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The Structure and Function of the Mouth-Parts, Rostrum and Fore-Gut of the Weevil Calandra granaria L.

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THE STRUCTURE AND FUNCTION OF THE MOUTH-PARTS, ROSTRUM AND FORE-GUT OF THE WEEVIL *CALANDRA GRANARIA* L.

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CONTENTS

The mouth-parts of *Calandra granaria* are situated at the tip of an elongated rostrum. The mandibles are asymmetrical and possess a markedly oblique axis of rotation which determines the precise mode of action of their teeth. Extremely long bracons attached near their molar regions lie in the lumen of the pharynx.

The maxillae although considerably specialized still show to a large extent their constituent parts. They lie in an almost vertical plane against the lateral walls of the labium, and are chiefly concerned with the transport of food from the mandibles to the mouth opening. The mechanics of the movements of the maxillae are discussed.

No indication of the areas involved in the rigid labium is afforded by the presence of sutures. A dorsal ligula is present, and between the ligula and the main body of the labium a pair of labial palps is revealed by sectioning. A backward extension of the labial roof is fused to the floor of the pharynx and gives it support.

The muscles of the mouth-parts lie completely within the head capsule, and operate the mouth-parts through the intervention of long tendons. These tendons are supported and guided in the rostrum by apodemes.

The pharynx consists of a long trough with a thin roof. Only the roof is provided with muscles, capable of elevating and depressing it. A median tract of spines in the roof operates in conjunction with the pharyngeal bracons in the transport of food along the pharynx.

The stomatogastric nervous system, consisting of paired frontal ganglion connectives and labral nerves, and a median recurrent nerve, is described. The median frontal ganglion of the generalized nervous system is replaced by small paired lateral frontal and labral ganglia and a simple median plexus.

True maxillary glands, opening near the bases of the maxillae, are present.

The structure and function of the oesophagus, crop and proventriculus are described. The proventriculus functions as a sieve retaining food in the crop until partially digested.

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1. Introduction

By far the greater part of the attention that has been paid to the coleopterous family Curculionidae has been either purely taxonomic in scope, or has been concerned with the biology of those members of economic importance. During the present century many investigations have been made into the biology of two weevils, *Calandra granaria* and *C. oryzae*, found commonly infesting stored grain and rice, with the result that knowledge of their habits and behaviour has accumulated far more rapidly than has accurate and detailed information on their structure. It is with the object of partially correcting this lack of balance in the study of weevils that the following work, carried out at the suggestion of Professor J. W. Munro, is offered not only as a study in functional morphology but also with the hope that it may have some interest for those working in applied fields.

I am deeply grateful to Dr Roche Lynch for his generous loan of a Zeiss research microscope and photographic apparatus, which has greatly facilitated the work.

2. Methods and technique

The information presented in this paper has been derived from a study both of whole preparations and numerous series of thin sections of adult weevils. The whole preparations call for no comment, but the methods employed in the production of the sections may be of some interest.

Preliminary attempts were made to section both *C. granaria* and *C. oryzae*, but it was soon found that the former was cut rather more readily and offered more opportunity of obtaining useful sections. Attention has therefore been concentrated on this species.

Initially, young adults were obtained by allowing pupae removed from the grain to complete their development, but later it was found possible to section young adults after their natural emergence from the grain, that is, when about 2–3 days older. Individuals at this older stage have, with few exceptions, been used throughout.

Of all fixatives tried alcoholic Bouin has proved to be the most satisfactory, and has been consistently employed. Many of the reagents, including diaphanol, which have been stated to soften the insect integument, have been tried, but have proved to be without beneficial effect.* Prolonged infiltration with celloidin, followed by paraffin embedding, has yielded good sections, and in this connexion it was found that double-embedded blocks sectioned much better when some weeks old than when freshly prepared. This was possibly due to the elimination of diffusion gradients within the blocks, and embedded material was therefore stored for as long as possible at 25° C before use to hasten such a possible process. This procedure has given good results.

Sections have been cut at 8 or $10\,\mu$, and Mallory's triple stain has been extensively used. Drawings have been made with the use of a squared-net eyepiece or of a Zeiss projection drawing apparatus.

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* At the time when this paper was being prepared, however, it was found that, after treatment with diaphanol for one year, *C. granaria* was satisfactorily softened. These specimens have not yet been sectioned, and therefore it is not possible to comment on the state of the tissues.

