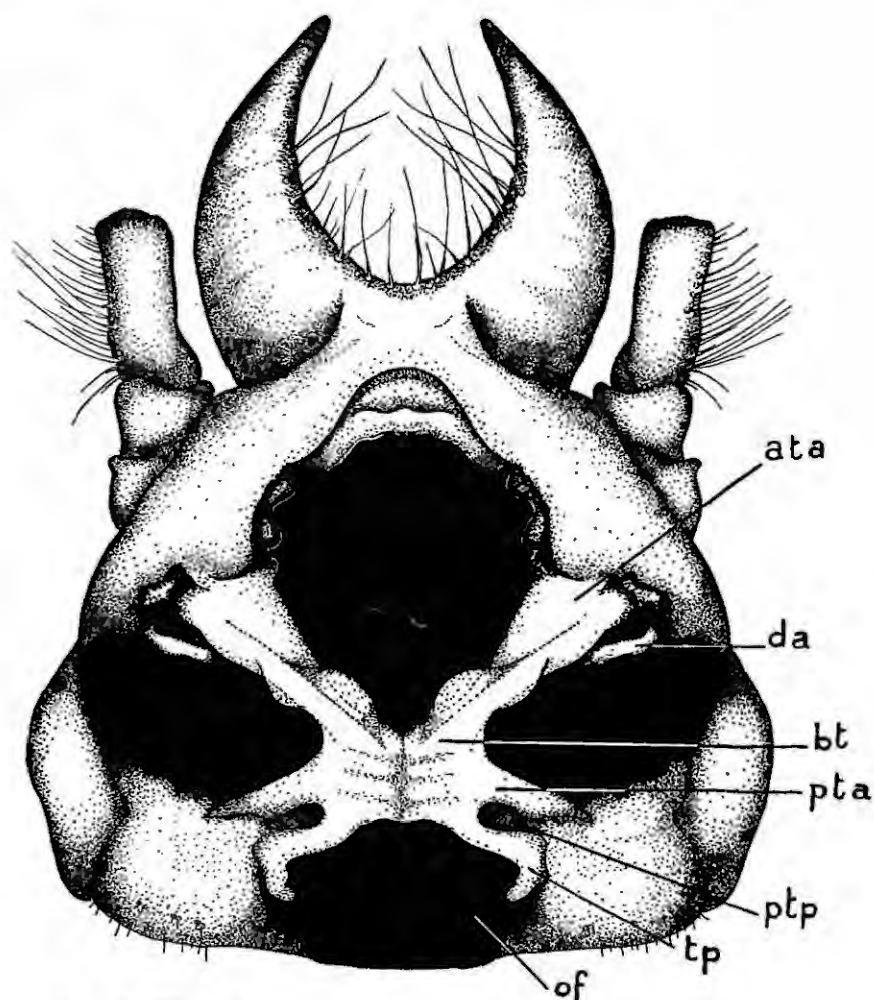
plate-like structure. The posterior tentorial arms are less well developed than the anterior tentorial arms and very much shorter. They arise as invaginations of the posterior tentorial pits, the latter occurring as deep depressions in the extremities of the post-occipital suture. The posterior tentorial 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.

Ephemeropteran larvæ of fossorial habit are exemplified by *Eatonica schoutedeni* (Navas), *Polymitarcys savigni* (Pict) and *Ephemerella* 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 tendinous 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.**

2mm.

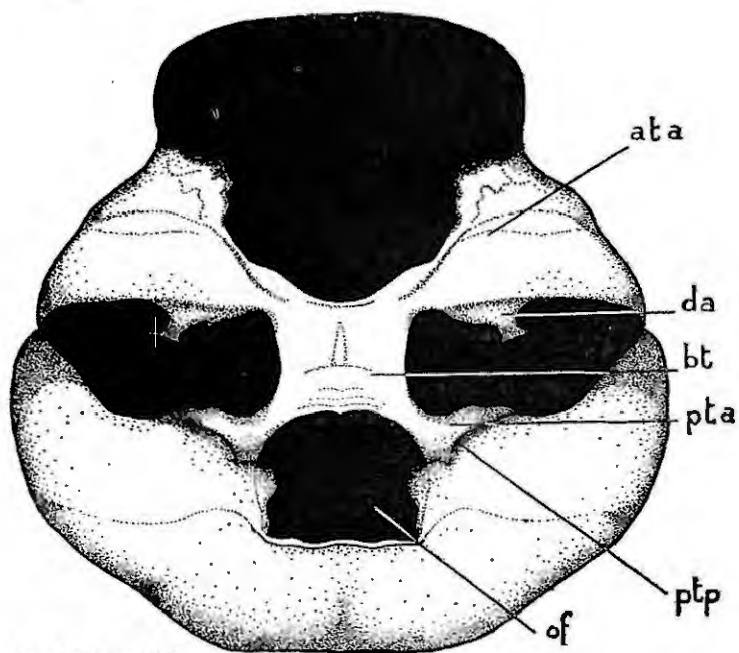
Fig. I. — Ephemeroptera. *Eatonica schoutedeni* (Navas).  
Larva. Postero-ventral aspect.

**ABBREVIATIONS USED IN FIGURES.**

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

In comparing the larval tentorium of *Polymitaecys savigni* (Pict) with that of *Eatonica schoutedeni* (Navas), a general similarity between the two may be discerned. However, in the tentorium of *Polymitaecys 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 *Afromurus harrisoni* Bnrd., *Adenophlebia auriculata* Eaton, *Acentrella natalensis* Crass, *Tricorythus discolor* (Burm.), *Torleya Belgica* L., *Coloburiscus humeralis* Eaton, and *Batis harrisoni* Bnrd., have been studied. The larvæ in all cases inhabit swift-flowing waters.

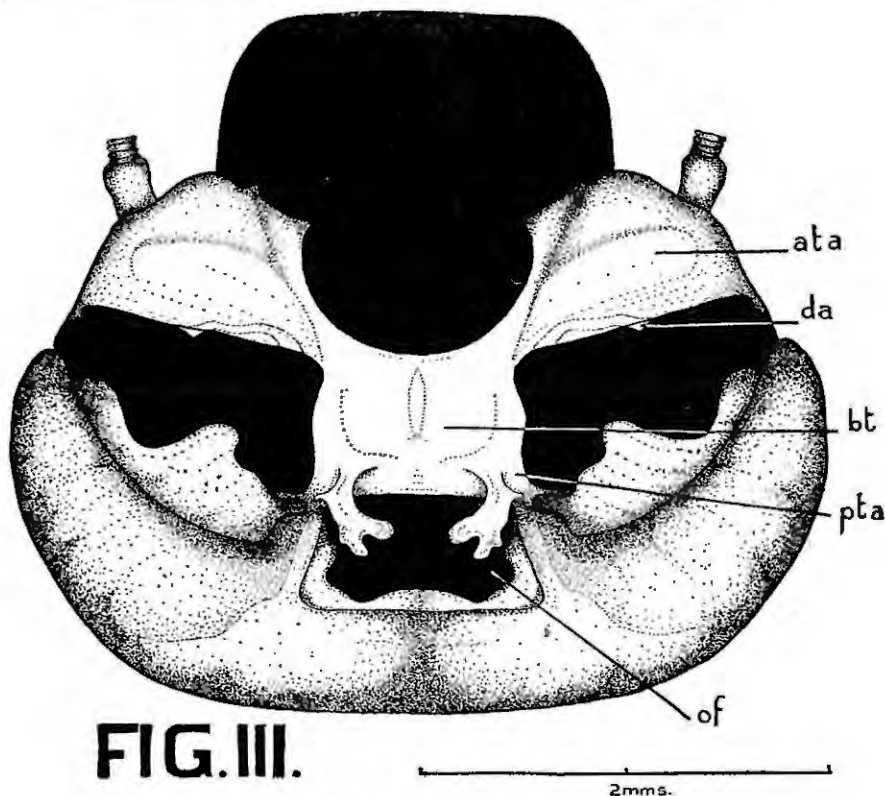


**FIG. II.**

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

In *Afromurus 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 tendinous 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 *Afromurus harrisoni* Burd., 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 *Afromurus harrisoni* Burd.



**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 *Afromurus harrisoni* Burd., 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.

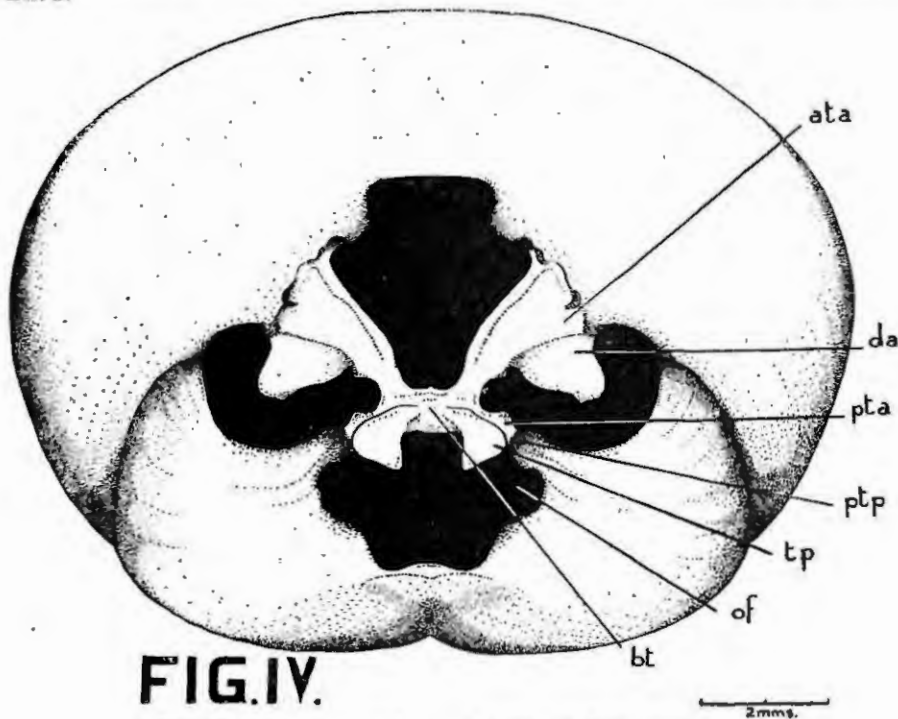


FIG. IV.  
Fig. IV.—Ephemeroptera. *Afronurus harrisoni* Bnrd.  
Larva. Postero-ventral aspect.

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 *Batis harrisoni* Brnd., 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 *Batis harrisoni* Brnd., 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 ephemeropteran 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 aquatic 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 (Fig. 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

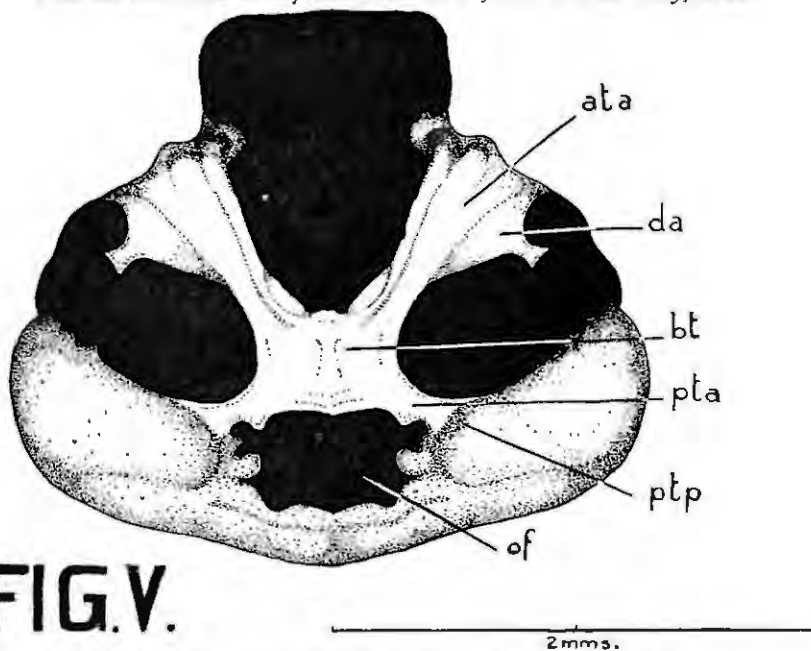


Fig. V. — Ephemeroptera. *Aprionyx tricuspidatus* Crass.  
Larva. Postero-ventral aspect.

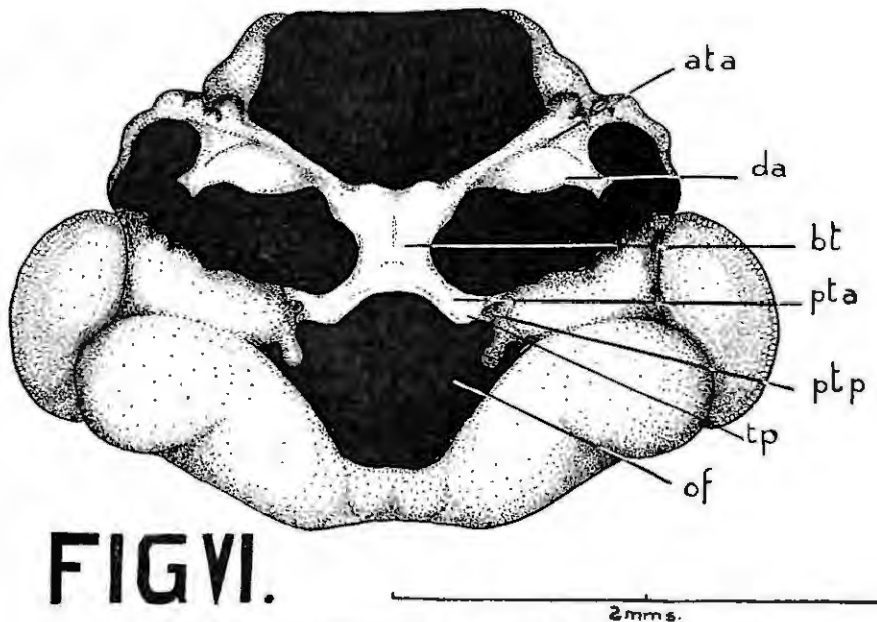


Fig. VI. — Ephemeroptera. *Potamanthus luteus* L.  
Larva. Postero-ventral aspect.

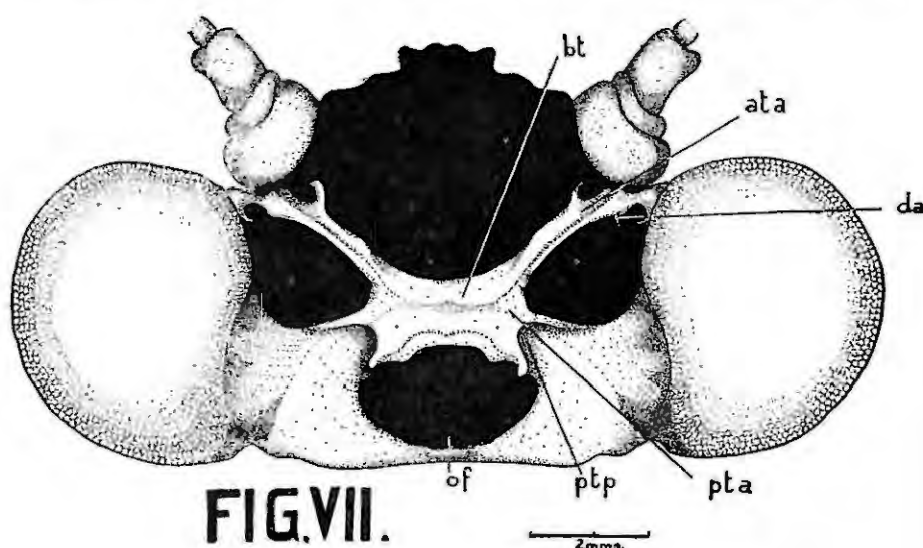
frontal area of the head-capsule may be triangular or rounded, and the large dorso-laterally placed compound eyes often occupy the greater part of the head-capsule, especially in the male Ephemeroptera. Three ocelli usually occur in the interocular region. The short antennæ are subulicorn, with two basal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

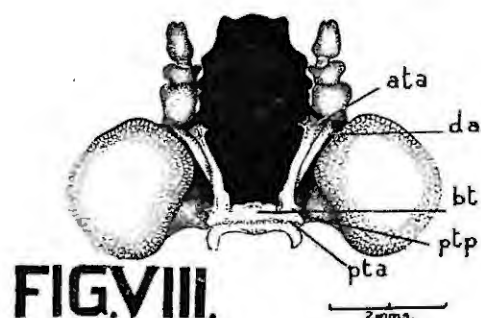
The tentorium in the Ephemeropteran adult *Eatonia schoutedeni* (Navas) whose larva is of fossorial habit, is fairly well developed (Fig. VII). The anterior tentorial arms arise as apodemes of the groove-like anterior tentorial pits, located above and outside of the clypeus (Fig. VII, ata.). The anterior 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 *Polymitaercys savignii* (Pict.). The anterior tentorial arms are fairly long, but narrower than in *Polymitaercys savignii* (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* Brnd., 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 *Accontrella 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 *Batis harrisoni* Brnd., 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.).

