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THE MORPHOLOGY OF THE TENTORIUM
OF THE ANISOPTERA
(ODONATA)

Thesis for the Degree of M. S.
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ABSTRACT

THE MORPHOLOGY OF THE TENTORIUM OF THE ANISOPTERA (ODONATA)

by Francis Edward Giles

The pi-shaped anisopteran tentorium is composed of the anterior arms, the dorsal arms, the posterior arms and the bridge. The anterior arms originate as cranial invaginations in the area of the subgenal sutures, while the posterior arms arise as invaginations of the head wall in the region of the postoccipital suture. These arms meet and coalesce to form the tentorial bridge. The dorsal arms arise as projections of the anterior arms and fuse with the antennal and ocular ridges.

The tentorium provides rigidity to the head, supports various internal organs, and serves the function of muscle attachment. The ventral mandibular adductor apodemes, and the ventral maxillary adductor apodemes originate from the anterior arms. A third mandibular adductor apodeme originates from the dorsal arms in the families Petaluridae, Gomphidae and Cordulegasteridae, but is not found in the families Aeshnidae and Libellulidae.

As the anisopterous head changes from a broad shallow head to a deep narrow head, the angles increase between the epistomal and subgenal sutures, and between the posterior arms and the bridge. Using these angles, and the presence and condition of the third mandibular adductor apodeme as criteria, an attempt has been made to equate the investigation with the phylogenetic relationships of other writers.

The contention of some investigators that the Gomphidae and Petaluridae are primitive forms, and that the Cordulegasteridae, Libellulidae and Aeshnidae, in that order, are evolved forms, is thought to be correct. However, the author finds no justification in assigning the highest position to the Aeshnidae. Hagenius brevistylus (Selys) has both primitive and evolved characteristics, and does not seem to follow the general gomphine development.

THE MORPHOLOGY OF THE TENTORIUM OF THE ANISOPTERA
(ODONATA)

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PROCEDURES

Heads of dried specimens were boiled in concentrated potassium hydroxide solution until the compound eyes were cleared of pigments. The heads were then washed in water and stored in eighty per cent alcohol. In dissecting, compound eyes and mouthparts were removed, and the specimens examined under alcohol. Drawings were made with the aid of a grid.

For a description of the musculature and position of the internal organs, living specimens were collected. These were fixed in Dietrich's solution for approximately twelve hours, transferred to eighty per cent alcohol, and then dissected under alcohol. The following fresh material was dissected:

Gomphus crassus Hagen

Opniogomphus rupinsulensis (Walsh)

Libellula luctuosa Burmeister

Libellula pulchella (Drury)

Pachydiplax longipennis (Burmeister)

Sympetrum rubicundulum (Say)

REVIEW OF LITERATURE

The hexapod tentorium is an important structure that has received little comparative investigation until recent years. The description of the tentorium of the orders Orthoptera, Plecoptera and Neuroptera by Comstock and Kochi (1902) closely parallels that of present day investigators. These two workers showed the tentorium to consist primarily of invaginations of the head wall, and of chitinized tendons. They established that the dorsal arms arose from the side of the tentorial body and extended to the frons or to the margins of the antennal sclerite. In an embryological study of Blatella germanica (Linn.), Riley (1904) found that the invaginations giving rise to the anterior arms appeared as early as the thirteenth day. The invaginations giving rise to the posterior arms occurred later, while the body of the tentorium was formed at about the twentieth day as a result of the fusion of the anterior and posterior arms. Riley also noted that the dorsal arms were formed by processes given off by the anterior arms. Snodgrass (1928), studying the orders Protura, Ephemeroptera, Odonata and Orthoptera, found that the anterior and posterior tentorial arms were hollow invaginations, the location of the roots being marked externally by pits. In the Pterygota, he observed that the anterior pits usually lay in the epistomal suture, in front of the anterior mandibular condyles, but that in the order Odonata, the anterior pits

occurred in the subgenal suture. The posterior pits were found at the lower ends of the postoccipital suture. He stated that the body of the tentorium was formed by the union of the anterior and posterior arms. Snodgrass further determined that the dorsal arms were derived from the anterior arms and extended to the facial wall in the region of the antennal bases. The dorsal arms were noted to sometimes fuse with the cuticle, but generally were attached only to the hypodermis.

The taxonomic importance of the odonate head characteristics was brought out by Lew (1933). In this work, the tentorium was described as arising from hollow invaginations of the head wall, and to consist fundamentally of three pairs of processes. The modification of these processes in the imago was found to occur mainly in the occipital region where the pits were so fused and atrophied, and the posterior arms so short and broad, as to be almost unrecognizable. Lew found that the naiadal head was not so modified, and both pits and posterior arms were readily discerned. He further stated that the posterior pits were closed, and that the dorsal arms originated from the anterior arms. Needham, Traver and Hsu (1935) wrote that the ephemeropteran dorsal arms were "ingrown arms or apodemes". In a study of the odonate naiad, Anax junius (Drury), Snodgrass (1954) determined that the posterior arms arose from pits in the postoccipital sulcus, and that the anterior arms arose from slits between the compound eye and

the base of the mandible. No mention was made of the origin of the dorsal arms, but Snodgrass described them as being "attached on the cranial wall by brushes of apparently non-muscular fibers". Short (1955), in a study of Aeschna cyanea (Müller), reported the dorsal arms in the naiad were attached to the cranial walls by nonmuscular fibers, and the imaginal dorsal arms were fused to the occular ridge. Short disagreed with Lew and stated that the posterior pits were open.

The only comprehensive work on the tentorium of the major insect orders was published by Hudson (1944, 1947, 1948, 1951). In the paper dealing with the Ephemeroptera, Hudson (1951) disagreed with Hsu and described the dorsal arms as being outgrowths of the anterior arms. Hudson's description of the tentorium agrees with that of Riley, Snodgrass, and Lew.