3. The morphology of the mouth-parts and mouth region

(i) *The apex of the rostrum.* The mouth-parts of *Calandra* are borne at the apex of an elongated rostrum formed by the prolongation anteriorly of the frons, and to a lesser extent of the vertex, of the head. This rostrum is in the female a little thinner, longer and more curved than in the male, but in both sexes it is about twice as long as the head. The female *Calandra* deposits eggs in holes previously bored by the rostrum in grain or rice, but, as Imms (1934, p. 507) remarks of weevils in general, the significance of the rostrum in the male is obscure. The feeding of adult weevils is not restricted to the drilling of holes; irregular excavations are also made, and some surface browsing is carried out.

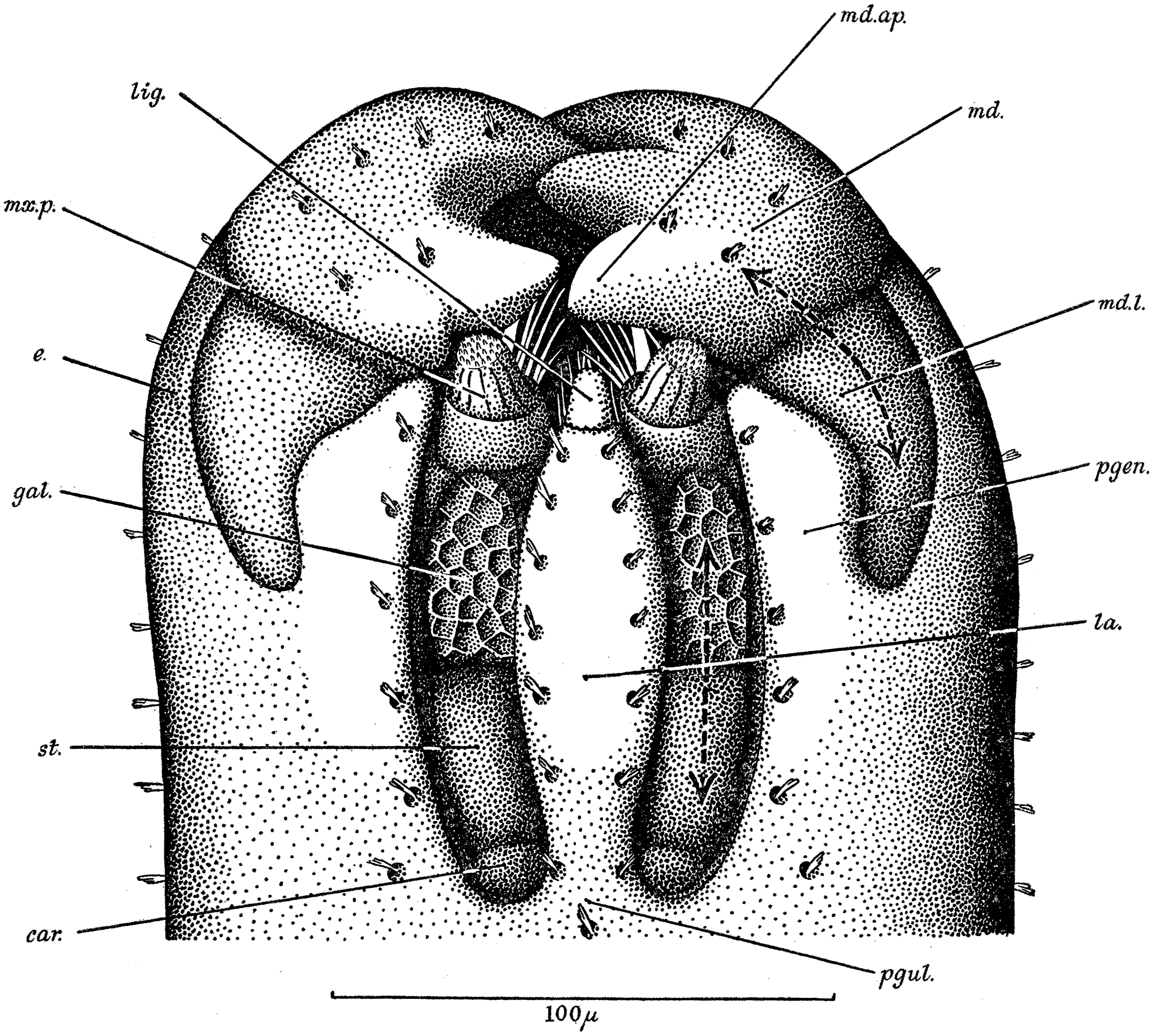

Figure 1. The mouth-parts of *Calandra granaria* in antero-ventral view. Arrows indicate the movements of the left mandible and maxilla.

