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FUNCTIONAL MORPHOLOGY OF THE FEEDING APPARATUS IN LARVAL AND ADULT *AESHNA JUNCEA* (L.) (ANISOPTERA: AESHNIDAE)*

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The head is prognathous in the larva, but hypognathous in the adult. In the larva, the prey is captured by the labial hooks. The labium is then flexed to bring the prey to the mandibles and maxillae for mastication. The labrum, maxillae and labium are moved out of phase with the mandibles. In the adult, the prey is captured by the front legs and the labium plays no part in food capture and little in feeding. However, the mandibles and maxillae are used as in the larva. The growth of the head capsule at metamorphosis of the larva into the adult is compared with the changes occurring in other Odon. and the differences are discussed.

INTRODUCTION

The anatomy of the head and mouthparts of the common earwig, *Forficula auricularia*, in relation to the feeding habits have been described by POPHAM (1959). Similar studies have been made for various mayflies (SEYMOUR BROWN, 1961), the larvae of the stonefly *Perla cephalotes* (CHISHOLM, 1962) and the beetles *Nebria brevicollis* and *Philonthus decorus* (EVANS, 1964). The form of the mouthparts in the Odonata have been described by BERLESE (1909), TILLYARD (1917), CRAMPTON (1923), LUCAS (1923, 1930), LEW (1934), WHEDON (1927, 1929), MUNSCHEID (1933), ASAHINA (1954), CHAO (1953), SNODGRASS (1954) and MATSUDA (1965), whilst ETIENNE (1977a, 1977b) has described the feeding behaviour of odonatan larvae. BUTLER (1904) made a comparative

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study of the labia, GRIEVE (1937) of the muscles of the head of *Ischnura verticalis* (Say), SNODGRASS (1954) and SHORT (1955) have given detailed accounts of the morphology of the heads of *Anax imperator* Leach and *Aeshna cyanea* (Müll.) respectively. There is a general lack of information on how feeding takes place and this paper will help to fill this gap in existing knowledge.

MATERIAL AND METHODS

The anatomy and morphology of *Aeshna juncea* have been studied using serial wax and thick celloidin sections stained with either haematoxylin and eosin or with Mallory's triple stain. Feeding has been studied with the aid of a binocular microscope using wild specimens fed under laboratory conditions.

LARVAE

HEAD AND MOUTHPARTS

As the anatomy and morphology of the larval stages of other dragonflies has been described by various authors, it is sufficient to summarise the

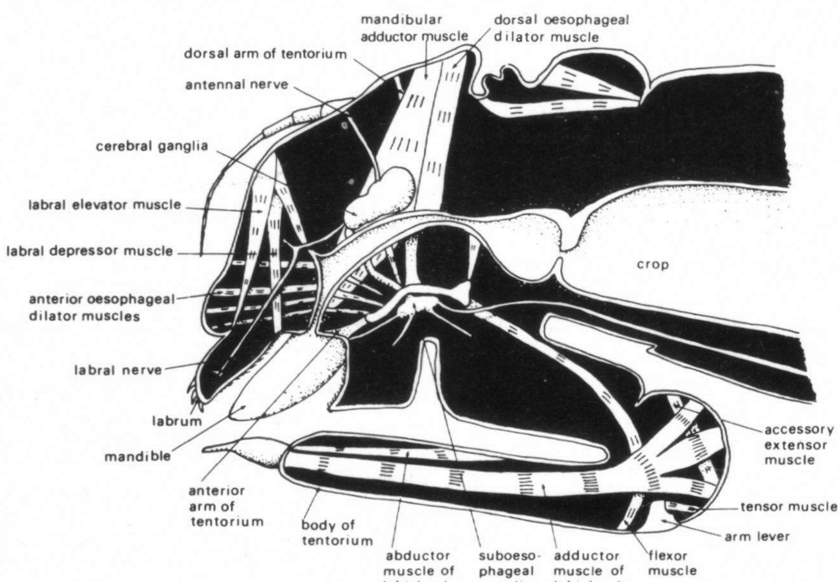


Fig. 1. Sagittal section of larval head of *Aeshna juncea* to show the cranial nervous system, tentorium and principal muscles.

essential features. The larva of *Aeshna juncea* has a prognathous head bearing a pair of large compound eyes meeting in the mid-dorsal line between which are a pair of short, forwardly directed antennae. The oblong labrum distally bears a number of rows of proprioceptive setae, while the mandibles have two distal teeth behind which is a hard molar area. Each of the paired maxillae is composed of an inner galeolacinia (MATSUDA, 1965), flanked on its outer surface by an unsegmented maxillary palp. The labium normally lies folded under the head with the postmentum directed backwards and prementum forwards. Distally the prementum bears a pair of hook-like structures. The homologies of these appendages have been discussed by most authors since BUTLER (1904) and TILLYARD (1917); but the explanation of CORBET (1953) and MATSUDA (1965) that they represent the paraglossae of other insects and a palpus is here adopted. The terminology of the various parts of the labium has been standardised by CORBET (1953) and is used in this paper