Asahina's (1954) morphological work on Epiophlebia superstes Selys (f. Epiophlebiidae), brings to light some interesting differences. In this species, the posterior pits occur in the upper ends of the ill-defined hypostomal sutures. The anterior pits do not lie in the subgenal or epistomal sutures, but appear as grooves running obliquely posterad from the anterior mandibular condyles.

GENERAL DESCRIPTION OF THE ANISOPTEROUS TENTORIUM

The tentorium may be regarded as the endoskeleton of the anisopteran head. It is a pi-shaped, internal bracing element that serves the function of muscle attachment and organ support. The anterior tentorial arms (Fig. 1) arise as invaginations of the head wall near the posterior mandibular condyles. Externally, they are marked by elongate pits which follow the subgenal suture and extend into the extremities of the epistomal suture. The shape of an anterior arm, from a dorsal aspect, is that of a triangle, the base being in the area of the pit. The inner ends of the arms are produced caudad and are convergent; the inner margins may develop swollen expansions.

The posterior arms arise from invaginations of the head wall. The origins of the posterior arms are marked externally by pits located in the postoccipital suture. These pits may be open or closed. The posterior arms are short and broad and merge with the anterior arms to form the body of the tentorium.

The body or bridge of the tentorium (Fig. 2) is a heavy, deeply sclerotized structure, adjacent to the posterior cranial wall. It divides the occipital foramen laterally into two unequal parts. The body may be sulcate and the anterior

edge varies in shape. In the middle of the posterior edge are found two processes, the ends of which are directed toward the meson to a varying degree. These processes articulate with the cervical sclerites and are here termed the cervical condyles.

The dorsal tentorial arms arise from the anterior arms at the point of junction of the anterior arms and the body of the tentorium. These curved, fan-shaped arms extend dorsad and are divergent. Distally, the dorsal arms become solidly attached to the antennal and ocular ridges and serve as the points of origin of the extrinsic antennal muscles.

At a point approximately half their length, the ventral surface of the anterior arms gives rise to the apodemes of the ventral mandibular adductor muscles. Other mandibular adductor apodemes may be present on the posterior surface of the dorsal arms, at the point of their junction with the anterior arms. The apodemes of the maxillary adductors originate ventrally at the junction of the anterior arms and the body of the tentorium. These apodemes are heavier than the mandibular apodemes and tend to be forked, giving them the appearance of two separate apodemes. On the ventral surface of the tentorial bridge, approximate to the cervical articulations, are the points of origin of the ventral longitudinal neck muscles. The apodemes of these muscles are delicate and may be destroyed by prolonged treatment with potassium hydroxide.

Dorsad of the bridge, the walls of the occipital foramen are produced inwardly into two large finger-like projections. These are the apodemes of the dorsal longitudinal cervical muscles.

The body of the tentorium provides support for the digestive and nervous system. The oesophagus lies dorsad on the tentorial body, and the digestive tract passes through the upper division of the occipital foramen. The brain is dorsad of the oesophagus and posterad of the dorsal arms. The circumoesophageal connectives lie against the anterior margin of the tentorial body and unite beneath it in the sub-oesophageal ganglion. The ventral nerve cord runs along the ventral side of the tentorial body through the lower section of the occipital foramen.

The tentorium provides rigidity at a critical point of the cranium, namely, the articulation of the mandibles. The tentorium thus transmits the stresses brought about by chewing to the epistomal ridge, the postoccipital ridge, and the antennal and ocular ridges.

Fig. 1. Sympetrum rubicundulum (Say), 24X. Frontal aspect to show the relationship between the tentorium and the external features of the head.

Fig. 2. Sympetrum rubicundulum (Say), 36X. Sagittal section, compound eyes and mouthparts removed.