The roof of the apex of the rostrum, or epistoma (figure 1, *e.*), is presumably formed by the reduced fronto-clypeal region of the head. Anteriorly its margin is smoothly and concavely curved. Two small sclerite-like thickenings situated antero-laterally and visible in ventral view perhaps represent the tormae, often taken (Crampton 1921, p. 68;

Snodgrass 1928, p. 41; 1931, p. 113) to mark the posterior limits of the labrum. Their presence here may indicate that a reduced and immovable labrum (figure 7, *l.*) is incorporated with and forms the anterior border of the epistoma.

The floor of the apex of the rostrum, or hypostoma, is composed of the median pregula (figure 1, *pgul.*) and the lateral pregenae (figure 1, *pgen.*). The pregula bears anteriorly the tongue-like and immovable labium (figures 1, 7, *la.*), which will be discussed later (p. 258). Anteriorly the pregenae are prolonged into horns, and henceforward in this account the term pregena will refer to these horns. They lie parallel with the labium but do not extend quite so far anteriorly as its tip. The hypostoma has therefore a marked tripartite appearance, emphasized by the fact that the anterolateral margins of the hypostomal area, external to the pregenae, commence at the bases of the pregenae and sweep anteriorly and dorsally to form the lateral margins of the rostral tip, which in turn are continuous with the emarginated anterior edge of the epistoma. A deep posteriorly directed cleft, occupied by the lateral plate of the mandible (figure 1, *md.l.*), therefore occurs lateral to each pregena.

As seen in lateral view the ventral surface of the labium and of the pregenae are inclined to some extent antero-dorsally, so that the tip of the rostrum presents a slightly obliquely truncated appearance (figure 7).

The areas forming the tip of the rostrum are not clearly defined owing to their close fusion with each other, and in this study, which is primarily concerned with the topography and mode of operation of the mouth-parts and related structures, no attempt has been made to determine their limits. The nomenclature adopted here is based on that employed by Hopkins (1911) in his description of *Pissodes*.

(ii) *The mandibles*. The mandibles of *Calandra* (figures 1, 7 and 8, *md.*; figures 2, 3 and 4) are massive and irregularly semi-globular, their inner faces being roughly plane, and their outer ones strongly convex. They bear prominent teeth on their anterior margins, and differences in the form and extent of the teeth result in the mandibles presenting a marked asymmetry. The left mandible possesses a conspicuous recurved apical tooth (figures 3, 4 L, *md.ap.*), which is followed by a rather stouter one, the subapical (figure 3, *md.sa.*). The median tooth (figure 3, *md.me.*) is the largest, and is bluntly rounded at its tip, while the molar tooth (figures 3, 4 L) is almost quadrangular and presents a slightly concave functional surface.

The right mandible, on the other hand, bears a greatly reduced apical tooth (figure 4 R, *md.ap.*), but the subapical and median teeth are very similar to those of the left mandible. The molar tooth of the right mandible is much larger than that of the left.

In other respects the mandibles are similar, each possessing the characteristic 'pharyngeal bracon' (Hopkins 1911) of the Curculionidae. These structures (figures 2, 3, 4, 7 and 8, *ph.b.*) appear to have been first described by McClenahan (1904) under the term 'pharyngeal process'. They reach their highest degree of development in the Calandridae (Ting 1936), where they are long, slender, chitinous rods lying free in the pharynx (figure 7, *ph.b.*) and extending in *Calandra* almost its full length. They are attached medially to the postero-dorsal angle of the mandible, behind the molar tooth, and in section through their bases are markedly concave, wrapping round the massive 'tendon' of the mandibular adductor muscle (figure 3, *md.ad.*). As they become more slender distally they become

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progressively oval and finally almost circular in section (figure 8 G, H, I, *ph.b.*). The surface of the bracons is thickly armed with short slender backwardly directed spines, which proximally are very dense over a triangular area of the median face, but elsewhere are more sparse and evenly distributed.

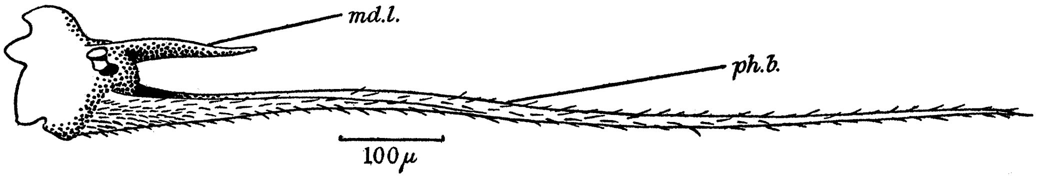

FIGURE 2. The left mandible as seen in median and somewhat ventral view, and rotated through approximately 90° as compared with the view obtained in figure 1, in which the apical tooth lies nearest the observer. The tendons are omitted, but the full extent of the pharyngeal bracon is shown.

