The Anatomy of the Head and the Alimentary Canal of Adult Eriocraniidae (Lep., Dacnonypha).

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CONTENTS

1. Introduction

The phylogenetic interrelationships between the primitive families in the Trichoptera-Lepidoptera-complex has been a subject of considerable interest and discussion. Especially the question concerning the position of the family Micropterygidae (s.str.) has caused much controversy. Originally considered genuine Lepidoptera, this family was given rank of a separate order, Zeugloptera, by Chapman (1917). Some of the later authors have fully supported this view (Hinton 1946 a, 1958, Kiriakoff 1948) or at least suggested it to be the correct one (Ehnbom 1948, Mortimer 1965), while others have maintained the true lepidopterous nature of the Micropterygidae (e.g., Tillyard 1919, 1923, Crampton 1920, Viette 1949, Dumbleton 1952, Hennig 1953, Sharov 1965, Ross 1967, Niculescu 1967 b). However, it is obvious from the literature cited that more research is needed for a full understanding of the early evolution of this order-complex. More detailed comparative anatomical investigations of the primitive Trichoptera, the Micropterygidae and the primitive undisputed Lepidoptera are needed, together with a critical re-evaluation of the similarities found to exist between these groups. As repeatedly stressed by Hennig, similarities due to common retention of original conditions (symplesiomorphies) are of no value for the tracing of evolutionary patterns.

The present paper gives an account of the anatomy of the head and the alimentary canal in adult insects of the lepidopterous family Eriocraniidae, which belongs to the primitive suborder Dacnonypha. Comparisons with primitive Trichoptera and with Micropterygidae are attempted primarily by using the descriptions available in the papers by Ehnbom (1948), Hannemann (1956), Mortimer (1965) and Klemm (1966). Comparisons are made also with other Lepidoptera in order to elucidate some of the trends in morphological evolution within the order (cp. Kristensen 1968a).

The Dacnonypha (with the single superfamily Eriocranoidea) comprises four families, viz. Agathiphagidae, Eriocraniidae, Mnesarchaeidae and Neopseustidae. Material suited for the study of internal structures was available only of the Eriocraniidae. The skeletal head-anatomy of the remaining families has been described elsewhere (Dumbleton 1952, Kristensen 1967, 1968b).

Descriptions of the external anatomy of the head-capsule and/or the mouthparts of the Eriocraniidae have previously been given by Genthe (1897), Busck & Böving (1914), Crampton (1920), Tillyard (1923) and Hansen (1930). None of these descriptions are very detailed, however, and some of them contain serious errors, e.g., that of Tillyard, which unfortunately forms the basis of the account given by Bourgogne (1951).

It should be noted that Crampton, Hansen and Ehnbom, following an outdated taxonomy, included the Eriocraniidae in the family Micropterygidae. Matsuda (1965) included the Eriocranoidea in the order Zeugloptera together with the Micropterygidae. However, the Eriocraniidae are considered to be quite distinctly separated from the Micropterygidae at the family level and to be genuine Lepidoptera by all other recent systematists including Hinton and Kiriakoff. Recently Niculescu (1967 b) has advanced a theory according to which the Eriocraniidae are even more primitive Lepidoptera than the Micropterygidae.

2. Material and methods

Dried specimens of representative species of the genera *Heringocrania, Dyseriocrania* and *Eriocrania* were cleared in KOH for the study of skeletal anatomy. For the study of internal anatomy fresh specimens of *H. unimaculella* (Zetterstedt), *E. semipurpurella* (Stephens) and *E. haworthi* Bradley (*purpurella* auct., *rubroaurella* auct.) were fixed in Bouin and dissected in 70 % alcohol. Whole mounts were prepared from the dissections and examined in ordinary light or phase contrasts; polarized light proved very useful for the study of musculature.

Sagittal and horizontal serial sections at a thickness of 8—15 μm were made after inbedding in celloidin and ester-wax. The sections were either stained with Ehrlich's haematoxylin-eosin, iron haematoxylin-Biebrich scarlet, or azan. As a supplement 50 μm celloidin sections stained with a modified Mallory phosphotungstic acid haematoxylin were examined.

No attempts were made to study the cephalic tracheal system.

The information concerning internal anatomy applies to *E. haworthi* unless otherwise stated.

3. Descriptive and comparative part

3. 1. The head-capsule

The head (figs. 1—2) is hypognathous, the anterior surface slightly convex, the posterior surface flattened. Posterodorsally the head has an impression in the midline. Anterolaterally is a pair of very short subgenal processes.

The relatively small compound eyes are situated laterally in the lower half of the head. Ocular costae ("Augenkapsel" of Hannemann 1956, "ocular sclerites" of Yagi & Koyama 1963) are well developed. According to the figures of Busck & Böving (1914), a narrow ocular sclerite (in the sense of Snodgrass, 1935) is present in *Dyseriocrania* (*Mnemonica* auct.) *auricyanea* Walsingham.

A pair of ocelli (fig. 1, oc) is present mediodorsad of the compound eyes.

The antennae are inserted between the eyes. No antennal sulcus is present. The head-wall is produced into a condylus which articulates with the scapus ventrally. The articular membrane is rather large.

The conspicuous anterior tentorial pits (fig. 1, at) are situated some distance ventrad of the lateral corners of the antennal sockets.

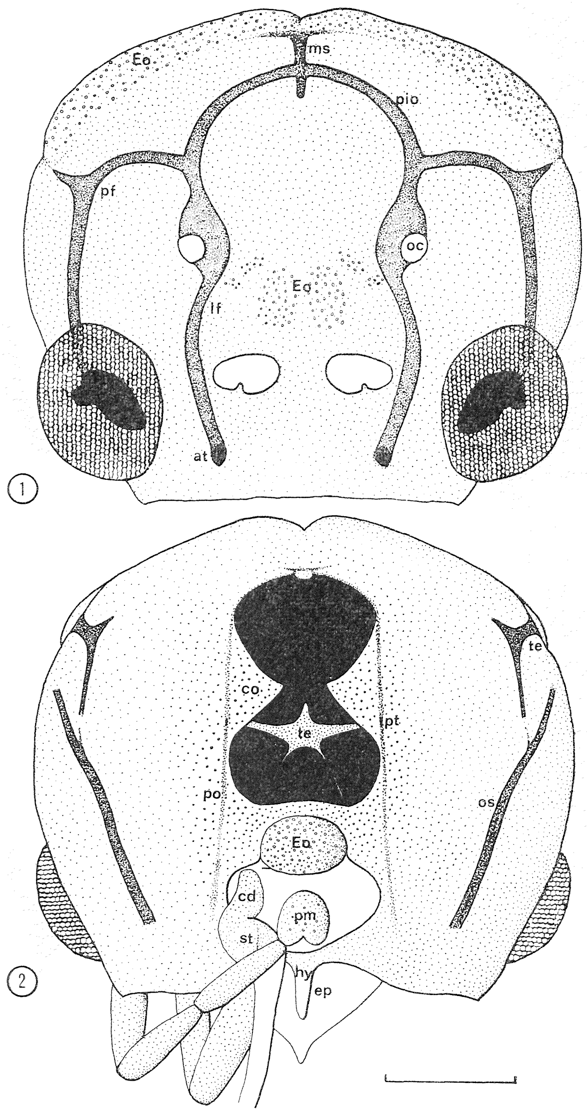
The clypeolabral suture is distinct.

The clypeus ("postlabrum" of Busck & Böving 1914) is not distinctly separated from the frons; a line of folded cuticle between the anterior tentorial pits may be the remnants of a transclypeal sulcus (cf. p. 245). Laterally the clypeus is limited by an indistinct cuticular fold, continuing ventrally into a deep inflection of the head-wall at the medial and ventral sides of the mandibular base.

The frons is bounded laterally by a mostly very distinct laterofacial sulcus (fig. 1, lf) which extends dorsally from the anterior tentorial pits and reaches the ocellus. As no exact criteria for laterally delimiting the frons are now recognized (e.g., Matsuda 1965), it seems of no morphological importance that the course of the sulcus in this family is laterad of the antennae. The two ocelli are connected by a distinct, posteriorly curved sulcus, here termed the postinterocellar sulcus (fig. 1, pio). The postinterocellar and the laterofacial sulci thus together delimit a median facial area, the most dorsal part of which belongs to the epicranium, as a pair of postcerebral pharyngeal dilators arises on it.

Some distance behind the ocellus a distinct sulcus branches off from the postinterocellar sulcus; curving on the epicranium it reaches the eye and may be continued on the ocular costa. It is termed here the postfrontal sulcus (fig. 1, pf).

A transverse lateral temporal sulcus (fig. 2, te) extends to the posterior surface of the head where it usually becomes indistinct;



Figs. 1—2. *Eriocrania*, headcapsule, weak cuticular folds and hairs omitted. (1) anterior view, antennae omitted. (2) posterior view, right mandible, maxilla and labial palp omitted. cd, cardo; co, occipital condyle; Eo, Eltringham's organs (alveoles indicated only); ep, epipharynx; hy, hypopharynx; lf, laterofacial sulcus; ms, midcranial sulcus; oc, ocellus; os, occipital sulcus; pf, postfrontal sulcus; pio, postinterocellar sulcus; pm, prementum; po, postoccipital sulcus; pt, posterior tentorial pit; st, stipes; te, corporotentorium resp. temporal sulcus. Scale 200 μm.

(The drawings are based upon a specimen of *E. sparmanella* but are modified to represent a generalized condition; e.g. the postoccipital sulcus is more strongly indicated than was actually the case).

in *D. auricyanea,* however, it almost reaches the occipital foramen (Busck & Böving 1914, fig. 27). Anteriorly this sulcus is more or less distinctly connected with a short branch from the postfrontal sulcus.

The occipital sulcus (fig. 2, os) is distinctly developed on the posterior cranial surface from a short distance above the subgenal processes. It usually becomes indistinct before reaching the temporal sulcus; in some specimens of *E. semipurpurella* and *E. sparmanella* (Bosc), however, it is seen to fuse with the latter. Sometimes it is bipartite at its upper end. It is possible that the mediodorsal part of the occipital sulcus at an earlier evolutionary stage has fused with the postinterocellar sulcus. This implies that most of the temporal sulci together with the dorsal parts of the postfrontal sulci actually belong to the occipital sulcus (cp. p. 246). Two very short sulci sometimes seen anastomosing with the postoccipital sulcus at its dorsolateral corners are presumably secondary strengthening devices rather than continuations of the occipital sulcus.

The postoccipital sulcus (fig. 2, po) is more or less distinctly present laterad and dorsad of the occipital foramen. The dorsal part of the postoccipital ridge is strongly developed and more or less produced medially. In the sulcus are located the posterior tentorial pits (fig. 2, pt). Above the latter the postocciput is medially produced as a pair of triangular occipital condyli (fig. 2, co) which may be large (e.g., *E. sparmanella*) or quite small (e.g., *D. subpurpurella* Haworth) and with which the laterocervicalia articulate. Ventrally the sulcus is continued as the hypostomal sulcus laterad of the maxillary bases; it becomes indistinct above the subgenal processes. Two hypostomal bridges are formed; the anterior, from which the hypopharynx projects, behind the mandibles, the posterior behind the maxillae and the labium.

A short midcranial sulcus (fig. 1, ms) is present dorsally on the epicranium; it terminates immediately in front of the postinterocellar sulcus.

In addition to the above-mentioned sulci the head-capsule is furnished with smaller cuticular thickenings in places where extra strengthening is needed.

The head is richly provided with Eltringham's organs (figs. 1—2, Eo). They occur on the epicranium (two pairs along the dorsal and lateral edge of the head, several pairs on the median facial area), medially on the frons and medially on the postmental area.

Comparative remarks. The head-capsule of Eriocraniidae has the same general proportions as that of Agathiphagidae, due to the small size and ventral position of the compound eyes. In most other Lepidoptera the eyes are enlarged and the dorsolateral areas of the epicranium correspondingly reduced.

A subgenal process is found also in Micropterygidae and Neopseustidae, as well as in Trichoptera and Mecoptera (Klemm, 1966) i. e., among the groups in the panorpoid complex having decticous pupae, and it may be the adult counterpart of the sclerotized frame of the posterior mandibular articulation in the pupa.

A comparison of the eriocraniid cephalic sulcus-pattern with that of related groups can be made tentatively only. The displacements of sulci in the different groups, necessiated by different feeding mechanisms, cranial dimensions and development of Eltringham's organs, tend to obscure the homologies.

In Micropterygidae (Issiki 1931, Hannemann 1956) the anterior tentorial pits are connected by a very well-developed sulcus, which according to general practice must be termed a transclypeal sulcus, since a pair of cibarial dilators (identified by their insertions being ventrad of the frontal ganglion connectives) originates dorsad of it. It appears reasonable to homologize the line of folded cuticle between the tentorial pits in Eriocraniidae with the transclypeal sulcus in Micropterygidae although the single pair of cibarial dilators arises entirely ventrad of it. A laterofacial sulcus is at most faintly indicated in Micropterygidae (e. g., *Micropteryx aruncella* (Scopoli), Issiki 1931, fig. 35 a). A postinterocellar sulcus is present in Micropterygidae and in some genera an interocellar sulcus is present as well. The occipital sulcus in the east-palaearctic micropterygid genera becomes indistinct near its dorsolateral corners, and in some *Sabatinca* and *Micropteryx* its dorsomedial part has fused with the postinterocellar sulcus; these are possibly initial stages in the evolution leading to the eriocraniid condition. A pair of temporal sulci dividing the occiput at the level of the dorsal corners of the foramen as in *D. auricyanea* is present in some micropterygid genera (Hannemann 1956, considered them to be the postoccipital sulci, but Klemm 1966, seems to be right in disputing this). The midcranial sulcus is variously developed; in some *Micropteryx* it is absent, in others it reaches the level of the antennal sockets.

The dacnonyphous family having the cephalic sulcus-pattern most similar to the Eriocraniidae is the Neopseustidae (Kristensen 1968 b). No distinct epistomal sulcus is present in this family. There occurs a distinct, uninterrupted occipital sulcus, which dorsally curves in forwards direction on the epicranium. On each side two sulci extend between this sulcus and the large compound eye; they are interpreted as the laterofacial and the postfrontal sulcus, respectively. If the above-advanced suggestions concerning the postinterocellar and postfrontal sulci in Eriocraniidae are correct, the patterns in the two families are basically similar. The laterofacial sulcus in Neopseustidae is on the anterior surface of the head present only ventrad of the anterior tentorial pits; on each side the area between the antennal socket and the pit is entirely occupied by a conspicuous Eltringham's organ. The temporal sulcus dividing the occiput is present. The midcranial sulcus reaches the occipital sulcus. In Agathiphagidae (Dumbleton 1952) the sulcus-pattern is much more reduced. *Agathiphaga vitiensis* Dumbleton has a V-shaped sulcus on the anterodorsal surface of the head, which may be homologous with the postfrontal sulci + medial part of postinterocellar sulcus in Eriocraniidae. Both *Agathiphaga* species have a long midcranical sulcus. In Mnesarchaeidae (Kristensen 1968 b) the head-capsule is devoid of sulci except for a vestigial temporal sulcus.

In higher Lepidoptera (Bourgogne 1951, Matsuda 1965) only the laterofacial sulcus consistently persists. The clypeal and frontal areas sometimes have fused in a complex way; in *Protoparce* pharyngeal dilators are stated to arise at the same level as, or even ventrad of, cibarial dilators (DuPorte 1956). The transverse sulcus often connecting the antennal sockets, which may (e. g., *Dilina*, Short 1951) or may not (e. g., *Danaus, Protoparce,* DuPorte 1956) coincide with the limit between the origins of pharyngeal and cibarial dilators, is probably in no case the primitive epistomal sulcus, but a secondary feature evolved independently several times for functional reasons. The apparent correlation between the interantennal distance and the presence of this sulcus in Papilionoidea (Ehrlich 1958) seems to support this view. The midcranial sulcus is distinct, e. g., in some Incurvariidae (Niculescu 1967a).

The primitive trichopterous genus *Rhyacophila* (Klemm 1966) has a weakly developed transclypeal sulcus (by Klemm tentatively called epistomal sulcus; however, as a pair of cibarial dilators arises dorsad of it, this is in conflict with current terminology). There occurs a laterofacial sulcus which from the anterior tentorial pit extends dorsally laterad of the antenna. On the posterior surface of the head is an occipital sulcus which gradually disappears dorsally and a temporal sulcus which extends from the dorsolateral corner of the occipital foramen and divides the occiput. In these aspects *Rhyacophila* shows greater similarities to primitive Lepidoptera than to the higher Trichoptera, as noted by Klemm.

3. 2. **The tentorium**

In the primitive genus *Heringocrania* the anterior tentorial arms are strongly sclerotized bars (fig. 15, aa). About their middle they give off equally well-developed dorsal arms which almost reach the head-capsule a short distance behind the antennae. Very near the occipital foramen the posterior tentorial arms together with the tentorial body form a short, stout bar provided with a medioposterior projection (figs. 11, t, 15, 16, pt). The tentorium in the genera *Dyseriocrania* and *Eriocrania* are specialized in having the anterior arm very much reduced behind the point where the dorsal arm arises; here they become colourless and extremely thin. They reach the posterior arms as hardly discernible strands (fig. 16).

Comparative remarks. It is difficult to decide whether the presence of dorsal tentorial arms in some Dacnonypha (they occur also in the Neopseustidae and the Mnesarchaeidae, Kristensen 1968b) is a primitive feature or a secondary specialization. As far as known they do not occur in the Agathiphagidae (Kristensen 1967) and in the Micropterygidae. The lepidopterous tentorium otherwise is very uniform, a simple π-shaped structure (Bourgogne 1951). A few Papilionidae do have dorsal arms (Ehrlich 1958); however, in this case there is little doubt that they have been secondarily evolved. Dorsal arms are present in primitive Trichoptera Integripalpia and are retained in some Limnephiloidea (Ross 1967).

The reduction of the posterior part of the anterior tentorial arms in higher Eriocraniidae is a most peculiar feature only paralleled in the Agathiphagidae (Kristensen 1967). However, because of the normal development of the arms in *Heringocrania* and in the Mnesarchaeidae and Neopseustidae (these families may be considered to constitute together the advanced sister-group of the Eriocraniidae, Kristensen 1968b), this similarity cannot be considered a homology.

The unpaired posterior projection from the corporotentorium is a character to which no attention has been paid in the literature. I have found it to be present also in *Micropteryx,* in the Neopseustidae and in the Mnesarchaeidae, but not in several primitive trichopterous genera examined (*Agapetus, Tinodes, Wormaldia, Agraylea); in *Rhyacophila* weak paired projections are present.

3. 3. The cervix

The cervical membrane between the head and the prothorax is rather large, especially ventrally. By this, considerable mobility of the head in the vertical plane is achieved; in living specimens the long axis of the head may form a very obtuse angle with that of the body.

The laterocervicalia (figs. 11, 17, lcv) are a single pair of rather large, anteriorly tapering plates. Anteriorly they articulate with the occipital condyli, posteriorly with the propleura; no sclerotic connexion between their posteromedial corners and the prosternum was found. The narrow anterior part bears a small hair-plate with minute setae (a proprioceptor, registering the movements of the head). Internally the laterocervicalia are furnished with a longitudinal costa which becomes indistinct posteriorly. Mediad of this costa is a suture (rather indistinct in some species, e. g. *E. semipurpurella*) which delimits the posteromedial part of the plate. This part may be homologous with the posterior cervical sclerite of generalized insects, the suture thus representing the line of fusion.