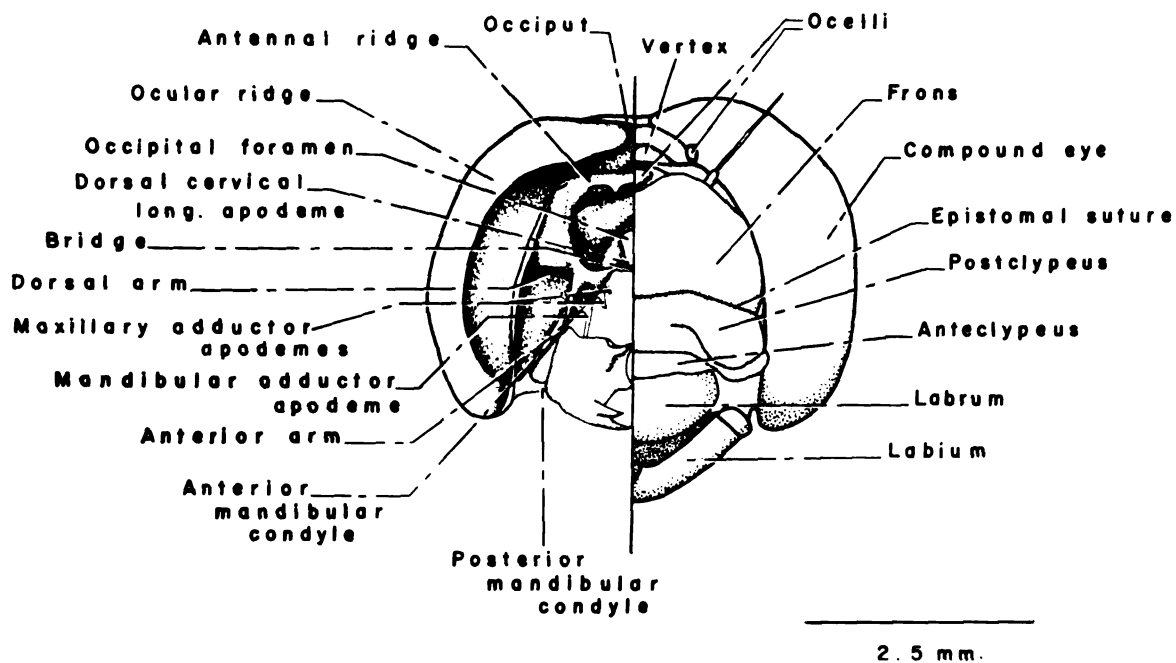


Figure 1

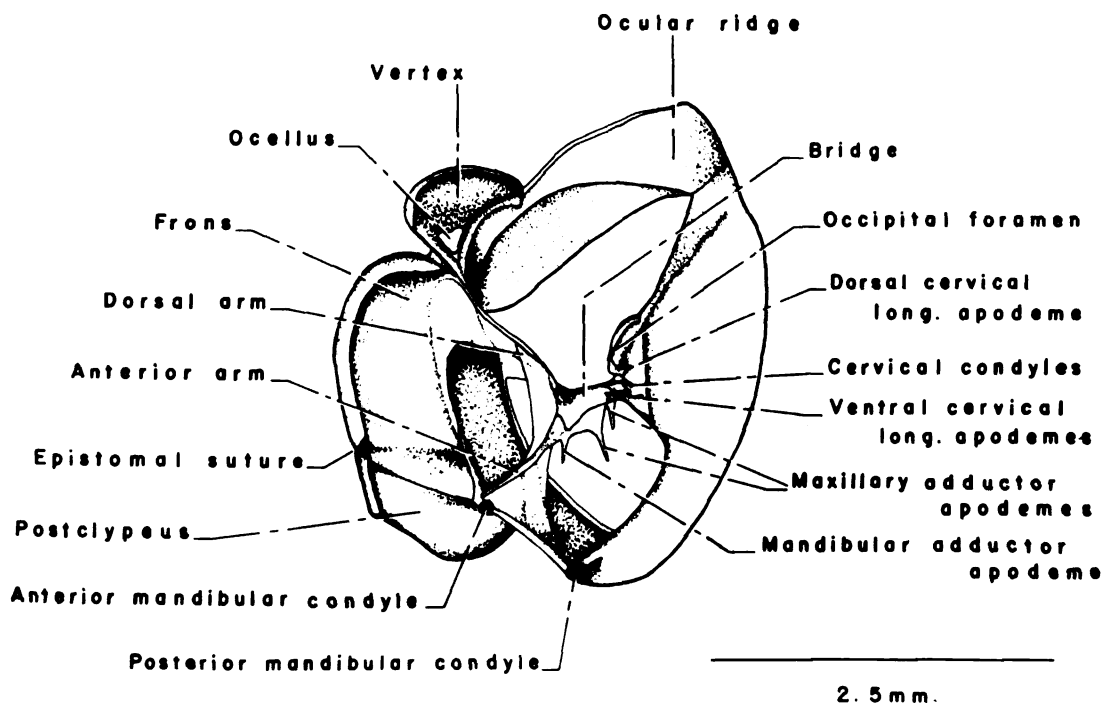


Figure 2

THE MORPHOLOGY OF THE ANISOPTEROUS HEAD

Family Petaluridae

Tachopteryx thoreyi Hagen (Fig. 3) was the only species available for study in this family. In following the angulations of the subgenal and epistomal sutures, the inner ends of the anterior pits of this specimen curve approximately thirty degrees. These pits give rise to moderately heavy anterior arms which follow the rearward curvature of the subgenal sutures. The posterior edges of the arms are concave, and the ectal ends are considerably wider than the inner ends. At a point near their junction with the tentorial bridge, the ventral surfaces of the anterior arms are produced into heavy projections. From these projections arise the mandibular and maxillary adductor apodemes.

At the junction of the epistomal and subgenal sutures, the anterior arms develop slight ridges, which are the beginnings of the dorsal tentorial arms. About one third the length of the anterior arms, these ridges curve upward and merge into the antennal and occular ridges. On the lower, posterior surface of the dorsal arms are found the heavy mandibular adductor apodemes.

The bridge of the tentorium is quite wide and deep. From the ventral, sulcated surface arise the well-developed

apodemes of the ventral cervical longitudinal muscles. As the posterior portion of the bridge is higher than the straight anterior edge, the cervical condyles lie above the main dorsal surface.

The posterior tentorial arms are short and meet at the bridge at an angle of approximately thirty degrees from the vertical. The moderately long posterior pits are slit-like, and are open.

Family Cordulegasteridae

The only representative of this family studied was Cordulegaster maculatus Selys (Fig. 4). Because the subgenal and epistomal sutures of this species meet at a distinct angle of approximately forty-five degrees, the anterior pits assume an L-shape.

Originating at the extremities of the subgenae, the outer ends of the anterior arms are quite wide, and the posterior edges are concave. Just before the arms unite with the bridge, the ventral surfaces are produced into slight projections which bear the mandibular and maxillary adductor apodemes.

Slight ridges arise on the anterior arms, in the area of the subgenal and epistomal sutures. These ridges, the dorsal tentorial arms, are almost immediately produced upward. The basal, posterior surfaces of the dorsal arms give rise to the light mandibular adductor apodemes.

The tentorial bridge is quite wide and deep. There is a moderate swelling on the anterior edge, and the ventral surface is sulcate. The longitudinal cervical apodemes are quite heavy. Because the posterior edge of the bridge curves upward, the cervical condyles lie above the dorsal surface of the bridge.

The open posterior pits are long and slit-like. They give rise to relatively long arms which meet the bridge at an angle of about forty-five degrees from the vertical.

Fig. 3. Tachopteryx thoreyi Hagen, 24X. Dorsofrontal aspect,
compound eyes and mouthparts removed.

Fig. 4. Cordulegaster maculatus Selys, 24X. Dorsofrontal aspect,
compound eyes and mouthparts removed.