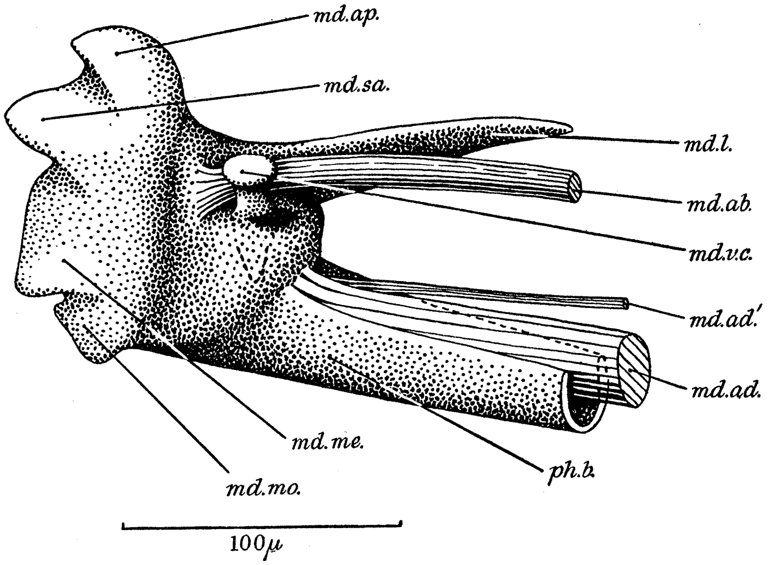

FIGURE 3. The left mandible seen from the same position as in figure 2, but enlarged to show the tendons, which with the pharyngeal bracon have been cut short. The position of the dorsal condyle is indicated in broken lines, and the setae of the bracon are omitted.

In the preceding paragraph it was stated for convenience that the bracons lie free in the pharynx, but actually this statement calls for slight modification. The articulation of the mandibles is so disposed that the basal parts of the bracons lie in the anterior portion of the pharynx, with the walls of which they are fused for a short distance in this region (figure 8 F, *ph.b.*). The lumen of the pharynx has therefore a somewhat hour-glass shape in section at this level. Hopkins (1911) refers to the pharyngeal bracons of *Pissodes* as forming 'a rigid support or brace to the lateral wall of the pharynx', but it will be seen later (p. 261) that, correlated with but not resulting from the fusion of the bracons to the pharynx, it is the pharyngeal floor that is rigid. In the neighbourhood of the bases of the bracons the walls of the pharynx are thin and flexible and allow of the movements of the bracons.

Ting (1936) has inferred from their fusion with the walls of the pharynx that the bracons are of stomodaeal origin and are only secondarily associated with the mandibles. Earlier (1933) this author had seen in the bracons the homologues of the prosthecae of staphylinid beetles, but in his later publication he states that the 'peculiar process attached to the inner basal angle of the mandibles is now known to belong to the pharyngeal or stomodaeal wall and is not a prostheca as previously termed by the author in a preliminary publication. It is attached to the mandible with the other pre-oral membrane and does not arise from a foramen on the mesal margin as Blackwelder (1934) has shown of the prostheca found on the mandibles of Staphylinidae'.

If Ting's later statement is correct, then the bracons show only homoplastic resemblances to the prosthecae of the Staphylinidae, but the features he mentions do not appear to afford conclusive evidence of this. The information derived from a detailed study of the development of the bracons in ontogeny, and from a study of their evolution throughout the Rhynchophora, should determine the true nature of these structures. In this connexion it is interesting to observe that McClenahan (1904) remarks on the budding, at one stage in the development of the rostrum and mouth-parts, of the pharyngeal processes from the mandibles, but she does not appear to have studied their development critically with a view to determining their precise homology.

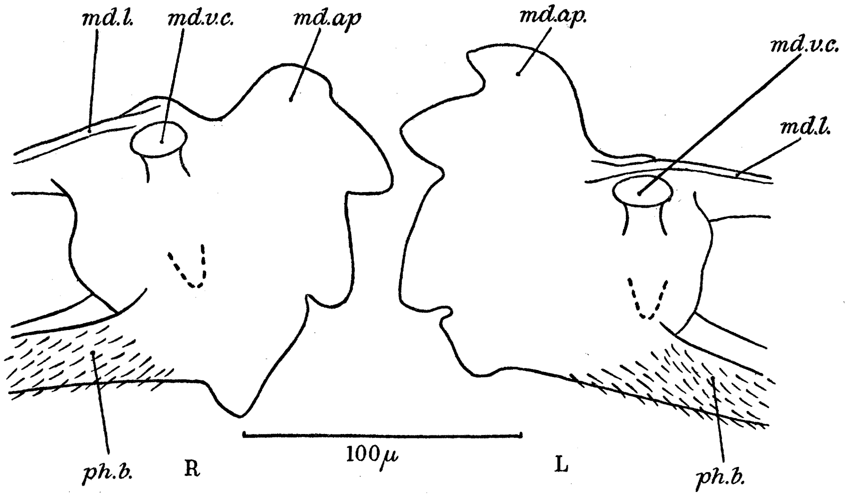

FIGURE 4. The right and left mandibles seen from the same position as in figures 2 and 3 to show their asymmetry. The dorsal condyles are indicated in broken lines.