The musculature of the cervix (fig. 11) consists of 10 sets of muscles inserting on the head and the laterocervicalia (the following account is based on *E. semipurpurella*):

1. M. pronoto-postoccipitalis, a pair of muscles arising medially on the pronotum and inserting on the postocciput.
2. M. propleuro-postoccipitalis, a group of very slender bands arising from the anterior margin of the propleuron and inserting on the postocciput.

3. M. laterocervico-postoccipitalis, a relatively strong muscle arising from the lateral half of the laterocervicale and inserting on the postoccipital ridge.

4. M. profurco-postoccipitalis, a narrow muscle arising on the lateral apical projection of the prosternal furca and inserting on the postoccipital ridge.

5. M. cervico-tentorialis, a group of slender bands arising dorsally on the cervical membrane and inserting partly dorsally on the corporotentorium, and partly on its posterior projection.

6. M. profurco-tentorialis, a relatively broad muscle arising subapically on the prosternal furca and inserting on the medial projection of the corporotentorium.

7. M. procoxo-tentorialis, a narrow muscle arising on the proximal rim of the procoxa immediately anterior of the pleural articulation of the latter; it extends to the tentorium close to 6.

8. M. propleuro-laterocervicalis, a relatively broad muscle arising from the anterodorsal corner of the propleuron and inserting anteriorly on the laterocervicale.

9. M. phragmo-laterocervicalis, arising on the first thoracic phragma and inserting on the internal costa of the laterocervicale at about the middle of its length.

10. M. profurco-laterocervicalis, arising from a medial apical projection of the prosternal furca. It is divided into two bundles, both of which insert on the internal costa of the laterocervicale, one near its anterior end, the other posterior to 9.

Comparative remarks. The laterocervicale of Eriocraniidae is similar to that of *Micropteryx* (Hannemann 1956) and primitive Trichoptera. In higher Lepidoptera and Trichoptera this sclerite acquires an L- or T-shaped outline (Bourgogne 1951, Ehrlich 1958, Tindall 1965).

The cervical musculature of *Eriocrania* is rather similar to that of *Micropteryx* (Hannemann 1956). The latter differs in having an additional m. profurco-laterocervicalis (this might, however, be homologous with the ventral bundle of 10), in having an additional pair of pronoto-postoccipital muscles originating laterally, in lacking homologues of 5 and 9 and in having a small prosterno-laterocervical muscle. A muscle originating from the anterodorsal corner of the propleuron and inserting on the corporotentorium is presumably homologous with 8 in *Eriocrania.*

In higher Lepidoptera muscles homologous with 2 and 5 apparently have not been described. No propleuro-laterocervical muscle has been described either, but a muscle between the anterolateral part of the pronotum and the laterocervicale (or the tentorium) found in all families examined by Maki (1938) and a muscle between propleuron and tentorium in *Telea* (Nüesch 1953) are perhaps homologous with it. A profurco-tentorial muscle is described only in *Fumea* (Dierl 1964); it may, however, be homologous with a muscle between profurca and the ventrolateral portion of the posterior end of the head also found in all families examined by Maki (1938). A m. phragmo-laterocervicalis occurs in *Plutella* (Maki 1938), *Fumea* (Dierl 1964) and *Telea* (Nüesch 1953; here it originates on the prealar arm). It is possibly homologous with a muscle between the phragma and the head in *Herse* (Berlese 1909), *Milina* and *Amata* (Maki 1938). The remaining muscles of *Eriocrania* may be straightforwardly homologized throughout the order. In some groups more sets of pronoto-postoccipital muscles are present.

The primitive trichopterous genus *Stenopsyche* (Maki 1938) lacks muscles homologous with 2, 5, 6, 7, 8 and the sterno-laterocervical muscle present in *Micropteryx*. The tentorio-procoxal muscle which was suggested to be a distinctive feature of the Lepidoptera (Berlese 1909, cp. Hannemann 1956) is present in *Rhyacophila* (Klemm, personal communication).

3. 4. **The antennae**

The antennae are filiform. The scapus (fig. 18, sc) is the largest segment; it is approximately cylindrical, narrowing somewhat towards the base. The basal edge is thickened except in the lateral part. Ventrally it is provided with a small ginglymus fitting the condylus of the antennal socket. At the joint between the scapus and the pedicellus the edge of the former is ventrally somewhat concave; in the wide membranous area thus produced is situated a small triangular sclerite (fig. 18, ts) covered with microtrichia. The pedicellus (fig. 18, pe) is about half the size of the scapus and also approximately cylindrical. Its proximal edge is thickened and dorsally slightly produced. The segments of the flagellum are cylindrical and very uniform.

The two basal segments are covered with narrow scales and long, raised setae. The flagellum is covered with depressed, narrow scales; ventrally in the anterior half of each segment a pair of setae are projecting from the scalecovering.

The Johnston's organ is of moderate dimensions, corresponding to the size of the pedicellus.

The extrinsic antennal musculature (fig. 3) consists of four muscles arising on the V-shaped structure formed by the strongly sclerotized part of the anterior tentorial arm and the dorsal arm:

11. M. tentorio-scapalis anterior, originating medially on the anterior arm rather close to the head-wall and inserting medially on the edge of the scapus.

12. M. tentorio-scapalis medialis, originating medially from the "bottom" of the "V" and inserting near 11.

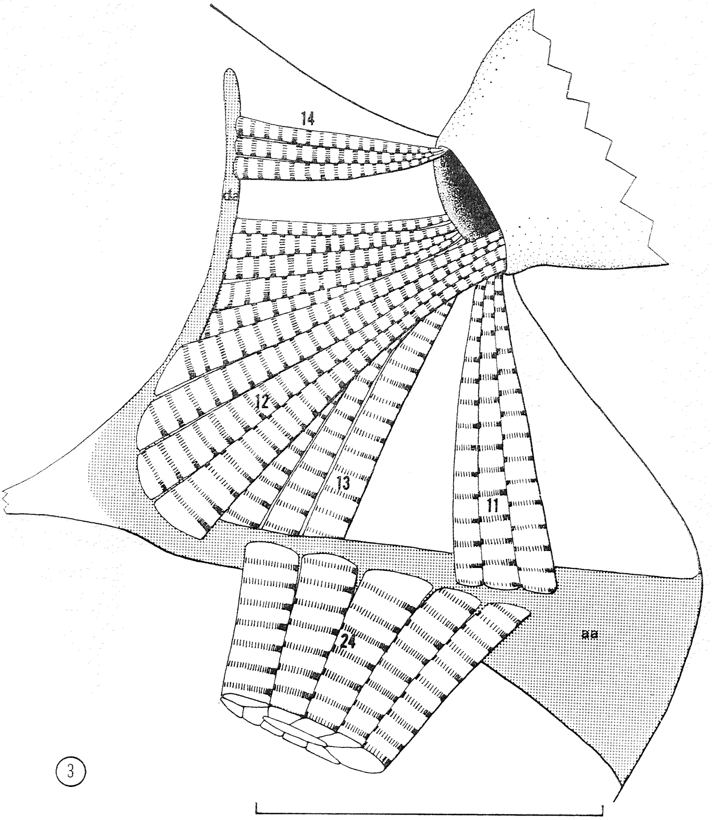


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Fig. 3. *E. haworthi,* tentorial musculature. aa, anterior tentorial arm; da, dorsal tentorial arm; 11, m. tentorio-scapalis anterior; 12, m. tentorio-scapalis medialis; 13, m. tentorio-scapalis lateralis; 14, m. tentorio-scapalis posterior; 24, m. tentorio-cardinalis. Scale 100 μm.

13. M. tentorio-scapalis lateralis, a very broad muscle; it originates laterally on both sides of the "V" and inserts laterally in the scapus.

14. M. tentorio-scapalis posterior, originating near the apex of the dorsal arm and inserting posteriorly in the scapus.

The intrinsic musculature consists of four muscles originating in the scapus and inserting near the proximal edge of the pedicellus:

15. M. scapo-pedicellaris dorsalis, arising on the dorsal wall of the scapus and inserting dorsally on the edge of the pedicellus.

16. M. scapo-pedicellaris posterodorsalis, a longer muscle inserting posterior to 15.

17. M. scapo-pedicellaris ventralis, originating from over a large area of the ventral scapal wall and inserting ventrally on the edge of the pedicellus.

18. M. scapo-pedicellaris posteroventralis, a straight muscle arising on the basal edge of the scapus and inserting on the triangular sclerite in the membrane between scapus and pedicellus.

(The orientation refers to the antenna being arranged perpendicular to the median plane of the head).

Comparative remarks. The shape and musculature of the antenna is of the type generally occurring in the most primitive groups of the Trichoptera-Lepidoptera-complex. Only in the Neopseustidae is the shape of the scapus and its articulation with the pedicellus of a more specialized type (Kristensen 1968 b). Four extrinsic muscles (or groups of muscles) presumably is the primitive condition in insects (Matsuda 1965), and four is a very common number in higher Lepidoptera (e. g., Ehrlich 1962) although it may vary from one to five (Schmitt 1938). Four intrinsic muscles likewise is the primitive condition; in most higher insects there are two (Matsuda 1965). Among higher Lepidoptera four are present in *Scirpophaga* (Pradhan & Aren 1941) and two in male Fumeinae (Dierl 1965). The size and shape of the antenna vary considerably within the order. The Johnston's organ is noteworthy enlarged only in the Papilionoidea (Ehnbom 1948).

3. 5. **The organs of ingestion and digestion**

Apparently adult Eriocraniidae have never been observed visiting flowers or other sources of fluid nutrients (e. g., honeydew).

However, in captivity they readily suck on waterdrops. It may therefore be suggested that the main function of the sucking mouthparts in this family is to facilitate the water uptake. As is well known, the cuticle of most terrestrial arthropods provides a most efficient protection against desiccation under normal conditions. However, insects of small size like the Eriocraniidae, which fly actively during the warmest hours of the day, are quite likely to experience a considerable waterloss through the spiracles, and a compensating oral uptake of water may therefore be important.

The sucking tube is constructed by the galeae, proximally roofed over by the labrum and closed laterally and ventrally by the mandibles and the hypopharynx, respectively.

3. 5. 1. The labrum

The outline of the labrum (fig. 19) is somewhat different in different species but usually approximately pentagonal. Its anterior surface is sclerotized and more or less densely covered by scales and microtrichia. The posterior surface, the epipharynx, is membranous, medially provided with papillae (fig. 20, el). These papillae were referred to as "taste buds" by Tillyard (1923); however, except for a few of the proximal papillae (fig. 20, es) they are not furnished with sense organs. In some of the papillae the fibres of the labral compressor muscle insert. Basally in the lateral labral wall is a pair of small sclerotizations, the tormae (fig. 19, to).

The extrinsic labral musculature (fig. 14) consists of:

19. M. fronto-labralis, the labral retractor. A pair of rather narrow muscles arising on the frons just mediodorsad of the anterior tentorial pits and inserting on the tormae.

20. M. clypeo-epipharyngealis arising on the clypeus and inserting on the base of the epipharynx. A muscle with a similar position in *Micropteryx* (no. 20 of Hannemann 1956) was by Matsuda (1965) interpreted as homologous with the anterior labral retractor in generalized insects. The latter, however, typically originates from the frons and inserts on the anterior edge of the labrum, which seems hardly compatible with the position of the muscle in question. In my opinion this is most likely to be an anterior median cibarial dilator which has shifted its point of insertion a short distance forward. In Eriocraniidae the fibres of

20 are very close to those of the lateral cibarial dilators (39).

The intrinsic labral musculature is:

21. M. labro-epipharyngealis, the labral compressor (fig. 14). Arising on the sclerotized medial area of the anterior wall its fibres insert in the epipharyngeal papillae.

Comparative remarks. A well-developed labrum with a pentagonal outline like that of Eriocraniidae is present in Micropterygidae and one of the two agathiphagids, *Agathiphaga queenslandensis* Dumbleton. *A. vitiensis* has an equally well-developed labrum which is trilobed. The large labrum of Neopseustidae is trapezoidal. In Mnesarchaeidae the labrum is not distinctly delimited from the clypeus. In the two last-mentioned families sensilla are present on the epipharynx as in Eriocraniidae (Kristensen 1968 b). The micropterygid epipharynx has certain specialized features evolved in connexion with the pollen-feeding habit (Tillyard 1923, Hannemann 1956). The absence on the eriocraniid (and neopseustid) labrum of lateral groups of long setae, so characteristic of Lepidoptera, is presumably secondary since such setae are present in Micropterygidae and Agathiphagidae.

In *Hepialus* (Mortimer 1965) the labrum is greatly reduced but still has a convex outline. In higher Lepidoptera, including Stigmellidae and Incurvariidae (Genthe 1897) the ventral edge of the labrum is strongly indented, the lateral corners (the "piliferes") being left with the epipharynx projecting between them. The frontal retractors are lost.

The labrum in primitive Trichoptera is difficult to delimit since in *Rhyacophila* (Klemm 1966) no evident clypeolabral suture and frontal labral muscles are present. (Klemm's identification of a pair of muscles from the sulcus below the tentorial pits inserting on the epipharynx at the level of the functional mouth as mm. flexores labrales posteriores is not compatible with the interpretation advanced above of the sulcus being transclypeal). The apical part of the clypeolabrum, partly delimited by grooves, is rather similar to the labrum of Micropterygidae, Agathiphagidae and Eriocraniidae in shape and in being membranous distally; it may therefore be regarded as alone constituting the labrum.

3. 5. 2. The mandibles

The mandibles (fig. 4) are a pair of small but distinct lobes

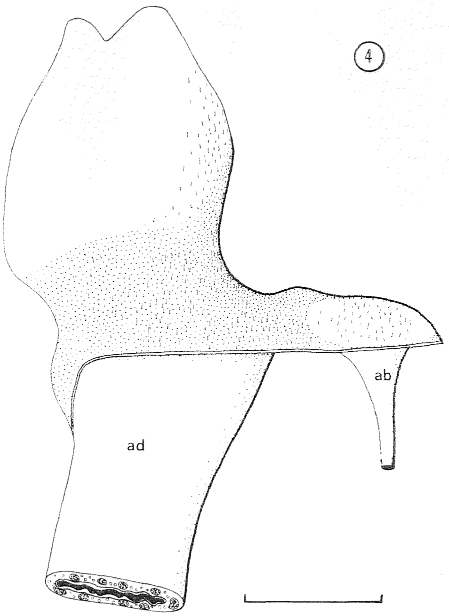


Fig. 4. *E. haworthi,* mandible cut away from headcapsule, dorsal view. ab, apodeme of abductor; ad, apodeme of adductor (glandular portion). Scale 50 μm.

which are distally membranous, proximally sclerotized; their anterior surface is sclerotically continuous with the head-capsule. In horizontal section they are approximately triangular, inwardly tapering (fig. 22). It has been stated that the mandibles in this family are entirely devoid of teeth (Walter 1885, Genthe 1897, Tillyard 1923). In *E. haworthi,* however, their medial margin is provided with a distinct subapical projection (sometimes obscured by the margin being folded); in *E. semipurpurella* the margin is only bluntly produced. Laterally the mandibles are covered with numerous microtrichia which are lacking medially. Laterad of the mandibles is a wide membranous area furnished with dense microtrichia.

The mandibular musculature was correctly observed by Busck & Böving (1914) in *D. auricyanea;* Chapman (1893) and Tillyard (1923) erroneously stated it to be absent in the family. It consists of:

22\. M. cranio-mandibularis internus, the mandibular adductor (fig. 14). The very numerous bands of this muscle arise from a large area of the lateral and dorsal parts of the head-capsule and are attached to a long apodeme (figs. 4, 14, ad, 21). This apodeme is formed as a tubular invagination of the head-wall. Externally the invagination forms a slit along the medial and ventral edge of the mandible (figs. 21, 22, mi, vi). Eventually the medial part of the slit becomes closed; the posterior mandibular surface is continuous with the anterior wall of the apodeme. No muscle-fibres are attached to the apodeme tube in the part immediately following the mandible. Here the cuticular intima is pale and folded, the epithelial cells are enlarged, have large nuclei and contain numerous vacuoles, indicating a secretory function (fig. 21, gla; fig. 23). Behind the glandular portion the epithelium of the apodeme becomes attenuated and the cuticle dark, sclerotized, accomodating the insertions of the muscle fibres (fig. 21, sa); the lateral part of the tube is the first to become changed. The tube is gradually flattened into a thin and relatively broad plate (figs. 24—25) which terminates some distance from the dorsal cranial wall.

23. M. cranio-mandibularis externus, the mandibular abductor. In general structure this muscle is similar to 22, but it is much smaller. Its fibres originate from the lateral part of the head-wall ventrocaudad to those of 22. Its apodeme (fig. 4, ab), which has no glandular portion, is attached to the lateral edge of the mandible.

In the pharate adult stage the mandibular muscles have the important function of moving the pupal mandibles during emergence from the cocoon (Hinton 1946b). The lack of an articular membrane anteriorly is no hindrance to the mobility of the mandibles as the tanning of the exocuticle presumably has not yet taken place at this time. After the shedding of the pupal cuticle the mandibles are functionless, and their muscles to some extent are histolysed, as suggested by Hinton (1946b) (figs. 24—25). In some of the specimens examined the fibres were exeedingly thin, without any distinct organisation and with degenerating nuclei. However, in all cases their presence was quite evident, and it is hardly likely that the musculature can entirely disappear during the brief free imaginal stage.

Comparative remarks. The functional mandibles of Micropterygidae of course differ in many aspects from those of Eriocraniidae, having well-developed articulations, specialized incisor and molar areas and very rigid apodemes (Hannemann 1956). Articulated mandibles with a medial tooth are present also in Agathiphagidae (Dumbleton 1952). More simple, unarticulated mandibles similar to those of Eriocraniidae occur also in Neopseustidae, Mnesarchaeidae (very small and hitherto overlooked, Kristensen 1968 b), Hepialidae and several higher Lepidoptera (Genthe 1897, Mortimer 1965). Mandibular muscles too may be present even in higher Lepidoptera having adecticous pupae. Both adductor and abductor-apodemes are present in the very small mandible of *Hepialus* (Mortimer 1965), and in *Scirpophaga* a single muscle (interpreted as the abductor) with a long apodeme is present (Pradhan & Aren 1941). Whether the apodemes are glandular in some of these cases is unknown; in no other adult Lepidoptera has any kind of mandibular gland been described.

Simple lobe-like mandibles are present in several Trichoptera (Crichton 1957, Klemm 1966). The primitive mandibular musculature in this order differs from that of Micropterygidae and Eriocraniidae in having an additional small tentorial adductor and in having the long apodeme of the cranial adductor dorsally forked as in Mecoptera (Klemm 1966).

3.5.3. The maxillae

The maxillary bases are placed in indentations in the hypostoma (figs. 1, 26). The cardo (figs. 2, 12, 26, 27, cd) is present as a slightly convex sclerite. Anterolaterally it is continuous with the stipes; for this reason it was not considered by Tillyard (1923) to be a clearly defined separate sclerite. Hansen (1930 pl. IX fig. 5, "*Micropteryx fastuosella*") figured the maxilla of *D. subpurpurella* incorrectly, showing cardo and stipes separated by a wide membranous area. Usually the cuticle along the anteromedial margin of the cardo is somewhat thickened. The stipes (figs. 2, 12, 14, 26, 27, st) is a rather broad, distally tubular segment. Its sclerotized posterior wall is strengthened by the costa (figs. 12, 26, lc) of a longitudinal sulcus, terminating between the palp and the galea. Its anterior wall is mostly membranous.