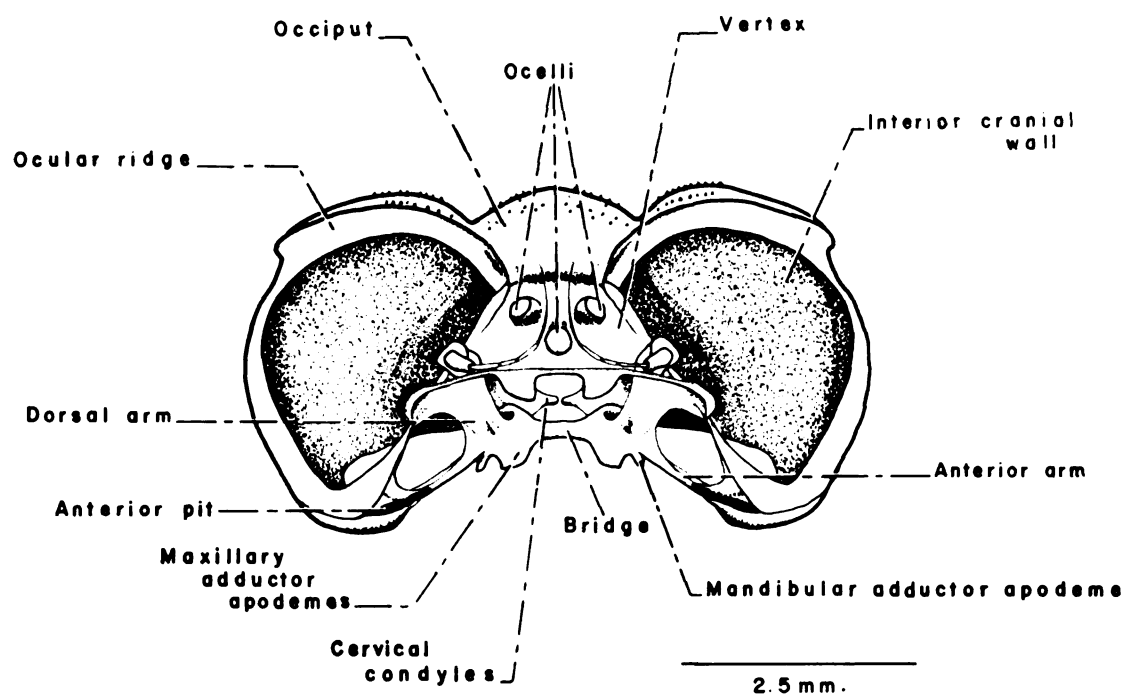


Figure 3

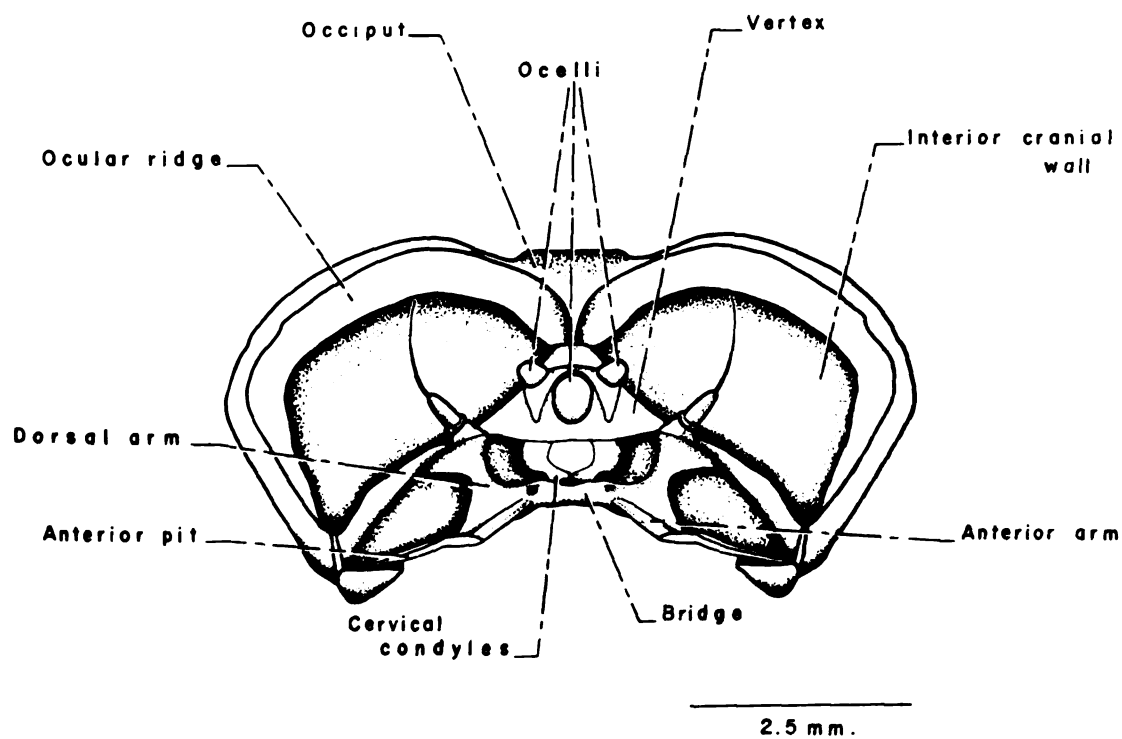


Figure 4

Family Gomphidae

From the front, the anterior pits of Gomphus exilis (Selys) (Fig. 5) form a smooth curve that is bent approximately thirty degrees at the inner ends. The anterior arms begin at the outer extremities of the subgenal sutures. They do not, however, follow the rearward curvature of the subgenae. The posterior margins of the arms are straight and are strengthened by a thickened edge. Ventrally, the arms produce moderate projections which give rise to the mandibular and maxillary apodemes.

The dorsal tentorial arms arise as slight ridges on the top surfaces of the anterior arms. These ridges start in the vicinity of the anterior mandibular condyles, and are produced upward about one half the length of the anterior arms. The moderately heavy mandibular adductor apodemes arise from the basal, posterior surfaces of the dorsal arms.

The moderately sized bridge has a straight anterior edge. As the posterior edge of the bridge is produced upward, the cervical condyles are positioned considerably above the sulcate, dorsal surface of the bridge.

The slit-like posterior pits are moderate in size and open. The short posterior arms meet in the bridge at an angle of about fifteen degrees from the vertical.

The construction of the tentoria of the ensuing four species so closely follows that of G. exilis, that only a few notes are necessary to describe their differences.