In addition to the pharyngeal bracons the mandibles each bear postero-laterally a backwardly directed flap-like flexible plate (figures 1–4, *md.l.*), devoid of setal or spinous armature, and of only small extent compared with the bracons.

The extrinsic articulation of the mandibles with the rostral tip is effected by a pair of characteristically shaped condyles. The ventral condyle (figures 3, 4 and 8, *md.v.c.*) is columnar and expanded distally, having the shape of a capstan. It arises obliquely from the median face of the mandible near its ventral border. The dorsal condyle (figure 8 C, D, *md.d.c.*) is peg-like and surrounded by a distinct annular depression or fossa. This condyle also arises obliquely, but from the dorso-lateral face of the mandible. Its long axis lies in line with that of the ventral condyle, so that the axis of articulation passes through the almost plane median surface of the mandible (see figure 8 C, D).

The ventral condyle of the mandible is received by an acetabulum excavated in the dorsal surface of the tip of the pregena, which extends forwards as an outrigger supporting the mandible. The margin of this acetabulum is infolded around the neck of the condyle (figure 8 D, *md.v.c.*). The dorsal condyle lies in an acetabulum formed laterally in the ventral surface of the epistoma, and here the acetabular margin is raised as an annular elevation projecting into the fossa surrounding the condyle (figure 8 C, D, *md.d.c.*). It will be apparent that this arrangement of condyles and acetabula confers on the articulation of the mandibles great rigidity in planes outside that of rotation.

It has been mentioned that the axis of rotation passes obliquely through the mandible. In addition to this obliquity the dorsal acetabulum is placed anterior and lateral to its ventral fellow, so that the axis of rotation slopes upwards, forwards and outwards with respect to the rostrum. The obliquity of the axis of rotation to both mandible and rostrum will be shown later (p. 276) to be of great functional significance.

The lateral plates, mentioned earlier (p. 252) as being borne by the mandibles, serve to close the cleft on each side of the hypostoma lateral and dorsal to the pregenae (figures 1 and 8 C, D, E, *md.l.*). This cleft is necessary to allow the mandible its wide arc of movement, and any structure closing it must be flexible and move with the mandible. These conditions are met by the lateral plates, which as may be seen from figure 3 protect the underlying abductor 'tendons' of the mandibles.

The muscles of the mouth-parts of *Calandra* are all situated in the cranium, and are anchored to its inner wall or to the tentorium. They operate the mouth-parts through the intervention of long 'tendons', necessarily running the full length of the rostrum, in which their precise arrangement is described in a separate section of this paper (p. 263). Although the term 'tendon' is descriptive of the function of these structures, they appear not to be true tendons. In them neither bundles of collagen fibres, nor nuclei, are apparent; indeed, they present an almost completely uniform appearance, staining a light Cambridge blue, resembling that attained by the endocuticle, in Mallory's triple stain. They are to be correctly regarded as long, slender, and flexible apodemes derived from the integument of the mouth-parts. McClenahan (1904) has described the development of the mandibular tendons in *Mononychus* as tubular ingrowths of the hypodermis of the mandibles. Short apodemes intervene between the mandible and its muscles in many insects, and are represented by the 'tendons' in *Calandra*. For convenience, however, and on account of their function, the long apodemes of *Calandra* will be referred to henceforward without further qualification merely as tendons.

On the mandibles are inserted three tendons. The largest of these is that of the adductor muscle. It runs down the rostrum and passes close to the lateral wall of the pharynx, where it is partially surrounded by the pharyngeal bracon (figures 3, 8 E, F, *md.ad.*). The insertion of this tendon on the mandible occurs just posterior to the attachment of the bracon and median to the axis of rotation.

A second rather smaller tendon, that of the abductor muscle (figures 3, 7 and 8 F, G, H, I, *md.ab.*), runs more laterally and ventrally down the rostrum. It passes beneath the lateral plate of the mandible, around and lateral to the ventral condyle, and is inserted a little anterior to the condyle. The third tendon (figures 3, *md.ad.'*, and 8 F, G, H, I, 1) is much more slender than the first and second tendons, and lies dorsal to the large adductor muscle in the rostrum, but is inserted with it on the mandible. From its position this third tendon may be referred to as the tendon of the accessory adductor muscle of the mandible.