The maxillary palp (figs. 13, 14, 27, mp) is covered with scales (except the distal segment) and richly provided with setae and microtrichia. As usually stated it is 5-segmented, but it clearly represents a transitional stage to the 4-segmented condition. The flexor muscle between the second and third segment is lost, and the distal edge of the former is not thickened. The fourth segment is the longest; subapically it has an unsclerotized zone (why Tillyard (1923) stated this portion to be "darkly pigmented" in *E. semipurpurella* is not clear, as also in this species it is colourless) which was not found to be invested with special organs. Busck & Böving (1914) erroneously counted the part of segment four distad of the membranous zone as a separate segment in *D. auricyanea;* as shown by Philpott (1927) the palp in this species is 5-segmented as in other Eriocraniidae. The short fifth segment is apically furnished with a group of basiconic sensilla (presumably chemoreceptors) (fig. 28, sb). In *E. haworthi* (figs. 13, 14, 28) and *E. sangii* Wood the apex is distinctly forked, but not in the other species examined, although Genthe (1897) stated the same condition to be present in *E. sparmanella* and *E. semipurpurella.* In the resting position the second and third segments are pressed against the head and have the fourth segment pressed against themselves.

The galea (figs. 5, 14, 27, ga) is elongated and medially concave except for the most proximal portion. The two galeae together form a proboscis, being linked together dorsally and ventrally and enclosing the foodchannel between them. In the resting position the proboscis is coiled, forming a spiral of about 2½ turns. The proximal galeal portion (figs. 12, 27, sga) is sclerotized and somewhat thickened, as described by Tillyard (1923); by Genthe (1897) it was mistaken for a vestigial lacinia. It will here be termed the subgalea (although this term is usually applied to a part of the stipes), being presumably homologous with the portion of the *Micropteryx* galea called so by Hannemann (1956). The remainder of the galea is sclerotized only in the most dorsal part. The lateral wall is strongly arched and densely covered with small spinose exocuticular tubercles, which may show a tendency of being arranged in vertical rows. The wall of the medial groove is made by a large series of plates, each slightly overlapping that distally to it. The plates show a fine vertical striation; however, whether they consist of tightly packed laminae like the bars in the medial wall of the galea of *Pieris* (Eastham & Eassa 1955) cannot be seen with the light microscope.

The dorsal linking mechanism consists of a series of ventrally bent and mediodistally directed sclerites (fig. 5, dl) corresponding to the "lance-shaped plates" of Eastham & Eassa (1955). Proxim-

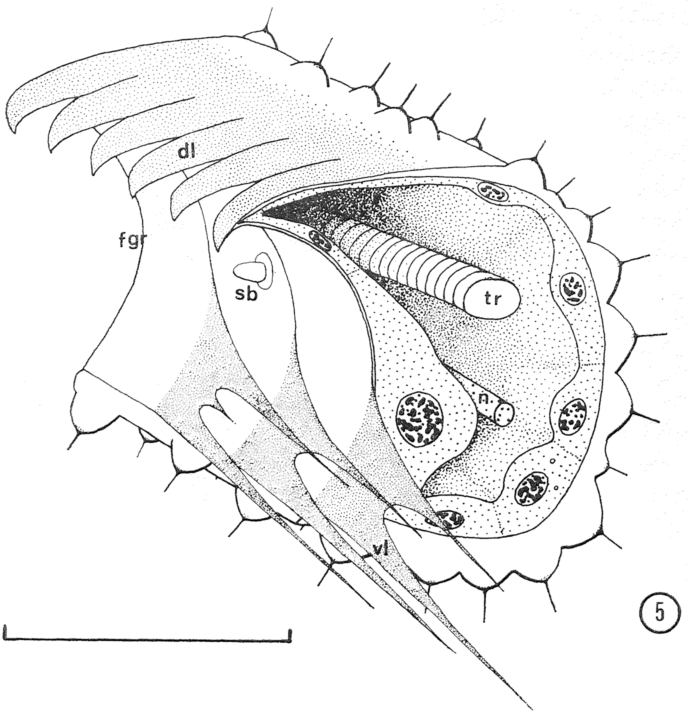


Fig. 5. *E. haworthi,* portion of left galea, antero-medial view. Vertical striation in plates of food-groove omitted. dl, dorsal linking processes; fgr, food-groove; ne, nerve (with pigment granules); sb, sensillum basiconicum; tr, trachea; vl, ventral linking process from anterior edge of plate in wall of food-groove. Scale 20 μm.

ally they are continous with the dorsal galeal wall, no special basal structures being present. The ventral linking mechanism consists of pigmented, mediodistally directed projections (fig. 5, vl) from the anterior (distal) edge of each plate in the medial wall. In the proximal part of the galea these projections are three-pointed, the most ventral point being by far the longest, the middle one the shortest. Distally the middle point is absent. The linkage produced apparently is not a very firm one. In fixed specimens the two galeae very easily come apart, and in living animals sucking from waterdrops in a petridish the apical portion of the proboscis was observed to split when pressed against the glass.

At the apex the galea is provided with several basiconic sensilla (chemoreceptors); a few also occur in the medial groove (fig. 5, sb). The epidermal cells in the galea, except those in the most dorsal part, are somewhat enlarged and may contain small vacuoles (fig. 5); the significance of this is not known. No dorsomedial unicellular glands, and no internal septa could be observed.

The lacinia (figs. 12, 14, li) is vestigial; it is presumably (cp. muscle 26) represented by a membranous protuberance mediad of the galea (which, by being hidden *in situ* by the prementum has been overlooked by previous authors). Its surface is covered with numerous small papillae.

The extrinsic musculature of the maxilla (figs. 12, 14) consists of:

24. M. tentorio-cardinalis, a very powerful muscle which originates ventrally on the anterior arm of the tentorial "V". It inserts on the anterior part of the cardo. A few of its fibres, however, actually insert on the medioproximal border of the stipes; it is likely therefore, that this muscle includes the m. tentorio-stipitalis as well. In *Micropteryx,* according to Hannemann (1956), the two muscles originate close to each other and are almost parallel.

25. M. cranio-stipitalis, a very narrow muscle arising from the lateral cranial wall just in front of the temporal sulcus and inserting with a long tendon in the stipes. Its size and course are similar to muscle no. 25 in *Micropteryx* (Hannemann 1956) and it is likewise supposedly derived from a cranio-cardinal muscle.

26. M. cranio-lacinialis, a rather well-developed muscle arising from the posterior hypostomal bridge and inserting at the base of the lacinial vestige.

The maxillary palp has two extrinsic and three intrinsic muscles (figs. 12—13):

27. M. stipito-palpalis anterior, the palp levator. It originates laterally in the stipes at the level of the distal edge of the cardo and inserts anterolaterally on the edge of the first palp segment.

28. M. stipito-palpalis posterior, the palp depressor. It arises from the stipital longitudinal costa and inserts in the first palp segment posterior to 27.

29. M. palpo-palpalis primus,

30. M. palpo-palpalis secundus and

31. M. palpo-palpalis tertius, originating basally in segments one, three and four respectively and inserting on the proximal edge of the following segment.

The galea has two extrinsic sets of muscles:

32. M. stipito-galealis internus, the galea levator. Its relatively broad bands fibres arise in the stipes mediad of and partly beneath 27 and insert anteromedially in the subgalea. From its origin and size it may be homologized with the stipito-lacinial muscle in *Micropteryx* (no. 29 of Hannemann 1956).

33. M. stipito-galealis externus, the ordinary galea flexor. It originates with several more or less separated bands anteromedially in the stipes and inserts anteriorly in the subgalea laterad to 32. In addition to adduction it may play a role also in the levation of the galea.

It is remarkable that no intrinsic muscles were found in the coilable part of the galea. The extension of the proboscis in Eriocraniidae then must be brought about by means of bloodpressure (a movement analogous with that of the antennal flagellum in many insects).

Comparative remarks. The cardo and stipes generally conform with those of Micropterygidae and the other dacnonyphous families. In the Hepialidae the entire maxilla is greatly reduced (Philpott 1927, Mortimer 1965). In the higher Lepidoptera (Schmitt 1938) the stipes is specialized to form a valve, as a closed proboscis haemocoele is necessary for the uncoiling when this is brought about through contraction of intrinsic proboscis muscles (Eastham & Eassa 1955). It is not known whether this also applies to the primitive heteroneurous groups.

The maxillary palp externally closely resembles that of *Micropteryx* in the relative length of the segments, the points of natural flexion and the presence of a desclerotization in the apical part of the fourth segment. In Agathiphagidae (Dumbleton 1952), the proportions of the palp of *A. queenslandensis* is more similar to the Eriocraniid type than that of *A. vitiensis,* in which the fourth and fifth segments are relatively shorter. In Neopseustidae the fifth segment is only little shorter than the long fourth. In Mnesarchaeidae the palp is three-segmented (Tillyard 1923, Kristensen 1968 b). A five-segmented, folded palp with a long fourth segment occurs in some monotrysian families (Stigmellidae, Opostegidae, some Incurvariidae) and in some primitive ditrysians (e.g., Tineidae). In several higher Lepidoptera the palp is four-segmented; in the most advanced groups the reduction has gone still further (Philpott 1927).

In Micropterygidae the galeae are small tapering processes. The subgalea of Micropterygidae and Eriocraniidae apparently is homologous with the thickened proboscis base in higher Lepidoptera. Haustellate galeae occur in all dacnonyphous families except the Agathiphagidae, in which they are unmodified lobes described as leaf-like (Dumbleton 1952). The eriocraniid proboscis, besides being much shorter, lacks several of the specializations present in advanced Lepidoptera such as *Pieris* (Eastham & Eassa 1955) which has coherent vertical exocuticular bands in the outer wall, "oval sclerites" and "triangular processes" at the base of the dorsal linking processes, dorsomedial unicellular glands (the secretion of which presumably serve to seal the linking), internal septa and an intrinsic musculature. The wall of the food groove and the ventral linking mechanism resembles that of Mnesarchaeidae, but is rather different from that of Neopseustidae and higher Lepidoptera (Kristensen 1968b).

A distinct lacinia is present in Micropterygidae and Agathiphagidae. No lacinial vestiges have been found in Mnesarchaeidae, Neopseustidae or the lower heteroneurous families, but may have been overlooked in some cases. Pradhan & Aren (1941) claimed a lacinial vestige to be present in *Scirpophaga;* the cranial muscle is absent in this case.

The extrinsic maxillary musculature resembles that of *Micropteryx* (Hannemann 1956), differing only in the entire absence of the small m. cranio-cardinalis and in the tentorio-stipital muscle at most being an insignificant portion of the m. tentorio-cardinalis. In higher Lepidoptera the extrinsic musculature typically consists of three powerful sets of stipital muscles, an anterior and a posterior tentorio-stipital (these may be subdivided into more bundles) and a cranio-stipital. These are all considered to be derived from the tentorio-stipital muscle of generalized insects (Schmitt 1938, Matsuda 1965). All three sets are present in the incurvariid genus *Tegeticula* (Schmitt 1938). Independent reduction of one or two sets have taken place in several families. In *Papilio* a tentorio-cardinal muscle is present (Srivastava, cited in Matsuda 1965) and in *Pieris* a tentorial retractor galeae inserting at the junction between the stipes and galea has been described (Eastham & Eassa 1955); presumably these muscles too have been secondarily derived from the tentorio-stipital muscle.

The stipital musculature of the palp and the inner lobes in Eriocraniidae is very similar to that of *Micropteryx* (Hannemann 1956) if the given interpretation of muscle 32 in the former family is correct. *Micropteryx* has retained the second intrinsic palp muscle. In the higher Lepidoptera a single extrinsic palp muscle has been described in *Tegeticula* (Schmitt 1938). In *Scirpophaga* (Pradhan & Aren 1941) the palp has no extrinsic muscles, but a single intrinsic one between segments one and two; one stipito-galeal muscle is present. Homologizing of muscles 32 and 33 with the basal proboscis-muscles of higher Lepidoptera seems possible only from a study of intermediate forms.

The maxilla of *Rhyacophila* (Klemm 1966) in some aspects resembles that of Micropterygidae, notably in the structure of the cardo, the presence of a m. cranio-cardinalis and the common origin of mm. tentorio-cardinalis and tentorio-stipitalis. It differs, e.g., in having a special cardinal portion of the palp levator and in lacking the cranio-stipital muscle. The palp, although likewise five-segmented, is of a very different type, having a swollen second segment, the fourth segment considerably shorter than the third, and both levator and depressor muscles being present between segments two-three and three-four. The inner maxillary lobes in Trichoptera are difficult to interpret, but both galea and lacinia may be present in some genera (Matsuda 1965).

3.5.4. The labium

Posteromediad of the cardines is a small sclerotized lobe representing the prementum (figs. 2, 26, 29, pm). Anteriorly it is slightly widened and has a median impression. Above the prementum and posteriorly fusing with the posterior hypostomal bridge is an oval convex sclerite furnished with long setae (an Eltringham's organ) (figs. 2, 26, Eo). It was termed the submentum by Genthe (1897) and the gular plate by Tillyard (1923). It is certain that it includes a postmental portion; a more exact morphological identification is impossible, since no muscles are associated with it.

The labial palp (figs. 14, 29, lp) arises anterolaterally on the prementum. It is three-segmented, covered with setae and narrow scales. The third segment is somewhat swollen and is apically furnished with a chemoreceptive organ: a group of basiconic sensilla projecting into the lumen of a pit-like invagination (fig. 29, so). In the resting position the palp is outwardly and upwardly curved.

No structures corresponding to paraglossae and glossae are present. The process considered by Genthe (1897) to be the labial "Lobus internus" is the hypopharynx, and the "Wärzchen" considered to be the "Lobi externi" and figured for *E. sparmanella* are a pair of conspicuous campaniform sensilla present in that species.

The labial musculature consists only of the extrinsic and intrinsic palp muscles:

34. M. praemento-palpalis (fig.14), arising posterolaterally in the prementum and inserting laterally on the proximal edge of the first palp segment.

35. M. palpo-palpalis primus and

36. M. palpo-palpalis secundus, two very slender muscles arising dorsally in the distal part of the first and second palp segment respectively and inserting medially on the proximal edge of the following segment.

Comparative remarks. The labium in *Micropteryx* (Hannemann 1956) is much more primitive than in the dacnonyphous families, having retained a distinct mentum and submentum, paraglossae and fused glossae. The musculature is the most complete found in the labium of any endopterygote insect according to Matsuda (1965). Dorsally the labium is fused with the hypopharynx. A postmental Eltringham's organ is sometimes present (Busck & Böving 1914).

The labium in Dacnonypha is rather similar to that of higher Lepidoptera, having lost the paraglossae and glossae, the distinct subdivision and delimitation of the postmentum and the extrinsic musculature. In a few heteroneurous Lepidoptera small lobes are present apically on the labium; they may be paired (*Tegeticula*, *Grapholitha*) or unpaired (*Scirpophaga*) but in no case are muscles associated with them (Schmitt 1938, Pradhan & Aren 1941). Probably they are secondary structures. The labium of *Hepialus* is fused with the hypopharynx (Mortimer 1965).

Three labial palp segments is the primitive number in insects and the usual number in Lepidoptera although there may be fewer. A few *Sabatinca* species (Micropterygidae) and *Agathiphaga* are stated to have four (Issiki 1931, Dumbleton 1952), but it is likely that the basal "segment" in these species is actually a part of the prementum (Kristensen 1967). The "basal spot", an area on the first palp segment densely covered with sensilla and suggested by Reuter (1888) to be a typical feature of the Lepidoptera, is absent in Micropterygidae as well as in all Dacnonypha. The sensory pit on the apical palp segment is a character common to the Micropterygidae, Agathiphagidae, Eriocraniidae and most higher Lepidoptera. In some families, however, the sensilla-group is not invaginated (Börner 1939, Kristensen 1968 b). The presence of only a single extrinsic palp muscle in *Eriocrania* seems to be a specialization since two are present in *Micropteryx* and several higher Lepidoptera. The loss of one or both muscles has occurred several times within the order (Schmitt 1938).

In Trichoptera the labial specialization has evolved along an entirely different line. As in the Lepidoptera the postmentum is obliterated and the paraglossae and glossae are lost, but the prementum and the hypopharynx fuse to form a large, soft, retractile lobe, the haustellum. One epicranial and two tentorial muscles insert on the prementum in *Rhyacophila* (Klemm 1966); in *Phryganea* (Chrichton 1957) all three are epicranial. Matsuda (1965), apparently misunderstanding Crichton, believed four extrinsic muscles to be present in Trichoptera, and interpreted the submento-mental muscle in *Micropteryx* as an originally postmento-premental muscle in order to homologize the musculature in these two groups. A premento-salivarial muscle and two extrinsic palp-muscles are present. The palp is nearly always three-segmented in this order.

3.5.5. The hypopharynx, the salivary glands and the sucking pump

The hypopharynx (figs. 2, 6, 7, 14, 31) is a narrow, elongated, distally tapering structure projecting beneath the labrum. Laterally it is continuous with the head-capsule through the anterior hypostomal bridge (figs. 6, 7, 31, hb). Its posterior proximal part is sclerotized, otherwise it is membranous; its apex is covered with minute microtrichia. Subapically on its anterior surface is the opening of the salivarium (figs. 6, so, 14). This opening was by Tillyard (1923) misinterpreted as the mouthopening although its true identity had already been discovered by Busck and Böving (1914). Basally the anterior hypopharyngeal wall is strengthened by a pair of linear sclerotic arms (figs. 6, 7, 31, su) which are laterally continuous with the hypostomal bridge. These arms are on basis of the musculature identified as the hypopharyngeal suspensoria.

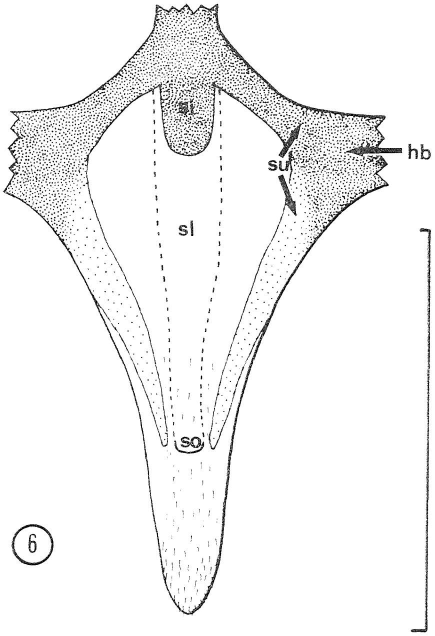


Fig. 6. *E. haworthi,* distal part of hypopharynx. hb, hypostomal bridge; si, sitophore; sl, salivarium; so, salivary opening; su, hypopharyngeal suspensorium. Scale 100 μm.

Proximally the suspensoria are strongly sclerotized and fuse medially with the sitophore. The latter (fig. 6, si), beginning as a heavy sclerotization in the midline on the anterior hypopharyngeal surface a short distance in front of the functional mouth, is continued as a large sclerotized triangular plate, the cibarial plate (figs. 7, 14, 32). This sclerite, extending to the morphological mouth at the level of the frontal ganglion, forms the floor of the sucking pump. The posterior border of the plate is slightly produced medially and laterally; in its lateral parts it is furnished with several campaniform sensilla (figs. 7, 32, 33, sc) (proprioceptors, the function of which here presumably is registering the amount of filling of the sucking pump by reacting to tensions in the cuticle).

The salivarium is crescentic in horizontal section; its cuticular intima is thick posteriorly, thin anterorly. Its opening on the anterior hypopharyngeal surface is a feature most unusual in insects (it occurs, e.g., in some Dermaptera, Popham 1959, quoted in Matsuda 1965).

The musculature of the salivarium (figs. 7, 14, 31) consists of:

37. M. hypopharyngeo-salivarialis anterior, the dilator of the salivarium. It originates with several fibres from the lateroproximal wall of the hypopharyngeal lobe and from the suspensoria and inserts on the thin anterior (dorsal) salivarial wall.