The joint between the postmentum and the prementum calls for special comments. On the dorsal side of the labium, between the pro- and postmentum, there is a large semioval area of arthrodial membrane (Fig. 2). In the centre of this area is a small invagination, which extends proximally between the ends of the great premento-glossal muscles, which adduct the prementum, to be attached by two divergent ligaments to a pair of apodemal knobs, at the basal margin of the prementum. According to SNODGRASS (1954) tension is maintained in this plicated fold by a pair of small tensor muscles, which originate, one on each side, on the end of the postmentum, lateral to the lever arms and which are inserted on the posterior edge of the anterior lever lobes. If the abdomen is squeezed, the labium as a whole is rotated forwards in front of the head and the movable hooks are abducted. Both TILLYARD (1917) and SNODGRASS (1954) have suggested the hydraulic action of haemolymph as a major mechanism for labial extension. Even if these suggestions are accepted, the role of the muscles must also be considered. The large prementoglossal muscles are inserted on the lever arms,

Fig. 2. Relative positions of the mandible and maxilla at four stages of the mouthpart feeding cycle.

only a short distance behind the hinge. Although the mechanical advantage of this lever system is low, the prementum can be rotated through a large angle as a result of only a slight contraction of these muscles and is of adaptive significance in rapidly capturing the prey. Further extension of the labium causes the volume of the appendages to increase and the arthrodial membrane at the pre-postmentum junction would be dilated, which, if uncontrolled, could inhibit the opening of the moveable hooks by haemocoelic fluid pressure. This possibility is prevented by the invagination at the base of the prementum becoming partially everted during labial extension and thereby directing haemocoelic fluid into the palps. The increase in the number of labial setae in successive instars, as described by CORBET (1951) for *Sympetrum striolatum* (Charp.) increase the efficiency of the labium for gripping the prey.

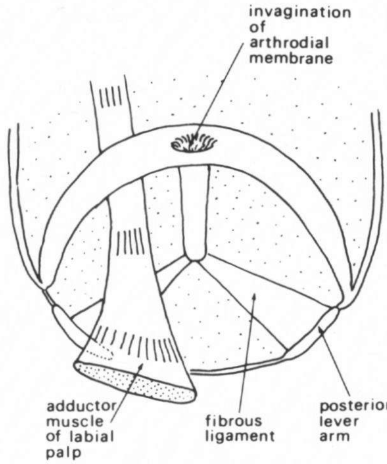


Fig. 3. Dorsal view of the labial hinge of the larval *Aeshna juncea*.

THE TENTORIUM

The tentorium of *Aeshna juncea* consists of a transverse central body joined to the inner cranial wall by three pairs of arms. The anterior arms are formed by invaginations from a pair of slit-like pits situated laterally, one of each side, in the pleurostomal part of the subgenal sulcus. These arms expand slightly along their line of cranial attachment, which occurs immediately posterior to the dorsal half of each mandible, and then pass obliquely backwards to the central shaft. The comparatively short dorsal arms of the tentorium arise as branches of the anterior arms and extend upwards to the cranial roof. These dorsal arms also expand along their line of cranial attachment near the outer margin of the frons, lateral to the antennal scape. The junction of the dorsal arms and frons, which is internally effected by short non-muscular fibres, is indicated externally by a pair of elliptical depressions known as the tentorial maculae. The short, posterior tentorial arms arise as invaginations of the cranial edge, immediately behind the invaginations of the maxillae.

The shaft of the tentorium divides the posterior occipital foramen into upper and lower halves. The lower passage accommodates the nerve cord, the upper one the oesophagus, salivary ducts (only present in the final nymphal instar) and the longitudinal tracheal trunks. The function of the tentorium is to form an internal brace to the head capsule and to act as the origin for the antennal, maxillary, labial and cervical muscles.

THE NECK

The head of *A. juncea* is attached to the thorax by a narrow neck or cervix. Dorsally, it appears as a very narrow transverse membrane, strengthened by sclerites. The anterior margin is supported dorsally and dorso-laterally by the post occiput. Behind this is an almost circular, median, dorsal sclerite in which the ecdysial sulcus is usually discernible. Immediately behind this sclerite, a pair of very slight sclerites run transversely in the neck membrane. When the neck is in a retracted position a transverse dorsal fold occurs in the neck membrane immediately posterior to these transverse sclerites and the pronotal collar almost impinges on the epicranial ridge of the head. Posterior to the outer extremity of each transverse sclerite is a small slightly sclerotised, oval area (the latero-dorsal cervical sclerite), from the back of which another slightly sclerotised, postero-dorsal, cervical sclerite runs obliquely outwards on either side. The postero-dorsal and dorso-lateral margin of the neck is attached to the front of the pronotum, which anteriorly forms a collar-like structure (the pronotal collar). Both the dorsal sclerites and the anterior margin of the pronotal collar bear numerous proprioceptive setae, which are used to inform the insect of the position of the head relative to the thorax.