The mandibles of *C. granaria* have been described, although inadequately, by Müller (1928), and Ting (1936) has referred to those of the Rhynchophora in his paper on the mouth-parts of this group.

The action of the mandibles will be discussed later in describing the feeding movements of the mouth-parts (p. 275).

(iii) *The maxillae.* The maxillae of *Calandra* occupy the longitudinal clefts at each side of the labium (figure 1), and lie in an almost vertical plane (figure 8 E, *mx.*). This position has been attained by a secondary rotation of the maxilla, resulting in the presentation of the morphologically dorsal (primitively anterior) surface to the exterior, facing the pregena. The apparent ventral surface of the limb is the morphologically exterior border. In the following description the terms employed will refer to the present topographical position of the limb.

Even after specialization the component parts of the maxilla are on the whole readily recognizable, even if the limits of these parts are obscure. The main body of the limb is thin and membranous, without obvious transverse articulations, but massively sclerotized areas indicate to some extent the relations of parts. Posteriorly and ventrally a pair of prominent sclerites, representing at most presumably only parts of the cardo and stipes (figure 5, *car.* and *st.*), are flexed in a characteristic manner, enclosing an angle of about 90°. The cardo does not articulate with the rostrum by a basal condyle, but towards the proximal end of its posterior margin it is excavated so as to form an acetabulum, the pararthris, into which projects an anteriorly directed process, the proarthris (figure 5, *pr.*), arising from the postero-median wall of the cleft between the labium and pregena (p. 262). An elevation on the posterior face of the cardo, distal to the acetabulum, forms the site of attachment of the maxillary remotor tendon.

Whether or not the sclerite articulating with the cardo represents the full extent of the stipes is not altogether clear, but several features suggest that it is merely a marginal strip of this area of the limb. It may therefore perhaps correspond with the 'eustipes' which has been recognized by Crampton (1916, 1921) in the stipes of more generalized maxillae, although it is true that in median view it shows a slight longitudinal furrow which might be interpreted as an indication that it is the complete stipes, and that in it are represented both an outer 'eustipes' and an inner 'parastipes'. Snodgrass (1928), in referring to the views expressed by Crampton, uses the terms 'verastipes' and 'juxtastipes', and states that the groove delimiting the verastipes in the more generalized maxilla is nothing more or less than the outward indication of an inner ridge on which are inserted the adductor muscles of the stipes. In *Calandra*, however, no muscles are inserted on the stipes, and it might therefore be argued that their absence renders the significance of the groove as still more cogent evidence of the inherent division of the stipes into two parts. From a consideration of the areas of attachment of the lacinia, galea, and palp, however, it appears that the sclerite under discussion cannot represent the full extent of the stipes, but in view of the specialization of the maxilla it is not possible to state whether it truly corresponds with the eustipes or is merely an independent thickening of some other area of the limb.

The lacinia of the maxilla (figure 5, *lac.*) is a smoothly rounded flattened lobe which projects upwards and slightly inwards, so that it lies almost vertically against the sloping lateral wall of the labium (figure 7, *lac.*). It bears on its inner surface a number of stout tooth-like setae, and on its outer surface numerous more slender setae regularly arranged. All these setae are set near the upper margin of the lacinia. They project upwards and forwards, but are recurved so that their tips are directed somewhat posteriorly.