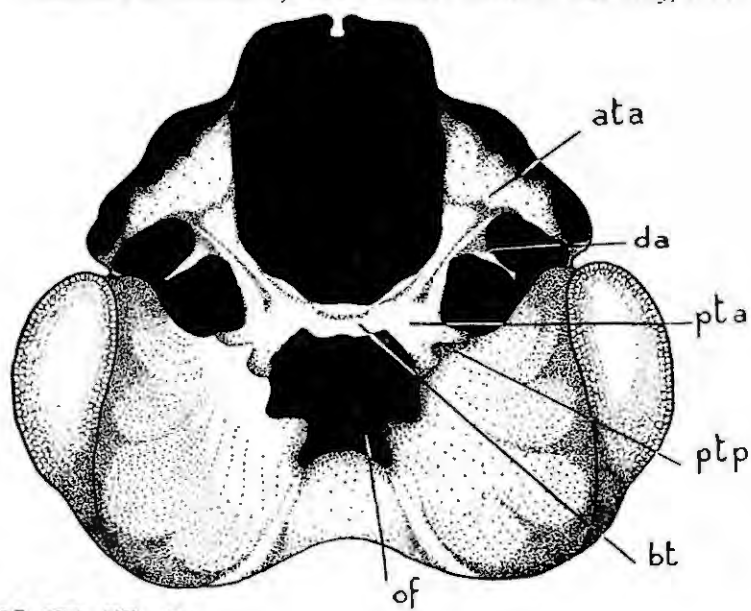
**FIG. IX.**

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

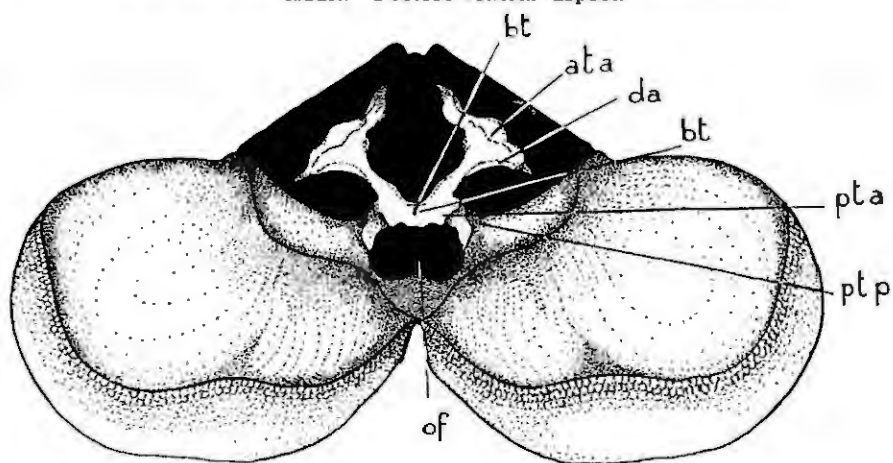
**FIG. X.**

Fig. X. — Ephemeroptera. *Afromurus 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 aquatic 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 savignyi* (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 ephemeropteran larvæ inhabiting swift-flowing waters may possess tentoria which resemble those of fossorial types; e.g. the tentorium of *Afromurus 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 aquatic 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

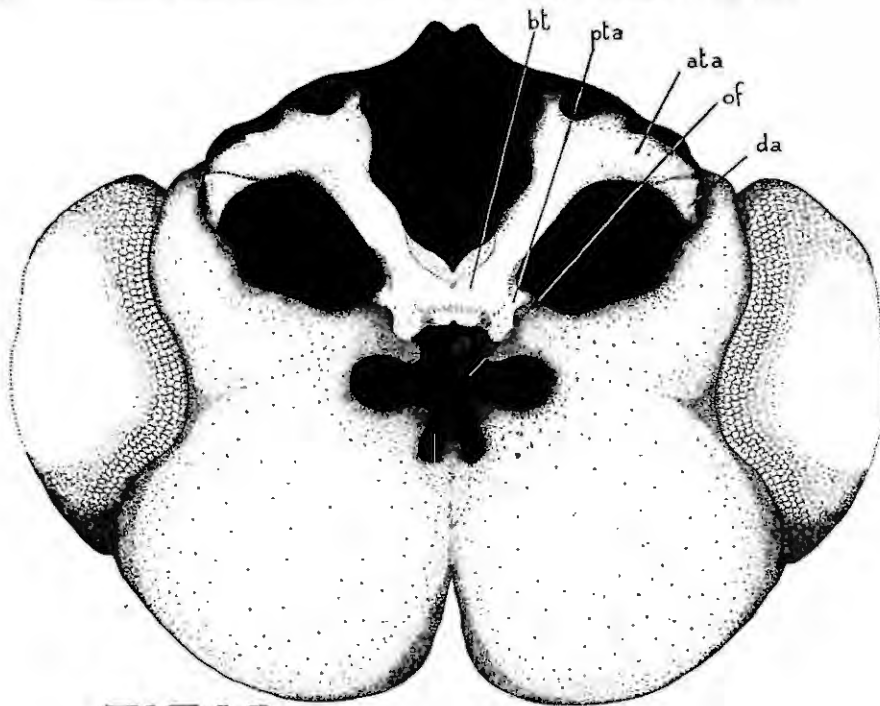
**FIG. XI.**

Fig. XI.—Ephemeroptera. *Baetis harrisoni* Brnd.  
Adult. Postero-ventral aspect.

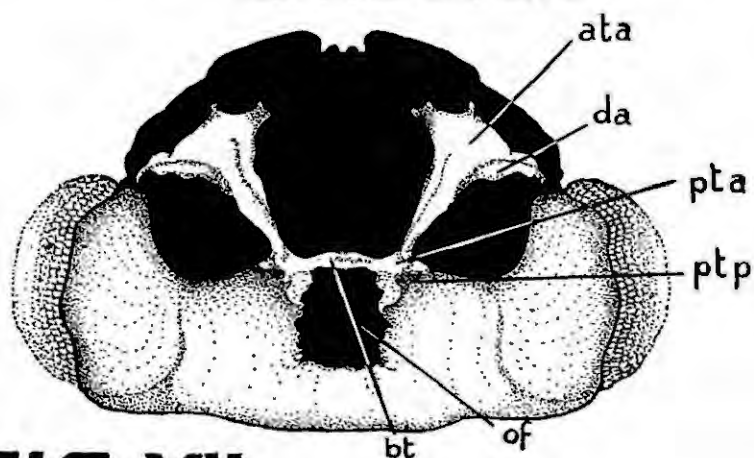
**FIG. XII.**

Fig. XII.—Ephemeroptera. *Aprionyx tricuspatus* 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* Brnd., *Adenophlebia ariculata* Eaton, and *Batis harrisoni* Brnd. 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 *Acetrella 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 *Batis harrisoni* Brnd., 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 *Batis harrisoni* Brnd., 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 musculature 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.

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STUDIES IN THE COMPARATIVE ANATOMY AND  
SYSTEMATIC IMPORTANCE OF THE  
HEXAPOD TENTORIUM.

V. ZORAPTERA, PSOCOPTERA, MALLOPHAGA AND ANOPLURA.

GERDA BLAND HUDSON, M.Sc., F.R.E.S.

INTRODUCTION.

A study of the tentorium of the Zoraptera, Psocoptera, Mallophaga and Anoplura was in progress, when Symons (1952) published a paper which dealt extensively with the head-capsule and tentorium in the three last named groups, Symons being apparently unaware of the writer's earlier publications on the Hexapod tentorium. In order, therefore, to avoid duplication of work, but for comparative purposes, only descriptions of the tentoria of species not previously investigated by Symons, have been given and figured in this paper, and Symons's work has received careful consideration throughout these researches.

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

## 2.

Grateful acknowledgment is tendered herewith to Dr. Kimmins, of the British Museum, for the identification of material, to the Director and Staff of Veterinary Services, Onderstepoort, for the presentation and identification of material, and to Professor Carpentier, Miss B. Bradford and Mr. R. Rand for the gift of material.

Appreciation is again extended to the Council for Scientific and Industrial Research and Dr. van der Walt, of the National Chemical Research Laboratory, for the loan of a Watson microscope, and to Professor J. Omer-Cooper for the loan of a camera-lucida.

The writer further wishes to express sincere thanks to Professor J. Omer-Cooper for his kind interest and assistance in this work.

### TECHNIQUE.

Several methods of clearing specimens were employed.

- (1) Specimens were placed in a cold 10 per cent potassium hydroxide solution for a period of two or three days, after which they were rinsed and preserved in 70 per cent alcohol. In order

3.

to accelerate the process of clearing the soft internal tissues, in some instances the specimens were placed in the potassium hydroxide solution and heated on a slow oven.

- (2) The second well known technique necessitated the specimens being placed in lactic acid and heated on an oven overnight. When clear specimens were transferred to liquid phenol for half an hour and then examined.
- (3) A combination of these two techniques yielded surprisingly satisfactory results. Specimens were transferred from the caustic potash solution, after slight draining, into liquid phenol and left for at least an hour.

Symons (1952) found that the second technique described here often showed up the tentorium better than the first technique. However, in specimens where the tentorium was only observed with great difficulty the writer found that the third method was employed with success.

In previous studies of the tentorium the head of each

specimen was usually dissected off the body and the mouthparts removed, but in this study whole mounts of specimens were made.

#### MATERIAL.

The following species were selected and examined :-

#### ZORAPTERA.

Zorotypus Hubbardi Caud.

#### PSOCOPTERA.

Liposcelis sp.

#### MALLOPHAGA.

Eumenacanthus Stramineus Nitzsch.

Heterodexius longitarsus (Piaget).

Austrorhynchus sp.

Eidmanniella pellucida Rudow.

Saunderssonia gonothorax Giebel.

Pectinopygus acutifrons (Rudow).

Pectinopygus afer (Kellogg).

Bovicola ovis (Schrank).

Bovicola Equi (Linn.).

Pediculus humanus L

Haematopinus euryesternus Nitzsch.

Linognathus setosus Olfers.

#### ZORAPTERA.

The head-capsule in the Zoraptera is prognathous, and the biting mouthparts anteriorly directed. The tentorium in the apterous form, Zorotypus Hubbardi Caud., (Figure 1.) is readily seen in cleared whole mounts and is sclerotised and well-developed. The anterior tentorial pits occur in the subgenal suture and arising as invaginations from them are the anterior tentorial arms. The latter proceed caudomesadly in the head-capsule to coalesce in the strong rectangular structure which forms the body of the tentorium. The dorsal arms are outgrowths of the anterior tentorial arms and occupy a slightly antero-dorsal position on the antennal ridge. The posterior tentorial pits are large and obvious. They occur in the post-occipital suture and give rise to the broad, stout posterior tentorial arms which curve somewhat before meeting in the well developed body of the tentorium.

#### PSOCOPTERA.

The head in the book lice and their allies (Psocida) is

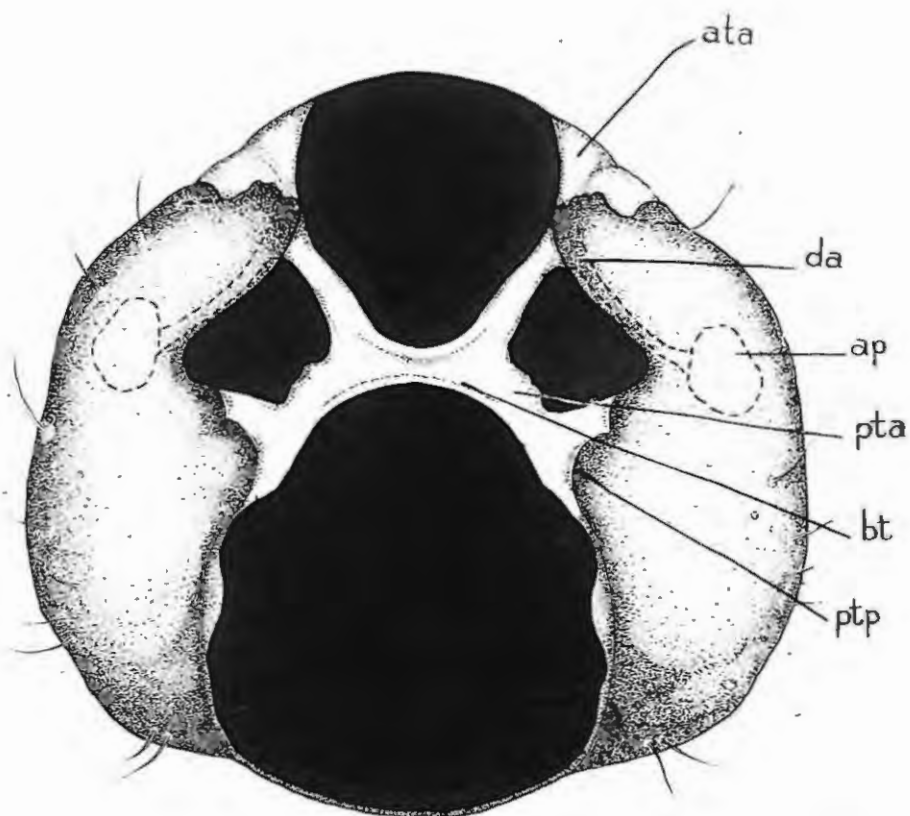


Fig.1.

FIGURE I. Zorotypus hubbardi Caud.

Ventral view of head with mouthparts removed.

- 
- ap - position of antennal sclerite.
  - ata - anterior tentorial arm.
  - bt - body of tentorium.
  - da - dorsal arm.
  - pta - posterior tentorial arm.
  - ptp - posterior tentorial pit.

usually large, mobile and prognathous although hypognathous forms are known to occur. In the Liposcelis sp. studied (Figure II.) the head is prognathous with the mouthparts forwardly directed, and the long filiform antennae antero-laterally placed.

The V-shaped tentorium in the Liposcelis sp. is robust and well sclerotised and obvious in cleared whole mounts. The anterior tentorial pits occur on either side of the margin of the head in the sub-genal suture. Badonnel (1934) studying the hypognathous species Stenopsocus stigmaticus Imhoff and Labrum, finds the anterior tentorial pits occurring in the clypeo-frontal suture. Symmons (1952) detects the anterior tentorial pits of Lepinotus in the subgenal, referred to as the "tentorial suture" by Ferris (1934) and termed the "pleurostomal suture" by Snodgrass (1935). Symmons draws attention to the fact that the sub-genal and clypeo-frontal sutures are partially fused under the sub-genal area which may account for these differences of opinion.

The dorsal arms occur as outgrowths of the anterior tentorial arms, a short distance from their proximal end, and are attached to the head-capsule somewhat laterad of the antennae. The anterior tentorial arms are well developed and proceed in a caudo-mesal direction to meet in the body of the tentorium.

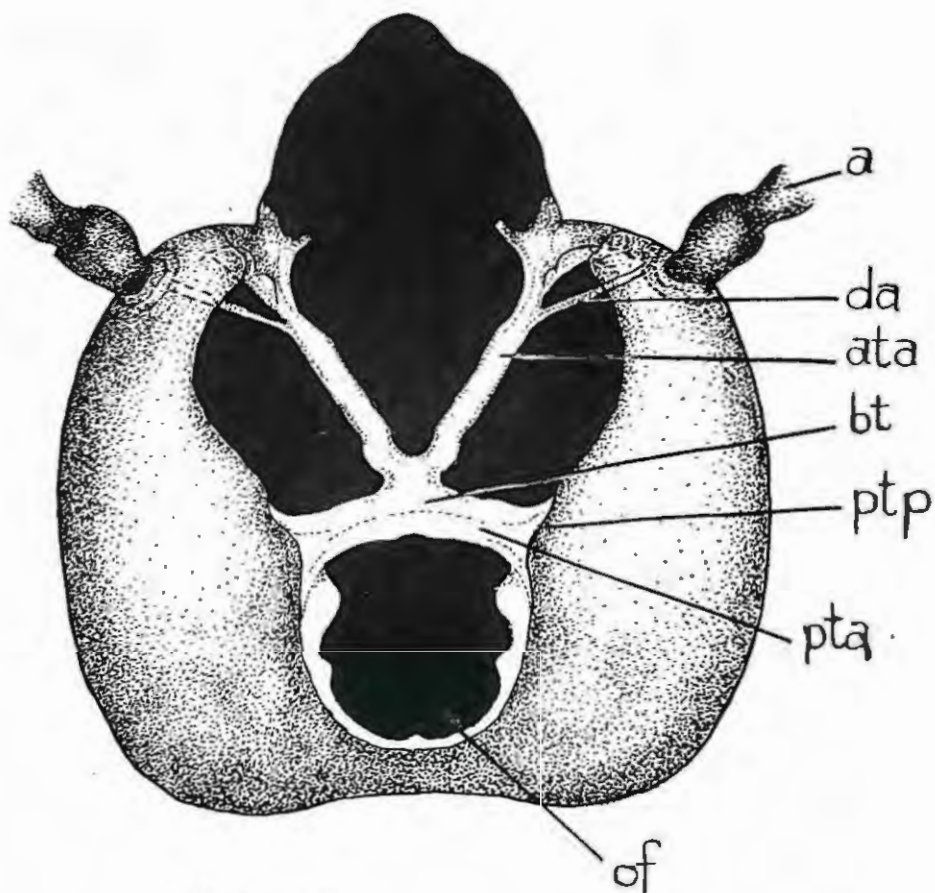


FIG. II.