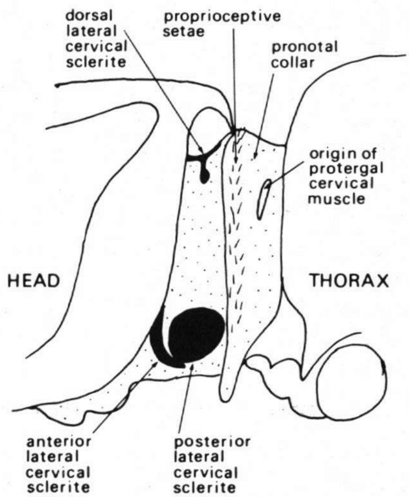


Fig. 4. Lateral view of neck of *Aeshna juncea*.

The ventral surface of the neck is very long, owing to the backward inclination of the posterior margin of the head. Being entirely membranous, the ventral surface of the neck is extremely flexible, a factor which enhances the forward thrust of the labium during protraction. The anterior margin of the neck is supported ventrally by a small elliptical gular sclerite, which is continuous anteriorly with the proximal ventral wall of the labium. The posterior margin of the ventral neck membranes is attached to the basisternum of the prothorax.

A pair of lateral cervical sclerites on each side of the neck cover the lateral regions. The anterior sclerite of each pair articulates dorsally with a small sclerite, the cephaliger, which is hinged to the postoccipital rim and ventrally with the posterior lateral cervical sclerite of that side. The latter articulates posteriorly with the anterior margins of the sternum. This arrangement of the sclerites allows the head to be raised and lowered, while, as CHISHOLM (1962) points out, the hinge between the two pairs of sclerites facilitates slight lateral movements.

FUNCTIONAL MORPHOLOGY OF THE NECK

Head movement in the larva is slight and ponderous when compared with the versatility and alacrity of movement of the adult head. Elevation and depression of the head are produced by the dorsal and ventral sets of muscles traversing the neck and running through the occipital foramen.

The head is raised forwards and upwards by the contraction of:

(A) The dorsal longitudinal muscles of the prothorax:

(1) A pair of large medial dorsal muscles, which originate on the first dorsal phragma and pass forwards through the neck to insert on the dorsal postoccipital ridge. A small branch from each of these muscles arches upwards into the pronotal collar and is inserted on the anterior rim of this collar.

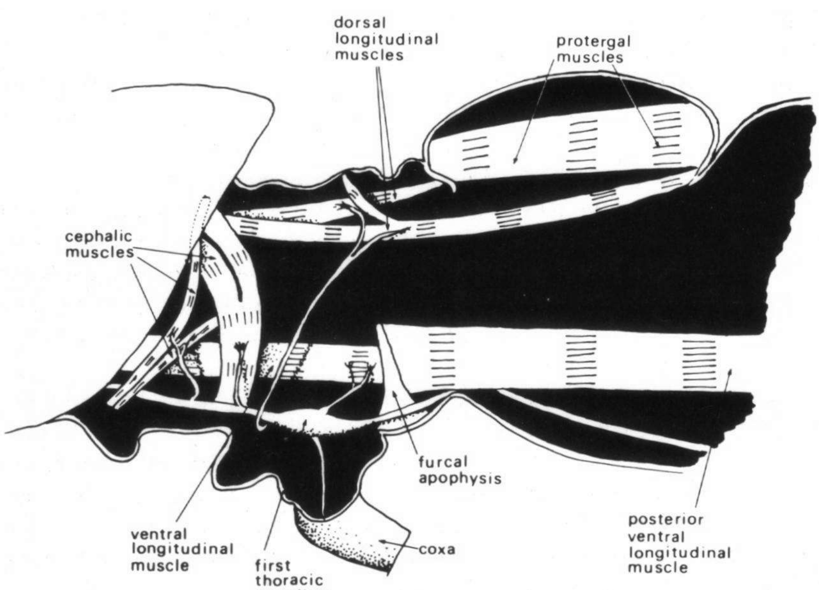


Fig. 5. Diagram to show the main cervical muscles of the larva of *Aeshna juncea*.

(2) A pair of smaller dorsal muscles, which originate on the anterior surface of a small median pronotal apophysis and insert on the postoccipital rim immediately anterior to the insertions of muscles (1) above.

(B) The protergal muscles of the head:

(3 & 4) These two pairs of muscles originate on the anterior wall of the first dorsal phragma and run forwards to insert on the pronotal apophysis.

(C) The cephalic muscles of the cervical plates:

(5 & 6) These two pairs of muscles originate on the postoccipital ridge, lateral to the insertions of muscles (1) and (2) above and insert within the concavity of the posterior lateral cervical sclerites and indirectly raise the head.

(7) A pair of muscles which originate ventro-laterally within the pronotal collar and pass almost vertically upwards between muscles (5) and (6) to insert on the postoccipital ridge.