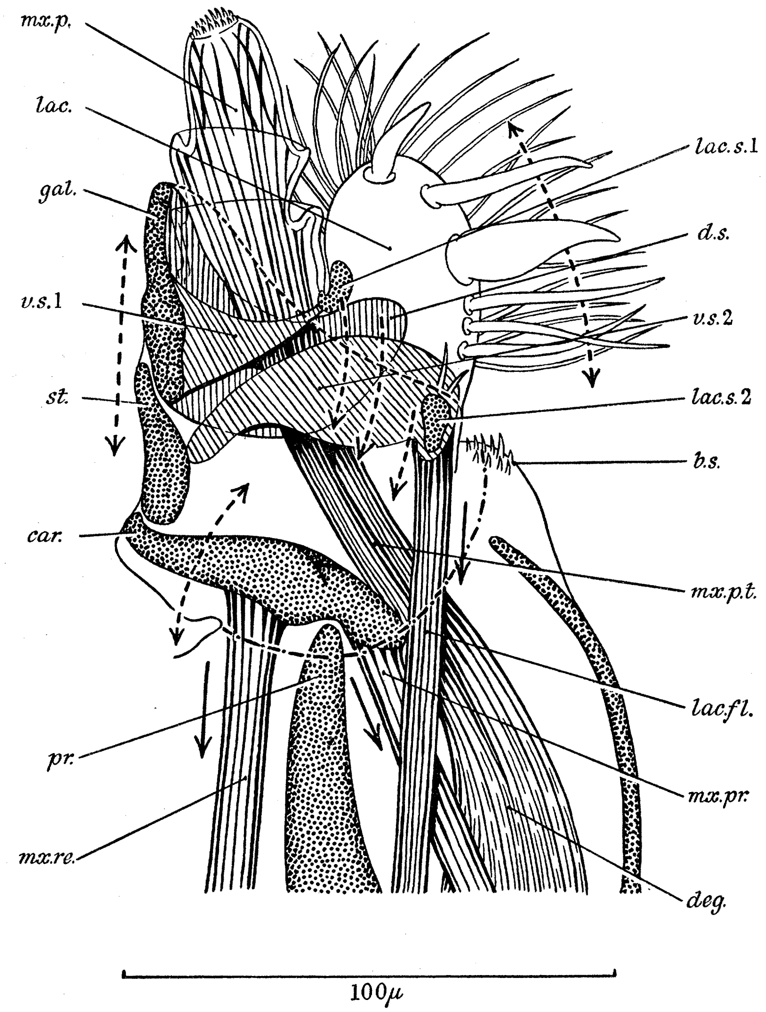

Figure 5. The right maxilla detached and seen in median (morphologically ventral) view as a transparent object, showing the sclerites and the internal tendons which are slightly displaced.

The galea is represented in part by a moderately stout sclerite (figures 1, 5, *gal.*) lying in line with that of the stipes. Its ventral surface bears a distinctive pattern of depressed reticulations, the significance of which is obscure. Three prominent sclerites, then, those of the cardo, stipes, and galea, are seen in line in a ventral view of the maxilla, and these sclerites Müller (1928) has mistakenly identified as the three joints of the labial palp (Unterlippentaster) and so illustrated them in his second figure. What I believe are the true labial palps are described later in this paper (p. 259). The full extent of the galea is possibly indicated by a delicate flap of the integument of the limb, indicated in figure 5 by a broken line, which extends on its outer surface from the tip of the galeal sclerite across the bases of the palp and lacinia to the dorsal margin of the lacinia just anterior to the second lacinial sclerite.

The maxillary palp, inserted between the galeal sclerite and the lacinia, is short and composed of three broad segments deeply retracted one into another. It is to this deep retraction that Ting (1936) ascribes the rigidity of the palp throughout the Rhynchophora, but this rigidity will be again referred to in describing the musculature of the limb. The terminal segment of the palp bears distally a number of short papilla-like setae, and its walls are indented by longitudinal grooves which give it a fluted appearance (figure 1, *mx.p.*). The grooves are referred to by Ting (1936) as structures opening into the haemocoele. No evidence is given in support of this statement, and my sections do not reveal any such openings. McClenahan (1904) describes the maxilla of the larva of *Balaninus* as consisting of cardo, stipes, lacinia, and a palp-like galea of two segments. The maxilla of the imago is stated to be similar with the exception that the galea is four-jointed. The palp proper is stated to be absent, but from the illustration given by this author it would appear more probable that it is the galea and not the palp which is absent.

It will be appreciated that while the galeal sclerite articulates with the stipital sclerite, the lacinia, palp, and the remainder of the galea, as indicated by the membranous flap referred to, are borne by an area dorsal to the stipital sclerite and presumably representing the remainder of the stipes. It appears, then, that the stipital sclerite cannot represent the full extent of the stipes, and the cardo and stipes are probably, as Snodgrass (1928) remarks of the orthopteran maxilla, strongly convex sclerites, without an inner wall, set upon the wall of the head. Here, however, in *Calandra*, the greater parts of the full extents of the sclerites are thin and membranous, and only prominent marginal thickenings remain to indicate their identity.

The membranous parts of the extreme basal region of the maxilla constitute or are indistinguishable from the arthrodial membrane of the limb, and are continuous with the membranous areas of the remainder of the limb. On the whole I am inclined to regard the broken line drawn in figure 5 from the basal setae to the ventral margin of the limb as indicating the extreme posterior limit of the cardo-stipital region.