FIGURE II. Liposcelis sp.

Ventral view of head with mouthparts removed.

- 
- a - part of antenna.
  - ata - anterior tentorial arm.
  - bt - body of the tentorium.
  - da - dorsal arm.
  - of - occipital foramen.
  - pta - posterior tentorial arm.
  - ptp - posterior tentorial pit.

The latter is posteriorly placed in the head-capsule and is a strong slightly curvate structure. Laterally the short, broad posterior tentorial arms fuse in the body of the tentorium. They arise from the well-formed posterior tentorial pits located in the post-occipital suture. The general structure of the tentorium of the Pscoptera is, therefore, comparatively simple to observe and to interpret.

#### MALLOPHAGA.

In biting lice and bird lice the head is large, free, dorso-ventrally flattened, somewhat triangular in shape, and often strongly chitinated. The mouthparts are modified for biting and are anteriorly directed, so that the head is usually prognathous. The prognathous condition in the Mallophaga and Anoplura is secondary, and may be achieved in two ways. The neck membrane may become elongated to form an area known as the gula, which may or may not be chitinated to form a plate, or the prognathous condition of the head-capsule may be brought about by the elongation of the ventral surface of the head. According to Symmons (1952) increase in the size of the gular region carries the posterior tentorial pits forward on the head and away from the

occipital foramen, but they remain close to the posterior articulations of the mandibles. Lengthening of the post-genal area, on the other hand, moves these pits back nearer to the foramen so that the distance from the posterior jaw articulations to the posterior pits and base of the sub - or post-mentum is increased.

In studying the tentorium of the Mallophaga and Anoplura it is essential that the anterior tentorial pits and the posterior tentorial pits are first located. This point is also stressed by Symmons (1952) who refers to the pits as "landmarks" on the Mallophagan head. The anterior tentorial pits occur on the ventral surface of the head in the subgenal suture (= tentorial suture = pleurostomal suture). According to Snodgrass (1935) this position of the anterior tentorial pits is more primitive than that in which the anterior tentorial pits develop in the epistomal suture, for the former mode of origin is encountered in the Chilopoda and the Diplopoda. The posterior tentorial pits arise approximately half way along thickly chitinised internal ridges which run on the ventral surface of the head-capsule from the lateral margins of the occipital foramen to the posterior jaw articulations. According to Symmons (1952) the portions of the ridges posterior to the pits must be in part, the post-occipital

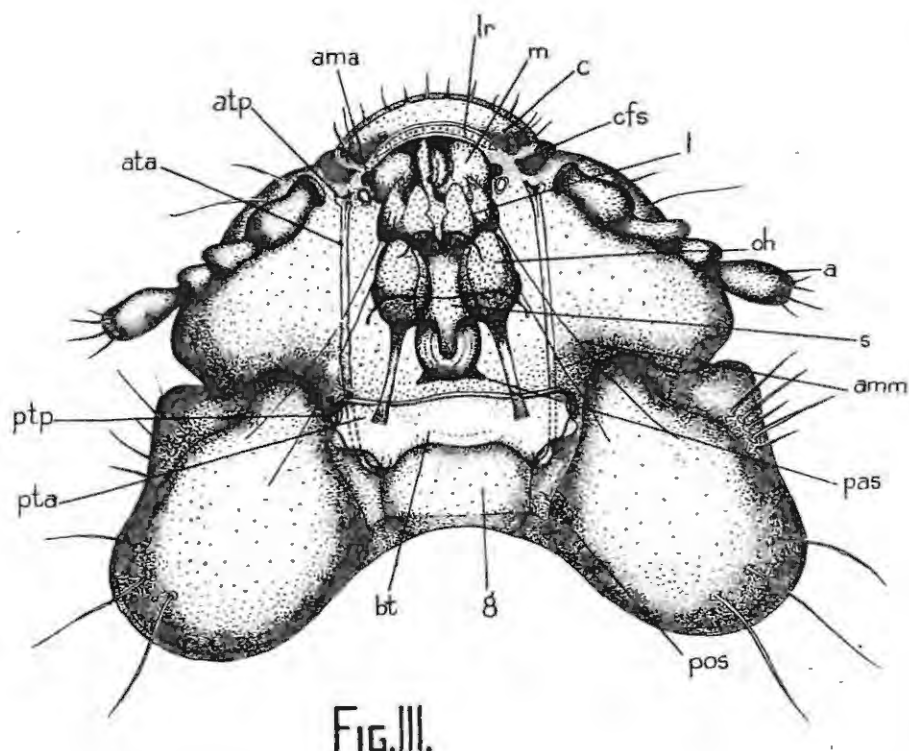


FIG. III.

FIGURE III. Eomenacanthus Stramineus Nitzsch.

Ventral view of head as seen in cleared whole mount.

- |  |                                    |
|--|------------------------------------|
| a - antenna.                                 | g - gula.                          |
| ama - anterior mandibular articulation.      | l - labium.                        |
| amm - apodeme of mandibular adductor muscle. | lr - labrum.                       |
| ata - anterior tentorial arm.                | m - mandible.                      |
| atp - anterior tentorial pit.                | oh - oval sclerite of hypopharynx. |
| bt - body of tentorium.                      | pas - posterior arm of sitophore.  |
| c - clypeus.                                 | pos - post-occipital suture.       |
| cfs - clypeo-frontal suture.                 | pta - posterior tentorial arm.     |
|  | ptp - posterior tentorial pit.     |
|  | s - sitophore.                     |

Maxillary palps and lacinia not figured.

sutures since the posterior tentorial pits usually occur in these particular sutures.

The tentorium of the Amblyceran species Eomenacanthus stramineus Nitzsch conforms to the general pattern described by Symons (1952) for the tentorium of Colpocephalum subaequale Burmeister. In Eomenacanthus stramineus Nitzsch (Figure III.) the tentorium is well developed. The anterior tentorial pits occur, on either side, in the subgenal suture on the ventral surface of the head and arising from these anterior tentorial pits are the two anterior tentorial arms. In Eomenacanthus stramineus Nitzsch, these are slender, tubular apodemes which proceed inwardly at a slight angle to the median, and meet in the broad rectangular body of the tentorium. As all the antennal muscles originate on the anterior tentorial arms, the presence of dorsal arms is superfluous, and they are therefore absent as outgrowths from the anterior tentorial arms. The posterior tentorial pits are large and readily discernable on the ventral surface of the head where they occur on heavily chitinised internal ridges and give rise to the posterior tentorial arms. the latter are short and broad and meet horizontally in the body of the tentorium.

The tentorium of the louse Heterodoxus spiniger (Enderlein)

studied by Symmons (1952) shows interesting features with the general form approaching more closely to the conditions found in the Ischnocera, than any other Amblyceran. Symmons (1952) describes a small laterally flattened and sclerotised enlargement arising from the anterior tentorial arm of this louse, which she interprets as the sclerotised base of the clypeal ligament in conjunction with a projection of the anterior arm, whereupon are found the origins of the antennal muscles. In the species Heterodoxus longitarus (Piaget) the rod-like anterior tentorial arms proceed from the anterior tentorial pits, the latter located on either side in the subgenal suture in close proximity to the point of fusion of this suture with the clypeo-frontal suture. The anterior tentorial arms are very difficult to detect in cleared mounts owing to their partial lack of sclerotisation. The flattened enlargement from each anterior tentorial arm as observed by Symmons (1952) in Heterodoxus spiniger (Enderlein) was seen in Heterodoxus longitarus (Piaget) as a slight out-growth on the median side of the anterior tentorial arm. The posterior tentorial pits are situated in a somewhat advanced position on the head, and give rise to the well developed posterior tentorial arms which broaden to meet in the body of the tentorium, the latter narrowing medianly to become thin and

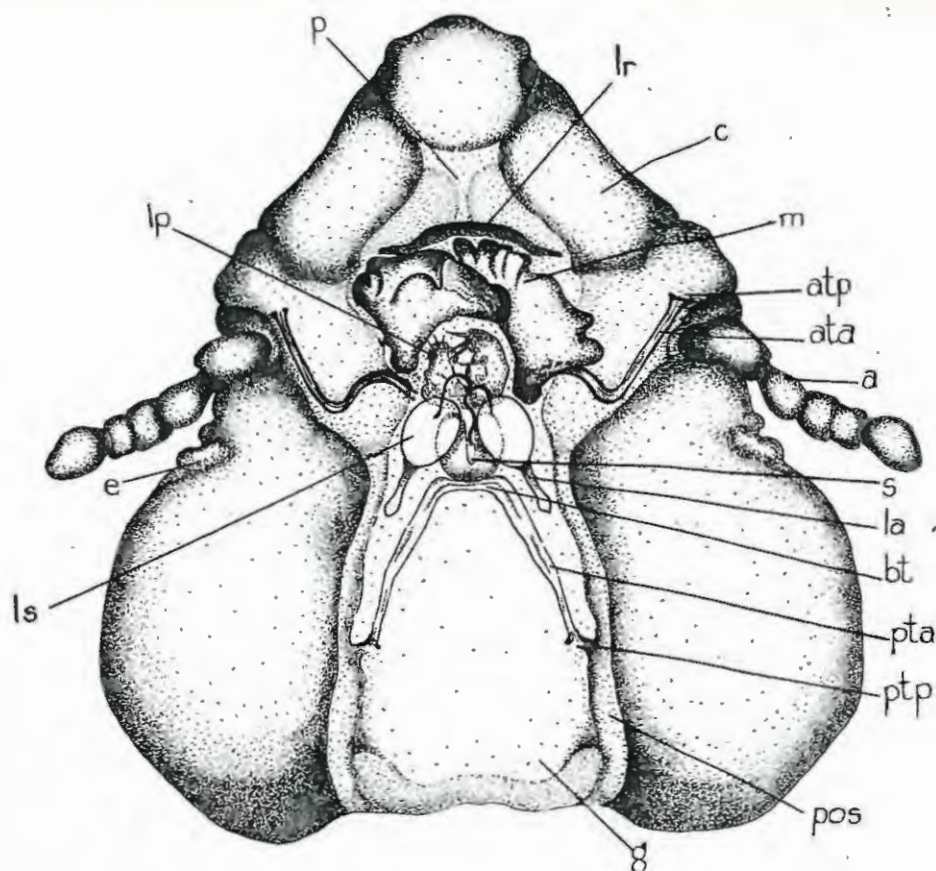


FIG. IV.

FIGURE IV. *Pectinopygus afer* (Kellogg).

Ventral view of head as seen in cleared whole mount.

a	- antenna.	lr	- labrum.
ata	- anterior tentorial arm.	ls	- lingual sclerite.
atp	- anterior tentorial pit.	m	- mandible.
bt	- body of the tentorium.	p	- pulvinus (clypeo-labral suture).
c	- clypeus.	pos	- post-occipital suture.
e	- eye.	pta	- posterior tentorial arm.
g	- gula.	ptp	- posterior tentorial pit.
la	- lingual apodeme.	s	- sitophore.
lp	- labial palp.		

Lacinia not figured.

somewhat filamentous.

The tentorium in Pectinopygus afer (Kellogg) (Figure IV.) is difficult to observe in cleared whole mounts, and specimens cleared by means of the potassium hydroxide technique proved more suitable for study than those subjected to the lactic-acid and liquid phenol method.

In Pectinopygus afer (Kellogg) the anterior tentorial pits are minute, occurring in the subgenal suture some distance from the margin of the head. According to Symmons (1952) the anterior tentorial pits of Phlopterus atratus Nitzsch could only be distinctly identified in sections of the head-capsule, but in the Phlopterid species described here, viz. Pectinopygus afer (Kellogg) the anterior tentorial pits could be located in well cleared mounts under high magnification. From the anterior tentorial pits the very delicate anterior tentorial arms proceed. Proximally they are slightly sclerotised and Symmons (1952) states that in Phlopterus atratus Nitzsch, the anterior tentorial arms are linked by a ligament innervated by the clypeal nerve to the dorsum of the head. Symmons (1952) interprets the anterior tentorial arm in Phlopterus atratus Nitzsch as equivalent to the comparatively small projection from the anterior tentorial arm of Heterodoxus spiniger (Enderlein). Symmons (1952)

describes the anterior tentorial arm of Philoferus stratus

Nitzsch as

"a small chitinous rod, only heavily sclerotised in its proximal part. Distally, this rod changes its nature by reduction in degree of sclerotization ----- and passes up towards the dorsum of the head to which it is linked by a ligament innervated by the clypeal nerve; this ligament is therefore the clypeal ligament often chitinised in Ischnocera, and the anterior arm equivalent to the comparatively small projection from the arm of Heterodoxus -----"

The writer tends to agree with this interpretation by Symmons.

Kéler (1938) in describing the tentorium of Trichedectes melis

Fabricius states that the anterior arms of the tentorium observed were rudimentary dorsal arms with the anterior arms fused to the head-capsule, but Kéler makes no mention of attachment of these so-called dorsal arms to the dorsal surface of the head. However, dorsal arms when present are always outgrowths of the anterior tentorial arms and it seems unlikely that dorsal arms such as described by Kéler would occur in the apparent absence or complete fusion of the anterior arms to the head-capsule. As anterior tentorial arms are invaginations of the head-capsule the presence of the anterior tentorial pits indicates that anterior tentorial arms exist and have not merged into the head-capsule. The

posterior tentorial pits in Pectinopygus afer Nitzsch are present in the post-occipital suture. As noted by Symmons (1952) they are less clearly defined than in the Amblycera. The posterior tentorial arms originate from the posterior tentorial pits. The former are short, sclerotised and join in the arcuate body of the tentorium. According to Symmons (1952) prior to her study, a tentorial bridge connecting the two posterior arms had not been detected in the Ischnocera. In cleared whole mounts of Pectinopygus afer Nitzsch careful examination definitely revealed the structure of the body of the tentorium, which appears to be very delicate and suggests some attachment to the sitophore. Symmons (1952) refers to the attaching membrane as the tentorio-hypopharyngeal ligament.

In Pectinopygus acutifrons Rudow the tentorium assumes much the same structure as that described for Pectinopygus afer (Kellogg). Again, the anterior tentorial pits are very difficult to locate, and the anterior tentorial arms are not readily traceable. The posterior tentorial pits are large and well developed and in Pectinopygus acutifrons Rudow the posterior tentorial arms and the arcuate body of the tentorium are very clearly visible in cleared whole mounts, so that this portion of the tentorium affords no difficulty in observation or interpretation.