In G. fraternus Say, the anterior pits as seen from the front, have a slight L-shaped appearance, due to the angle at which the subgena and epistomal sutures meet. The rear edges of the anterior arms are concave, and follow the curvature posterad of the subgenae. The dorsal arms are produced upward about one third of the length of the anterior arms. There is a slight bulge on the anterior edge of the bridge.

The subgenae of G. spicatus (Hagen) is not continued to the rear, and although the outer ends of the anterior arms arise at the extremities of the subgenae, the posterior edges of the arms are straight. Ventrally, the projections giving rise to the mandibular and maxillary apodemes are quite heavy. The forward edge of the bridge has a slight bulge.

In Ophiogomphus rupinsulensis (Walsh), the outer ends of the anterior arms follow the backward curvature of the subgenae, and the posterior edges of these arms are concave. The forward ridges of the dorsal arms, before they are produced upward, are moderate in size.

The subgenae of Progomphus obscurus (Rambor) are not produced to the rear, and the posterior edges of the anterior arms are straight. From the ventral surfaces of these arms

arise only slight projections for carrying the adductor apodemes. The posterior pits are open and round.

The most heavily constructed tentorium of all species examined was found in Hagenius brevistylus (Selys). The anterior pits of this species are bent at an angle of about forty-five degrees at the inner ends. These pits are not straight slits, but curve outward as they follow the subgenal sutures. From a frontal aspect, the pits appear roughly L-shaped. The outer ends of the anterior arms follow the rearward curvature of the subgenae, and the posterior edges of the arms are concave. On the ventral surfaces of the anterior arms, adjacent to the bridge, are heavy projections which bear the maxillary and mandibular adductor apodemes.

The dorsal arms arise as slight ridges on the upper surface of the anterior arms approximate to the anterior mandibular condyles. These ridges are produced upward about one third the length of the anterior arms. On the basal, posterior surface of the dorsal arms are found heavy mandibular adductor apodemes.

As the posterior area of the bridge is produced upward, the heavy cervical condyles lie above the dorsal surface of the bridge. Both dorsal and ventral surfaces of the bridge are sulcate, and the anterior edge of the bridge is slightly concave.

The open posterior pits are long and wide. The short posterior arms meet the bridge at an angle of approximately ten degrees from the vertical.

Family Aeshnidae

The anterior pits of Aeshna constricta (Say) (Fig. 6) are smoothly curved as they follow the subgenal and epistomal sutures. These pits are bent at an angle of approximately forty-five degrees at the inner ends. Arising from the pits are heavy anterior arms that follow the rearward curvature of the subgenae. The concave posterior margin of the arms are strengthened by a round, swollen edge. At the end of the subgenal sutures, the tips of the anterior arms are dorsally extended and fuse into the ocular ridges. Ventrally, the arms give rise to the mandibular adductor apodemes, directly below the point at which the dorsal arms are produced. Immediately posterad of these apodemes, the ventral surfaces of the anterior arms develop large projections which extend backward to the bridge. These projections are long, and the inner edges form an ellipse that is almost closed at the distal ends. From the tips of these projections are produced the maxillary adductor apodemes.

Just inside the point of junction of the subgenal and epistomal sutures, ridges are produced on the upper surfaces of the anterior arms. These ridges, the dorsal arms, rise abruptly within one fifth the length of the anterior arms. Part of the ocular ridge is ventrally extended to meet and fuse into the posterior surface of the dorsal arms. This leaves a portion protruding from the outside edge of the arm,

making it appear to have a shallow keel. A faint carina runs from each anterior mandibular condyle to merge into the posterior surface of each arm. There are no mandibular adductor apodemes attached to the posterior surfaces of the dorsal arms.

The large tentorial bridge has a concave, sulcated forward edge. Ventrally, the surface of the bridge is smooth and bears well developed ventral cervical longitudinal apodemes. The cervical condyles are in the same horizontal plane as the sulcated dorsal surface of the bridge.

The slit-like posterior pits are long and open. The long posterior arms meet the bridge at about a forty-five degree angle from the vertical.

The tentoria of A. canadensis (Walker), A. interrupta (Walker) and Anax junius (Drury) vary little from that of A. constricta. In all of these species the posterior pits are round. The projections of the anterior arms, which bear the maxillary adductor apodemes, form a more ovate-rectangular figure on the inner edges. In keeping with this inner configuration, the tips of the projections are widely separated. From a frontal aspect, the anterior pits of A. canadensis appear L-shaped.

Fig. 5. Gomphus fraternus Say, 24X. Dorsofrontal aspect,
compound eyes and mouthparts removed.

Fig. 6. Aeschna constricta (Say), 24X. Dorsofrontal aspect,
Compound eyes and mouthparts removed.