38. M. hypopharyngeo-salivarialis posterior, a bundle of extremely short fibres connecting the salivarium with the hypopharyngeal floor.

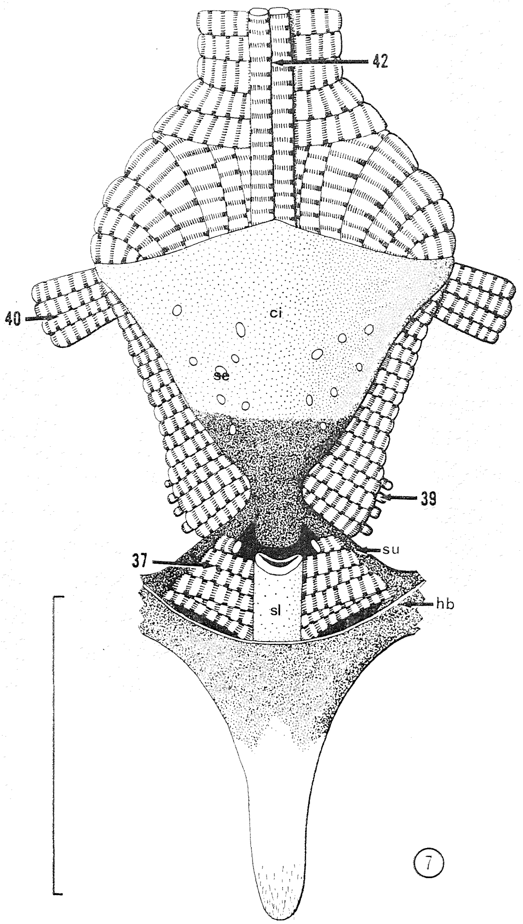


Fig. 7. *E. haworthi,* hypopharynx and sucking pump, ventral view. ci, cibarial plate; hb, hypostomal bridge; se, sensilla campaniformia in cibarial plate; sl, salivarium; su, hypopharyngeal suspensorium; 37, m. hypopharyngeo-salivarialis anterior; 39, m. clypeo-cibarialis; 40, m. fronto-pharyngealis anterior; 42, m. tentorio-cibarialis. Scale 100 μm.

No labial muscles of the salivarium are present.

The common salivary duct (fig. 14, sd) is relatively long, reaching the cervical region. It is of the usual type, the intima being invested with taenidia. The salivary glands (fig. 30) are of the normal lepidopterous type. They are long, filamentous tubes extending into the abdomen; their cells are large and have big, branched nuclei except for the few large cells which form the apex of the tube.

The sucking pump (figs. 7, 14) is a well-developed organ, attaining its greatest width at the level of the morphological mouth. It is derived partly from the cibarium, partly from the anterior pharynx, the borderline being marked by the frontal ganglion connectives. Its floor, as stated above, is formed by the cibarial plate. The dorsal cuticular intima is pale and folded. The muscularis (pump compressor) consists of an outer layer of circular muscles and an inner layer of longitudinal muscles (fig. 14, lm, mu); in the most anterior pharyngeal part, however, only the latter are present. The sucking pump leads into the narrow part of the pharynx.

The sucking pump is provided with three pairs of powerful dilatormuscles (fig. 7, 14):

39. M. clypeo-cibarialis, arising on the clypeus postero-laterad of 20 and inserting anteriorly on the cibarium.

40. M. fronto-pharyngealis anterior, originating laterally on the frons anterior to the antennae and inserting laterally on the sucking pump immediately behind the frontal ganglion connectives.

41. M. fronto-pharyngealis posterior. A pair of muscles arising medially on the frons behind the antennae. Running very close together they insert on the posterior pharyngeal part of the sucking pump.

A single pair of muscles is attached to the cibarial floor:

42. M. tentorio-cibarialis, a pair of rather narrow muscles arising on the corporotentorium; extending very close together they insert on the medial projection on the hind edge of the cibarial plate. As their course is mediad of the circum-oesophageal connectives they cannot be homologous with the tentorial hypopharyngeal retractors in generalized insects. Presumably they are postcerebral pharyngeal dilators which have shifted their insertions forwards.

Comparative remarks. In *Micropteryx* (Hannemann

1956) the broad hypopharynx is fused with the labium, the salivary opening being apical on the composite structure. The sitophore is partly specialized to form a spine-covered cavity in which the pollen is triturated; proximally it continues as a rather short sclerite, corresponding to the cibarial plate in Dacnonypha. The sclerite is connected to the epipharynx by lateral apodemes and the hypopharynx has a ligamentous connexion with the mandibular base. Laterally in the hypopharyngeal wall is a slender sclerite termed the suspensorium and distally a pair of similar sclerites, the "salivia". At least the last-mentioned are undoubtedly true suspensoria, since muscles to the dorsal and ventral walls of the salivarium originate on them. The salivary glands are sack-like.

The dacnonyphous families Agathiphagidae and Neopseustidae have a free distal hypopharyngeal lobe with a dorsal salivary opening like the Eriocraniidae. In the Mnesarchaeidae the distal lobe is distinct but shortened; the salivary opening is possibly apical (Kristensen 1968 b). The shape of the hypopharyngeal lobe and its lateral connexion with a hypostomal bridge in the first-mentioned families are characters reminiscent of the condition in some Mecoptera (Heddergott 1938). The cibarial plate is rectangular in Neopseustidae, triangular and inwardly narrowing in Mnesarchaeidae (Kristensen 1968b).

In higher Lepidoptera the free distal part of the hypopharynx is lost; the plate in the cibarial floor, however, is always present (Schmitt 1938). The dorsal dilators of the salivarium originate from this plate (Schmitt 1938, Eastham & Eassa 1955), indicating that the suspensoria may have become incorporated in it.

The haustellum of Trichoptera is rather different from the hypopharynx-labium lobe in *Micropteryx* (Crichton 1957, Klemm 1966). The hypopharyngeal surface is specialized for the uptake of fluid nutrition; branched microtrichia form channels through which liquid may be drawn by capillary forces. As in the Micropterygidae, the Dacnonypha and the higher Lepidoptera, the sitophore forms a sclerotized floor of the cibarium. A premental salivarium-muscle is present but no hypopharyngeal ones. A longitudinal muscle on the anterior surface of the salivarium is a Mecoptera-like feature (Grell 1938). The salivary glands are sack-like.

The sucking pump of Eriocraniidae is much more developed than that of Micropterygidae, in which group the sucking function does not play a direct role in the mechanism of ingestion. The muscularis in *Micropteryx* (Hannemann 1956) apparently is represented only by a small group of circular muscles (no. 47) in the anterior part of the cibarium. Apart from the additional proximal dilator (no. 49) mentioned p. 245, the number and arrangement of the dilators of the sucking pump and of the labrum agree with those of Eriocraniids, but they are much weaker.

In the higher Lepidoptera the dilators usually form very powerful bundles, but may be much reduced in non-feeding forms (Schmitt 1938); their number and arrangement vary considerably (Schmitt 1938, Ehrlich 1962). The muscularis in *Pieris* (Eastham & Eassa 1955) differs from that of Eriocraniidae in having the innermost layer formed by the circular muscles, followed by a layer of longitudinal muscles and finally a layer of diagonal muscles.

The sucking pump of Trichoptera is rather well developed, as in Eriocraniidae and higher Lepidoptera, undoubtedly a convergence resulting from both groups feeding on liquid matters. As in Eriocraniidae there is an inner layer of longitudinal muscles and an outer of circular muscles (Klemm 1966). The arrangement of the preoral dilators in *Rhyacophila* is difficult to compare with that of Micropterygidae-Dacnonypha because of the uncertainty in the interpretation of the clypeolabrum. If the delimitation of the labrum suggested here is correct, the homologies may be: lateral 1 cplr = the labral compressor; medial 1 cplr = the clypeo-epipharyngeal muscle; 2 cplr = the proximal cibarial dilator; 1 dlcp, 2 dlcp, mlrp have no counterpart; 1 dlphy = 49 in *Micropteryx*. *Rhyacophila* has two more pairs of pharyngeal dilators of the sucking pump. The ventral tentorio-cibarial muscle is common to all three groups.

3.5.6. The alimentary canal.

The portion of the pharynx (fig. 14, 34) behind the sucking pump is a rather narrow tube. Its wall consists of a somewhat folded squamous epithelium with a thick intima. The muscularis comprises inner longitudinal and outer circular fibres. The former are well developed only along the dorsal wall, otherwise very slender and scattered; the latter form several relatively strong bundles.

Two pairs of postcerebral pharyngeal dilatores (fig. 14) are present:

43. M. epicranio-pharyngealis, arising immediately in front of the postinterocellar sulcus and inserting on the dorsal pharyngeal wall.

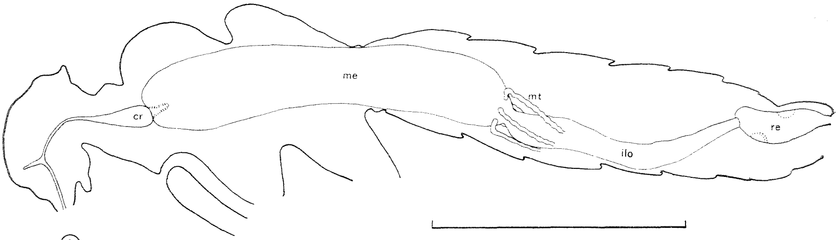
44. M. postoccipito-pharyngealis, arising on the occipital condyli and inserting on the ventral pharyngeal wall.

The oesophagus extends to the metathorax. Posteriorly it is somewhat dilated, forming a simple crop (figs. 8, 36, cr) with a diameter much smaller than that of the midgut. As in the pharynx, the wall consists of a squamous epithelium; the cuticular intima is particularly thick in the anterior part. The oesophageal wall is more or less distinctly thrown into six longitudinal folds (fig. 35); also some transverse folding occurs. The muscularis is quite weak, but both longitudinal and circular fibres are present, forming an open network.

The oesophageal valve (fig. 36) is a simple funnel-shaped invagination of the oesophagus into the anterior part of the midgut. The oesophageal epithelium is folded down and extends a short distance forwards before joining the midgutepithelium. The valve is surrounded by slender muscle fibres; circular fibres internally, longitudinal fibres externally.

The midgut (mesenteron) is by far the largest part of the alimentary canal; it extends from the mesothorax to the fourth abdominal segment (fig. 8). It is a simple wide tube which is encountered in variable states of distension.

The midgut epithelium apparently undergoes a partial decomposition during the adult life when no real feeding takes place (cp. p. 252) (figs. 37—38). In a newly emerged specimen (judging



⑧

Fig. 8. *E. haworthi*, diagram of alimentary canal. cr, crop; me, mesenteron; mt, Malpighian tubules; ilo, ileo-colon; re, rectal sac with rectal papillae. Scale 1 mm.

from the condition of the mandibular musculature) the epithelial cells are approximately cuboidal, have large nuclei and a discernible brush-border (fig. 37, bru). At this stage even a few regenerative cells (fig. 37, rc) could be observed. Some cells were seen discharging cytoplasmic globules (fig. 36, gl) into the lumen, a characteristic feature of disintegrating midgutcells. In older specimens the epithelium is extremely thin and without a discernible brush-border. When not maximally distended the epithelium is seen to be folded longitudinally and transversely. The muscularis consists of an open network of circular and longitudinal fibres.

No peritrophic membrane could be observed.

The six Malpighian tubules (figs. 8, 39, 40, mt) open into the alimentary canal at the posterior end of the midgut. Each tubule opens separately into the gut. The openings are arranged with equal mutual distance in a circle around the latter. The tubules are of an unspecialized, submoniliform type. No muscular fibres were found in their walls.

The hindgut is distinctly divisible in an anterior ileo-colon and a posterior rectum (fig. 8). The former, which is found in various states of distension (mostly, however, thrown into six longitudinal folds), has a rather thick epithelium (fig. 43). The apical portion of the cytoplasm has a striated appearance as is usually the case in insects. The intima is hardly discernible.

The rectum is a greatly distended sack. Its wall is an attenuated squamous epithelium having a well-developed intima. By the opening of the ileo-colon into the sack a short distance behind its anterior end a small caecum is formed. Three rectal papillae (figs. 8, 44) are present, two anterolateral and one posteromedial. The papillae have a central cavity (fig. 44, cv) which is not always distinct, however. Proximad of the cavity is a layer of cells having the apical cytoplasm striated. Distad of the cavity is a small number of very large cells with large nuclei, surrounded by a peripheral layer of cells with somewhat smaller but still large nuclei.

The entire hindgut has a relatively weakly developed muscularis comprising both longitudinal and circular fibres (figs. 41—42). In the ileo-colon both kinds of fibres are very narrow, forming a rather regular open network. The circular fibres are especially close together a short distance behind the openings of the

Malpighian tubules; this arrangement may be considered as a reduced pyloric sphincter. In the rectum the circular fibres are somewhat coarser and the network less regular; branching and anastomosing of the fibres are frequent.

Comparative remarks. The pharyngeal musculature of *Micropteryx* (Hannemann 1956) differs from that of Eriocraniidae in having two discrete bundles corresponding to 44 and two ventral sets of tentorial dilators (of which the anterior presumably is homologous with 42). The alimentary canal of Eriocraniidae closely resembles that of *Micropteryx,* described by Mortimer (1965). Important similarities are the simplicity of the oesophagus and the oesophageal valve. No crop is described in *Micropteryx;* however, as the diameter of the oesophagus is stated to be progressively increasing from anterior to posterior, the condition is rather similar to that in *Eriocrania.* Furthermore, the two families agree in the great size of the midgut and the number and position of the rectal papillae. The circular muscles around the oesophageal valve and behind the Malpighian tubules are distinctly weaker than in *Micropteryx* and the midgut epithelium is somewhat simpler. These differences may be explained by the differences in feeding habits. No cavity in the rectal papillae was found by Mortimer.

The higher Lepidoptera generally have the crop very well developed although it may be much reduced or entirely absent in non-feeding Lymantriidae, Lasiocampidae and Arctiidae (Dauberschmidt 1933, Mortimer 1965). The crop may be a mere dilation of the posterior oesophagus or it may be a distinct diverticulum. The latter condition is prevalent among the more advanced families; however, both types occur in Hepialidae and monotrysian Heteroneura (Dauberschmidt 1933, Bourgogne 1951). Some advanced species which feed regularly have the posterior oesophagus surrounded by strong circular muscles and the intima provided with spines and bristles (e. g. Mortimer 1965). The midgut usually is relatively short. Its simple shape is retained in many families, the most noteworthy modifications occurring in Sphingidae, Noctuidae (swelling of anterior portion) and Nymphalidae (presence of glandular outgrowths) (Dauberschmidt 1933). The arrangement of the Malpighian tubules in Eriocraniidae is more primitive than in higher Lepidoptera. The normal condition is two lateral groups of three tubules having a common opening and (except in a few Arctiidae, Veneziani 1905) a common duct which may be more or less bladder-like distended. In some Monotrysia (Stigmellidae, Incurvariidae) the number of tubules is reduced to four, and in some lower Heteroneura (Tineidae, Monopidae) only two persist. Simple filamentous or moniliform tubules are prevalent in most families; more or less regularly ramified tubules occur, e.g., in some Sphingidae, Saturniidae and Galleridae (in the latter family the number of tubules in each lateral group may exeed three) (Dauberschmidt 1933, Bourgogne 1951, Richards & Davies 1957). The hindgut is generally similar to that of Eriocraniidae. There is considerable variation in the development of the rectal caecum in advanced families; in a few group it is entirely absent (Zygaenidae, some Papilionoidea) (Dauberschmidt 1933). The number of rectal papillae is always higher than three, varying from four (*Hepialus, Fumea casta* ♀) to about 500 (some Noctuidae) (Bordas 1920, Dierl 1964, Mortimer 1965). Histologically the eriocraniid papillae conform with those of *Hepialus* and differ from those of higher Lepidoptera (Bordas 1920, Mortimer 1965) in having more than four large cells apically.

The alimentary canal in the Trichoptera examined has by convergence in some aspects become more similar to the types occurring in higher Lepidoptera than in Micropterygidae and Eriocraniidae, having a large crop formed by a simple oesophageal dilation, a relatively short midgut and several rectal papillae. In *Limnephilus* the intima immediately in front of the oesophageal valve is furnished with bristles. The six Malpighian tubules are, however, arranged in the same primitive way as in Eriocraniidae (Glasgow 1937, Korboot 1964,, Mortimer 1965).

3.6. **The nervous system**

3.6.1. The central nervous system

In the brain (figs. 14, 47, br) the protocerebrum (fig. 9, pr) is well developed, dorsally somewhat indented in the midline. The corpora pedunculata do not form elevations of the brain surface. The optic lobes (fig. 9, ol) arise immediately above the level of the dorsal tentorial arms and extend lateroventrally toward the compound eyes. They are widest some distance before entering the eyes. The short ocellary nerves arise dorsolaterally from the protocerebrum.

The deutocerebrum (fig. 9, deu) is relatively well developed, forming a pair of distinct anteroventral protuberances on the brain. The antennal nerves (figs. 9, 10, na), arising from these protuberances, give off branches to the extrinsic antennal musculature and to the postantennal Eltringham's organs (fig. 10, na 1) before entering the antennae. The nerves constituting the last-mentioned branch are presumably of tritocerebral origin. In the scapus the nerve divides into two branches both of which extend throughout the antenna, supplying the Johnston's organ and the numerous other sensilla.

The tritocerebrum is not externally distinctly delimited from the proto- and deutocerebrum. From the tritocerebrum the frontal ganglion connectives and the labral nerve arise anteroventrally (fig. 10, nla), the two being separated immediately at their origin. Each labral nerve gives off branches to the floor of the sucking pump (fig. 10, nla 1) and to the frontal Eltringham's organ (fig. 10, nla 2). A pair of nerves which may be interpreted as the nervi tegumentales (fig. 10, nt) arises from the back of the brain, being basally united with the external nervi corpori cardiaci. After giving off a branch (fig. 10, nt 1) to muscles 43 they extend to the dorsal part of the headcapsule, supplying the dorsal Eltringham's organs. The tritocerebral commissure (fig. 46, tr) is not free. It has been incorporated in the suboesophageal ganglion immediately under the anterior surface of the latter. The oesophageal ring is

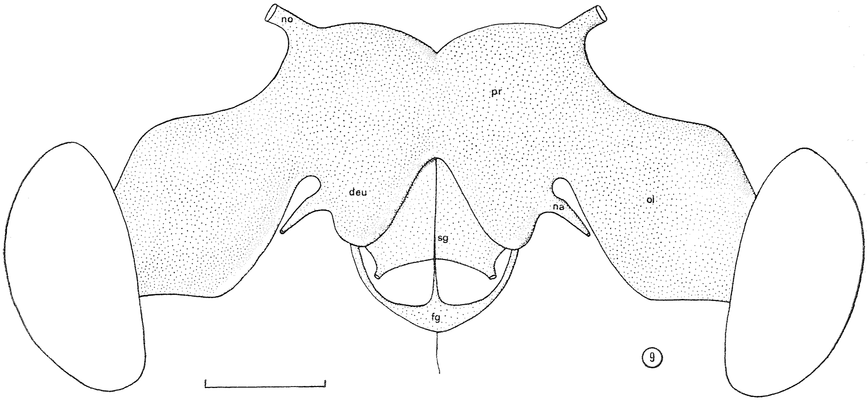


Fig. 9. *E. haworthi,* cephalic nervous system, anterior view. deu, deutocerebrum; fg, frontal ganglion; na, antennal nerve; no, ocellary nerve; ol, optic lobe; pr, protocerebrum; sg, suboesophageal ganglion. Scale 100 μm.

relatively large, leaving ample space around the oesophagus and the aorta (fig. 47).