As the head is moved upwards and forwards, the length of the dorsal side of the neck is reduced by the infolding of the arthrodial membrane behind the transverse, dorsal cervical sclerites. At the same time the two ventral cervical folds of arthrodial membrane, which occur posterior to the gular and lateral cervical sclerites unroll, thus facilitating the forward and upward movement of the head. When the head is lowered, the opposite occurs. The lowering of the head is achieved by the contraction of the following muscles:

(D) The ventral longitudinal muscles of the prothorax:

(8) A pair of stout muscles arising on the prothoracic fureal apophysis. These muscles pass through the neck and occipital foramen and insert laterally on the posterior tentorial bridge.

(E) The protergal muscles of the first cervical plate:

(9) A pair of stout muscles, which originate dorso-laterally on either side of the pronotal collar. They pass obliquely downwards to their anterior insertions on the posterior surface of the anterior lateral cervical sclerites. Contraction of these muscles probably depresses the head by retracting and elevating the posterior ventral cervical region.

(F) The prosternal muscles of the anterior cervical sclerites:

(10) A narrow band of muscle, which originates on the anterior surface of the coxa of each foreleg, internal to the coxal armature, and crosses over to insert on the inner dorsal extremity of the anterior lateral cervical sclerite on the opposite side.

Lateral movement of the head is effected by the contraction of the muscles 3, 4, 5, 6, 7 and 9 on one side of the head.

PREFEEDING BEHAVIOUR

ETIENNE (1977) has shown that the larvae of *Aeshna cyanea* are ambush hunters, which first swim towards their prey and then rapidly decelerate to walk and creep towards a potential victim, until it is within striking distance. If the prey escapes at this stage, the larva freezes, steps backwards and changes its direction of orientation, thereby bringing unsuccesful hunts to a halt and reducing the chances of future encounters with unobtainable prey.

FOOD CAPTURE

The larva either remains motionless until the victim is within reach, or stealthily stalks its prey until it is close enough to strike. The mask is then extended with great rapidity and at the same time the palps are forced wide apart. Contraction of the palpus adductor muscles results in the palps closing and gripping the prey. The flexor muscles of the labium contract and draw the prey backwards, where it is gripped firmly by the lacinial teeth of the maxillae before being passed to the mandibles.

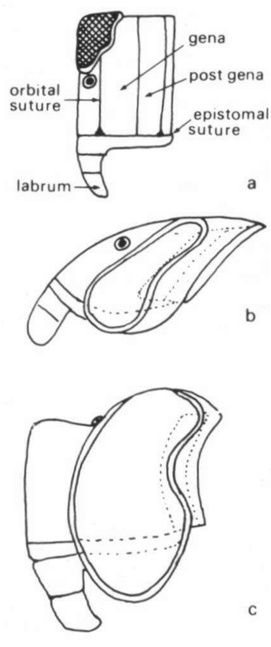


Fig. 6. Diagrams of: (a) hypothetical ancestral insect head (after SNODGRASS, 1954), — (b) lateral view of the head of the larva of *Aeshna juncea*, — (c) the same of the adult.

FEEDING

The mandibles and maxillae move during feeding as follows. The maxillae manipulate the food by a rotatory action. First the maxillae are retracted and abducted to a depressed position, with the laciniae and palps ventral and posterior to the mandibles (Fig. 2a). The maxillae are then gradually protracted, adducted and elevated (Fig. 2b). As this happens, the laciniae and palps slide along the median edage of the mandibles (Fig. 2c). Retraction of the maxillae follows immediately and is accomplished by a dorsalward rotation of the laciniae (Fig. 2d). The maxillae are then rotated outwards and distally depressed, but meanwhile the mandibles have converged. As they approach the mid-line, the labrum is depressed and also retracted by the contraction of the labral depressor muscle. At the same time, the distal part of the flexible anteclypeus is turned inwards. Mandibular closure is accompanied by elevation of the hypopharynx. As the mandibles re-open, the labrum is elevated and the hypopharynx is depressed. The movements of the mandibles are out of phase with those of the labrum, hypopharynx and maxillae.

As the maxillae are adducted, the mandibles open and the prey is pushed backwards between the closing mandibular teeth, which cut it into slices by their scissor-like action. Since the lacinial teeth are sharply pointed, they help to collect food particles and push them upwards into the cibarial cavity. At the same time, the labrum is lowered, the hypopharynx raised and a quantity of saliva flows on to the food particle. Orally directed cuticular processes on the inner labral edge and on the surface of the hypopharynx prevent loss of food particles to the outside and encourage their movement towards the oesophagus. After reaching the cibarium, the food material is moved by peristalsis through the oesophagus into the crop.