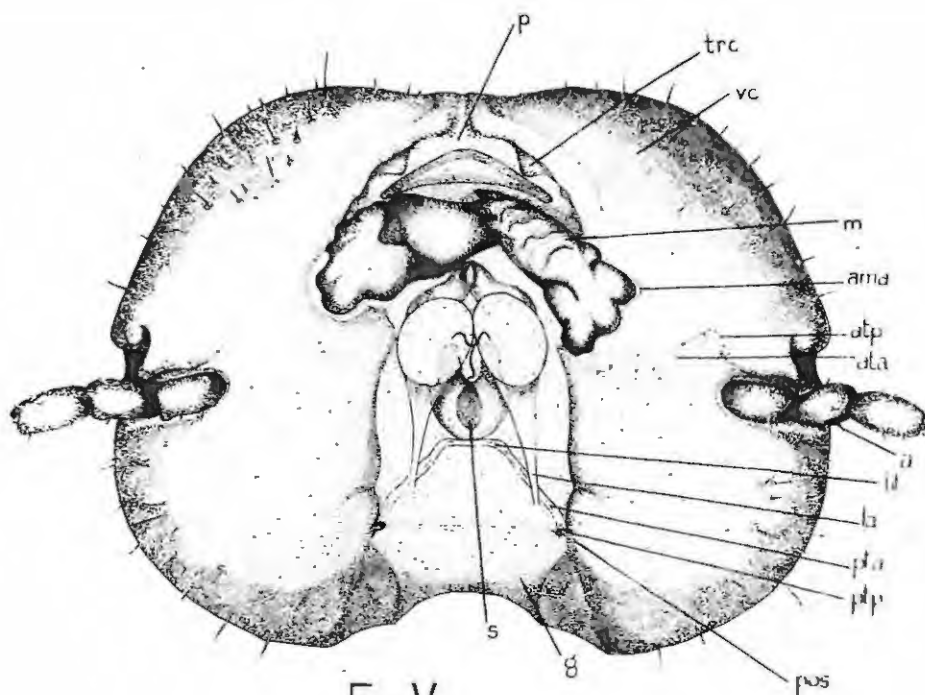


FIG. V.

**FIGURE V. *Bovicola Equi* (Linn.)**

Ventral view of head as seen in cleared whole mount.

a - antenna.	m - mandible.
ama - anterior mandibular articulation.	p - pulvinus (clypeo-labral suture).
ata - anterior tentorial arm.	pos - post-occipital suture.
atp - anterior tentorial pit.	pta - posterior tentorial arm.
bt - body of the tentorium.	ptp - posterior tentorial pit.
g - gula.	s - sitophore.
la - apodeme of lingual sclerite.	trc - thickened rim of the clypeus and pulvinus.
	vc - ventral portion of clypeus.

Lacinia not figured.

The tentorium of Bovicola Equi (Linn.) (Figure V.) and that of Bovicola ovis Schrank are less difficult to determine than are the tentoria of either of the two former species of Ischnocera described. Both anterior and posterior tentorial pits are easily seen in cleared mounts and the anterior and posterior tentorial arms may be observed arising from these pits. The anterior tentorial arms are better developed and more easily seen than those of Pectinopygus afer (Kellogg) or Pectinopygus acutifrons Rudow although similar in origin and general formation. The posterior tentorial arms meet in the curvate body of the tentorium, in much the same manner as observed in the other species of Ischnocera examined.

In the Rhyncophthirina, Symmons (1952) working on Haematomyzus elephantis Piaget, indicates the presence of minute posterior tentorial pits with very short inwardly projecting arms, on each of which a single oesophageal muscle originates, but no other parts of the tentorium were found. Kéler, in a private communication to Symmons in 1950, stated that he found rudiments of posterior tentorial arms in Haematomyzus. Unfortunately despite considerable effort no material of the elephant louse was made available for further investigation by the writer.



ANOPLURA.

Prolonged and careful scrutiny of the head-capsule of three different species of Anoplura, viz. Pediculus humanus L., Haematopinus eurytetrus Nitzsch and Linognathus setosus Olfers revealed complete absence of tentorial pits or tentorial structure. These findings are in agreement with those of other workers who have studied the head-capsule of Anoplura. Florence (1921), Stojanovich (1945), and Symmons (1952).

CONCLUSIONS.

In the classification of the recent hexapod insects, advanced by Omer-Cooper (1939) the Psocoptera and the Zoraptera are placed in separate orders of their own, and both are somewhat removed from the Mallophaga and Anoplura. According to Lums (1934) the Psocoptera is an order of insects which includes both book-lice and their allies, the bark-lice, i.e. Psocida and Zoraptera, the affinities of the Zoraptera being regarded as close to the Psocida in their similarity of structure of wing-venation. This conception of the close relationship of the Psocida and Zoraptera is shared by many workers, and is adopted by Hopkins (1949)

whose classification of Mallophaga and related insects reflects the modern beliefs of their relationships. From a study of the tentorium, however, it would appear to the writer that the Zoraptera show greater affinity to the Embioptera than they do to the true book-lice. A comparison of the tentorium of Zorotypus Hubbardi Caud. with that of Haploembia cespensis Esb. Pet., (Hudson, 1947) readily indicates striking similarity in structure, which is not observed to the same degree in comparing the tentorium of the Zoraptera with the tentorium of the Psocida.

In Zorotypus Hubbardi Caud. the anterior tentorial arms originate from the anterior tentorial pits, the latter occurring in the subgenal suture. The anterior tentorial arms are broad and well developed apically, proceeding caudo-ventrally to meet in the strong body of the tentorium. They are strikingly similar to the anterior tentorial arms of the Embiopteran species, Haploembia cespensis Esb. Pet., as are the dorsal arms which, in both Zoraptera and Embioptera occur as somewhat delicate structures arising as outgrowths of the anterior tentorial arms and becoming attached to the head-capsule on the antennal ridge. It is, however, in the structure and position of the body of the tentorium and the posterior tentorial arms that the similarity

between these two groups of insects is most pronounced. In both the Zoraptera and the Embioptera the well developed broad posterior tentorial arms, arising from the posterior tentorial pits located in the post-occipital suture, proceed in an arcuate manner for a short distance before coalescing in the body of the tentorium, the latter appearing in both cases as a short rectangular imperforate plate.

The tentorium in the Psocoptera, while indicating better development than that encountered in the Mallophaga, shows no such striking similarity in form to the Zoraptera, as is observed between the Zoraptera and the Embioptera. The tentorium in the Psocoptera is "V-shaped", with the narrow anterior tentorial arms meeting in the short posteriorly placed body of the tentorium. The dorsal arms are attached to the head-capsule meso-laterad of the antenna. The posterior tentorial arms are, however, more transverse than arcuate in structure and are shorter than those of the Zoraptera.

Thus from a study of the tentorium, the writer prefers to regard the Psocoptera as an order of insects which includes the book-lice only, devoting a separate order, the Zoraptera to include the bark-lice, this latter order being placed in close proximity to the order Embioptera. Omer-Cooper (1939) states

that the Zoraptera as a group

"is imperfectly known; if it is united with the Psocoptera serious difficulty accrues. The Psocoptera are a compact and easily recognized group with affinities to the Embioptera and, possibly, to the Anoplura. If the Zoraptera are added the group becomes loose and difficult to define; it would then be hard to find valid reason for the exclusion of the Embioptera. From a practical and morphological standpoint such indefinite groups are undesirable. Their only interest is to the phylogenist. To destroy a most satisfactory little Order for the purpose of finding a home for an obscure group of doubtful affinities appears a wanton act ----".

Omer-Cooper (1939) then proceeds to classify the Zoraptera and Psocoptera each in separate orders which are placed near to the orders Plecoptera, Embioptera and Isoptera, and are distantly removed from the orders Mallophaga and Anoplura. The writer, from an examination of the tentorium agrees with Omer-Cooper's classification and separation of the Zoraptera and Psocoptera into individual orders. However, in the complete absence of a tentorium in the Anoplura, the writer cannot countenance the suggestion of possible similarity occurring between the Zoraptera and the Anoplura.

From a detailed study of the Mallophagan head, Symons (1952) came to the conclusion that

"——the fundamental similarities between the heads of all Mallophaga, evident from the fact that a generalised plan could be made, rules out the possibility of external form offering any phylogenetic significance applicable to main groups within the suborder. Variations which occur are of a detailed nature valuable for taxonomic purposes relating to the lower categories. The inadvisability of using modifications of mouth-parts and external cranial structure for phylogenetic studies, because of their adaptability to environment and feeding habits of the lice, has been put forward by Clay (1949a 1949b). However, the possibility that tentorial form in Mallophaga and related insects may have meaning in this connection was suggested by the following observations made during the present study; variations of tentorial form occur which

- ( i ) exhibit progressive reduction of parts and sclerotization from one extreme (complete form) to the other (total absence),
- ( ii ) are separable into distinct types,
- ( iii ) are most different in genera known to be distantly related (i.e. between suborders and superfamilies),
- ( iv ) are most similar in genera known to be closely related,
- ( v ) show no parallel sequence within groups known to be unrelated.

The range of tentorial variation is wide, but series within it are limited to one different type in each of Psocoptera, Ischnocera Rhyncophthirina, and Anoplura, and at least five in Amblycera, and, consequently, cannot be applied to relationships below superfamily rank in Psocoidea, and family rank in Amblycera ———".

Symmons (1952) working independently has, therefore, reached the same conclusions as the writer, (Hudson, 1951) that tentorial form is of phylogenetic significance as applicable to main groups of insects.

In the Mallophaga studied here, the Amblyceran species, Eumenacanthus stramineus Nitzsch and Heterodoxus longitarus (Piaget) are comparable and similar to the Amblyceran species studied by Symmons (1952). The anterior tentorial pits occur in the subgenal suture and rod-like anterior arms of the tentorium proceed inwards to meet in the well developed body of the tentorium. The posterior tentorial pits are readily detected, and from them the short, stout posterior arms originate as invaginations, and coalesce in the body of the tentorium. This general tentorial structure is typical of the Amblycera, and differs distinctly from that encountered in the Ischnocera.

In the Ischnocera investigated in this study, Pectinopygus acutifrons (Rudow), Pectinopygus afer Nitzsch, Bovicola ovis Schrank, and Bovicola Equi (Linn.) the tentorial structure appears to be similar to that of Ischnocera studied by Symmons (1952) and differs considerably from the structure seen in the Amblycera. The anterior tentorial pits are not easy to locate and reduction of the anterior tentorial arms is apparent, so that they also

provide some difficulty in detecting. The body of the tentorium is distinguishable in cleared whole mounts, but prior to Symmons's (1952) paper, the body of the tentorium, connecting the two posterior arms had not been described in the Ischnocera.

The Amblycera and the Ischnocera differ strikingly from the Anoplura, where tentorial pits and tentorial structure are entirely lacking.

In the Rhyncophthirina, Symmons (1952) reports the presence of minute posterior tentorial pits with short inwardly projecting arms, features which she regards as a possible connecting link between the Amblycera and Ischnocera where a tentorium is present and the Anoplura where the tentorium is entirely absent.

From a study of the tentorium it is therefore apparent that the Mallophaga and Anoplura may be divided into four clearly defined groups, viz :-

- (1) Amblycera, where the tentorium shows variation from robust to less well-developed forms.
- (2) Ischnocera, where the anterior tentorial arms are considerably reduced and do not coalesce in the body of the tentorium, the latter being of fragile structure.

- (3) Rhyncophthirina, where only the rudiments of posterior tentorial pits and posterior tentorial arms are reported to exist.
- (4) Anoplura, where tentorial pits and tentorial structure are completely absent.

In the first three instances, some form of tentorial structure is present, whereas in the Anoplura, this is entirely lacking, which would suggest a distinct difference between the Mallophaga and the Anoplura. Omer-Cooper (1939) designates the Anoplura to a separate order of their own as apart from the order which is occupied by the Mallophaga, indicating that in the structure of the mouthparts, the thorax, and the general body form, they are distinct and easily recognised groups. From a study of the tentorium it is observed that tentorial structure occurs in all the Mallophaga but is entirely absent in the Anoplura, thus providing further evidence for the separation of these two groups. Symmons (1952) in suggesting that the Rhyncophthirina and Anoplura share a common origin and that the former is more closely linked to Anoplura than Ischnocera in a position between these groups reservedly indicates that it is assumed the characters taken into account were not developed along independent lines. The writer

believes that common ancestry cannot be offered as proof that the two groups should be classified in one order, and on the evidence of tentorial structure would suggest that the Mallophaga and Anoplura be placed each in a separate order as suggested by Omer-Cooper (1939). This classification is therefore in disagreement with that of Hopkins (1949). In his classification included under the super-order Osecoides, are the two orders Psocoptera and Pthiraptera. Under the latter order, falls the sub-order Mallophaga, which is subdivided into four super-families, the Rhyncophthirina, the Amblycera, the Ischnocera and the Anoplura.

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## GENERAL DISCUSSION.

### 1. NOMENCLATURE.

The endoskeleton of the insect head consists of invaginations of ectodermal origin, which meet and coalesce to form a chitinous internal structure known as the tentorium.

A generalised insect tentorium is composed of :-

#### (a) A pair of anterior tentorial arms.

The anterior tentorial arms are caudadly directed apodemes within the lumen of the head, and originate from hollow anterior invaginations, known as the anterior tentorial pits. In most pterygote insects, the anterior tentorial pits develop in the epistomal suture, which is also known as the clypeo-frontal suture. In the Odonata, Ephemeroptera, Dermaptera, Zoroptera, certain Psocoptera Mallophaga and some Orthoptera, the anterior tentorial pits occur in the anterior region of the sub-genal suture referred to as the "fronto-genal suture", Duporte (1946), and also termed the "pleurostomal suture" by Snodgrass (1935) and the "tentorial suture" by Ferris (1943).

(b) A pair of posterior tentorial arms.

The posterior tentorial arms are invaginations of the posterior tentorial pits. The posterior tentorial arms are forwardly directed apodemes which usually unite with the anterior tentorial arms to form the body of the tentorium. The posterior tentorial pits are located in the lateral extremities of the post-occipital suture.

(c) The body of the tentorium.

The apodemes arising from the anterior tentorial pits and the posterior tentorial pits may coalesce internally at their bases to form a chitinous cross-bar or plate, known as the body of the tentorium. This may contain an aperture (Blattidae, Mantidae, Isoptera) for the passage of circum-oesophageal connectives. Anteriorly the aperture is bounded by the frontal plate or anterior base of the body of the tentorium, formed by the union of the anterior tentorial arms. Posteriorly, the aperture is bounded by the bridge formed by the coalescence of the posterior tentorial arms. The body of the tentorium is the

3.

part to which the name tentorium was originally applied. Comstock and Kochi (1902).

(d) A pair of dorsal arms.

In addition to the anterior tentorial arms and the posterior tentorial arms, a pair of dorsal arms is usually present. The dorsal arms, however, occur as secondary outgrowths of the anterior tentorial arms, and do not originate as invaginations of the cuticular layer. They are attached to the head-capsule in the region of the antennal or ocular ridges, and the depressions or dark spots where the dorsal arms unite with the epicranial wall are termed "tentorial maculae" by Snodgrass (1935).

Tendonous outgrowths may occur on the anterior tentorial arms, or the body of the tentorium (Odonata, Orthoptera, Ephemeroptera). These tendonous outgrowths are formed by the chitinising of tendons connecting muscles to the tentorium.

In the foregoing description of a generalised insect tentorium the writer favours the use of simple nomenclatures. In the

following table, an attempt has been made to clarify the varied and confusing nomenclatures which exist in literature on the endoskeleton of the head.

COMPARISON OF NOMENCLATURES EMPLOYED IN THE  
DESCRIPTION OF THE TENTORIUM OR ENDOSKELETON OF  
THE INSECT HEAD.

(1) <u>ANTERIOR TENTORIAL PITS.</u>	= <u>PRETENTORINA.</u>
Walker (1935)	Yuasa (1920)
Inns (1934)	MacGillivray (1923)
Snodgrass (1935)	Hoke (1924)
Symmons (1952)	Crampton (1928).
	= <u>TENTORIAL INVAGINATIONS.</u>
	Du Porte (1946)
(2) <u>ANTERIOR ARMS OF THE TENTORIUM, OR ANTERIOR TENTORIAL ARMS.</u>	= <u>PRETENTORIA.</u>
Comstock & Kochi (1902)	Yuasa (1920.)
Stielmeier (1923)	MacGillivray (1923)
Wu (1923)	Hoke (1924)
	Crampton (1928)

## (2) Contd.

ANTERIOR ARMS OF THE  
TENTORIUM, OR ANTERIOR  
TENTORIAL ARMS.

Walker (1933)

Inns (1934)

Snodgrass (1935)

Du Porte (1946)

Weber (1949)

Symons (1952)

= ANTERIOR BRANCHES.

Hansen (1930)

= PAIR OF INCROTHS.= TWO RODS.

Tillyard (1917)

= ANTERIOR PAIR OF INVAGINATIONS.= INTERNAL LATERAL BRANCH AND  
INTERNAL BRANCH.

Berlese (1910)

(3) DORSAL ARMS.

Comstock &amp; Kochi (1902)

Wu (1923)

Walker (1933)

Snodgrass (1935)

Weber (1949)

Symons (1952)

= SUPRATENTORIUM.

Ynaga (1920)

MacGillivray (1923)

Hoke (1924)

Crompton (1928)

= SUPERIOR OR TERTIARY BRANCH.