From the suboesophageal ganglion the mandibular nerve arises anteriorly (fig. 10, nmd). It loops around muscle 24 and on the external surface of the latter it forms a swelling from which more branches are given off to the mandibular musculature.

The maxillary nerve (fig. 10, 14, nmx), which arises a considerable distance posterior to the mandibular nerve, is the strongest nerve arising from the suboesophageal ganglion. Immediately after its origin it gives off a branch (fig. 10, nrg) to the retro-

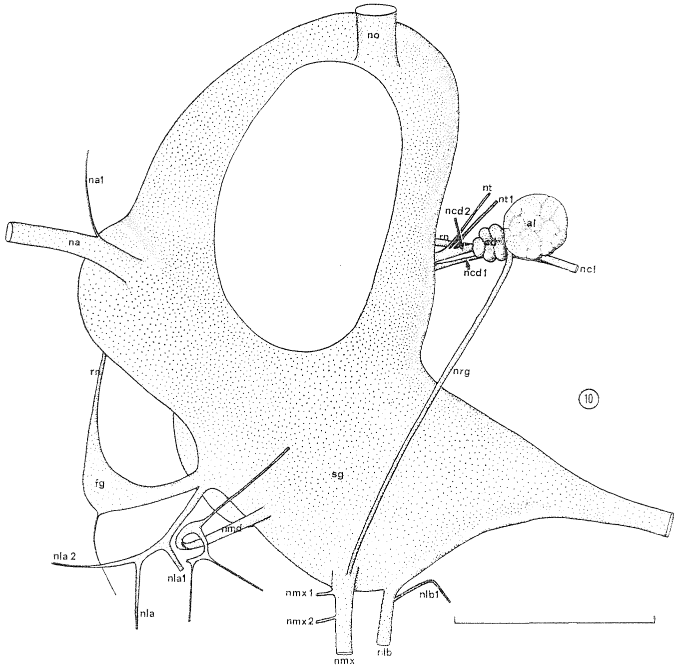


Fig. 10. *E. haworthi*, cephalic nervous system, lateral view. Left optic lobe cut off. al, corpus allatum; cd, corpus cardiacum; fg, frontal ganglion; na, antennal nerve; na 1, nerve to postantennal Eltringham's organ; ncd 1, internal nerve of corpus cardiacum; ncd 2, external nerve of corpus cardiacum; ncl, caudal nerve; nla, labral nerve; nla 1, nerve to sensilla in cibarial plate; nla 2, nerve to frontal Eltringham's organ; nlb, labial nerve; nlb 1, nerve to postmental Eltringham's organ; nmd, mandibular nerve; nmx, maxillary nerve; nmx 1&2, nerves to m. tentorio-cardinalis; no, ocellary nerve; nrg, nerve from suboesophageal ganglion to retrocerebral glands; nt, tegumentary nerve; nt 1, branch of tegumentary nerve to m. epicranio-pharyngealis; rn, recurrent nerve; sg, suboesophageal ganglion. Scale 100 μm.

cerebral complex (see below). A couple of small branches (fig. 10, nmx 1 & 2) supply muscle 24. In the stipes the nerve divides into two branches which supply the palp and the galea, respectively.

The labial nerve (figs. 10, 14, nlb) arises a rather short distance posteromediad of the maxillary nerve. It gives off a branch to the postmental Eltringham's organ (figs. 10, 14 nlb 1) and one to the salivarium (fig. 14, nlb 2); eventually it extends through the prementum and the labial palp.

Posteriorly from the suboesophageal ganglion originates a pair of nerves to the oesophagus.

The two connectives between the suboesophageal ganglion and the prothoracic ganglion are enclosed within a common sheath.

Comparative remarks. The cephalic nervous system of Micropterygidae is described by Ehnbom (1948). An *Eriocrania* sp. is listed among the Micropterygidae examined in his paper, but no special mention of it occurs in the text. However, the Eriocraniidae differ from the Micropterygidae in the incorporation of the tritocerebral commissure in the suboesophageal ganglion and in the unpaired condition of the connectives between the suboesophageal ganglion and the prothoracic ganglion. In these characters the Eriocraniidae resemble the higher Lepidoptera. With regard to the first-mentioned feature the family actually represents a transitional stage, since the commissure is still distinctly delimited and forms the most anterior layer of the suboesophageal mass. The oesophageal connectives in Eriocraniidae apparently are a little broader than in Micropterygidae (figured in Ehnbom 1948, p. 89), but the dimensions of the oesophageal canal still are much more similar to those of the latter family than to those of higher Lepidoptera, where the brain and suboesophageal ganglion are broadly fused laterally, leaving only a very narrow canal for the aorta and the foregut. The mandibular nerve is absent in advanced Lepidoptera.

In most Trichoptera, including *Rhyacophila* (Crichton 1957, Klemm 1966), the oesophageal ring is wide, the tritocerebral commissure is free and the connectives between the suboesophageal ganglion and the prothoracic ganglion is paired as in *Micropteryx*. Contrary to the original condition in Lepidoptera, the frontal ganglion connectives and the labral nerve are surrounded by a common neurilemma sheath for a considerable distance after leaving the tritocerebrum (Ehnbom 1948).

3.6.2. The sympathetic nervous system

The frontal ganglion (figs. 9, 10, 14, fg) is located on the anterior wall of the sucking pump ventrad of the brain. Ventrally it gives off a slender nerve which supplies muscles 39 and the cibarial muscularis. Dorsally the ganglion tapers into the strong recurrent nerve (figs. 9, 10, 14, 34, 48, rn) which gives off fine branches to muscles 40 and 41, forming a bend upwards between the two muscles of the latter set. Where reaching the ventral wall of the aorta the nerve forms a small ganglion-like swelling, from which arise several slender nerves to the pharyngeal wall. Subesequently the nerve enters the aorta and runs inside the latter through the oesophageal ring, continually giving off slender branches which penetrate the aortawall and supply the pharynx. Behind the brain is formed a small hypocerebral ganglion (figs. 14, 50, hg), consisting of an assemblage of discrete neuron-bodies with large, often vacuolated nuclei, situated on the surface of the nerve. Immediately behind the hypocerebral ganglion the recurrent nerve breaks through the aortawall and continues its course along the dorsal wall of the oesophagus where apparently it eventually fuses with the nervi caudales (see below) from the corpori cardiaci. A terminal swelling of this fused nerve, the ganglion ventricularis, is formed at the level of the crop.

The paired corpori cardiaci (figs. 10, 14, 49, 50, cd) are situated on either side of the oesophagus at the level of the hypocerebral ganglion. Their external surface is uneven due to the large size of the neurosecretory cells (figs. 49, 50, ns) constituting the outer layer. Medially is a neuropile mass (fig. 50, nm). The anteromedial portion consists of small cells with small nuclei; it is continuous with the wall of the aorta. Each corpus cardiacum is connected to the back of the brain by the internal and external nervi corpori cardiaci (fig. 10, ncd 1 & 2), mediad and laterad of muscle 43 respectively. Laterally the corpus cardiacum receives a nerve which has branched off from the maxillary nerve (cp. p. 277). Immediately behind the entrance of this nerve arises the very short nervus corporis allatus. From the medial side of the organ arises a strong nerve (fig. 10, ncl) which extends along the oesophagus; a similar nerve was termed the nervus caudalis by Ehnbom (1948). As stated above, the nervi caudales fuse with the recurrent nerve. The corpori cardiaci of the two sides are connected by a transverse nerve below the aorta, which arises from the roots of the caudal nerves; presumably they have also nervous connexions to the hypocerebral ganglion.

The corpora allata (figs. 10, 14, 49, 50, al) are approximately sphaerical bodies with a smooth surface. The number of cells with large nuclei (secretory cells) is relatively high (about 15 in a central section, thickness 10 μm). No connective tissue cells were identified.

Comparative remarks. The course of the recurrent nerve within the aorta is a feature which apparently has not been described from other Lepidoptera. The ganglion-like swelling in front of the aortic ampulla has been described also in *Pieris napi*. The hypocerebral ganglion is weakly developed in most Lepidoptera (Ehnbom 1948).

A ganglion-like organization of the corpus cardiacum as in *Eriocrania,* which has a distinct medial neuropile mass, according to Ehnbom (1948), does not occur in other Lepidoptera, the main portion of the corpus being occupied by the small cells which in *Eriocrania* are concentrated anteromedially. However, in *Hepialus hecta,* figured by Ehnbom (p. 119) a distinct neuropile does appear to be present. The arrangement of the neurosecretory cells is rather similar to that of other Lepidoptera. The nerve supply of the corpus cardiacum differs from that of other Lepidoptera in the presence of the nerve from the suboesophageal ganglion. The entrance of this nerve very close to the origin of the corpus allatum nerve may suggest that the fibres of the former are continued to the corpus allatum. A suboesophageal innervation of the latter organ has been described in, e.g., Ephemeroptera (Cazal 1948, quoted by Hinton 1951); it is certainly a primitive condition in insects. Caudal nerves were found in several higher Lepidoptera by Ehnbom (1948) (contrary to the statement by Hinton 1951). A transverse nerve connecting the two corpori cardiaci has been described, e.g., in *Odezia.* Connexions to the hypocerebral ganglion are mostly very indistinct; exceptions occur, however, even in advanced families. The corpus allatum resembles that of most other Lepidoptera. In some Noctuidae they are separated into discrete cell-groups. In a few Sesiidae and Hyponomeutidae they have fused medially (Ehnbom 1948).

The trichopterous retrocerebral complex differs from the lepidopterous mainly in that the hypocerebral ganglion and its lateral connexions to the corpori cardiaci are always well developed. No suboesophageal innervation of the retrocerebral complex has been described; a nerve extends from the corpus cardiacum to a bundle of lateral muscles or to the salivary glands (Ehnbom 1948). In Trichoptera, as generally in insects, aortic nerves arise from the recurrent nerve; the course of the latter is below the aorta. (Ehnbom 1948, Klemm 1966).

3.7. The visual organs

The compound eyes, (figs. 1, 2) as already stated, are relatively small. The ommatidia are eucone; no corneal processes are present (figs. 51, 52). The length of the crystalline cone (fig. 52, cn) is at most about twice the thickness of the corneal lens. The crystalline cone cells are exceedingly attenuated. The rhabdoms (fig. 52, rh) reach the apex of the crystalline cones. The distal parts of the ommatidia are isolated from each other through abundant pigment in the iris cells and retinular pigment cells (terminology of Yagi & Koyama 1963). Proximad of this pigmented layer is a zone containing relatively little pigment. In this zone are located the nuclei of the retinular sense cells (figs. 51, 52, sn); the chromatin in these nuclei is evenly distributed. The proximal part of the eye again appears strongly pigmented due to the presence of well-developed basal cells in addition to the inter-ommatidial pigment (fig. 51). The eye is inwardly bordered by the basal-membrane, penetrated by the retinula cell axons which eventually enter the optic lobe.

Occasionally aberrant specimens occur in which the amount of pigment in the eye is very much reduced (the distal part of the rhabdom is visible only in such specimens) (fig. 52).

The two ocelli (figs. 1, 53) are enclosed in a heavily sclerotized capsule and have their optical axes directed laterally. The cornea is a convex-concave lens (fig. 53, le) which is not thickened. The corneagen cells form a thick vitreous body (fig. 53, vb) under the cornea and extend along the posterior wall of the capsule; their nuclei are concentrated proximally in the body. Most internally is a mass of sense cells (fig. 53, sn), the axons of which form the ocellary nerve.

Comparative remarks. The eriocraniid compound eyes in many aspects resemble those of Trichoptera, Micropterygidae and Hepialidae (Ehnbom 1948), differing mainly in having considerably shorter crystalline cones. In this aspect they are more similar to Sesiidae and other diurnal lower Heteroneura. Ehnbom claimed that a strong development of the proximal pigmented zone is characteristic of the trichopterous eye. However, apart from the Eriocraniidae, also the Hepialidae have it well developed (Yagi & Koyama 1963). The eyestructure in higher Lepidoptera varies considerably; several cases of convergent evolution make a phylogenetic interpretation of the similarities difficult.

The loss of the median ocellus is a specialization common to the Micropterygidae, the Dacnonypha and the higher Lepidoptera. In Agathiphagidae, Neopseustidae and Mnesarchaeidae also the lateral ocelli are absent, as is the case in several other Lepidoptera. The eriocraniid ocelli agree closely with the type common to Micropterygidae and Trichoptera (Ehnbom 1948); it may be suggested that the curious "connective tissue membrane" described and figured from these groups, is a shrinkage-artifact representing the vitreous body. In higher Lepidoptera the cornea is thickened and there are no cells between it and the sense cells (except in the specialized ocelli of Zygaenidae and Sesiidae, Ehnbom 1948).

3.8. **The circulatory system**

The cephalic aorta extends as a closed tube through the oesophageal ring. In front of the brain the tube widens to an aortic ampulla which anteriorly is closely associated with muscles 41; eventually it becomes attached to the head-wall. Anterolaterally the ampulla extends to the antennal bases where it communicates with a well developed antennal artery. No further distinct blood-vessels could be distinguished in the head.

Comparative remarks. The eriocraniid cephalic aorta conforms to the normal lepidopterous type (Bourgogne 1951). As in Micropterygidae and Hepialidae there are no paired glands associated with the aortic ampulla. Such glands are characteristic of higher Lepidoptera. They are also absent in *Zygaena* and *Cossus* (Ehnbom 1948), but this may be a secondary reduction.

4. **Discussion**

From the preceeding comparative remarks it is evident that the Dacnonypha, the Micropterygidae and the primitive Trichoptera exhibit considerable similarity in their anatomy. This is in accordance with the generally accepted conception of a common ancestry of these groups. Furthermore, evidence is provided for a certain pattern of phylogenetic interrelationships of the groups in question.

It is apparent that the Micropterygidae have diverged from the evolutionary line at a later date than the Trichoptera although they have retained some primitive characters which are lost in the latter order. Micropterygidae are similar to the Trichoptera in some of the characters in which they differ from the Dacnonypha, e.g., the distinct tentorio-stipital muscle, the free tritocerebral commissure, and the paired posterior connectives from the suboesophageal ganglion. These are, however, essentially symplesiomorphies, i.e., characters pertaining to the generalized insect organization. On the other hand, Micropterygidae and the Dacnonypha are similar in a number of characters representing a more advanced condition than that of Trichoptera (or: advanced in another direction than in Trichoptera):

1. Presence of medial posterior process on corporotentorium.
2. Presence of lateral seta-bundles on labrum (in Dacnonypha present in Agathiphagidae).
3. Lack of tentorial adductor of mandible.
4. Relative length of maxillary palp segments and points of natural flexion of palp.
5. Lack of antagonistic muscles at base of segments two and three of maxillary palp.
6. Presence of a separate slender cranio-stipital muscle.
7. Presence of an Eltringham's organ on postmental area.
8. Presence on apical labial palp segment of an invagination containing chemoreceptive sensilla.
9. Lack of dorsal longitudinal muscle of salivarium.
10. Number and position of rectal papillae.
11. Immediate separation of frontal ganglion connective and labral nerve.
12. Lack of median ocellus.

Considering the number of similarities in advanced characters between the two groups it appears most unlikely that they should all have arisen by convergence; certainly the most straightforward explanation would be that they (or at least most of them) are true synapomorphies, indicating a common line of evolution of the Micropterygidae and the Dacnonypha after the separation of the Trichoptera. Consequently there can be no phylogenetically based objection to including the Micropterygidae in the Lepidoptera without including the Trichoptera in the same order. This view may be corroborated by considerations concerning other anatomical features (Hennig 1953).

The recent proposal by Niculescu (1967b) that the Dacnonypha be considered as more primitive Lepidoptera than the Micropterygidae appears unacceptable for several reasons. Niculescu argues that the micropterygid biting mouthparts are highly specialized, and as it is generally recognized that specialized structures do not evolve from other specialized structures it is claimed that the higher Lepidoptera having a specialized proboscis cannot be derived from Micropterygidae. On the other hand, the mouthparts of Eriocraniidae having "non-functional" mandibles and a short proboscis are considered to represent a primitive condition similar to a type from which both Micropterygidae and higher Lepidoptera could have evolved.

There is, however, overwhelming evidence that the Micropterygidae are more primitive than the Dacnonypha. The eriocraniid unarticulated mandible and short proboscis are certainly secondary derivations from an articulated (i.e., permanently functional) mandible and an unspecialized galea, respectively, as occurring in Micropterygidae and the dacnonyphous family Agathiphagidae. Other traits in micropterygid anatomy which have not acquired the apomorph conditions characteristic of Dacnonypha and higher Lepidoptera include, e.g., the very generalized labium, the free tritocerebral commissure, the paired posterior connectives from the suboesophageal ganglion, the sack-like salivary glands and several details in organs not discussed in this paper (notably in larval anatomy). In several aspects the Eriocraniidae actually represent a transitional type between the primitive organization-type of Micropterygidae (which, concerning adult anatomy, is largely retained in Agathiphagidae also) and higher Lepidoptera. This is particularly evident in the structure of the mandible and its musculature, the maxilla and its musculature, the external brain-structure and the alimentary canal.

The misconception inherent in Niculescu's theory is primarily due to the exaggerated significance attached to the specializations of the micropterygid mouthparts. Insufficient allowance is made for the adaptions acquired during the evolution of the Micropterygidae after the separation of their ancestral form from the lepidopterous line of evolution. Recent Micropterygidae feed as adults on pollen and for the triturating of the pollen-walls some specializations of the mouthparts have been developed (epipharyngeal brush, asymmetrical mandibles, hypopharynx formed as a triturating basket), but this is likely to be a relatively late evolutionary event. Every recent natural group of animals is likely to possess analogous specializations. The Eriocraniidae, e.g., can equally not be considered an ancestral group of higher Lepidoptera since they have a specialized, cutting, functional ovipositor and legless larvae. However, modern phylogenetic taxonomy is concerned not with deriving one group of recent animals from another, but with determining the relative times of their divergence from a common evolutionary line. It is in these terms that the Dacnonypha can be stated to represent a transitional stage between the Micropterygidae and the higher Lepidoptera.

Acknowledgments

I wish to express my sincere gratitude to my teachers of entomology, Dr. A. Nielsen (University of Copenhagen) and Prof. H. E. Hinton (University of Bristol), for inspiring discussions and valuable criticism. (I have not, however, always agreed with their ideas, so the responsibility for the opinions expressed is entirely my own). My best thanks are also due to Dr. S. L. Tuxen, head of the Entomology Department, Zoological Museum (University of Copenhagen) and Prof. B. Christensen (University of Copenhagen) for their interest in the work and for providing facilities. I thank Dr. N. Klemm (Mainz) for valuable information. For help on technical matters I am indebted to Mrs. Joyce Ablett (Bristol) and Mrs. Grete Ulstrup (Copenhagen).

Summary

1. The heads in the genera *Heringocrania, Dyseriocrania* and *Eriocrania* are externally basically similar.

2. The cephalic sulcus-pattern includes elements absent in higher Lepidoptera. In some aspects it is comparable to that of Micropterygidae and Neopseustidae.

3. Dorsal tentorial arms are well developed. In *Dyseriocrania* and *Eriocrania* the anterior arms are posteriorly extremely weak; in *Heringocrania* they are normal.

4. The cervical musculature does not agree exactly with either that of Micropterygidae or of any higher Lepidoptera.

5. One of the scapo-pedicellar muscles inserts on a triangular sclerite in the membrane between the two segments.

6. The well-developed labrum has retained the frontal retractors.

7. Mandibles are distinct but without articulations. A great cranial adductor and a smaller abductor are present; their fibres are partly histolysed during the free adult life. The adductor apodemene is glandular anteriorly and has an external opening.