ADULTS

The transition from an aquatic larva into a terrestrial adult involves profound changes in the form of the head, which are associated with changes in the habitat and method of feeding. In the adult, the mouthparts assume a hypognathous position and the role of the labium, in capturing the prey and

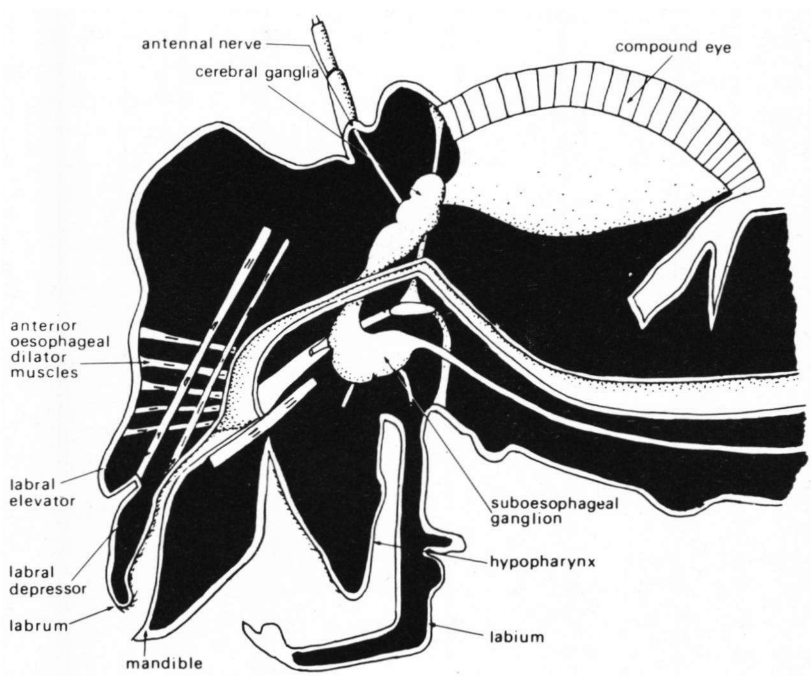
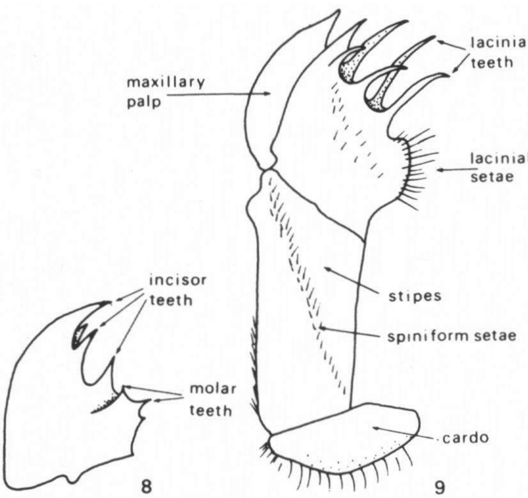


Fig. 7. Sagittal section of the head of adult *Aeshna juncea*.

holding it whilst it is masticated is taken over by the forwardly directed legs of the thorax. A change from a prognathous larval head to the hypognathous adult condition is achieved by a relatively greater growth of the dorsal side of the head and the expansion of the compound eyes until they meet in the mid-dorsal line. At the same time, the pre- and postmentum segments of the labium become relatively shorter and are no longer used for capturing the prey. The labial palps are also reduced and there is a corresponding enlargement of the lacinial teeth for lifting the prey upwards towards the mandibles. The mandibles change from a rectangular shape with medially directed teeth to triangular structures with the teeth directed downwards and inwards. Inspite of these changes in shape, the basic organisation and arrangement of muscles and nerves remains largely unchanged. In contrast the neck is greatly modified to allow the head greater mobility.



Figs. 8-9. Mandible (Fig. 8) and maxilla (Fig. 9) of the adult *Aeshna juncea.*

THE NECK

The neck of the adult dragonfly is exceedingly small and slender, pivoting the head almost on a point, and allowing it to turn in practically every direction. So mobile is the head, in fact, that the observation of a dragonfly cleaning its head and eyes with its fore-legs usually evokes in the onlooker a sense of apprehension lest the head should topple off its apparently precarious pivot.

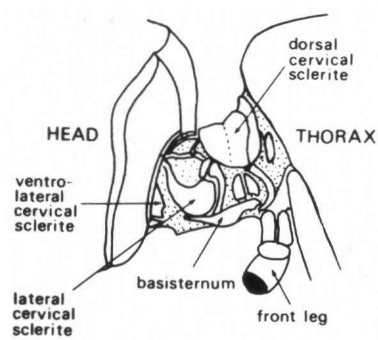


Fig. 10. Lateral view of the neck of adult *Aeshna juncea.*

Dorsally, the membranous neck extends from the occiput anteriorly to the pronotal collar posteriorly. It is strengthened by several small sclerites. A small, median T shaped sclerite (the antero-dorsal cervical sclerite) gives a certain amount of rigidity to the more anterior part of the dorsal surface. Posterior to this occurs a median crescentric sclerite (the dorsal cervical sclerite) to the outer margin of which is hinged a pair of backwardly-directed longitudinal, dorsal cervical sclerites. When the neck is in the normal retracted position, the main dorsal cervical sclerite fold occurs directly behind this crescentic sclerite. This fold is rendered possible by the flexing of the lateral cervical sclerites, the proximal halves of which become dorsal to the distal portions, so that the crescentic sclerite comes to lie dorsally, or even posterior, to the posterior dorsal cervical sclerite, which runs transversely across the neck at this point. This last sclerite, together with another two pairs of small dorso-lateral cervical sclerites immediately behind it, supports the posterior region of the neck. The outer edges of the neck membrane are attached to the posterior extensions of the lateral cervical sclerites.