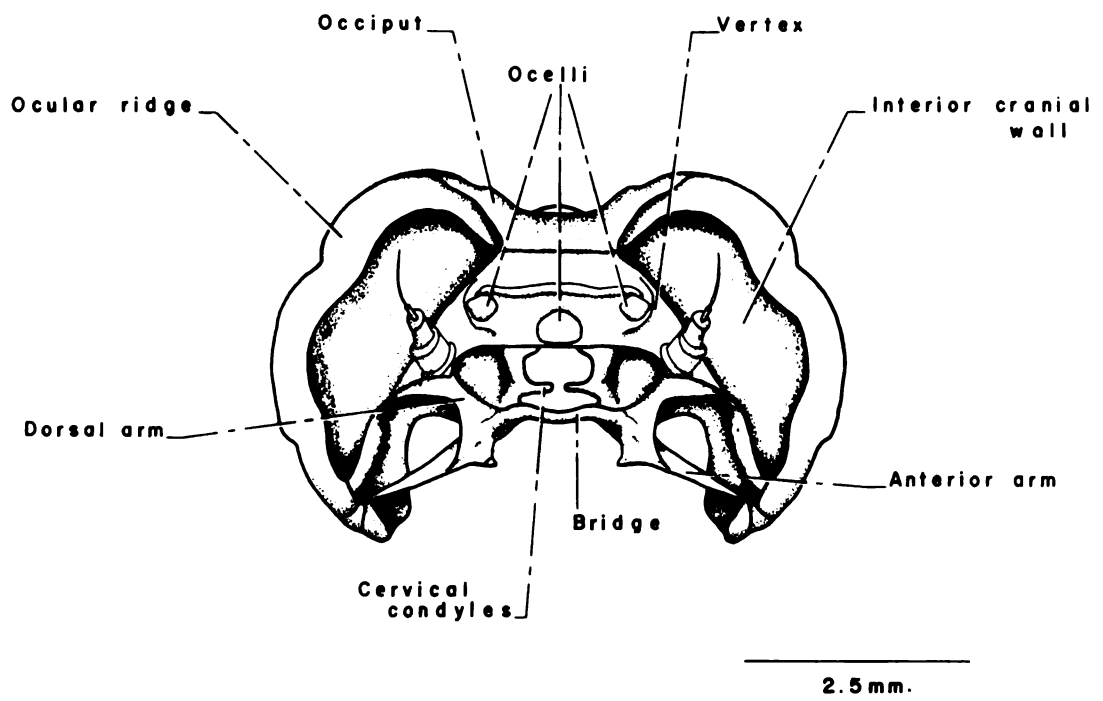


Figure 5

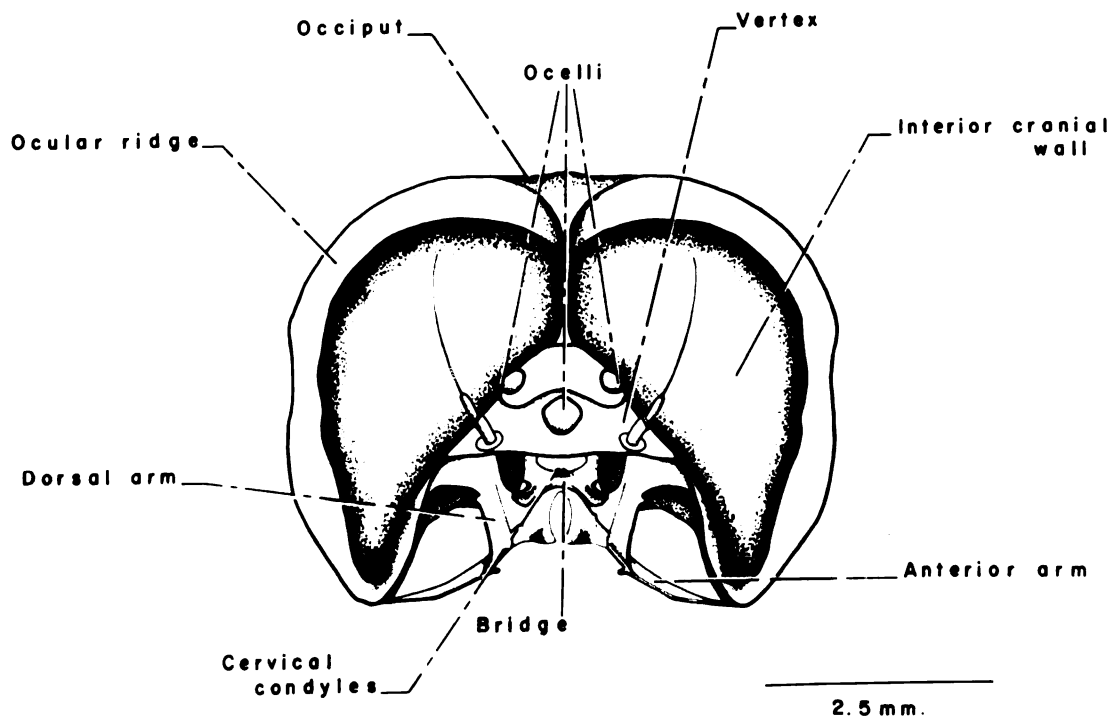


Figure 6

Family Libellulidae

In the subfamily Macrominae, only Macromia illinoisensis (Walsh) and Didymops transversa (Say) were examined. As the tentoria of these species are almost identical, a description of M. illinoisensis will suffice for this taxon. This description will also serve as a model for the typical libelluline tentorium (Figs. 1 and 2).

The anterior pits of M. illinoisensis are not straight slits, but curve smoothly outward as they follow the subgenal and epistomal sutures. The inner ends of the pits are curved approximately forty-five degrees. As the anterior arms follow the rearward curvature of the subgenae, the ectal ends of the arms become quite wide and their posterior edges concave. At the termination of the subgenae, the tips of the arms are dorsally produced and fuse with the lower portion of the ocular ridge. Anterad of the bridge, the ventral surfaces of the arms give rise to slight projections which bear the maxillary adductor apodemes. Forward of these projections, the ventral surfaces of the arms bear the mandibular adductor apodemes.

The dorsal arms arise as shallow ridges on the anterior arms. These ridges, originating near the anterior mandibular condyles, are produced upward within one quarter the length of the anterior arms. Segments of the ocular ridges extend downward to meet the dorsal arms. Because the forward

parts of these segments fuse to the posterior surfaces of the arms, the anterior edges of the arms remain free and appear as carinae. There are no mandibular adductor apodemes on the posterior surfaces of the dorsal arms.

Both surfaces of the tentorial bridge bear a sulcus, as does the straight anterior edge. The ventral cervical longitudinal apodemes, which originate on the under surface of the bridge, are delicate. Because the posterior end of the bridge is produced slightly upward, the cervical condyles lie just above the dorsal surface of the bridge.

The open posterior pits are quite large and crescent shape, and give rise to crooked arms which meet the bridge at an angle of about forty-five degrees from the vertical. The only significant differences between the tentoria of M. illinoisensis and D. transversa appear in the posterior arms and the cervical condyles. In the latter species, the arms are shorter and straighter, and the cervical condyles are level with the dorsal surface of the bridge.

With slight modifications, the design of the tentoria of subfamily Cordulinae is similar to that of the subfamily Macrominae. Unless noted, the details of the following species are in agreement with M. illinoisensis.