8. The cardo, stipes and maxillary palp both externally and in the musculature in many aspects are similar to those of Micropterygidae. The galeae form a functional, coilable proboscis as in higher Lepidoptera. The proboscis has no internal musculature and the ventral linking mechanism (resembling that of Mnesarchaeidae) is quite different from that of higher Lepidoptera. The lacinia is a membranous protuberance, its cranial flexor is retained.

9. The labium, like that of higher Lepidoptera, has only the prementum and the palp distinctly developed.

10. The distal part of the hypopharynx is a free lobe; the salivary opening is located on its anterior (dorsal) surface. The cibarial plate, formed by the sitophore, is laterally furnished with campaniform sensilla. The salivary glands resemble those of higher Lepidoptera.

11. The oesophagus is slightly dilated posteriorly, forming a very small crop. The midgut is the greatest part of the alimentary canal. The six Malpighian tubules each open into the gut. Three rectal papillae are present.

12. The cephalic central nervous system has a relatively wide oesophageal ring. The tritocerebral commissure is incorporated in the suboesophageal ganglion. The mandibular nerve is well developed. The posterior connectives from the suboesophageal ganglion are fused.

13. The recurrent nerve extends through the brain inside the aorta. The retrocerebral complex receives a nerve from the suboesophageal ganglion.

14. No paired glands are associated with the aortic ampulla.

15. The compound eyes differ from those of other very primitive Lepidoptera in having shorter crystalline cones. The lens of the ocellus is not thickened. The corneagen cells form a vitreous body.

16. Several synapomorphies of Micropterygidae and Dacnonypha seem to exist. The former family may therefore be included in the Lepidoptera. Niculescu's (1976b) theory of the Eriocraniidae being more primitive than Micropterygidae is not accepted.

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Figures 11—53.

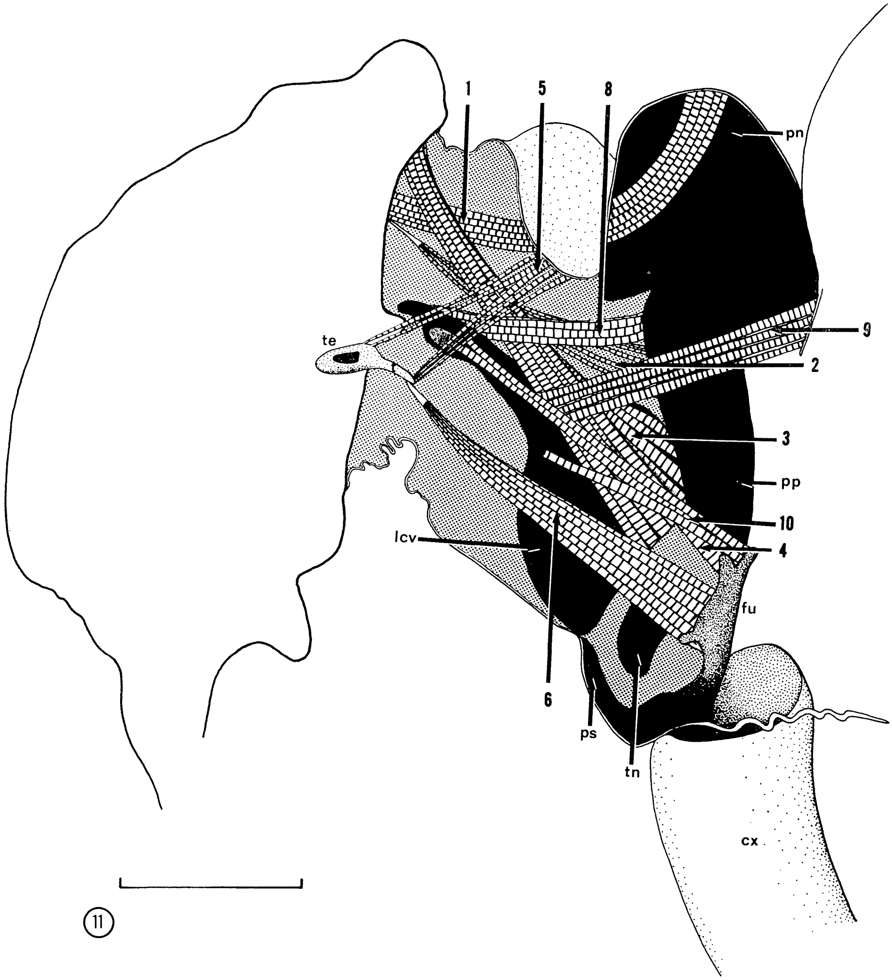

Fig. 11. *E. semipurpurella,* cervical region, medial sagittal section. cx, procoxa; fu, prosternal furca; lcv, laterocervicale; pn, pronotum; pp, propleuron; ps, prosternum; t, posterior projection of corporotentorium; te, corporotentorium; tn, trochantin; 1, m. pronoto-postoccipitalis; 2, m. propleuro-postoccipitalis; 3, m. latero cervico-postoccipitalis; 4, m. profurco-postoccipitalis; 5, m. cervico-tentorialis; 6, m. profurco-tentorialis; m. propleuro-laterocervicalis; 9, m. phragmo-laterocervicalis; 10, m. profurco-laterocervicalis.

(The procoxo-tentorial muscle is almost entirely hidden by muscle 6 in this view).

Scale 200 μm.

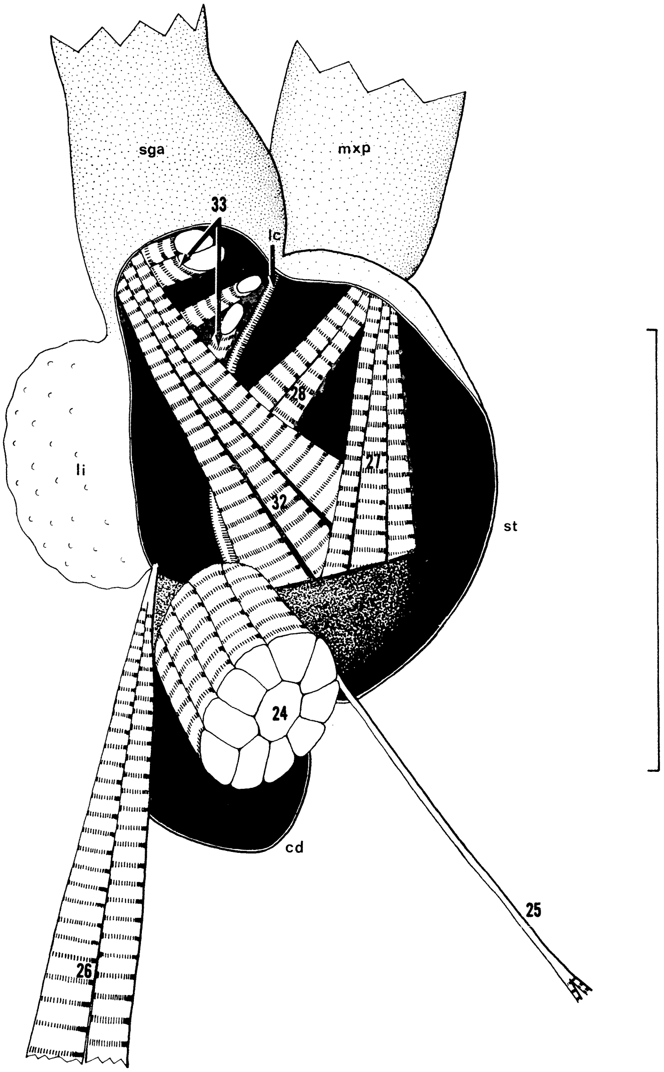

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Fig. 12. *E. haworthi,* maxillary base cut away from head, anterior stipital wall removed. cd, cardo; lc, longitudinal costa on posterior stipital wall; li, lacinia-vestige; mxp, maxillary palp; sga, subgalea; 24, m. tentorio-cardinalis; 25, m. cranio-stipitalis; 26, m. cranio-lacinialis; 27, m. stipito-palpalis anterior; 28, m. stipito-palpalis posterior; 32, m. stipito-gallealis internus; 33, m. stipito-galealis externus. Scale 100 μm.

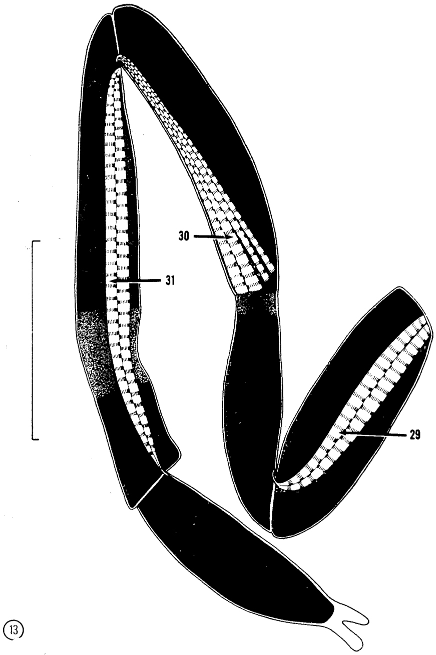

Fig. 13. *E. haworthi,* maxillary palp. 29, 30, 31, m. palpo-palpalis primus, secundus and tertius. Scale 100 μm.

Fig. 14. *E. haworthi,* head, medial sagittal section. aa, anterior tentorial arm; ad, apodeme of mandibular adductor; al, corpus allatum; am, aortic ampulla; ao, aorta; br, brain; d, corpus cardiacum; fg, frontal ganglion; ga, galea; hg, hypocerebral ganglion; hy, hypopharynx; li, lacinia-vestige; lm, longitudinal fibres in sucking pump muscularis; lp, labial palp; mp, maxillary palp; mu, circular fibres in sucking pump muscularis; nlb, labial nerve; nlb 1, nerve to postmental Eltringham's organ; nlb 2, nerve to salivarium-musculature; nm, neuropile mass; mx, maxillary nerve; no, ocellary nerve; oe, oesophagus; ph, pharynx; rn, recurrent nerve; sd, salivary duct; sg, suboesophageal ganglion; sp, sucking pump lumen; st, stipes; te, corporotentorium; 11, m. tentorio-scapalis anterior; 12, m. tentorio-scapalis medialis; 13, m. tentorio-scapalis lateralis; 14, m. tentorio-scapalis posterior; 19, m. fronto-labralis; 20, m. clypeo-epipharyngealis; 21, m. labro-epipharyngealis; 24, m. tentorio-stipitalis; 26, m. cranio-lacinialis; 34, m. praemento-palpalis; 37, m. hypopharyngeo-salivarialis anterior; 38, m. hypopharyngeo-salivarialis posterior; 39, m. clypeo-cibarialis; 40, m. fronto-pharyngealis anterior; 41, m. fronto-pharyngealis posterior; 42, m. tentorio-cibarialis; 43, m. epicranio-pharyngealis; 44, m. postoccipito-pharyngealis. Scale 200 μm.

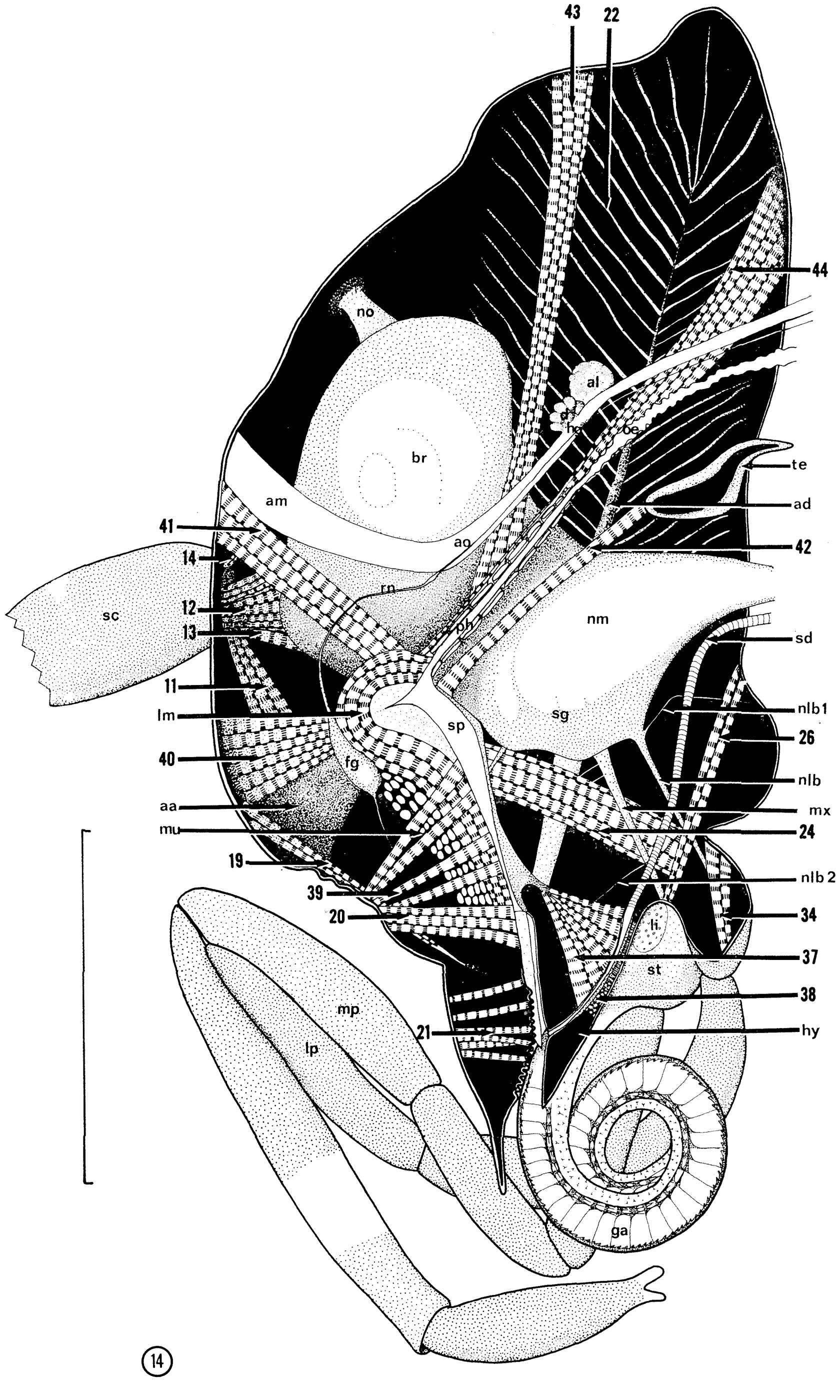
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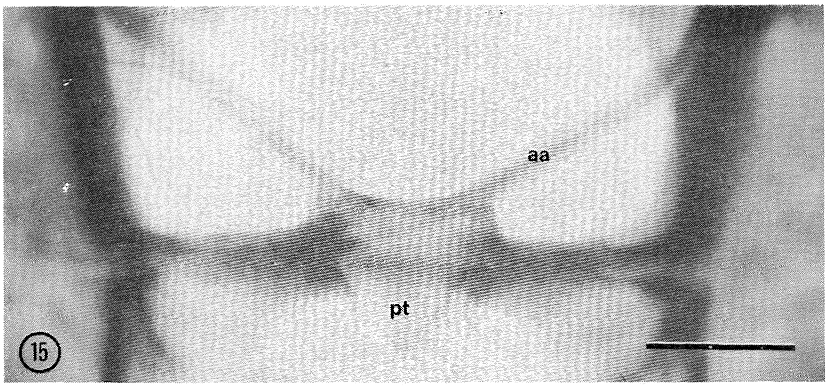
Fig. 15. *H. unimacullella,* occipital foramen with tentorial bridge, posterior view. (Macerated specimen). aa, anterior tentorial arm; pt, posterior process on corporotentorium. Scale 50 μm.

Fig. 16. *E. semipurpurella,* occipital foramen with tentorial bridge, posterior view. (Macerated specimen). pt, posterior process on corporotentorium. Anterior tentorial arms not discernible. Scale 50 μm.

Fig. 17. *E. sparmanella.* lcv, laterocervicale. Scale 100 μm.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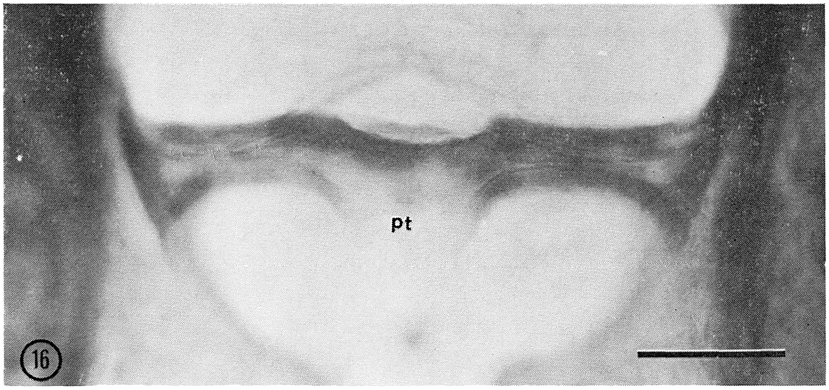
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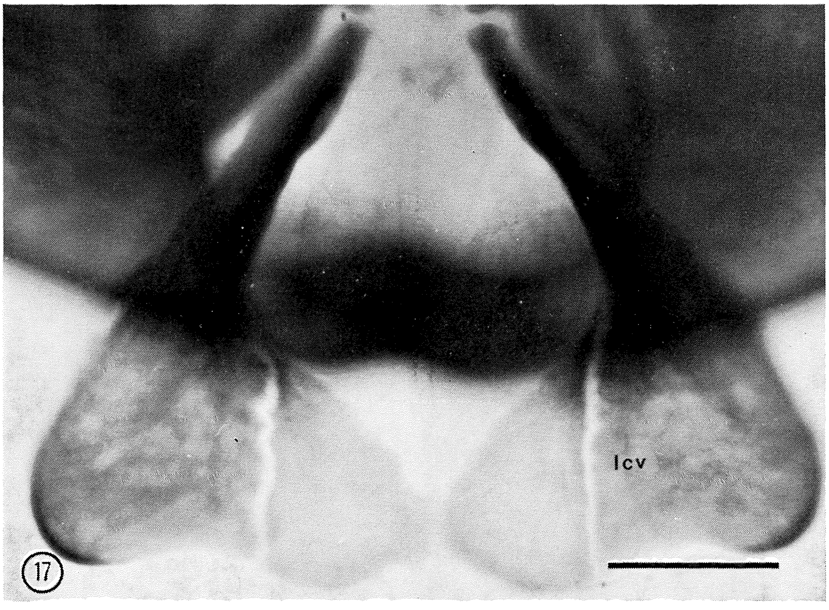
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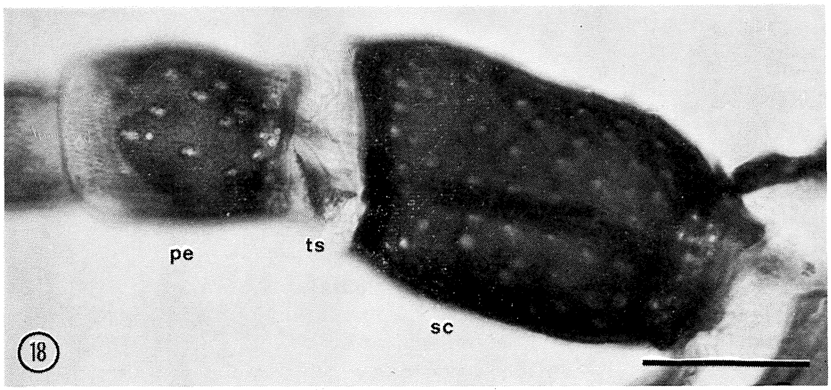
Fig. 18. *E. haworthi,* antennal base. pe, pedicellus; sc, scapus; ts, triangular sclerite. Scale 50 μm.