The ventral surface of the neck is almost entirely membranous, being strengthened by only three slight, posteriorly-placed ventral cervical sclerites. One of these is medially-placed, the posterior pair being lateral to it. Anteriorly, the ventral surface of the neck is medially attached to the gular sclerite and peripherally to the proximal ventral margin of the labium. The posterior ventral surface of the neck is attached to the basisternum.

A pair of substantial lateral cervical sclerites support the ventro-lateral and lateral walls of the neck membrane. The anterior extremity of each of these neck plates continues antero-dorsally as the cephaliger or head bearing process, and finally meets its fellow from the opposite side in the mid-dorsal line. Just in front of each lateral cervical sclerite a pair of ventro-lateral cervical sclerites occur, which are not found in the larval neck, but here give extra rigidity where it is needed.

FUNCTIONAL MORPHOLOGY OF THE NECK

When compared with that of the larva, the neck of the adult dragonfly is greatly reduced in size, and the muscles are proportionately also reduced. Numerically, however, the cervical musculature of the adult is more complex than that of the larva. This, combined with the decrease in the size of the neck, is associated with the great mobility of the adult head.

As in the larva, elevation and depression of the head are produced by the dorsal and ventral cervical muscles as follows.

(A) The dorsal longitudinal muscles:

(1) A pair of slender horizontal muscles originating on the anterior surface of the first dorsal phragma, on either side of the mid-line. These muscles pass forwards until they reach the pronotal apophysis. Here they diverge, one passing on each side of the apophysis, and are inserted on the outer extremities of the

crescentric dorsal cervical sclerite. The effect of the contraction of this pair of muscles is to cause a dorsal cervical transverse fold to occur in the neck membrane, immediately behind the crescent-shaped sclerite. This change helps in the elevation of the head.

(2) The formation of the dorsal cervical fold is also produced by the contraction of a small pair of dorsal muscles, which originate on the anterior face of the first dorsal apophysis and run outwards to insert laterally on the crescentic sclerite lateral to muscles (1) above.

(3) A median longitudinal muscle originates on the anterior wall of the pronotal apophysis and passes forwards dorsal to the gut and gives off two branches to the gut wall. This muscle is inserted on the postoccipital ridge.

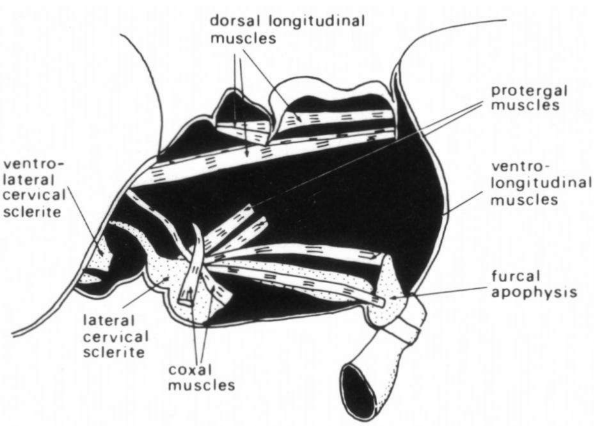


Fig. 11. Cervical muscles of the neck of adult *Aeshna juncea.*

(B) The protergal muscles:

(4) A pair of longitudinal muscles occur within the pronotal collar. They originate along the posterior wall of the collar and converge as they run forwards to insert on the pronotal apophysis.

(5) A slender, median muscle originates on the median ventral tip of the first dorsal phragma, between the origins of muscle (1) and passes forward between these muscles to insert on the corresponding tip of the pronotal apophysis.

(C) The cephalic muscles:

(6, 7 & 8) Two oblique muscles on the inner ventral wall of each lateral cervical sclerite and passing antero-dorsally to their insertion. The outer margin of each pair of muscles is dorso-laterally inserted on the postoccipital ridge while the inner muscle is attached to the body of the tentorium, in close proximity to a third oblique muscle

This muscle originates on the posterior wall of the lateral cervical sclerite on either side and passes internal to muscles (6) and (7). Since the cervical area posterior to the lateral cervical sclerites is heavily sclerotised it has considerable stability and it seems likely that the contraction of muscles 6, 7 and 8 will cause a backward movement of the dorsal region of the head, rather than an elevation of the cervical sclerites themselves.

The head is lowered by the contraction of the following muscles:

(D) The ventral longitudinal muscles of the prothorax:

(9) The ventro-lateral muscles originate, on each side, on the anterior face of the furcal apophysis and pass forwards to its proximal insertion on the body of the tentorium.

(E) (10) A second muscle arises ventrally on the coxa of each leg, passes ventral to muscle (9) and crosses over to its insertion on the lateral cervical sclerite of the opposite side.