All of the species of this subfamily have cervical condyles that lie on the same level as the bridge, except

Cordulia shurtleffi (Scudder) where the condyles are slightly above the bridge. As seen from the front, the anterior pits of C. shurtleffi, Dorocordulia libera Selys, Somatochlora minor Calvert, and Tetragoneuria cynosura (Say) are straight. The dorsal arms are not produced upward as quickly as in M. illinoisensis, but arise about one half the length of the anterior arms. The anterior edge of the bridge of these species is round and sulcate, with the exception of S. minor which is straight and sulcate. C. shurtleffi and D. libera have posterior arms that are short and straight, while those of S. minor and T. cynosura are identical to the crooked arms of M. illinoisensis. All of these species have moderately long, slit-like posterior pits except T. cynosura, which has large, crescent-shaped pits, and Tetragoneuria spinigera Selys. The latter species has S-shaped pits that are moderate in size. Although the tentorium of T. spinigera is stouter than the general macromine and corduline tentoria, the bridge is thinner in construction. The anterior edge of the bridge is round and not sulcate. Dorsally, the surface is hollow and lies above the ectal ends of the bridge. The posterior arms of this species are short and thick.

Of the fourteen species of subfamily Libellulinae examined, none of them differed radically from subfamilies Macrominae and Cordulinae. Exceptions to the general structure of the tentoria of M. illinoisensis occur in the following species.

The tentoria of Libellula cyanea (Fabr.), L. pulchella (Drury), L. quadrimaculata Linn., and Nannothemis bella (Uhler) all differ from that of M. illinoisensis in having L-shaped anterior pits. The tentorium of N. bella is unique in its slightly longer posterior arms. In all of these species, the moderate sized posterior pits are slit-like, and give rise to short posterior arms. The dorsal surface of the bridge is level with the cervical condyles, and the sides curve downward so as to be below the level of the center portion of the bridge.

Sympetrum obtrusum (Hagen) and S. rubicundulum (Say) have indistinguishable tentoria. They both differ from M. illinoisensis in having slit-like posterior pits. The cervical condyles lie on the same level as the smooth, dorsal surface of the bridge. The anterior edge of the bridge is round.

The tentoria of Pachydiplax longipennis (Burm.) and Perithemis tenera (Say) are quite similar. Both have slit-like posterior pits and cervical condyles that are on the same level as the dorsal surface of the bridge. P. tenera, however, does not have a sulcated bridge. Perithemis lydia (Drury) conforms to the design of M. illinoisensis, except for the cervical condyles, which are angled upward and lie slightly above the bridge.

The following five species are not consistent in their structural variations from other members of the Libellulinae.

Both Erythemis simplicicollis (Say) and Erythrodiplax minuscula Rambur have tentoria with L-shaped anterior pits. The tentorium of E. simplicicollis has S-shaped posterior pits and the anterior edge of the bridge is round. In E. minuscula, the posterior pits were found to be closed. The tentorium of Celithemis elisa (Hagen) has round posterior pits and a thin bridge that is sulcate on the ventral surface only. In Ladonna sp., the large posterior pits are slit-like, and the dorsal surface of the bridge is without a sulcus. Leucorrhinia intacta (Hagen) is also characterized by slit-like posterior pits in the tentorium, but these are moderate in size. Here, the ventral surface of the bridge is not sulcate.

DISCUSSION

The description of the dorsal arms as ingrown apodemes, by Needham, Traver and Hsu (1935), was not substantiated by this investigation. A careful examination of boiled heads shows no signs of any external pits which such invaginations would produce. All observations show that these arms must arise as projections of the anterior arms. In some heads, deep pigmentation of the antennal and ocular ridges produces a distinct line of demarcation at the point of fusion with the dorsal arms. Prolonged boiling of many heads in potassium hydroxide have caused the ridges and arms to separate at this point. The ventral extension of the ocular ridges to the arms in the families Aeshnidae and Libellulidae, further delineates these two structures and their mode of junction.

Snodgrass (1928) states that the primitive location of the anterior pits is in the subgenal area. Neither he nor Hudson (1948) mention that the ectal ends of the anisopteran pits extend into the outer regions of the epistomal sutures. Hudson's (1944, 1947, 1948, 1951) work on the tentorium is extensive. His section dealing with the Odonata (1948), however, is too general to be used in a definitive study of the suborder Anisoptera. Hudson does not identify the mandibular and maxillary adductor apodemes which originate on the tentorium or the cervical condyles. He refers to these,

respectively, as the tendinous outgrowths and the semi-circular projections. He states further that the ventral cervical longitudinal apodemes "may possibly be regarded as the tendons of the flexors of the head.....". These structures were found to be of extreme importance in this study.

Lew's (1933) work on the odonate head, based largely on external features, reports that heavy sclerotization has closed and obscured the posterior pits in the adult forms. This condition was not found by the author. All heads, except E. minuscula, had posterior pits that were open and readily visible. This discrepancy may possibly be ascribed to desclerotization produced by the boiling of the heads in potassium hydroxide. Another difference was noted in the nomenclature used. Lew calls the tentorial bridge "the floor of the foramen magnum" and the aperture below the bridge, the labial cavity. As the ventral nerve cord passes through the latter opening, this opening must also be part of the occipital foramen, which is divided into two parts by the bridge. Although Lew does not give a comparative study of the tentorium, his overall analysis of the phylogeny of the head is thorough. Using the size of the compound eyes and the interocular distance as the most important characteristic, Lew places the families Gomphidae and Petaluridae closest to the primitive form. He considers the families Cordulegasteridae, Libellulidae and Aeshnidae, in that order, to be higher in development.