Berlese (1910)

(4) <u>POSTERIOR TENTORIAL PITS</u>	= <u>METATENTORINA.</u>
Walker (1933)	Yuasa (1920)
Imms (1934)	MacGillivray (1923)
Snodgrass (1935)	Hoke (1924)
Symmons (1952)	Crampton (1928)
(5) <u>POSTERIOR ARMS OF THE TENTORIUM OR POSTERIOR TENTORIAL ARMS.</u>	= <u>METATENTORIA.</u>
Comstock & Kochi (1902)	Yuasa (1920)
Wu (1923)	MacGillivray (1923)
Walker (1933)	Hoke (1924)
Imms (1934)	Crampton (1928)
Snodgrass (1935)	= <u>POSTERIOR PAIR OF INVAGINATIONS. FOURTH BRANCH.</u>
Weber (1949)	Berlese (1910)
Symmons (1952)	= <u>PAIR OF RAMI.</u>
	Hansen (1930)

(6) BODY OF THE TENTORIUM.

Comstock &amp; Kochi (1902)

Wu (1923)

Walker (1933)

Innes (1934)

= CORPOTENTORIUM.

Yuasa (1920)

MacGillivray (1923)

Weber (1949)

= TRANSVERSE ROD.

Tillyard (1917)

= BRIDGE OF THE TENTORIUM  
TENTORIAL BRIDGE.

Snodgrass (1935)

Symmons (1952)

= UNPAIRED PLATE.

Hansen (1930)

= TRANSVERSE BAR  
FIFTH BRANCH.

Berlese (1910)

(7) FRONTAL PLATE.

Comstock &amp; Kochi (1902)

= ANTERIOR BRIDGE.

Walker (1933)

Snodgrass (1935)

	<p>= <u>CEPHALIC BRIDGE</u>.</p> <p>Stickney (1923)</p> <p>= <u>LAMINATENTORIUM</u>.</p> <p>Yuasa (1920)</p> <p>MacGillivray (1923)</p> <p>Hoke (1924)</p> <p>Crampton (1928)</p>
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2. A BRIEF REVIEW OF THE STUDY OF THE TENTORIUM IN CERTAIN GROUPS OF PTERYGOTE INSECTS.

(a) A Study of the tentorium in some orthopteroid Hexapoda.

The tentorium in this group of insects is usually X-shaped and of robust construction, consisting of well-developed anterior and posterior tentorial arms, which are united caudo-mesally to form the body of the tentorium. Dorsal arms are present and the anterior and posterior tentorial pits are always distinct.

It has been demonstrated that the head-capsule in the orthopteroid Hexapoda may be primitively prognathous,

as in the Phasmidae, hypognathous, as observed in the Mantidae, Blattidae, most Gryllidae, Tettigonidae, and most Acrididae, or the head-capsule may become secondarily prognathous, as encountered in Gryllotalpa africana Pal., and Oecanthus capensis Saus. By examination of the tentorium in the orthopteroid Hexapoda, it is possible to differentiate between primitive and secondary prognathism. In the Phasmidae, one striking feature of the tentorium is the length attained by the anterior tentorial arms. The posterior tentorial arms are somewhat short and transverse. A second noticeable feature of the tentorium in the Phasmidae is the posterior position of the short body of the tentorium. In contrast to this tentorium of the primitively prognathous Phasmidae, the body of the tentorium in both of the secondarily prognathous species studied, shows marked elongation, whereas there is no suggestion of elongation of the anterior tentorial arms. Anterior and posterior tentorial arms are of moderate length. It is, therefore, apparent that as the mouthparts have changed from a ventral to an anterior position, the tentorium has altered to contend with the new

arrangement, and so the body of the tentorium has become greatly elongated, whereas the anterior and posterior tentorial arms are relatively unaffected.

From the data accumulated on the tentorium of the orthopteroid Hexapoda, it is evident that these insects may be divided into three distinct groups. The first group contains the primitively prognathous Phasmidae, whose somewhat "V-shaped" tentorium differs from that of the remaining orthopteroid insects. The second group includes the Blattidae and the Mantidae, and is distinguished by the unique feature of a median aperture in the body of the tentorium, which separates the Blattidae and Mantidae from all other orthopteroid Hexapoda. The third group embraces all the saltatorial types, the Gryllidae, Tettigonidae and Acrididae where the tentorium is typically X-shaped. From a study of the tentorium it appears that the Tettigonidae show a close relationship to the Acrididae, but the relationship of the Acrididae and the Tettigonidae to the Gryllidae is less conspicuous.

- (b) Studies in the comparative anatomy and systematic importance of the hexapod tentorium.  
II. Dermaptera, Embioptera and Isoptera.

In the Dermaptera the head is secondarily prognathous. Since the publication of this paper, Strenger (1950), in a study of the head of Forficula auricularia has further ratified this point. The secondary prognathous condition has resulted in the dorsal elongation of the head, accompanied by an elongation of the ventral region, so that the base of the labium has lengthened between the post-genae and an additional plate, the gula, has been formed. Considerable controversy still persists amongst morphologists as to the true origin and nature of the gula region of insects, and arising out of this study of the tentorium it appears to the writer that further investigation into the gula region of insects would be of value to entomologists.

The tentorium of the Dermaptera exhibits well-developed anterior tentorial arms which coalesce in the body of the tentorium. The posterior tentorial arms are somewhat short and transverse. Dorsal arms are

present and are attached to the head-capsule in the inter-ocular region. The imperforate body of the tentorium is X-shaped and much elongated, the latter feature being associated with the secondary return to the prognathous condition. The anterior tentorial pits lie in the epistomal suture, and the posterior tentorial pits are located in the extremities of the post-occipital suture.

The head in the Embioptera is again, secondarily prognathous, a true gula being absent, but an additional sclerite or plate performing the same function as the gula, occurs in the cervical membrane, posterior to the base of the labium and fused with the margins of the post-genae.

In the Embiopteron tentorium, the anterior tentorial arms are wedge-shaped, and narrow to unite in the short, rectangular, medianly-placed body of the tentorium. There is no median aperture in the body of the tentorium. The posterior tentorial arms are strong and arcuate proceeding anteriorly for some distance into the lumen of the head, before coalescing in the body of the tentorium. Dorsal arms are attached to the head-

capsule on the anterior aspect of the antennal ridge. The anterior tentorial pits occur in the epistomal suture, and the posterior tentorial pits may be found in the post-occipital suture.

The Isoptera in their structure of the head-capsule indicate a secondary return to the prognathous condition. The elongation of the ventral region of the head has caused an elongation of the submentum in the region of the posterior tentorial pits, but as the submentum remains undivided a true gula has not been formed.

In the Isoptera the tentorium is somewhat X-shaped. The anterior tentorial arms are widely expanded and triangularly shaped. They converge to unite medianly in the frontal plate of the tentorium. The posterior tentorial arms are short, broad and transverse, and coalesce to meet in the posterior portion of the body of the tentorium. The body of the tentorium is medianly perforated by an aperture, the latter bounded anteriorly by the frontal plate, and posteriorly by the posterior portion of the body of the tentorium, sometimes referred to as the posterior bridge. Dorsal

arms occur which are often difficult to locate. They are attached to the head-capsule on the antennal ridge or in the inter-ocular area. The anterior tentorial pits lie in the epistomal suture. In the soldier caste, the posterior tentorial pits occur as grooves at the sides of the gular region of the labium, but in other castes the posterior tentorial pits are found in the extremities of the post-occiput.

The findings in this study of the tentorium in the Dermaptera, Embioptera and Isoptera indicate that these three groups of insects show no close relationship to one another. However, the tentorium of the Isoptera shows remarkable similarity to the tentorium of the Blattidae and Mantidae in the possession of a median aperture in the body of the tentorium. The general structure of the Isopteron tentorium also indicates resemblances shared with the Blattidae and Mantidae on the one hand, and the Isoptera on the other. It is, therefore, suggested that on tentorial structure the Isoptera merit classification with the Blattidae and Mantidae (= Dictyophora of Omer-Cooper, 1939).

- (c) Studies in the comparative anatomy and systematic importance of the Hexapod tentorium.  
III. Odonata and Plecoptera.

The structure of the tentorium was examined in both larval and adult forms of Odonata and Plecoptera. In the Odonata the larva and the adult exhibit the hypognathous type of head, whereas prognathism or semi-prognathism persists in larval and adult Plecoptera.

In the Odonata, the tentorium is pl-shaped in the larva and the adult. In both stages, the long anterior tentorial arms are well-developed and usually bear tendinous outgrowths. The anterior tentorial arms meet in the broad, posteriorly placed body of the tentorium. The posterior tentorial arms are short and meet transversely in the imperforate body of the tentorium. Dorsal arms are present, but are better developed in the adult than in the larva, though they are obvious structures in both. The dorsal arms are attached to the head-capsule on or near the mesal margin of the antennal ridge. The position of the anterior tentorial pits in the lateral extremities of the sub-genal suture has been indicated as a more primitive condition than that encountered in the orthopteroid Hexapoda, where

the anterior tentorial pits usually occur in the fronto-clypeal suture. The posterior tentorial pits are located in the depths of the post-occipital region.

In all but the highly specialised Plecoptera, the tentorium is X-shaped and may be compared with that of the orthopteroid insects. The anterior tentorial arms are stoutly developed, and the posterior tentorial arms curve and proceed some distance into the head cavity before coalescing in the imperforate body of the tentorium which is generally of rectangular shape. Well-developed dorsal arms are present and attached to the head on or near the antennal ridge. The anterior tentorial pits lie near the extremities of the epicranial arms, or, when present, in the lateral limits of the epistomal suture. The posterior tentorial pits occur in the extremities of the post-occipital suture.

The conclusions reached in a study of the tentorium of the Odonata and the Plecoptera, indicate that there is little similarity between these two groups. The Odonata appear to be far removed from the orthopteroid Hexapoda, Dermaptera, Embioptera and Isoptera, in a comparison of the tentorium. Furthermore the Odonata

share no noticeable similarities of tentorial structure with the Plecoptera.

The tentorium of the Plecoptera exhibits certain orthopteroid features and in the generalised Plecoptera the typical X-shaped tentorium of the orthopteroid insects is encountered. It has also been demonstrated that certain features in the structure of the Plecopteron tentorium may be compared with similar features observed in the Embioptera.

- (d) Studies in the comparative anatomy and systematic importance of the Hexaped tentorium.  
IV. Ephemeroptera.

The tentorium in both the larval and adult stages of the Ephemeroptera was investigated. It was observed that in larvae inhabiting a variety of aquatic conditions, no diagnostic features of the tentorium were present, which could be used as a means of differentiating larvae living in one type of environment from larvae showing a preference for an entirely different type of environment. The larvae of the Ephemeropteron species chosen for study were prognathous with the exception of Baetis harrisoni Brnd. which was hypognathous. A comparison between

the tentorium of the hypognathous adult and the prognathous larva did not provide striking dissimilarities.

The tentorium in the adult Ephemeroptera is usually pi-shaped. The anterior tentorial arms are of surprisingly length, and brace the larger portion of the head-capsule, converging medianly and tapering to meet in the short, narrow, posteriorly placed body of the tentorium. The posterior tentorial arms are very short. The band-shaped, somewhat delicate body of the tentorium is imperforate. Dorsal arms are present and are attached to the head-capsule on or adjacent to the antennal ridge. The anterior tentorial pits are of groove-like structure, occurring above and outside of the clypeus, a position described by Snodgrass (1928) as

"lying at the edges of the inflected ventral areas of the genae, before the bases of the mandibles".

This position of the anterior tentorial pits only differs from the Myriapoda and Apterygota in that the bases of the hypopharyngeal apodemes have moved outward from the hypopharynx to the lateral walls of the cranium. The

posterior tentorial pits are located in the lower extremities of the post-occipital suture.

From a study of the tentorium in larval and adult Ephemeroptera it has been revealed that the tentorium, not being chiefly functional by nature, is a structure of phylogenetic significance.

A comparison of tentorial structure as observed in the Ephemeroptera and the orthopteroid Hexapoda, Dermaptera, Embioptera and Isoptera previously studied, provides no similarities for proving that the Ephemeroptera bear close relationship to any of the insect groups mentioned. The position of the anterior tentorial pits suggests that the Ephemeroptera are more primitive than any of the pterygote insects studied thus far.

In comparing the tentorium of the Ephemeroptera with that of the Odonata and Plecoptera, it is seen that in general structure, the tentorium of the Ephemeroptera shares some resemblance with that of the Odonata. The Ephemeroptera, from the position of the anterior tentorial pits, are regarded as the more primitive of the two groups, for in the Odonata, the anterior tentorial

pits lie in the sub-genal sutures. The Odonata, in turn, have been shown to differ widely from all other groups studied. There are no close similarities of structure to be seen in a comparison of the tentorium in the Ephemeroptera with that of the Plecoptera and it is therefore considered that on tentorial structure these two insect groups show no close relationship to each other.

- (e) Studies in the comparative anatomy and systematic importance of the Hexapod tentorium.  
V. Zoraptera, Psocoptera, Mallophaga and Anoplura.

The head is prognathous in the Zoraptera. The tentorium in the apterous form Zorotypus Hubbardi Caud. is well sclerotised and somewhat X-shaped. The anterior tentorial arms incline medianly to meet in the strong rectangular body of the tentorium. The posterior tentorial arms are broad, robust and arcuate. They proceed for some distance into the lumen of the head before uniting in the body of the tentorium, a feature which recalls a similar position found to occur in the Embioptera and the Plecoptera. Dorsal arms are present

and are attached to the head on the antennal ridge. The anterior tentorial pits occur in the sub-genal suture, whereas the posterior tentorial pits are located in the post-occipital suture.

In the Psocida the head is prognathous, though hypognathous forms are known to exist. In the prognathous Liposcelis sp. examined, the tentorium is V-shaped, and the anterior tentorial arms are remarkably long and slender rods bracing the greater portion of the head-capsule and converging postero-mesadly to meet in the narrow body of the tentorium. The posterior tentorial arms are short and coalesce in the body of the tentorium. Dorsal arms occur as outgrowths of the anterior tentorial arms and are attached to the head-capsule slightly laterad of the antennal ridge. The anterior tentorial pits are found in the sub-genal suture. The posterior tentorial pits take their origin in the post-occipital suture.

The prognathous condition of the head-capsule in the Mallophaga and Anoplura is secondary. From a study of the tentorium it would appear that these insects may be divided into four clearly defined groups.

In the Amblycera, e.g. Eomenacanthus stramineus Nitzsch, Heterodoxus longitarsus (Plaget) the tentorium shows variation from robust to less well-developed forms. The anterior tentorial arms in this group are usually slender, tubular apodemes varying in their size and degree of sclerotisation. The posterior tentorial arms are short, broad and transverse. The body of the tentorium may be reduced to a ligamentous bridge, or it may take the form of a well chitinized bar. Dorsal arms are usually absent. The anterior tentorial pits are found in the sub-genal suture, while the posterior tentorial pits are found in the extremities of the post-occipital suture.

In the Ischnocera, e.g. Pectinopygus afer (Kellogg), Pectinopygus acutifrons Rudow, Bovicola ovig Schrank, Bovicola Equi (Linn.) the anterior tentorial arms are considerably reduced and do not coalesce in the body of the tentorium. The body of the tentorium is delicate, ligamentous and slightly curved. The posterior tentorial arms are short, sclerotised and unite in the body of the tentorium. There is an attachment of the body of the tentorium to the posterior face of the

sitophore. Dorsal arms are absent. The anterior tentorial pits in the Ischnocera are difficult to locate in the subgenal suture, but the posterior tentorial pits, though smaller than those in the Amblycera, penetrate the post-occipital sutures.

In the Rhyncophthirina only the rudiments of the posterior tentorial pits and posterior tentorial arms are reported to exist.

In the Anoplura tentorial pits and tentorial structure is entirely lacking.

A study of the tentorium in the Mallophaga and Anoplura therefore suggests that in the former, tentorial structure showing a varying degree of development is present, whereas complete reduction of tentorial structure occurs in the Anoplura. As common ancestry cannot be regarded as a satisfactory criterion on which to base classificatory evidence, the writer, considering only the tentorial structure in these insects, prefers to place the Mallophaga and the Anoplura each in a separate order.

A note on the tentorium in the Apterygota.

Before proceeding to discuss the phylogenetic relationships of the groups studied, it is advisable at this stage to consider briefly existing knowledge of the tentorium in some apterygotan insects.