(F) The protergal muscles of the lateral cervical sclerites:

(11 & 12) On each side there is an oblique muscle (11) which originates laterally on the anterior rim of the pronotal collar and passes antero-ventrally to its insertion on the anterior portion of the lateral cervical sclerite of that side. A similar, but slightly more horizontally-placed muscle occurs internal to muscle (11) on either side. Contraction of muscle (11) probably effects the lowering of the head, while contraction of muscle (12) retracts the head.

Lateral movements of the head are effected by the contraction of muscles 6, 7 and muscles 10, 11 and 12 of one side only. Because no two of these muscles have identical origins and insertions, the effect of their contraction will be to enable the head to turn in a variety of directions to various degrees.

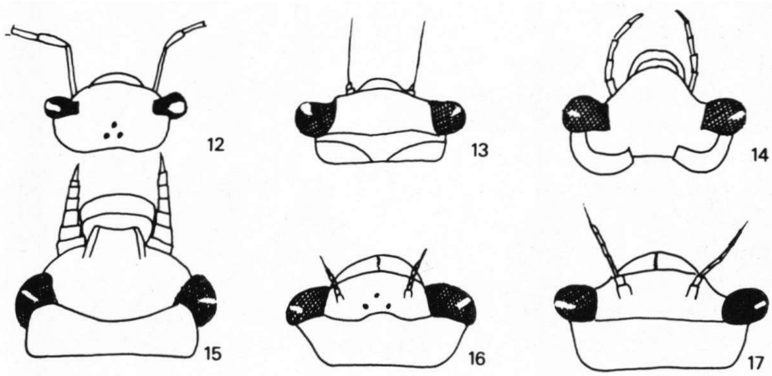
FOOD CAPTURE AND FEEDING

The adults of *A. juncea* feed exclusively on the wing on small Diptera, Coleoptera and other available insects. The prey is seized by the forwardly directed forelegs and held in this position whilst the food is examined and eaten. Artificial feeding of starved adults with meal worms showed that the mouthpart movements followed the same sequence as in the larva, except that the labium takes little part in feeding. The food is passed from the legs to the laciniae, which at this stage are depressed and abducted. As the mandibles open, the maxillae are adducted and thereby lift the food particles upwards into the cibarium between the mandibular teeth. At the same time, the labrum is lowered and the labium flexed forwards. The food particles are then crushed between the closing mandibular teeth. At the same time saliva is added to the food to help in the process of digestion in the crop. As a second portion of food is pushed by the maxillae between the open mandibular teeth, the previous food particle is pushed upwards into the cibarium, where it is held in position by the orally directed cuticular processes on the epipharynx and on the front of the hypopharynx. Here the food particles are crushed by the molar areas of the mandibles before being drawn upwards by peristaltic movements through the oesophagus.

DISCUSSION

It is generally agreed that the hypognathous type of insect head is primitive, in as much as the mouthparts retain the position of ambulatory appendages. Such a view overlooks the principle that all stages in the life cycle have been subject to the influence of evolution and that the final form of the adult is the result of various growth processes occurring at all stages of the life cycle. The less specialised Orthoptera have a hypognathous head in both the larva and the adult and there is relatively little change in head structure between the early instars and the adult. In contrast, cyclorrhaphous Diptera have very specialised heads in the adult stage, which, though hypognathous, have developed from a greatly reduced prognathous larval head with virtually no mouthparts but hook like mandibles. The hypognathous heads of Thysanura, such as *Machilis*, have a large pair of compound eyes situated near the top of the head and antennal sockets situated immediately ventral to them. This type of insect head can be regarded as primitive firstly because the positions of the compound eyes, antennal sockets and labrum are closely associated with the corresponding cerebral ganglia and secondly because it is a generalised type from which the forms of head capsule in other Exopterygote insects can be derived. If this is so, it follows that the head of the adult anisopteran can be regarded as primitive in so far as it is hypognathous, but the large compound eyes meeting on the top of the head and the reduced antennae situated medially between the eyes are to be regarded as secondary specialisations. So too are the mouthparts of the adult, which are adapted to enable the adult to feed whilst flying. In contrast, the larval head may be regarded as unspecialised in the size and position of its compound eyes and in resembling the Thysanura and many Orthoptera in collecting its food with the labium and then passing it forwards to the maxillae and mandibles.