As far as is known, the presence of a third mandibular adductor muscle on the dorsal arms of only three out of the five anisopterous families has not been described before. Both Snodgrass (1935) and Short (1955) consider the retention of this muscle a primitive feature. The fact that this muscle is found in the families Petaluridae, Gomphidae and Cordulegasteridae is an indication that these groups are close to the primitive type. Using the size of the muscle apodeme as a criterion, the closeness to the condition where the adductor was normally functional can be hypothesized. Because the muscle apodeme is heaviest in the Petaluridae, it would seem that this family has the most primitive musculature. The moderately constructed adductor apodeme of the Gomphidae would place this group in an intermediate condition, while the lightly constructed muscle apodeme of the Cordulegasteridae would indicate that this group has evolved further along the line leading to the loss of the muscle. The presence of a heavily constructed adductor apodeme in H. brevistylus would indicate that this species has developed along different lines than the rest of the Gomphids. Both families Aeshnidae and Libellulidae have evolved far enough to have lost the third mandibular adductor.

It would appear that in the anisopteran head, the development has been one of both contraction and elongation. The wide heads of the Petaluridae and Gomphidae have compound

eyes that are separated by a broad occiput and vertex. These families have a tentorial bridge that lies almost in the same vertical plane as the anterior arms. During development, the anisopteran eyes have drawn closer together. In the Cordulegasteridae, the eyes are very close together, limiting the size of the occiput and vertex. The head of the Cordulegasteridae is still broad, however, and the tentorial bridge still lies close to the vertical plane of the anterior arms. Families Aeshnidae and Libellulidae have narrower and deeper heads than the preceding groups. The compound eyes of these families have migrated toward the meson, constricting the vertex and occiput. As a result of this general ventral elongation of the head, the anterior pits have migrated downward and the anterior arms come to lie considerably below the level of the bridge. A lower position of the aeshnine and libelluline anterior arms would be necessary to provide support to the lower portions of this form of head.

In the transformation from a broad, shallow head to a deep, narrow head, the angle between the subgenal sutures (and hence the anterior pits which are located there) and the epistomal suture has been increased. In the Petaluridae and Gomphidae this angle is thirty degrees. (H. brevistylus is the only variation found in the latter family, having an angle of forty-five degrees.) As the subgenal sutures are drawn ventrad, the angles are increased to forty-five degrees in the Libellulidae and Aeshnidae. These sutures also form an angle

of forty-five degrees in the Cordulegaster which would indicate that this family has begun developing along similar lines as the preceding two families.

The lengthening of the anisopteran head can also be traced by comparing the angles between the tentorial bridge and the posterior arms. These structures form an angle of thirty degrees in Petaluridae, and fifteen degrees in the Gomphidae. (An exception to the last measurement is found in H. brevistylus, in which species the angle is ten degrees.) In the Cordulegasteridae, Aeshnidae and Libellulidae, the posterior arms are ventrally produced, and the angle formed with the bridge is forty-five degrees.

In the Petaluridae and Gomphidae, the position of cervical articulation is well above the level of the bridge, and the occipital foramen extends upward toward the occiput. The same condition exists in the family Cordulegasteridae, except that the cervical condyles are only slightly dorsad of the bridge. As head shape changes, a shift in position of these structures is noted. The occipital foramen occupies a more central position in the cranium of families Aeshnidae and Libellulidae, and with three exceptions, the cervical condyles are on a level with the bridge. (It is quite possible that the discrepancy in the species M. illinoisensis, C. shurtleffi and P. lydia are due to malformations or damage to the head.) This migration of the position of the cervical condyles seems to follow the shift

in the position of the occipital foramen. It would appear that a modification in the shape of the head would change the point of balance and require a relocation of the cervical condyles.

Further modifications of the tentorium occur in the Aeshnidae and Libellulidae. In both of these families, the ocular ridges have been ventrally produced to fuse with the dorsal arms (Fig. 2). As the edges of these two structures meet at an angle, the arms are left with a slight carina. This carina acts as a strengthening corrugation and gives rigidity to the tentorium. Rigidity is also provided by the extreme tips of the anterior arms, which are curved upward to fuse with the flanges of the ocular ridges (Fig. 2). With this modification, the arms present a broader surface and a curved buttress which absorb stresses more efficiently than those of other families which merge in a sharp taper.

H. brevistylus was the only species examined which differed appreciably from its family characteristics. The retention of a heavy, third mandibular adductor apodeme, and the shallow angle made by the posterior arms and the bridge, appear to be primitive characteristics. A more advanced condition is noted in the angle of the subgenal and epistomal sutures, which is equal to that of the higher evolved Libellulidae and Aeshnidae. It is possible that a further study of this species would confirm the author's supposition that

this species has diverged from the general gomphine development.

The works of Lew (1933) and Sargent (1937) indicate that there is not sufficient justification to arrange the phylogeny of an order on the basis of any one morphological characteristic. Sargent investigated the development of the scalariform thoracic apodemes and the curvature of the mesopleural sutures which serve to strengthen the pterothorax of the Anisoptera. He stated that in regard to the thoracic apodeme, the Cordulegasteridae are the most primitive in development, the Aeshnidae are an intermediate group, and the Gomphidae the most advanced. He reported the Libellulidae as being a divergent form, progressing along a line that developed the mesopleural suture rather than the scalariform apodeme. Lew, using the size of the eyes and the interocular distance of the odonate head, considered the Gomphidae and the Petaluridae to be primitive types, and the Cordulegasteridae, Libellulidae and Aeshnidae, in that order, to be evolved forms. These two works serve to point out that a phylogenetic arrangement of a group will differ when based upon different morphological criteria. Furthermore, these works show that a highly evolved form does not necessarily achieve maximum specialization in all aspects of its morphology. Conversely, a relatively primitive group, such as the Gomphidae, may develop great specialization in a given structure.

The author fully realizes the difficulties involved in using a single structure, such as the tentorium, for drawing conclusions on the phylogeny of the group. Nevertheless, he is inclined to consider the arrangement of Lew to be nearer the true phylogeny. It would appear, however, that the Cordulegasteridae have evolved to a higher level than attributed by Lew, and may possibly be developing along lines that diverge from the other anisopterans. Both Aeshnidae and Libellulidae are highly evolved forms, but the results of this investigation do not justify the assignment of the highest position to the Aeshnidae.

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