Fig. 19. *E. haworthi,* labrum, dorsal view. to, torma. Scale 50 μm.

Fig. 20. *E. haworthi,* median part of epipharynx. el, epipharyngeal papillae; es, epipharyngeal sensillum. Scale 25 μm.

Fig. 21. *E. haworthi,* apodeme of mandibular adductor, longitudinal section. gla, glandular portion of apodeme; sa, sclerotized portion of apodeme; vi, invagination of headwall ventrad of mandible, continuous with apodeme. Scale 50 μm.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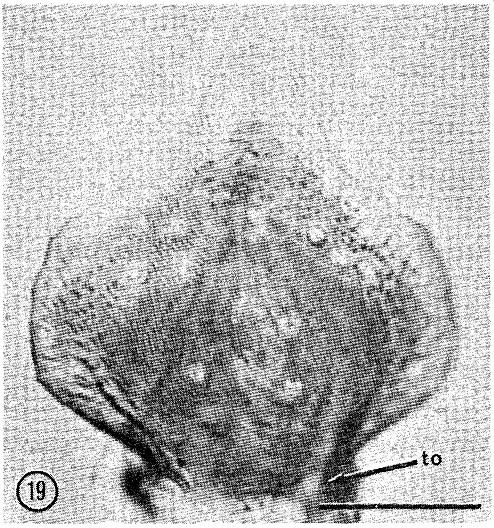
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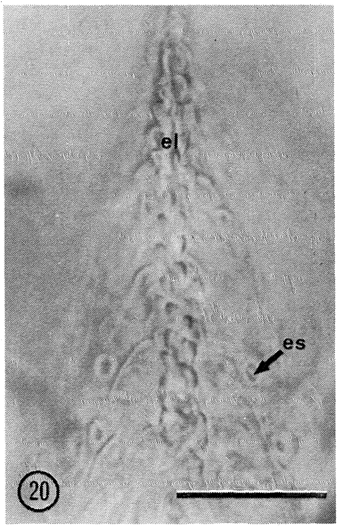
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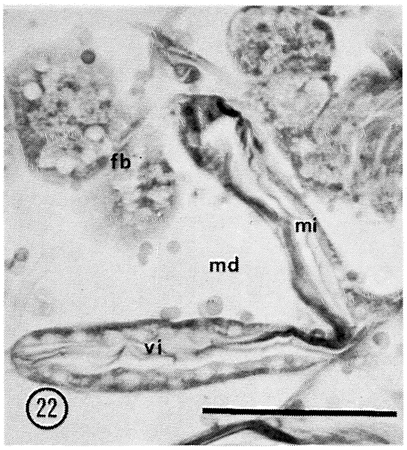
Fig. 22. *E. haworthi,* mandible, horizontal section. fb, fat body cells; md, mandible; mi, invagination of headwall mediad of mandible which eventually is closed; vi, invagination of headwall ventrad of mandible which eventually is continued as the adductor apodeme. Scale 50 μm.

Fig. 23. *E. haworthi,* apodeme of mandibular adductor, horizontal section. in, intima. Epithelium glandular, containing numerous large vacuoles. Scale 25 μm.

Fig. 24. *E. haworthi,* fibres of mandibular adductor in a presumably newly emerged specimen, horizontal section. fb, fat body cells; tr, trachea. Arrow indicates level of apodeme-plate. Scale 50 μm.

Fig. 25. *E. haworthi,* fibres of mandibular adductor in a presumably older specimen, horizontal section. nu, degenerating nuclei. Arrow indicates level of apodeme-plate. Scale 50 μm.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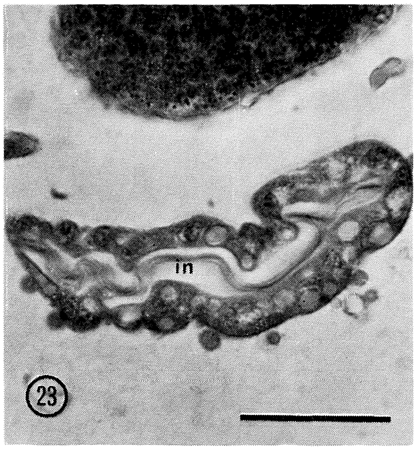
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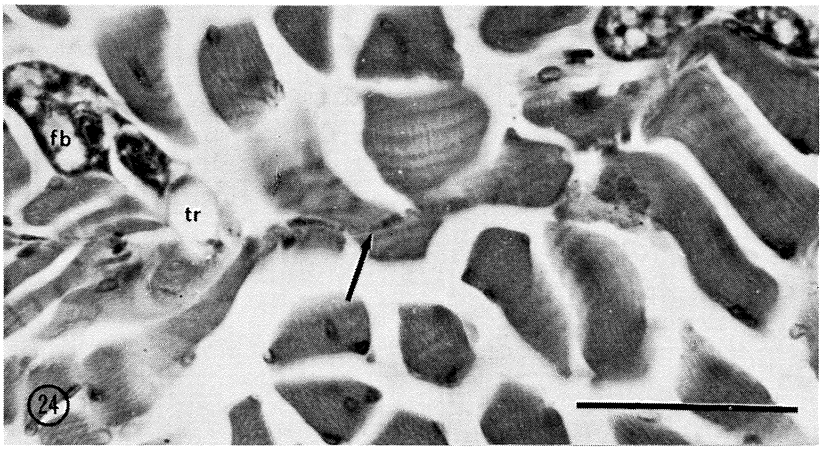
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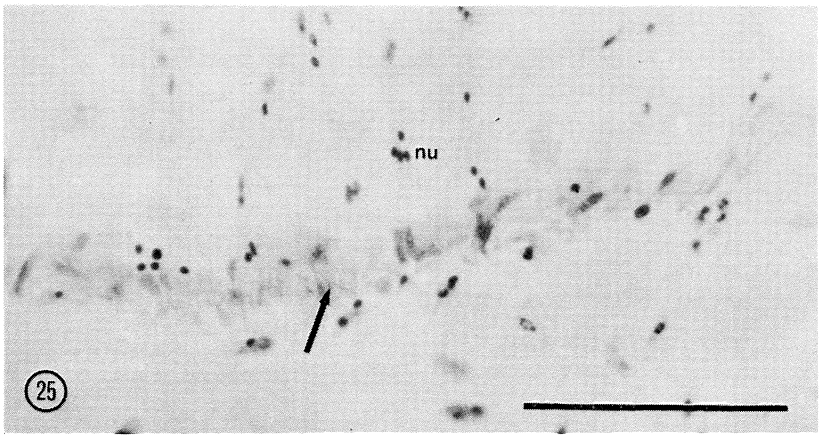
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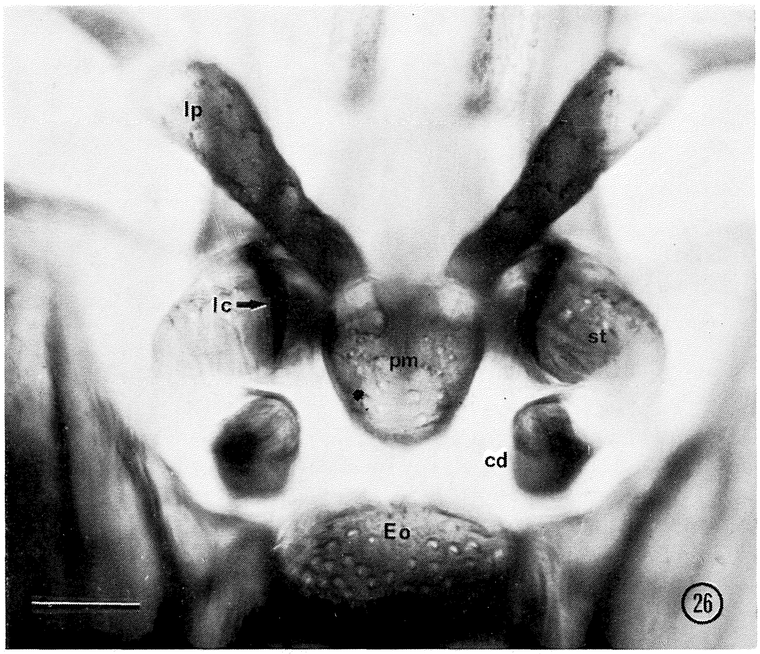
Fig. 26. *E. haworthi,* mouthparts, ventral view. cd, cardo; Eo, Eltringham's organ on postmental area; lc, longitudinal costa in ventral stipital wall; lp, labial palp; pm, praementum; st, stipes. Scale 50 μm.

Fig. 27. *E. semipurpurella,* maxilla, medial view. cd, cardo; ga, galea; mp, maxillary palp; sga, subgalea; st, stipes. Scale 100 μm.

Fig. 28. *E. haworthi,* apical segments of maxillary palp (phase-contrast). sb, sensillum basiconicum. Notice the forked shape of the distal segment in this species. Scale 50 μm.



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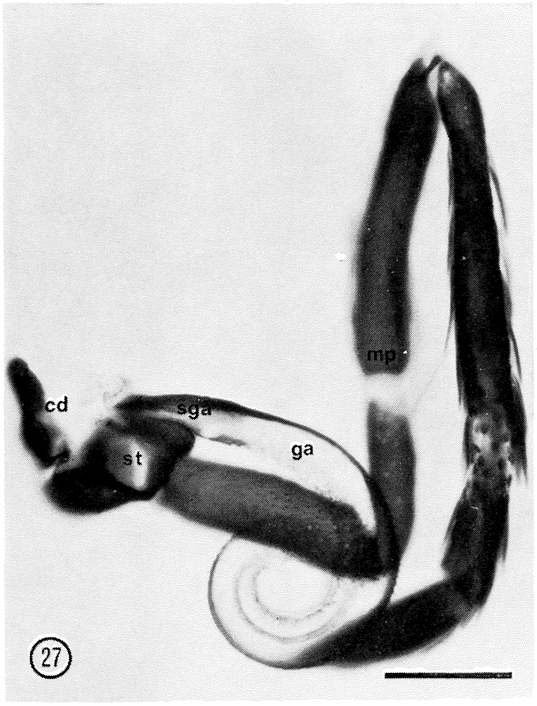

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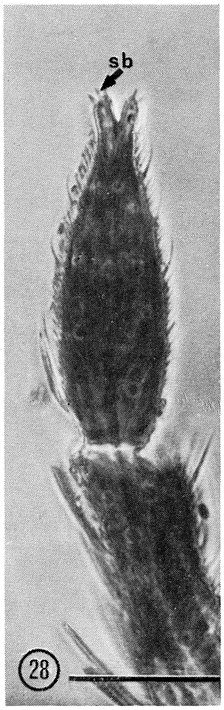

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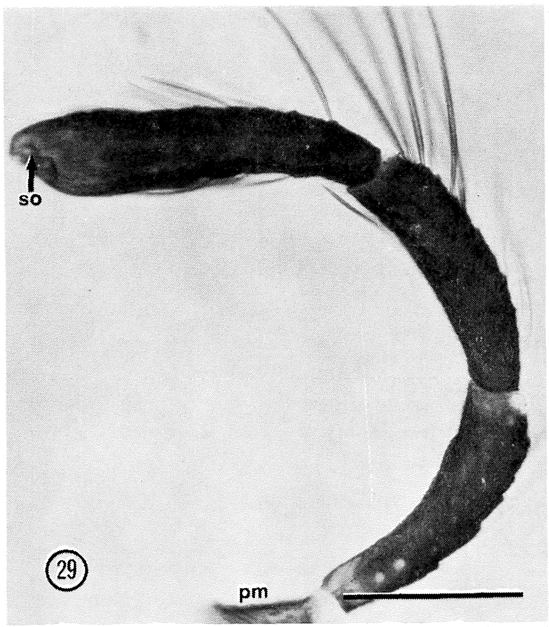
Fig. 29. *E. haworthi,* labial palp. pm, praementum; so, sense organ. Scale 100 μm.

Fig. 30. *E. haworthi,* salivary gland, tangential section. nu, nucleus. Scale 10 μm.

Fig. 31. *E. haworthi,* hypopharynx, horizontal section. hb, hypostomal bridge; md, mandible; sl, salivarium; su, hypopharyngeal suspensorium; 37, m. hypopharyngeo-salivarialis anterior; 38, m. hypopharyngeo-salivarialis posterior. Scale 25 μm.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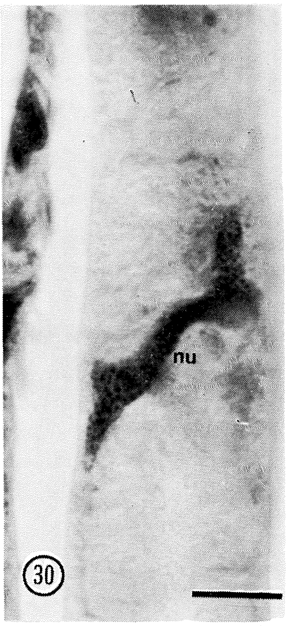
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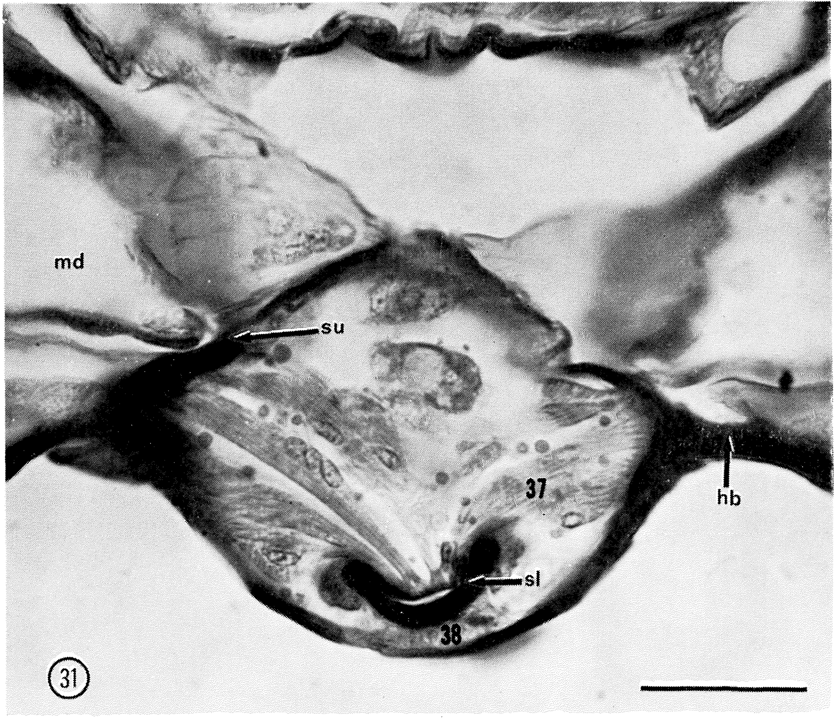
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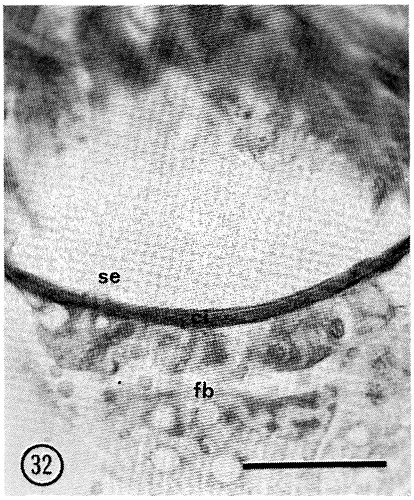
Fig. 32. *E. haworthi,* cibarium, horizontal section. ci, cibarial plate; fb, fat body; se, sensillum campaniformium. Scale 25 μm.

Fig. 33. *E. haworthi,* cibarial plate with sensilla campaniformia (scanning electron micrograph, courtesy of Prof. H. E. Hinton, Bristol). Scale 10 μm.

Fig. 34. *E. haworthi,* pharynx surrounded by brain and suboesophageal ganglion, horizontal section. ao, aorta; rn, recurrent nerve; 42, m. tentorio-cibarialis. Scale 10 μm.

Fig. 35. *E. haworthi,* oesophagus, horizontal section. in, intima; mu, circular fibres in muscularis. Scale 10 μm.

Fig. 36. *E. haworthi,* oesophageal valve, sagittal section. cr, crop; fb, fat body; gl, cytoplasmic globules; me, lumen of mesenteron; oev, oesophageal valve. Scale 50 μm.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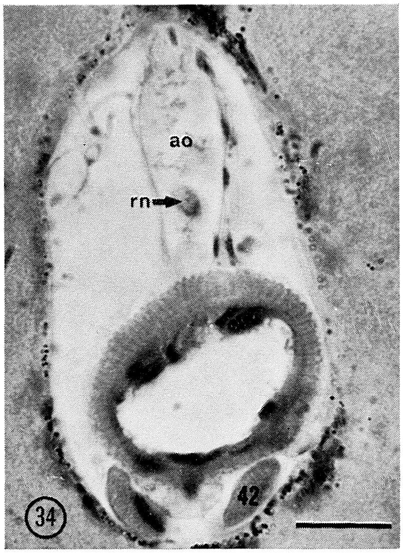
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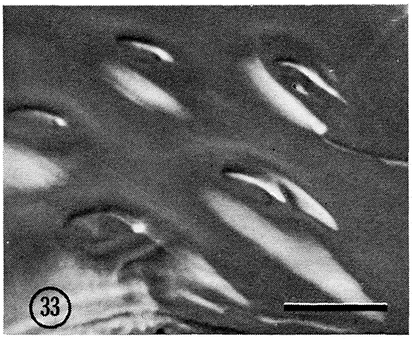
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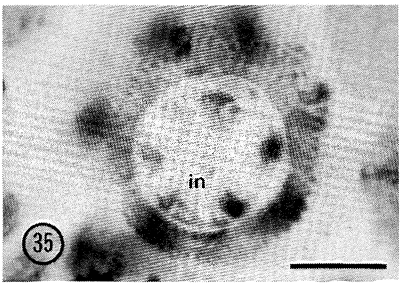
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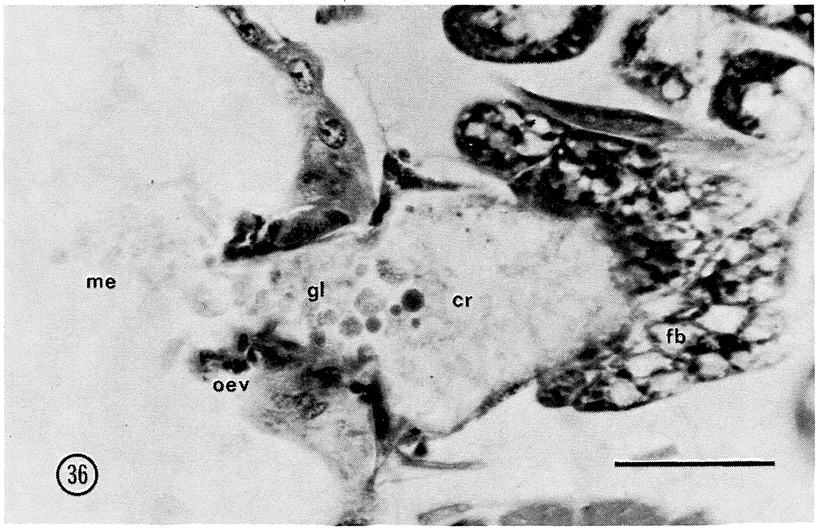
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Fig. 37. *E. haworthi,* wall of mesenteron in a presumably newly emerged specimen, horizontal section. bru, brush-border; lu, lumen of mesenteron; rc, regenerative cell. Scale 10 μm.