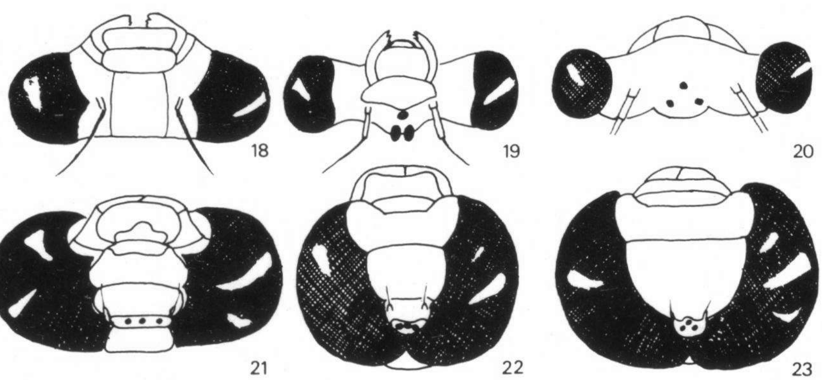
Nevertheless, the specialised form of the individual mouthparts, and especially of the labium, must be regarded as specialisations for the feeding methods used. In addition, the larval head is prognathous as an adaptation to carnivorous feeding habits. The prognathous form of the larval head is produced by a relatively greater growth of the underside of the neck and the ventral surface of the head between the bases of the mandibles and maxillae. As a result of these growth differentials in the embryonic stage, the maxillae of the larva come to be horizontal, with the mandibles directed slightly downwards and the labium slightly upwards. This development of prognathism at this stage is associated with a slightly dorso-posterior rotation of the cerebral ganglia, accompanied by a tendency for the antennal sockets to shift towards the apex of the cranium — a tendency which is absent in some Zygoptera. At metamorphosis, the change from the prognathous larval head to the hypognathous form of the adult head is achieved by a relatively more rapid growth of the upperside of the head, especially in the region of the frons, while the increase in the number of ommatidia in the eyes causes them to grow towards each other in the mid dorsal line. These changes are accompanied by a corresponding lateral growth of the protocerebra lateral to the antennal nerves.



Figs. 12-17. Dorsal view of the heads of the larvae of: (12) *Calopteryx virgo* (L.), — (13) *Lestes dryas* Kirby, — (14) *Pyrrhosoma nymphula* (Sulz.), — (15) *Gomphus vulgatissimus* (L.), — (16) *Libellula quadrimaculata* L., and — (17) *Sympetrum striolatum* (Charp.).

The ecological significance of such cranial differences is that the larvae and the adults of each species have developed independent adaptations to carnivorous feeding habits in water and in flight respectively. It is possible that the ancestral Odonata were carnivorous, terrestrial insects, but that selective pressure from the more specialised insects has largely driven them off the land into water and into the air respectively. The Odonata have survived by evolving aquatic larvae and by a rapid metamorphosis converting them into adults which can feed and mate on the wing. In this respect, adult Ephemeroptera have evolved a stage further in as much as the adult is solely concerned with mating and reproduction and the lack of feeding has reduced the adult life to a minimum.

The work of ASAHINA (1954) on the functional morphology of the relic dragonfly *Epiophlebia superstes* Sel. and of CHAO (1953) on the unspecialised dragonfly *Onychogomphus ardens* Needham suggests that the ancestral Odonata had the heads of the larva and the adult with moderately separated eyes and the same number of ommatidia in each stage. The antennae were situated in an antero-lateral position, the frons of the adult was not inflated and the anteclypeus was small. The mandibles of the larva comprised a number of forwardly directed teeth and a molar area. The mandibles of the adult were similar. The maxillae of the adult and larvae comprised a lacinia with about six spines and the galea formed a palp-like appendage. In the larval labium, the glossae were fused to produce a median lobe, which enlarged in the adult. In both the larva and the adult, the paraglossae were represented by the lateral lobe and the palp by a moveable hook.



Figs. 18-23. Dorsal view of the heads of the adults of: (18) *Calopteryx virgo*, — (19) *Lestes dryas*, — (20) *Pyrrhosoma nymphula*, — (21) *Gomphus vulgatissimus*, — (22) *Libellula quadrimaculata*, and — (23) *Sympetrum striolatum*. The heads are drawn with the mouth upwards for comparison with the corresponding diagrams of the larval heads.

If the head of *Epiophlebia superstes* is typical of unspecialised Odonata, it follows that those dragonflies in which other forms of the larval and adult heads show the greatest similarity, must be regarded as showing an unspecialised level of Odonatan organisation. Figures 12-17 show that there is a general similarity in the form of the larval heads of both the Zygoptera and the Anisoptera, both having well developed antennae. In contrast, Figures 18-23 show that there is a wide range in the form of the adult heads. In Zygoptera, such as *Calopteryx virgo* (L.) there is a large measure of similarity between the head of the larva and that of the adult. In the Zygopteran adult, the antennae are well developed and there are the same number of ommatidia in the eyes of both larva and adult. In the Anisoptera, the heads of *E. superstes* and *Gomphus vulgatissimus* (L.) show a general similarity to those of their larvae, but in the more specialised Anisoptera, such as *Libellula depressa* L. and *Sympetrum striolatum* (Charp.), the antennae are greatly reduced, the eyes are greatly enlarged and there is also a greater difference between the mouthparts of the larva and those of the adult. The life cycles of *Epiophlebia superstes* and *Calopteryx virgo* show a primitive level of odonatan organisation, whereas the more specialised anisopteran species such as *L. depressa* and *S. striolatum* have evolved a type of life cycle with greater changes taking place at metamorphosis than in other species of Odonata.

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