The hypopharyngeal skeleton of Japyx was first described by Meinert (1867). Von Stummer-Traunfels (1891) redescribed it and termed the hypopharyngeal skeleton the "Stützeagerüst" or supporting framework of the hypopharynx. Folsom (1899) gave a description of the hypopharyngeal skeleton of Orchesella cincta and stated that it consisted of a thin median plate with paired anterior, dorsal and posterior arms, the anterior arms being united with the lateral lobes of the hypopharynx. This structure, Folsom pointed out, is homologous with that of the Orthoptera and other insects. Berlese (1910) described the tentorium of the Protura, and this was further investigated by Prell (1913). The anterior arms of the tentorium were found to be united in a median bar, with each arm forked anteriorly. Prell observed that the fork made connections with the base of the hypopharynx and with the fronto-olypeal ridge of the head. Both Berlese and Prell identified this structure as the tentorium of the Protura, and

Prell further homologises it with the "Zungenapparat" of Collembola, which Snodgrass (1928) corroborates as being correct.

Snodgrass (1928) figures the tentorium of Machilis where an inter-mediate stage of tentorial development is observed. Here the anterior and posterior regions are still independent of each other. The hypopharyngeal apodemes arise from suspensorial plates connected laterally with the cranial walls, but their points of origin from these plates are at the basal angles of the clypeus. Snodgrass mentions a well-developed posterior tentorial bar which extends transversely through the back of the head from pits in the lower ends of the post-occipital suture. The maxillary cardines are usually attached to the margin of the cranium, slightly anterior to these posterior tentorial depressions. The inner ends of the hypopharyngeal apodemes, or anterior tentorial arms, of Machilis become weak and fibrous. A two-branded fiber extends downward in the head from the middle of the posterior bar. Snodgrass indicates that in most pterygote insects, the anterior and the posterior tentorial arms are united with each other, and typically the lateral elements are fused across the median line to form the body of the tentorium. However, the median plate or body of the tentorium is not developed in all cases. Snodgrass quotes two examples, the caterpillar, and the adults of the higher Hymenoptera to support

this statement. In the caterpillar the posterior arms form a slender bar through the back of the head to which the anterior arms are laterally attached, and in the Hymenoptera the posterior bar appears as a slender yoke between the posterior ends of the anterior tentorial arms.

Denis (1928) studying the anatomy of the head of certain Collembola, states that we owe to Folsom (1900) what little knowledge was then available on the tentorium of the Anurida. Denis then proceeds to describe in fair detail the tentorial structure of the Anurida. He differentiates the tentorium into an anterior tentorium and a posterior tentorium. The posterior tentorium is a chitinous plate situated above the oesophagus and consisting of three pairs of arms, the ventro-median arms (= bras ventraux médians), the ventro-lateral arms (= bras ventraux latéraux) and the uniting arms (= bras d'union). The anterior tentorium has a complicated structure and is composed of lateral arms which together form "une sorte de cadre au cerveau". Anteriorly they produce a branch which gives attachment to antennal muscles and muscles to the pharynx. Median arms are also present.

From the knowledge available on the apterygotan tentorium it would appear that the pi-shaped tentorium, present in certain pterygote insects, bears a closer resemblance to the tentorium of

the apterygota than does the X-shaped tentorium, and it is, therefore, concluded that in pterygote insects the pi-shaped tentorium is more primitive than the X-shaped tentorium.

### 3. PHYLOGENETIC SIGNIFICANCE OF THE HEXAPOD TENTORIUM.

In Paper IV it has been demonstrated that the tentorium is of importance in establishing relationships, being a structure which is not chiefly functional by nature.

The positions of the anterior and posterior tentorial pits have frequently been used by morphologists in phylogenetic studies of the head-capsule and it is surprising that so little attention has been paid to the endoskeleton of the head.

Symons (1952) in a study of the comparative anatomy of the Mallophagan head, reached the conclusion that tentorial form in the Mallophaga and related insects is of phylogenetic significance. Symons found that the tentorium is almost identical in lice known (on other morphological characteristics) to be closely related, but becomes markedly different in

genera of more remote ancestry. Thus Symmons working independently on the tentorium, has corroborated the writer's hypothesis that the tentorium is of phylogenetic significance.

Results of the study of the tentorium in certain pterygote insects, indicate that the range of variation of the tentorium is wide, but series within this range are limited. Insects grouped together on other morphological evidence are frequently found to possess tentorial structure which provides further proof of their relationships.

In considering the affinities of any group of insects, it is evident that the entire structure of the body should be taken into account. It is beyond the scope of this work to do so, but it may be of value to examine relationships suggested by the findings of these studies on the tentorium and also to note how they compare with the affinities suggested by workers whose conclusions were reached after pursuing investigations in other fields of morphology.

(a) Relationships of the orthopteroid Hexapoda.

Considerable variation of opinion exists with regard to the phylogeny and classification of the

orthopteroid Hexapoda.

Some of the early taxonomists included the Dermaptera amongst the insects to be classified under the order Orthoptera.

Packard (1883) places the Orthoptera under a Super-order Phyloptera, the latter including the orders Dermaptera, Orthoptera, Pseudoneuroptera and Neuroptera, a somewhat heterogeneous group in the light of present day knowledge. Packard remarks on the similarities of the Gryllidae to the Locustariae (= Tettigonidae) and closely allies the Phasmida with the Acridii, while the order Mantidae is regarded as standing next to the lowest group of Orthoptera, the Blattariae.

Brauer (1885) who laid the foundation of a modern classification of insects placed the orthopteroid Hexapoda in an order, Orthoptera genuina, and this order included the Orthoptera and the Embioptera. Brauer was thus responsible for dividing the old assemblage Neuroptera into separate sections, each of ordinal value.

Sharp (1899) and later Shipley (1904), placed the Dermaptera with the orthopteroid insects in single order,

which they called the Orthoptera.

Börner (1904) separated the Dermaptera from the Orthoptera and in his classification each of these insects came to occupy an order of their own.

Handlirsch (1908) in his revolutionary system, partly adopted by Brues and Melander (1932) divides the orthopteroid insects between two sub-classes. The Orthopteroides, the first sub-class includes the Orthoptera (= Saltatoria) Phasmoidea, Diploglossata, (= Hämimeridae) Dermaptera and Thysanoptera. The Blattaeformia is the second sub-class and this includes the Mantodea, Blattodea, Isoptera, Corrodentia (= Psocoptera) Mallophaga and the Siphunculata (= Anoplura).

From a study of the head and mouthparts of Orthoptera and Euplexoptera, Yusa (1920) shows that the Mantidae and Blattidae are closely related. They are followed by the Gryllidae (not regarded as having developed through the Mantidae) and then the Locustidae (= Tettigonidae) and the Acrididae. Yusa maintains that the Phasmodae appear to be remote from the Blattidae and considers their exact phylogenetic position

difficult to determine.

Walker (1922) in making a phylogenetic study of the terminal structures of orthopteroid insects, considers that the Mantodea and Blattodea belonged to a common stock and are more like one another than are the various families of Orthoptera. Walker, in his plan of the phylogeny of orthopteroid insects indicates that the Protoblattodea originated from Palaeodictyopteran stock. The Protoblattodea branched to give rise to the Orthoptera (Tettigonidae, Grylloidea, Tridactyloidea, and Acridoidea) and the remaining groups, Phasmoidea, Grylloblattodea, Zoraptera<sup>\*</sup>, Isoptera, Blattodea and Mantodea. The Orthoptera form one compact group, according to Walker, the Blattodea Mantodea and Isoptera are held to have many features in common, whereas the exact position of the Phasmoidea is regarded as doubtful. Certain affinities with the Grylloblattodea suggest the inclusion of the Zoraptera with the orthopteroid insects. Walker (1933) regards the Orthoptera as an order which includes the sub-orders, Isoptera, Dictyoptera (Blattidae and Mantidae) Phasmatodea

\* Query as indicated by Walker.

and Saltatoria.

Sedgewick (1927) includes in this order Orthoptera, the cursorial families, Forficulidae, Hemimeridae, Blattidae, Mantidae, and Phasmidae, while the Saltatoria include the Acridiidae, Locustidae and Gryllidae.

Crampton (1929) working on the terminal abdominal structure of female insects classifies the Blattidae and Mantidae together in one order, the Dictyoptera, while Grylloblatta and the Saltatoria are grouped in the order Orthoptera and the Phasmidae are placed in a separate order of their own, the Phasmoptera.

Crampton (1931) on the evidence of the mouthparts, neck and prothoracic sclerites and terminal abdominal structures of the female, indicates that the Blattids, Mantids and Isoptera form a compact super-order of insects, the Panisoptera.

Crampton (1932) in a study of the head-capsule, states that the Blattids and Mantids are grouped together to form the order Dictyoptera while the Isoptera are placed in a separate order, but all these insects are included in the super-order Panisoptera.

Crampton's super-order Panorthoptera comprises the Proorthoptera, Grylloblattidae saltatorial Orthoptera and Phasmids.

Bruce and Melander (1932) under the order Blattodea include the phasmids mantids and blattids grylloblattids, whereas the order Orthoptera includes the Tettigonidae and Acrididae only.

Inns (1934) draws attention to the fact that the original name of Dermaptera, applied by de Geer was subsequently replaced by Olivier, who used the name Orthoptera. Inns disapproves of dividing the Orthoptera into several distinct orders, and of restricting the original name to the saltatorial forms only. He maintains that this course is unwarranted, and largely due to differences of opinion with reference to characters of ordinal value only. Inns divides the order Orthoptera into the Cursoria and the Saltatoria, the Cursoria containing the Grylloblattidae, Blattidae, Mantidae and Phasmidae, the Saltatoria including the Acrididae, Tettigonidae and most Gryllidae.

Tillyard (1926), Wardle (1937) and Frost (1942) all classify the Orthoptera as an order of insects to include

the Blattidae, Mantidae, Phasmidae, Grylloblattidae, Gryllidae, Tettigonidae and Acrididae, Tillyard omitting the Grylloblattidae in his classification.

Essig (1942) divides the Orthoptera into several orders, and uses the term Orthoptera to include the families of Gryllidae, Tettigonidae and Acrididae, while separate orders are provided for the Grylloblattidae, Phasmida, Mantodea and the Blattaria.

Schwanwitsch (1943) proposes an interesting sub-division of the Insecta Pterygota into sub-ordinate groups using "the muscular motor of the wing" as a taxonomic criterion for the grouping of insect orders into larger units. He divides the wing motor musculature in insects into two main types. In the chiastomyaria, the levators of the wing are dorsal-ventral, the depressors longitudinal. Into this main group Schwanwitsch places all the Pterygota with the exception of the Odonata. In the latter all the wing muscles lie in the same direction, and so the Odonata comprise the second type, and the muscular motor is termed orthomyaria. The Chiastomyaria are sub-divided into the Anteromotaria, where the forewing becomes dominant,

while the hind one may be decreased, lost or transformed into a haltere, and the Posteromotoria, where the forewings are turned into elytra, halteres or undergo atrophy (many Phasmids) while the hindwings are the sole or principal organs of flight. The Anteromotoria are divided into three complexes of orders, the Panorpoidea, the Hemipteroidea and the Ephemeroidea. The Posteromotoria consist of the one complex, the Orthopteroides which includes the Orthoptera, Blattelliptera, Dermaptera, orders regarded as related to them, namely the Isoptera and Embioptera, and also the Placoptera which show according to Schwanwitsch some orthopteroid affinities as well. Coleoptera and Strepsiptera are also included in this complex.

Weber (1949), under a Super-order Orthopteroides includes the orders Saltatoria, Phasmida, Dermaptera and Diploglossata (Hemimerus). Placed in a second Super-order are the orders Mantodea, Blattaria, Isoptera and Zoroptera. This classification therefore separates the Phasmidae from the cursorial group with which they have been so consistently associated, and the Phasmidae have come to occupy a position in

proximity to the Saltatoria, a group with which they were thought to have affinities, by the early entomologists.

Thus it is observed that although much difference of opinion is encountered in the views held on the phylogenetic position and the classification of the orthopteroid Hexapoda, it is generally agreed, that the Mantidae and Blattidae are closely related and differ widely from the Phasmidae whose exact phylogenetic position appears difficult to determine. The Saltatoria form a well defined compact group whose marked characteristics differentiate them from the cursorial insects.

Omer-Cooper (1939) whose classification of the recent hexapod insects is supported, as will be shown later, by the writer's findings, abandons the old order Orthoptera on morphological grounds, maintaining that the four groups into which the orthoptera are usually divided do not appear to be of equal morphological value. He regards the Phasmidae as aberrant and very primitive forms, showing little resemblance to any other known group and he considers that their

association with the other orthopteroid insects appears to have been justified on negative considerations alone. The Saltatoria, according to Omer-Cooper, are a well-defined group with a characteristic morphology. He states that the Blattidae and Mantidae show no great structural dissimilarity from each other, all the differences being associated with their mode of life, and in no case have these differences involved radical morphological change. In his classification, he has placed the Blattidae and Mantidae each in a separate sub-order and together they form the Order Dictyophora (= Cothecaria) recognised by Leach and other early entomologists. Following Brues and Melander, Omer-Cooper places the little known Grylloblatta in a separate order, calling attention to the uncertainty which prevails with regard to their affinities.

From a study of the tentorium in the orthopteroid Hexapoda, the writer has demonstrated that the Phasmidae possess a tentorium which differs fundamentally from that of any of the other orthopteroid groups examined. The Phasmidae are also the only members of the orthopteroid insects studied which have retained a primitively

prognathous type of head. They do not exhibit the X-shaped tentorium characteristic of orthopteroid insects but possess a tentorium which displays greatly elongated anterior tentorial arms, with the body of the tentorium placed posteriorly in the head cavity. The body of the tentorium is imperforate, and the absence of a median aperture is a feature which separates the Phasmidae from the other cursorial groups the Blattidae and the Mantidae, with which the Phasmidae are usually classified. The Blattidae and Mantidae share many similarities of tentorial structure, both possessing well-developed anterior and posterior tentorial arms with the body of the tentorium perforated by a median aperture. In the Saltatoria, the tentorium is typically X-shaped, and shows similarity of structure in all the groups studied, Gryllidae, Tettigonidae and Acrididae, although the Tettigonidae and the Acrididae show closer relationship to each other than they do individually to the Gryllidae.

A study of the tentorium in the orthopteroid Hexapoda suggests that the Phasmidae deviate considerably from the Blattidae and the Mantidae, the latter

comprising the two cursorial groups with which the Phasmidae are usually associated. The Saltatoria form a compact group of insects all exhibiting much the same tentorial structure. The tentorium of the Saltatoria differs widely from that of the Phasmidae, and may be readily distinguished from that of the Blattidae and Mantidae in the absence of a median aperture in the body of the tentorium. The findings in this study of the tentorium in the orthopteroid Hexapoda suggest that the Phasmidae should occupy a separate order of their own. The Blattidae and Mantidae are satisfactorily classified each in a sub-order of the order Dictyophora, as designated by Omer-Cooper (1939). Further, the Saltatoria should be classified in a separate order. This is in agreement with Omer-Cooper's classification except that he has, however, divided this order into two, Sub-order Longicornuta (= Locustidae etc.) and Sub-order Brevicornuta (= Acrididae). The writer, considering the single feature of the tentorium, prefers to separate the Saltatoria into two Sub-orders, the first to contain the Gryllidae and the second to contain the

Tettigonidae and the Acrididae.

(b) Relationships of the Dermaptera, Embioptera and Isoptera.

The Dermaptera are considered to have affinities with the orthopteroid insects but workers disagree as to the extent of their relationships.

Packard (1883) regarded the Dermaptera as the lowest of his four orders (Dermaptera, Orthoptera, Pseudoneuroptera and Neuroptera) comprising the super-order Phyloptera. He refrained from associating the Dermaptera with the Orthoptera on the grounds of dissimilarities of thoracic structure, and the presence of overlapping abdominal tergites in the Dermaptera.

Brauer (1885) placed the Dermaptera in an order of their own under the sub-class Pterygogenea.

Sharp (1889) and Shipley (1904) modelling their system on that of Brauer, introduced the terms Exopterygota and Endopterygota, and placed the Dermaptera and the Orthoptera together in a single order of the Exopterygota.

Börner (1904) classified the Dermaptera as a

separate order, and placed the Dermaptera with the Hemimetabolous group of the Pterygota.

Handlirsch (1908) divides the Dermaptera into two orders, viz., Dermaptera and Diploglossata (= Hemimeridae) and both orders are classified under the subclass Orthopteroides.

Yansa (1920) noted the differences between the Orthoptera and the Euplecoptera (= Dermaptera) in the structure of maxillae, parapharynx and labium, but admitted that the Orthoptera and Dermaptera showed affinities in their more generalised features.