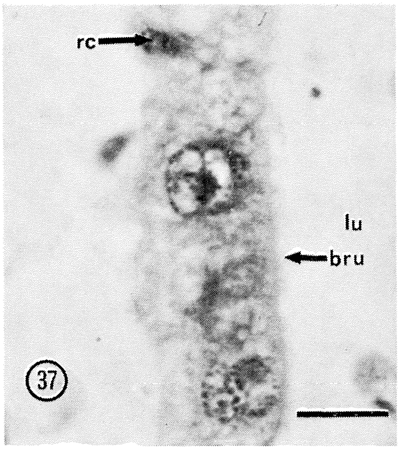
Fig. 38. *E. haworthi,* wall of mesenteron in a presumably older specimen, sagittal section. The wall is partially thrown in folds. lu, lumen of mesenteron; mu, circular fibres in muscularis; Scale 10 μm.

Fig. 39. *E. haworthi,* transition between mesenteron and proctodaeum, sagittal section. ilo, ileo-colon; me, mesenteron; mt, Malpighian tubules. Scale 100 μm.

Fig. 40. Part of preceeding figure at greater magnification. mt, Malphighian tubule. Scale 25 μm.

Fig. 41. *E. haworthi,* ileo-colon, whole mount (+ nicols). Notice regular network of longitudinal and circular fibres in muscularis. Scale 50 μm.

Fig. 42. *E. haworthi,* rectum, whole mount (+ nicols). Notice the irregular course of the fibres in muscularis and the weak development of the longitudinal fibres contrasted with that of the circular fibres. Scale 50 μm.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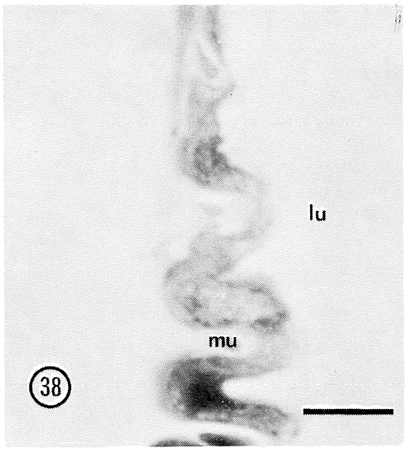
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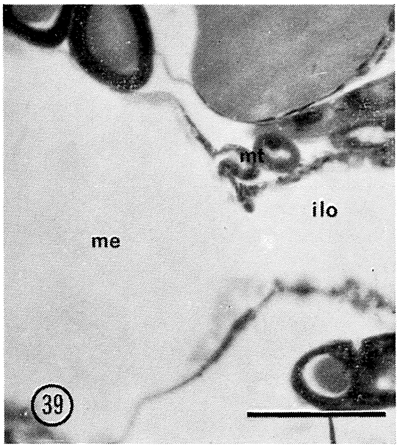
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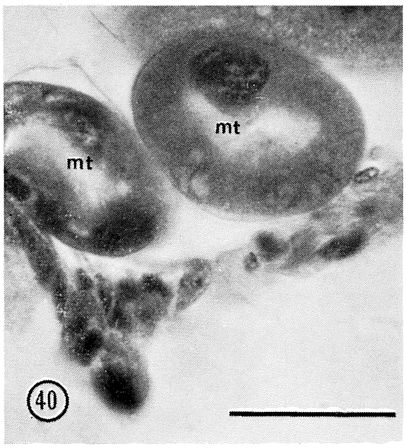
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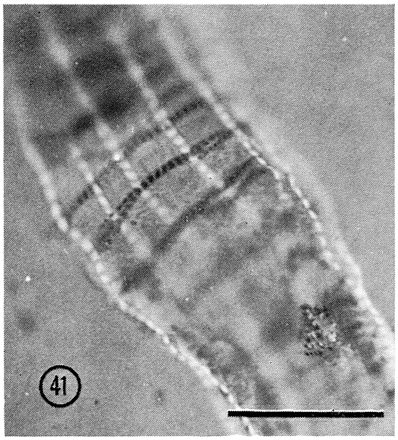
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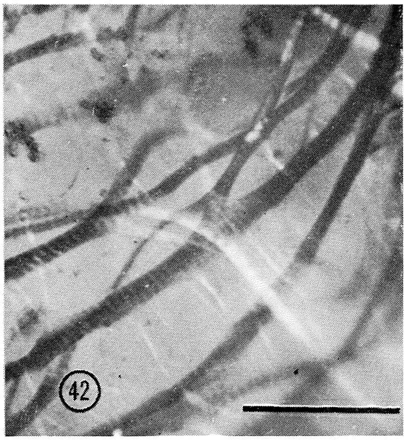
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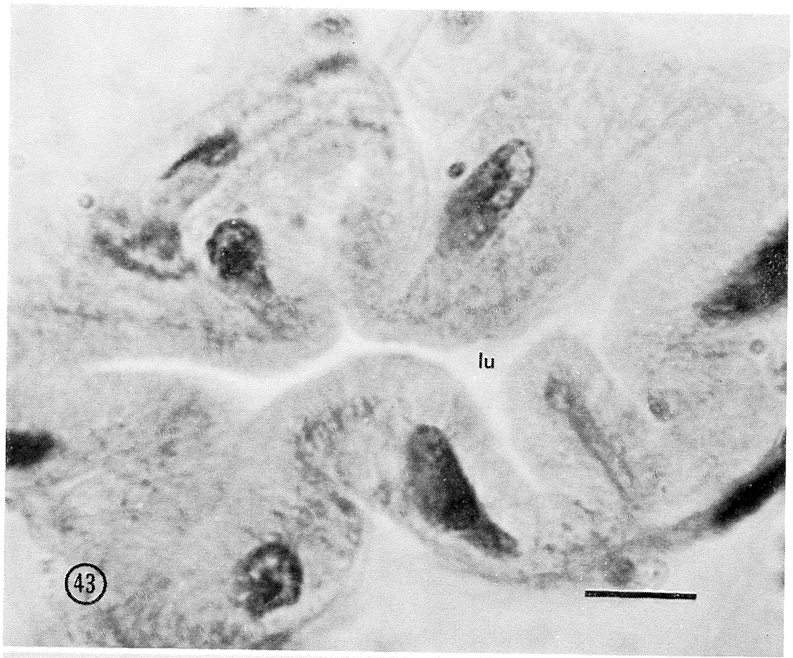
Fig. 43. *E. haworthi,* ileo-colon, transverse section. lu, lumen. Scale 10 μm.

Fig. 44. *E. haworthi,* rectal papilla, sagittal section. cv, basal cavity in papilla; lu, lumen in rectum. Scale 10 μm.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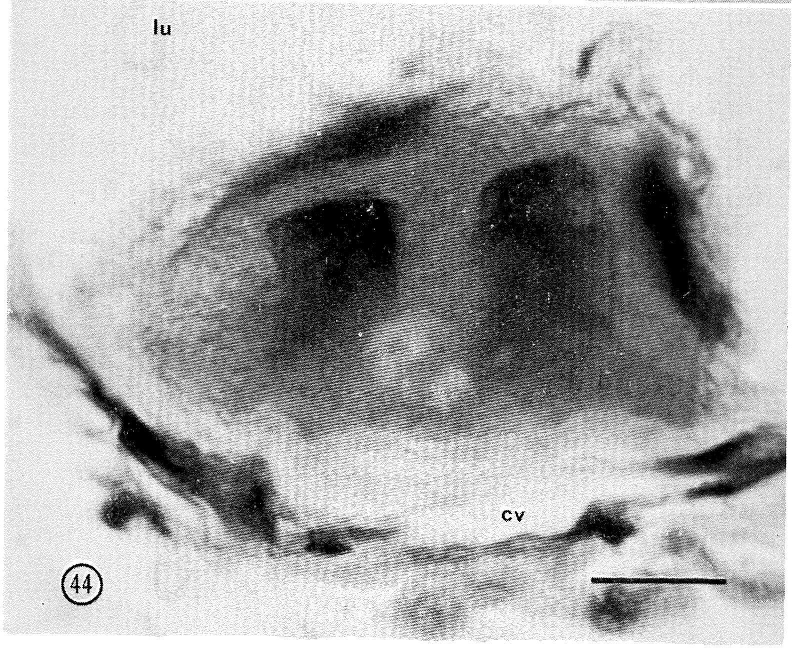
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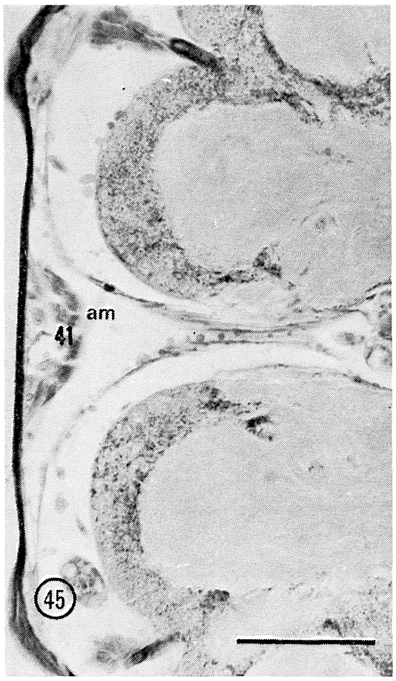
Fig. 45. *E. haworthi,* anterior part of head, horizontal section. am, aortic ampulla; 41, m. fronto-pharyngealis posterior. Scale 50 μm.

Fig. 46. *E. haworthi,* oesophageal ring and suboesophageal ganglion, horizontal section. sg, suboesophageal ganglion; tr, tritocerebral commissure. Scale 25 μm.

Fig. 47. *E. haworthi,* head, horizontal section. ad, apodeme of mandibular adductor; br, brain; sg, suboesophageal ganglion. Scale 100 μm.



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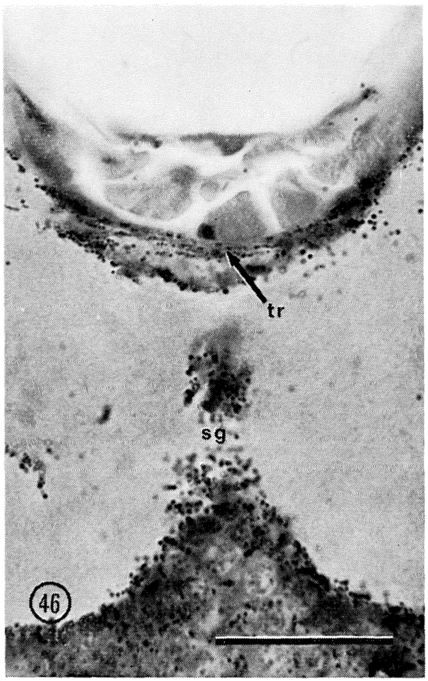

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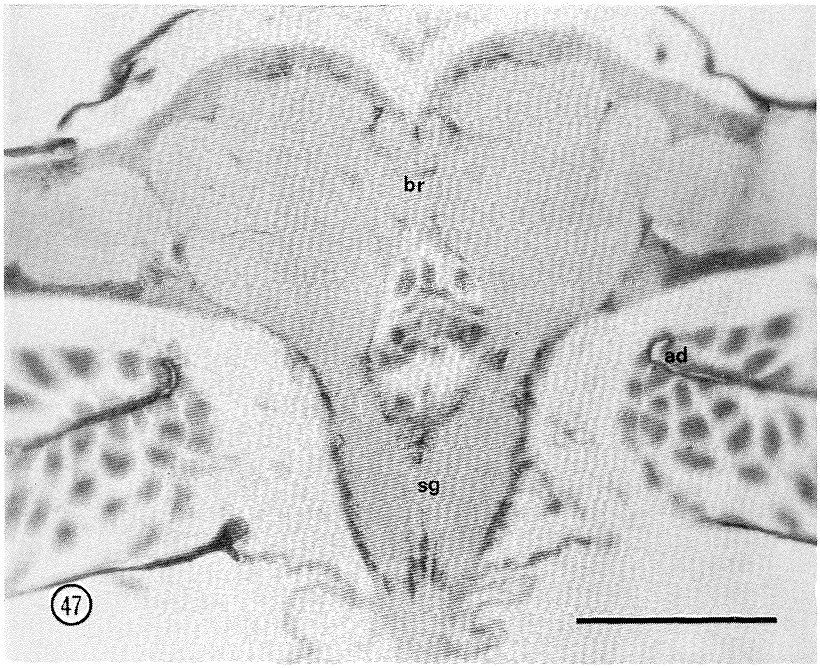

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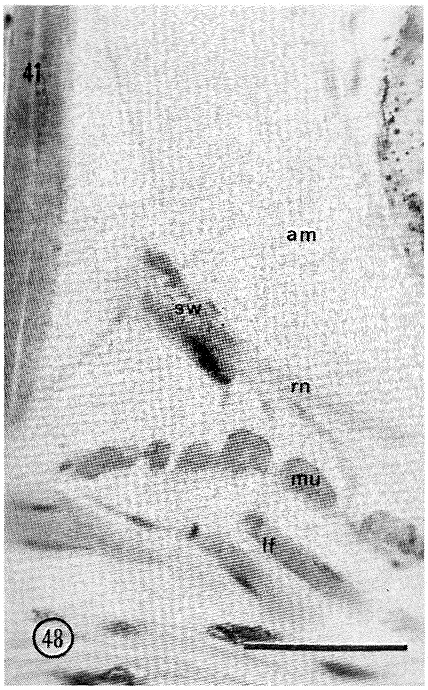
Fig. 48. *E. haworthi,* aortic ampulla and surroundings, sagittal section. am, aortic ampulla; lf, longitudinal fibres in pharyngeal muscularis; mu, circular fibres in pharyngeal muscularis; rn, recurrent nerve; sw, ganglion-like swelling on recurrent nerve; 41, m. frontopharyngealis posterior. Scale 25 μm.

Fig. 49. *E. haworthi,* retrocerebral glands, sagittal section. al, corpus allatum; cd, corpus cardiacum; nal, nervus corporis allatus; ns, neurosecretory cell in corpus cardiacum. Scale 25 μm.

Fig. 50. *E. haworthi,* retrocerebral glands, horizontal section. al, corpus allatum; ao, aorta; hg, hypocerebral ganglion; nm, neuropile mass in corpus cardiacum; ns, neurosecretory cell in corpus cardiacum. Notice the continuity between the tissue of the aorta-wall and the corpus cardiacum. Scale 25 μm.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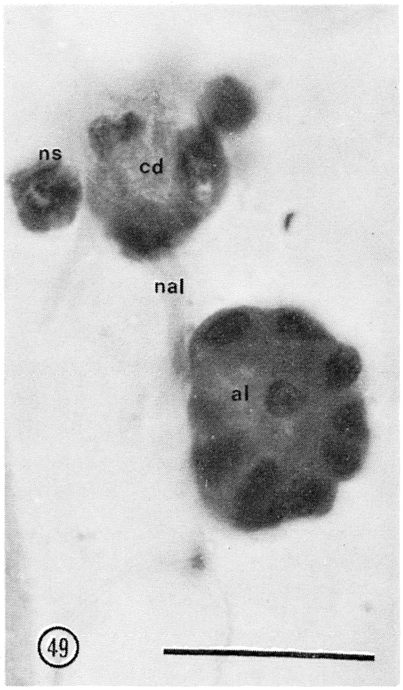
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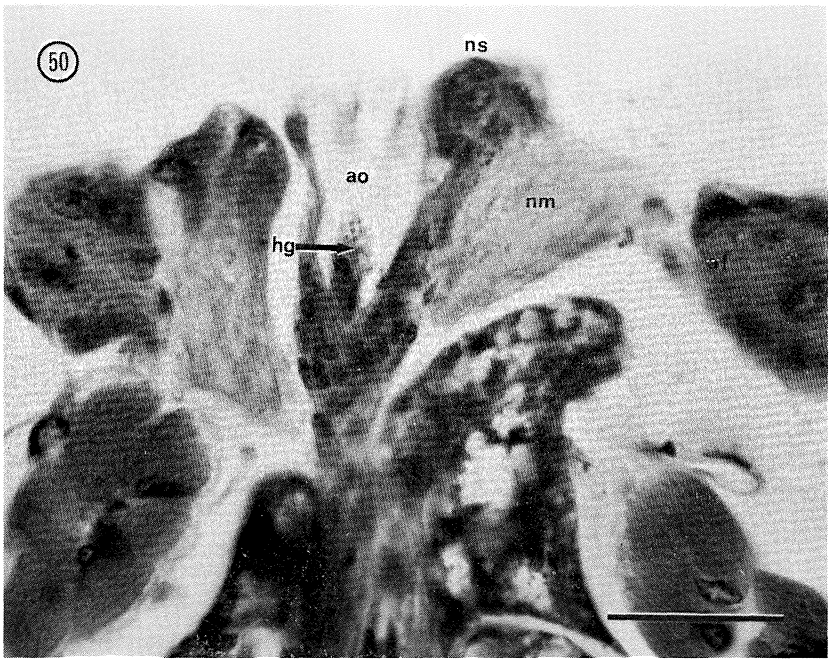
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Fig. 51. *E. haworthi,* compound eye, horizontal section. ln, lens; sn, sense cells. Notice the well developed basal pigment layer. Scale 25 μm.

Fig. 52. *E. semipurpurella,* compound eye, horizontal section. Abnormal specimen having pigmentation strongly reduced. cn, crystalline cone; rh, rhabdom; sn, sense cell. Scale 25 μm.

Fig. 53. *E. haworthi,* ocellus, horizontal section. le, lens; no, ocellary nerve; sn, sense cells; vb, vitrous body. Scale 25 μm.

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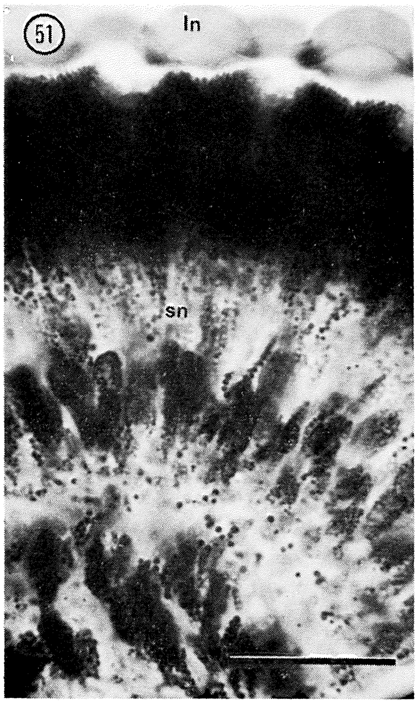

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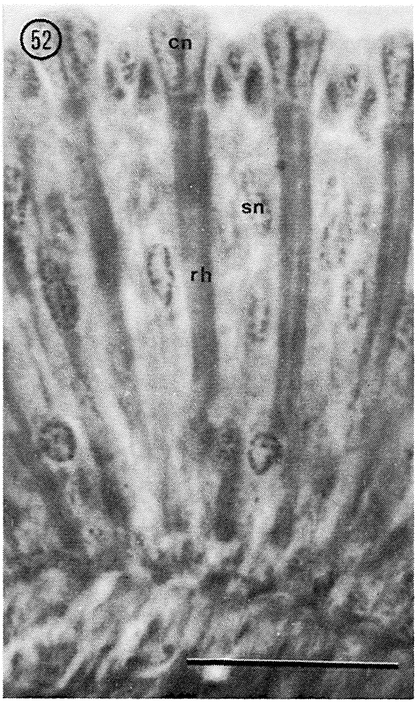

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