Walker (1922) in his plan of the phylogeny of orthopteroid insects indicates that the Dermaptera branched off from the original Palaeodictyopteran stock at the same period as did the orthopteroid insects. The original offshoot gave rise to two branches, the Dermaptera on the one hand and the Plecoptera and Embiidina on the other. These conclusions were reached on a phylogenetic study of the terminal structures of orthopteroid insects. Walker (1933) in a study of the anatomy of Grylloblatta campodeiformis Walker, considers that in its head and appendages, Grylloblatta

is nearest the Saltatorial Orthoptera, and as far as these parts are concerned, fits the hypothetical concept of a common ancestor for the Saltatoria and the Dermaptera.

Sedgewick (1927) classifies the Dermaptera in the cursorial sub-order of the Order Orthoptera. The Cursoria include the Families Forficulidae, Hemimeridae, Blattidae, Mantidae and Phasmidae.

Crampton (1929) in the study of the terminal abdominal structures of female insects, is uncertain as to whether the Dermaptera should be classified with the Panisoptera, comprising the order Dictyoptera (Blatta and Mantis), order Isoptera, or with the Panorthoptera comprising the order Orthoptera (Grylloblatt and Saltatoria) and order Phasmoptera (Phasma).

Crampton (1932) in his phylogenetic study of the head-capsule in certain Orthopteroid, Psocoid, Hemipteroid and Holometabolous insects again comments on the uncertain position of the Dermaptera.

Tillyard (1926), Brues and Melander (1932), Imms (1934), Wardle (1937) and Essig (1942) are all in

agreement in the classification of the Dermaptera, into a self-contained order.

In the subdivision of Insecta Pterygota proposed by Schwenkitch (1943) the Dermaptera are included in the Posteroanterior division of the Chlastryaria, and placed in the Orthopteroida complex. Thus the Dermaptera are classified with the Orthoptera and the Blattellera in the order Orthoptera.

Weber (1949) places the Dermaptera in a separate order, under the Super-order Orthopteroida which also includes the orders Saltatoria, Phasida and Diploglossata (Hemiptera).

Osner-Cooper (1939) classifies the Dermaptera as a separate order, which he further divides to include the sub-orders, Arxenia, Hemimerina, and Forficulina.

Results of an investigation into the tentorium of the Dermaptera indicate that these insects differ from the Embellera and the Isoptera. The Isoptera possess a characteristic median aperture in the body of the tentorium, which is not shared by the Dermaptera for the latter possess an imperforate body of the

tentorium. The tentorium in the Dermaptera is relatively longer than that observed in the Embioptera, and the posterior tentorial arms in the Dermaptera are transverse, whereas in the Embioptera the posterior tentorial arms are comparatively long and arcuate. Although the Dermaptera may show evidences of orthopteron affinity in their general morphological organisation, in the structure of the tentorium, the similarities are not sufficiently marked to warrant a close association of the Dermaptera with any of the orthopteroid insects studied. The writer corroborating Omer-Cooper's classification on this point considers that the Dermaptera should be retained in an order of their own, as is also indicated by many workers concerned with the taxonomic position of this group.

The affinities of the Embioptera are still somewhat undecided.

Packard (1883) frankly admits his inability to solve the relationships of his heterogeneous group, the Pseudoneuroptera, and comments on the close affinities of the Termitidae and the Embidae,

as well as of the Psocidae and the Perlidae. Packard then concludes that the Ephemerina, Odonata, Platyptera (Termitidae, Embidae, Psocidae, Perlina) as well as the Orthoptera and the Dermaptera are nearly equivalent and should take the rank of order.

Brauer (1885) includes the Embioptera with the Orthoptera in the order Orthoptera genuina.

Sharp (1899) and Shipley (1904) both classify these insects in a separate order of their own.

Handlirsch (1908) placed the Embioptera in the Sub-class Embideria to include the single order Embioptera.

Walker (1922) in a phylogenetic study of the terminal structures of orthopteroid insects states that

"The male genitalia of the Embiidae offer little or no evidence as to their relationships with other orders, but there is nothing in their structure to conflict with the view held by MacLachlan, Crampton and others that their nearest affinities are with the Plecoptera -----".

Walker (1933) maintains that the plecopteran head may be derived from a form similar to that of *Grylloblatta* and adds that the embiopteran head may equally well be derived from the same ancestral type.

Tillyard (1926) and Sedgewick (1927) both propose a single order for the Embioptera.

Crampton (1929) draws attention to evidence supporting the relationship of the Embioptera to the orthopteroid insects, and indicates that the terminal abdominal structures in these two groups fully confirm the evidence of relationship.

Crampton (1933) in two separate papers asserts that the Embioptera are the closest relatives of the Plecoptera and he proceeds to group these two orders in a super-order, the Pamphleoptera.

Brues and Melander place the Embioptera in a separate order of their own, Embioides, and as the order Embioptera they are likewise placed in a separate order by Lins (1934), Wardle (1937), Frost (1942) and Essig (1942).

Schwanwitsch (1943) in his Sub-division places the Isoptera and Embioptera together in the Orthopteroides complex of the Posteromotorian group of the Chiantomyaria. Mention is briefly made of the relationship regarded as existing between the Isoptera and Embioptera and the Orthoptera (Orthoptera, Blattoptera, Dermaptera).

Weber (1949) places the Embioptera in a super-order of their own, Embioidea, which contains the single order Embioidea.

Cner-Cooper (1939) classifies the Embioptera in an order of their own, which he places in proximity to the Plesoptera and the Isoptera.

From a study of the tentorium it would appear that the Embioptera warrant classification in a separate order. They show no marked resemblance in tentorial structure to either the Dermaptera or the Isoptera, and no striking similarities are encountered in a comparison of the Embiopteran tentorium with that of orthopteroid insects. The anterior tentorial arms are apically expanded and narrow before uniting in the imperforate body of the tentorium, which is rectangular in shape. Dorsal arms are present but not of robust construction. Curvate posterior tentorial arms are well-developed proceeding inwards for some distance before coalescing in the body of the tentorium. In the structure of the posterior tentorial arms, the Embioptera differ widely from the Dermaptera and Isoptera, while the

imperforate body of the tentorium immediately differentiates the Embioptera from the Isoptera. The tentorial structure in the Embioptera provides no evidence to support an association of the Embioptera with the Phasmoda, Dictyophora or Saltatoria.

Frequent reference is made in literature to the similarities existing between the Isoptera and the Dictyophora (more especially the Blattidae) but few systems of classification reflect this apparent relationship.

Packard (1883) includes the Isoptera (= Termitidae) with the Embidae, Psocidae and Perlina, all classified as members of his order Platyptera. Packard points out many features of similarity between the Termitidae and the Blattariae on the one hand, and the Termitidae and Embidae, as well as the Psocida and also the Perlidae on the other.

Brauer (1885) places the Isoptera together with the Psocoptera and Mallophaga in an order called the Corrodentia.

Sharp (1899) abandons the Corrodentia and the

Termitidae come to occupy a separate order of their own in his classificatory system.

Shipley (1904) has accepted Sharp's classification, but has changed the name of Sharp's order Termitidae, to that of Isoptera.

Börner (1904) places the Isoptera in an order of the Hemimetabolous pterygote insects.

Handlirsch (1908) allocates the Isoptera to a separate order, Isoptera, in proximity to the Mantodea and Blattodea orders of his Sub-class Blattaria.

Walker (1922) in a phylogenetic study of the terminal structures of orthopteroid insects considers that the Blattodea, Mantodea and Isoptera have so many features in common that they must belong to one common stock. However, Walker is uncertain of the exact relationship of the Isoptera to the Blattidae and Mantidae, and he notes that the form of the body and the position of the head of the Isoptera is more "plecopteroid" and hence more primitive than in the Blattidae and Mantidae unless it may be regarded as an adaptation to environment. Walker considers it best to regard the Isoptera as having arisen from the

Proteblattoidea, a palaeozoic order from which all three orders of the Blattoid group were developed.

Walker (1933) regards the Isoptera as a sub-order of the Orthoptera, because of their recognized close relationship with the Blattidae.

Tillyard (1926) and Sedgewick (1927) each suggest a single order for the Isoptera, in their classificatory systems.

Crampton (1929, (1933), considers that the Blattids, Mantids and Isoptera form a compact group of orthopteroid insects and he proceeds to classify them in the Panisoptera, a group in which he includes the Orders Dictyoptera, Isoptera and possibly the Dermaptera.

Inns (1934), Wardle (1937), Frost (1942) and Essig (1942) all classify the Isoptera in a separate order.

Schwenwitsch (1943) relates the Isoptera to the Embioptera, placing them with the Orthoptera in the Orthopteroides complex of the Posteropteria group of the Chiantomyaria.

Weber (1949) includes the Isoptera in the super-order Blattoides which includes the orders Mantodes,

Blattaria and Zoraptera.

Omer-Cooper (1939) classifies the Isoptera in a separate order which he places between the Embloptera and the Zoraptera.

It is apparent that many workers although aware of the relationships existing between the Isoptera and Dictyophora, still prefer to retain a separate order for this group of insects.

An examination of the tentorium in the Isoptera, fails to reveal any striking similarity between the Isoptera and the two groups, Dermaptera and Embloptera. The tentorium of the Isoptera does, however, show a marked resemblance to that of the Dictyophora especially to the Sub-order Blattidae. The anterior tentorial arms in both the Blattidae and Isoptera are widely expanded apically and converge to unite in the frontal plate of the tentorium. Dorsal arms are present in the Isoptera and the Dictyophora. The Isoptera also possess a median aperture in the body of the tentorium, a striking feature only encountered thus far in the tentorium of the Blattidae and Mantidae and differentiating these groups from all the

other groups examined. Posterior tentorial arms are stout and well-developed in both the Dictyophora and the Isoptera. Thus the findings in this study of the Isopteran tentorium indicate that the Isoptera show no close relationship to the Dermaptera and Embioptera, but reveal striking similarities to the Dictyophora. It is, therefore, suggested that the order Dictyophora, including the sub-orders, Blattidae and Mantidae be expanded to include in addition the sub-order Isoptera.

(c) Relationships of the Odonata and Plecoptera.

It is generally recognised that the Odonata next to the Ephemeroptera, are a most clearly circumscribed group, having no close allies amongst recent insects. It is considered that the Ephemeroptera and the Odonata separated from the main Pterygote stem at an early evolutionary stage, and their lack of close affinities with other insect groups is reflected in the consistent position as a separate order that they have retained in most systems of classification.

Packard (1883) in the order Pseudoneuroptera included the sub-orders Odonata, Ephemerina and

### Platyptera.

Thereafter it appears that most workers designated the Odonata as a separate order, as observed in the systems proposed amongst others, by Brauer (1885), Sharp (1899), Shipley (1904), who altered the name Odonata to that of Paraneuroptera, Börner (1904) and Handlirsch (1908), Walker (1922), Tillyard (1926) Sedgewick (1927), who followed Shipley in retaining the name Paraneuroptera in lieu of Odonata, Crampton (1929), Brues and Melander (1932) Hurd (1937), Omer-Cooper (1939), Frost (1942), Essig (1942) and more recently Weber (1949). Schwanwitsch (1943) in his Subdivision of the Insecta Pterygota into sub-ordinate groups based on wing musculature, places the Odonata as the only representatives of the Orthomyaria group, thus differentiating them from all the remaining groups of pterygote insects.

A study of the tentorium in the Odonata indicates that these insects differ widely from the Plecoptera, and provide no evidence of tentorial structure for suggesting affinities with any of the orthopteroid insects, or the Dermaptera, Embioptera and Isoptera.

The pi-shaped tentorium in the Odonata differs widely from the X-shaped tentorium of the orthopteroid insects and the generalised Plecoptera. The tentorium of both larval and adult Odonata was examined and there appeared to be no fundamental differences in the structure. The position of the anterior tentorial pits in the subgenal suture is regarded as an intermediate stage between the primitive condition found in the Chilopoda, Diplopoda and Apterygota and the final condition in which the anterior tentorial pits occur in the fronto-clypeal suture as is characteristic of most of the Pterygota.

The tentorium of the Odonata though differing fundamentally from the tentorium as observed in the remaining groups of Pterygota (with the exception of the Ephemeroptera) appears to be less primitive than the tentorium of the Apterygota. In the latter the endoskeleton may be simply united by slender, tendinous arms, or the component parts of the tentorium may be still unconnected, whereas in the Odonata union of the endoskeletal parts within the head has usually taken place.

It is, therefore, apparent that the Odonata, while differing widely from the pterygote insects studied, show in tentorial structure, features which suggest that they are more highly evolved than the Apterygota, but probably separated from the main Pterygote stem at an early evolutionary age. It is, therefore, suggested that in agreement with the majority of workers, the Odonata be classified in a self-contained order.

The Plecoptera are usually regarded as a very generalised group, a fact emphasised by Constock and Kochi (1902) and later by Crampton (1921), although Smith (1917) notes the highly specialised condition of the genitalia, while Tillyard points out specialisation in venation, the coriæ and the mouthparts of the Australian species. Hoke (1923) finds that the Plecoptera though regarded by many as a more generalised group of insects than the Orthoptera, show a greater degree of specialisation than the latter.

Packard (1883) classifies the Perlina in the Order Platyptera, which also includes the Termitidae,

Embiidae and Psocidae. Brauer (1885) provides a separate order for the Plecoptera, as does Sharp (1899) whose classification was modelled on that of Brauer.

The Plecoptera have thereafter been placed in an order of their own by many workers including Shipley (1904), Börner (1904), Handlirsch (1908), Walker (1922), Tillyard (1926) and Sedgewick (1927). The latter considers that the Plecoptera are most closely connected with the Orthoptera, especially the least specialised members of the family Phasmidae.

Crampton (1929), (1933), classifies the order Plecoptera with the order Embioptera under the Pimpliptera, maintaining that the Embioptera are the closest relatives of the Plecoptera. He bases his conclusions on the study of the terminal abdominal structure of female insects, and a phylogenetic study of the head-capsule.

Walker (1933) finds that the Plecopteran head may be derived from a form similar to that of Grylloblatta, for although in the majority of the order the head and its appendages are considerably different from this type, that of primitive forms

closely resembles it.

Inns (1934) places the Plecoptera in an order of their own, and mentions that the adults have the same general characters as the Orthoptera but he notes the differences in weaker mouthparts, wing texture and the coxae.

Wardle (1937), Omer-Cooper (1939), Frost (1942), Essig (1942), Weber (1949), all allot a separate order to the Plecoptera.

In the Subdivision of the Insecta Pterygota proposed by Schwanwitsch (1943) the Plecoptera share the Orthapteroidea complex of the Posteromotaria group of the Chiasatomyaria, with the Orthoptera and their related orders, the Isoptera and Embioptera.

Examination of the tentorium of the larval and adult Plecoptera shows that the tentorium of the Plecoptera is comparable with the X-shaped tentorium of the orthopteroid insects, but differs widely from the pi-shaped tentorium present in the Odonata. The anterior tentorial pits in the Plecoptera are located in the lateral limits of the fronto-clypeal suture indicating a less primitive condition than that observed in the Odonata where the anterior tentorial pits lie in

the subgenal suture.

Hoke (1923) finds that the Plecoptera shows some resemblance to the Embioptera. Similarities in tentorial structure confirm this assumption. It is observed that there is a closer association between the Plecoptera and the Embioptera than between the Plecoptera and the orthopteroideid insects. The relationship between the Plecoptera and the Embioptera is, however, not sufficiently marked to warrant these two orders being united into a single group.

The structure of the tentorium suggests that the Plecoptera should be placed in an order of their own, adjacent to that of the Embioptera. This conclusion, therefore, supports the classification proposed by Amer-Cooper (1939).

(d) Relationships of the Ephemeroptera.

The Ephemeroptera, together with the Odonata are regarded as very ancient forms of insects differing widely from the remaining Pterygota in musculature, wing venation, abdominal appendages and tentorial structure. In their line of descent, the Ephemeroptera probably separated off before the remaining

pterygote insects had been differentiated.

As in the Odonata, workers are in general agreement with regard to the classification and phylogenetic position of the Ephemeroptera.

Packard (1883) in his system regarded the Ephemeroptera as a sub-order of the pseudoneuroptera, which includes also the sub-order Odonata and the sub-order Platyptera. Classifications proposed thereafter, however, are in total agreement in the provision of a separate order for the Ephemeroptera, exponents including Brauer (1885), Sharp (1899), Shipley (1904), Börner (1904), who originated the name of Agnatha in lieu of Ephemeroptera, Handlirsch (1906), Walker (1922), Tillyard (1926), Sedgewick (1927), Crampton (1929) (1932), Bruce and Melander (1932) as Plecoptera, Ince (1934), Wardle (1937), Omer-Cooper (1939), Frost (1942), Essig (1942) and Weber (1949).

Schmidt (1942) in his utilization of the muscular motor of the wing as a taxonomic criterion places the Ephemeroptera in the third complex of the Anteromoteria, namely the Ephemeroidea, the Anteromoteria being a division of the Chlastomyaria.

The findings of a study of the tentorium in both larval and adult Ephemeroptera indicate that the Ephemeroptera differ considerably from all other groups investigated, with the exception of the Odonata, although it has already been demonstrated that the Odonata themselves differ from the other pterygote insects. The pi-shaped tentorium of the Ephemeroptera is similar to that observed in the Odonata, but does not resemble the X-shaped tentorium seen in the orthopteroid insects. In the Ephemeroptera the anterior tentorial pits lie at the edges of the inflected ventral areas of the genae, before the bases of the mandibles, a more primitive condition than that observed in the Odonata, and the remaining Pterygota.

The tentorium of the Ephemeroptera suggests a possible intermediate form between that found in the Apterygota, on the one hand and the Odonata and remaining Pterygota, on the other. The tentorium of the Ephemeroptera is considered less primitive than forms found in the Apterygota for the anterior and posterior elements of the endoskeleton in the tphemeroptera have coalesced to form a chitinised internal structure

whereas in the Apterygota the anterior tentorium may be unconnected to the posterior tentorium as seen for example in the Protura and Machilidae. Folsom (1899) describes the tentorium of the Collembolan Orchesella cincta as consisting of a thin median plate with paired anterior, dorsal and posterior arms. The tentorium of Orchesella cincta is less primitive form of tentorium from which the Ephemeropteran tentorium may well have been developed. The writer is tempted to suggest that an intermediate stage in the development of the tentorium, as seen in the Apterygota and the Ephemeroptera may possibly have existed in members of the former extensive order to which the present remnants of the Ephemeroptera belong.

It is, therefore, evident from a study of the tentorium in the Ephemeroptera that these insects have no near allies among recent insects, and the writer agrees with the consensus of opinion which places the Ephemeroptera in a separate order.

(e) Relationships of the Zoraptera, Psocoptera, Mallophaga and Anoplura.

The Zoraptera, Psocoptera, Mallophaga and Anoplura

are groups of insects whose affinities still remain somewhat doubtful.

The Zoraptera, first described by Silvestri in 1913 are a comparatively new and little known group.

Crampton (1922) placed the Zoraptera in the order Psocida

"on account of the great similarity of the wings, head-capsule, legs, testes, and other structures of the Zoraptera to those of the Psocids".

Crampton (1923) in a phylogenetic comparison of the maxillae throughout the orders of insects, observes that the maxilla

"---of the Zorotypid shown in Fig. 38 is as "orthopteroid" as any of the higher insects ----".

He finds similarity in the structure of the maxilla of a Zorotypid as compared with that of a Phasmid an Embiid, and an Isopteron. Crampton (1929) regards the Zoraptera as the most primitive representatives of the Psocids having departed the least from the ancestral type in the general character of their terminal abdominal structures. He refers to them as "merely peculiar Psocids". Crampton (1931) states

that

"the psocid Zorotypus is the best intermediate form for connecting the lower Holometabola in general with the Isoptera - like forebears of the Holometabola."

Crampton (1932) emphasises the fact that the Zoraptera are the most primitive representatives of the Psocids, and he, (1933), regards the nearest relatives of the Grylloblattids as the zorapterous psocids.

Walker (1922) observes that the Zoraptera appear to have affinities with the Grylloblattoidea and the Blattoidea, Mantodea and Isoptera. He tentatively regards the Zoraptera as a branch arising near the point of divergence of the Grylloblattoidea from the Protoblattoidea. However, Walker (1933) finally classifies the Zoraptera as a primitive suborder of the Psocoptera.

Tillyard (1926) places the Zoraptera provisionally in a separate order, closely allied to the Copeognatha (= Psocoptera). He suggests that the Zoraptera should be placed in a suborder of the Copeognatha.

Sedgewick (1927) does not include the Zoraptera in his classification of Insects which emphasises

the lack of knowledge of this group even in fairly recent times. Bruss and Melander (1932) place the Zoraptera in a separate order.

Imms (1934) commenting on the paucity of knowledge of these insects suggests affinities with the Psocida (after Crampton, 1922) but on general considerations he regards the Zoraptera as having relationships with the Isoptera on the one hand and with the Plecoptera and Psocida on the other.

Wardle (1937) includes the Zoraptera as a sub-order of the Psocoptera, but Frost (1942) and Essig (1942) both place the Zoraptera in a self-contained order in close proximity to the Corrodentia (= Psocoptera).

It must be assumed that Schwanwitsch (1943) in his sub-division of the Insecta Pterygota classifies the Zoraptera with the Psocoptera for no separate mention is made of this group. The Psocoptera are placed in the Anteromotoria group of the Chiasmataria and are included in the Hemipteroidea complex which also comprises the Hemiptera, Thysanoptera, Mallophaga and Siphunculata.

Weber (1949), classifies the Zoraptera in the super-order Blattoidea, together with the orders Mantodea, Blattaria and Isoptera.

Omer-Cooper (1939) regards the Zoraptera as an imperfectly known group with affinities to the Embioptera and possibly the Anoplura. He places the Zoraptera in a separate order apart from the order Psocoptera.

His classification, it has been demonstrated, is supported by evidence obtained in a study of the tentorium. This study reveals striking similarity of tentorial structure among the Embioptera and Zoraptera and to a lesser degree, the Plecoptera. It is, therefore, concluded that the Zoraptera, Embioptera and Plecoptera should be classified in separate orders but in close proximity to each other. Relationship frequently suggested between the Zoraptera and the Isoptera, is not apparent on the evidence of tentorium.

The Psocoptera, Mallophaga and Anoplura have frequently been associated in classifications so that it is convenient to consider these relation-

ships simultaneously.

The Psocoptera have been regarded as an order of insects including the Zoraptera and the Psocida (= Copeoginatha) while the name Anoplura now frequently refers to the Mallophaga together with the Siphunculata (= Anoplura).

Packard (1883) placed the Psocidae in the Order Platyptera together with the Termitidae, Embidae and Perlina.

Brauer (1885) included in the order Corrodentia the Isoptera, Psocoptera and the Mallophaga.

Sharp (1899) classified the Mallophaga and Anoplura together with the third order Siphonaptera in the Anapterygota, while the Psocidae were placed as an order in the Exopterygota.

Shipley (1904) adopted a similar classification, but he called the Mallophaga the Lipoptera and the Siphunculata or Anoplura, the Elliptoptera.

Borner (1904) showed preference for the name Corrodentia, an order he placed in the Hemimetabola and in it he included the Psocoptera and the Mallophaga.

Handlirsch (1908) classified the Corrodentia (= Psocoptera) Mallophaga and Siphunculata in the Sub-class Blattseformia.

Crampton (1923) included the orders Hemiptera with the Homoptera, Psocids, Mallophaga, Pediculids in a group which he calls the Panhemiptera. Of these insects the Psocids are shown to have retained the maxillae in the most primitive form, and this is regarded by Crampton as additional evidence to support the assumption that the Psocids have departed as little as any from the primitive condition of this super-order. The maxillae of the Psocids are further shown to possess striking similarity to those of the Mallophaga supporting the view that the Mallophaga were descended from Psocid-like ancestors. The mouthparts of the Anoplura are considered to be too highly specialised to offer clues to immediate relationships of the group. Crampton (1929) alters the above classification and comes to include in the group Panpsocoptera, the orders Psocoptera Nirmaptera (= Mallophaga) and Pediculaptera (= Anoplura). The Psocoptera include the Psocids and the Zeraptara.

Crampton (1932) refers to the Psocoid or Hemipteroid group which includes the Zoraptera and other Psocida Mallophaga, Anoplura, Hemiptera and probably the Thysanoptera, as being intermediate between the Orthopteroids on the one hand, and the Holometabola on the other.

Tillyard (1926) places the Psocoptera in an order excluding the Zoraptera, (which occupy an order of their own) and he regards the Psocoptera as an order of insects set far apart from all the other orders except the Zoraptera. The order Anoplura includes the Anoplura and the Mallophaga.

Sedgewick (1927) adopts Sharp's classification in its entirety.

Bruce and Melander (1932) place the Psocoptera, Mallophaga (Lipoptera) and Anoplura (Siphunculata) each in a separate order.

Ims (1934) in the order Psocoptera includes the sub-orders Zoraptera and Psocida, while the Anoplura are composed of the sub-orders Mallophaga and Anoplura. Ims, in classifying the Mallophaga and Anoplura together indicates that they are commonly

regarded as separate orders but are sufficiently closely related to merit their union into one order.

Wardle (1937) separates the order Carrodentia from the Zoroptera, but the Mallophaga and Anoplura are classified together under the order Anoplura.

Frost (1942) and Essig (1942) propose similar systems of classification but they place the Mallophaga and Anoplura in separate orders.

Schwanwitsch (1943) includes the Mallophaga Siphunculata and the Psocoptera in his Hemipteroidea complex of the Anteromoteria group of the Chlastomyaria.

Hopkins (1949) reflecting the modern conception of their relationships under the Superorder Psocoidea, includes the orders, Psocoptera, and Phthiraptera, the latter including also the Sub-order Mallophaga with the four super-families Rhyncophthirina, Amblycera, Ischnocera and Anoplura.

This classification is adopted by Symons (1952). From a study of the tentorium Symons states that the evolutionary sequence of members of the Psocoidea, may be : Order Psocoptera, followed by the order Phthiraptera, with the Anoplura least primitive of all.

Cooper (1939) places the Psocoptera in an order separate from that of the Zoraptera, which also came to occupy an order of their own. The Mallophaga and Anoplura are likewise placed in individual orders, somewhat removed from the former.

From a study of the tentorium in the Psocoptera, Mallophaga and Anoplura it is observed that whereas tentorial structure is always present though possibly reduced in the Psocoptera and Mallophaga, it is entirely absent in the Anoplura. It has been suggested by Symons (1952) that the Rhyncoptirina and Anoplura share a common origin and that the former is more closely linked to Anoplura than Ischnocera, in a position between these groups, although Symons indicates that it is assumed that the characters considered were not developed along independent lines.

The writer, however, holds the hypothesis that common ancestry cannot be regarded as a fundamental criterion for taxonomic purposes, and considers that morphology offers essential evidence for the determination of phylogeny.

The "V-shaped" tentorium in the Psocoptera differs widely from that encountered in the Mallophaga and

Anoplura. The wall chitinised and sclerotised anterior tentorial arms converge widely to meet in the posteriorly placed band-shaped body of the tentorium. Dorsal arms are present. The posterior tentorial arms are very short and transverse, meeting in the band-shaped body of the tentorium.

In the Mallophaga variations from primitive tentoria to tentoria which have undergone modifications by reduction in size and sclerotisation are apparent. The greatest degree of reduction is manifested by the presence of a delicate ligamentous body of the tentorium instead of a well chitinised bar. It has been demonstrated that the structure of the tentorium in the Mallophaga differs from that of the Psocoptera. Furthermore the Mallophaga may be distinguished from the Anoplura, the latter possessing no vestige of tentorial pits or tentorial structure.

A study of the tentorium in the Psocoptera, Mallophaga and Anoplura indicates that these three groups of insects may be clearly differentiated from each other. It is therefore suggested that they each be an allotted separate orders, the Mallophaga and

Anoplura remaining in fairly close proximity to each other, while the Psocoptera merit an order within the range of the Plecoptera, Embioptera and Zoraptera.

TABLE TO ILLUSTRATE COMPARISON BETWEEN THE  
CLASSIFICATION PROPOSED BY OMER-COOPER AND  
THAT SUGGESTED BY HUDSON.

OMER-COOPER.	HUDSON.
<u>SUB-CLASS PTERYGOTA.</u>	<u>SUB-CLASS PTERYGOTA.</u>
DIVISION : ARCHIPTERYGOTA	DIVISION : ARCHIPTERYGOTA
ORDER : EPHEMEROPTERA	ORDER : EPHEMEROPTERA
ORDER : COONATA	ORDER : COONATA
<u>DIVISION</u> NEOPTERYGOTA	<u>DIVISION</u> NEOPTERYGOTA
<u>SUB-DIVISION</u> EXOPTERYGOTA	<u>SUB-DIVISION</u> EXOPTERYGOTA
ORDER : PLECOPTERA	ORDER : PLECOPTERA
ORDER : EMBIOPTERA	ORDER : EMBIOPTERA
ORDER : ZORAPTERA	ORDER : ZORAPTERA

TABLE TO ILLUSTRATE COMPARISON BETWEEN THE  
CLASSIFICATION PROPOSED BY OMER-COOPER AND  
THAT SUGGESTED BY HUDSON.

OMER-COOPER.	HUDSON.
ORDER : PSOCOPTERA	ORDER : PSOCOPTERA
ORDER : PHASMIDA	ORDER : PHASMIDAE
ORDER : SALTATORIA	ORDER : SALTATORIA
Sub-Order Longicornula	Sub-Order Gryllidae
Sub-Order Breuicornuta	Sub-Order Tettigonidae and Acrididae.
ORDER : DICTYOPHORA	ORDER : DICTYOPHORA
Sub-Order Blattida	Sub-Order Blattida
Sub-Order Mantida	Sub-Order Mantida
	Sub-Order Isoptera
ORDER : DERMAPTERA	ORDER : DERMAPTERA
ORDER : MALLOPHAGA	ORDER : MALLOPHAGA
ORDER : ANOPLURA	ORDER : ANOPLURA

While the inadvisability of placing too much importance on deductions based on one morphological character is emphasised,

it is observed that the findings in this study of the tentorium and the classification proposed as a result thereof corroborate to a large measure the conclusions reached by Omer-Cooper (1939).

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S U M M A R Y.

1. The aim of the present investigation is to extend existing knowledge of the insect tentorium. This involves the clarification of nomenclature, the examination and interpretation of the tentorium in certain groups of insects and a dissertation of the phylogenetic significance, and classificatory value of the tentorium.
2. In Paper I a description is given of generalised tentorium, nomenclature is clarified and the functions of this structure defined. In particular the tentorium of the orthopteroid Hexapoda is described embracing in the cursorial group, the Phasmidae, Blattidae and Mantidae, and in the saltatorial group, the Gryllidae, Tettigonidae and the Acrididae.

The findings in this study indicate that it is possible to differentiate between primary prognathism and secondary prognathism from an examination of tentorial structure. The evidence suggests that the Phasmidae should be placed in a separate group from the Blattidae and Mantidae. Similarities of tentorial structure are shared by the Mantidae

and Blattidae, and by the Gryllidae, Tettigonidae and the Acrididae. A closer relationship is apparent between the Tettigonidae and the Acrididae than between the Gryllidae and the Acrididae.

3. In the second paper the tentorium of the Dermaptera, Embioptera and Isoptera is described. Microscopic analysis was improved by the use of a new technique for demarcating tentorial structure. The findings indicate that the differences of tentorial structure are sufficient to corroborate the existing separation of these groups into individual orders. Further, the evidence shows a close affinity between the Isoptera and the Dictyophora (Blattidae and Mantidae).

4. Paper III describes the tentorium of the larval and adult forms of the Odonata and Plecoptera. From an examination of the tentorium it is evident that there are considerable differences between these two groups. The Plecoptera show some association with the Embioptera whereas the Odonata differ from the groups previously studied.

5. Paper IV deals with the tentorium of the Ephemeroptera. The tentoria of larval forms representative of varying habitats as well as those of adult Ephemeroptera are described. The weight of evidence accumulated proves that the tentorium being a structure which is not chiefly functional by nature is of phylogenetic significance in establishing relationships between insect groups. Some slight resemblance is noted between the tentorium of the Ephemeroptera and the Odonata. Otherwise the Ephemeropteran tentorium has quite distinctive features from groups previously studied.
6. Descriptions of the tentoria of the Zoraptera, Psocoptera, Mallophaga and Anoplura are given in Paper V. Close similarities of tentorial structure were found to exist between the Zoraptera and the Embioptera. On the basis of the evidence the Psocoptera, the Mallophaga and the Anoplura are each placed in a separate order.
7. General conclusions are prefixed by a rationalisation of tentorial nomenclature, and also by a review of the studies of the tentorium in certain pterygote insects.

The importance of the tentorium as a factor of phylogenetic significance is generally established. Following on this an appraisal of the classifications of various workers has been made in the light of a system based upon tentorial structure. With due regard to the limited scope of the present study, and with the proviso that tentorial analysis should be supplemented by total morphological investigation the conclusions reached in the study of the tentorium in certain pterygote insects are presented in the belief that they contribute to some extent towards the clarification of insect relationships.