In addition to the stout rod-like sclerites already mentioned as forming the ventral margin of the limb, other sclerites, thin and plate-like, are discernible as thickenings of the delicate integument. Two, which from their morphological position I have called the first and second ventral sclerites, occur on the median surface. The first (figure 5, *v.s.*1) is roughly triangular. Its base rests on the basal half of the galeal sclerite, and its apex just reaches the lobe of the lacinia, where it impinges on a small but massive kidney-shaped sclerite, the first lacinial sclerite (figure 5, *lac.s.*1), situated at the base of the ventral margin of the lacinia. The second (figure 5, *v.s.*2) is somewhat pear-shaped. Its narrow end rests on the dorsal surface of the stipital sclerite, about half-way along its length, while its main mass lies across the base of the lacinia, where a clearly defined thickening at the base of the dorsal margin forms the second lacinial sclerite (figure 5, *lac.s.*2). The second lacinial sclerite is clearly shown by Ting (1936, fig. 78) in his illustrations of the maxilla of *Cylas* and of *Tachygonus*.

On the lateral surface of the appendage a morphologically dorsal sclerite (figure 5, *d.s.*), attached along the whole of the margin of the galeal sclerite, sweeps posteriorly through the base of the palp and dorsally into the lacinia. It passes through the region of the palp, galea, and lacinia, that is, through the region to be considered as representing the stipital area of the appendage, and terminates in a rounded apex which lies in the centre of the lacinial lobe.

The significance of these sclerites cannot be appreciated without reference to the tendons of the maxilla, but before these are considered two further points must be mentioned.

First, a long, slender, and curved sclerite supports the dorsal margin of the maxillary base; and, second, just anterior to the tip of this sclerite, and a little posterior to the base of the lacinia, there occurs a number of small spine-like setae, the basal setae (figure 5, *b.s.*). These setae are directed forwards and occur at the same transverse level as the hypopharyngeal lobe (p. 260 and figure 7, *hp.*) which itself bears setae. The basal setae and hypopharyngeal lobe no doubt together constitute a subsidiary triturating mechanism falling within the effective field of action of the pharyngeal bracons (p. 278).

The muscles operating the maxillae are, like those of the mandibles, situated in the head and their long and slender tendons pass down the rostrum to the appendages themselves. Only three maxillary tendons have been observed on each side in the rostrum. One of these, the lacinial flexor tendon (figures 5, 7, *lac.fl.*, and 8 F, G, H, I, 2), occupies a more median position that the other two, which are the promotor and remotor tendons of the cardo (figures 5, 7, *mx.pr.*, *mx.re.*, and 8 F, G, H, I, 3, 4). This disposition of the tendons is correlated with the position occupied by the maxilla. It has been mentioned (p. 254) that the lacinia lies against the wall of the labium and slopes slightly inwards as it projects upwards. The cardo, on the other hand, flexed at right angles to the stipes and projecting dorsally, slopes slightly outwards, so that its basal end is not only posterior but lateral to the base of the lacinia. While it is convenient, then, to describe the maxilla as lying in an approximately vertical plane, the limb as a whole is actually twisted, so that the lacinia and its tendon lie median to the cardo.

The promotor tendon of the maxilla (figure 5, *mx.pr.*) is attached to the basal end of the cardo, and the remotor tendon (figure 5, *mx.re.*) to the 'cardo process' at about the middle of the length of the cardo. These tendons, working antagonistically through the action of their muscles, are capable of swinging the cardo in see-saw manner about the fulcrum provided by the proarthris (figure 5, *pr.*). The hinging of the cardo to the stipes results in this semi-rotatory movement being translated as a linear fore and aft movement to the sclerites composing the ventral border of the limb, and as a consequence the maxilla as a whole is caused to carry out anterior-posterior movements of protraction and retraction. These movements are clearly indicated in figure 5.

The lacinia is capable of movements independent of those of the maxilla as a whole. As already described, the dorsal and ventral terminations of the margin of the lacinia are strengthened by the lacinial sclerites (figure 5, *lac.s.*1, *lac.s.*2) which provide abutments for the two ventral sclerites. The tendon of the lacinial flexor muscle is attached in the region of the second lacinial sclerite, suggesting that the muscle corresponds to the cranial flexor muscle of the lacinia in the more generalized maxilla (see Snodgrass 1935, p. 78). Its pull draws the lacinia back, the two ventral sclerites and the single dorsal sclerite, based on the sclerites of the stipes and galea, functioning as a parallel link mechanism and so defining the arc swept by the lacinia.

The recovery of the lacinia from its backward movement cannot be caused by the action of muscles and tendons, since the only other tendons discovered within the maxilla are those of the palp. Return of the lacinia may perhaps be accomplished by the elasticity of the sclerites forming the parallel link mechanism, or by the pressure of body fluid within the limb. It is noteworthy that in different Crustacea body-fluid pressure has been suggested to be the means whereby a limb is rendered turgid and therefore semi-rigid but elastic (Cannon 1935) and an epipodite is caused to perform its recovery beat (Dennell 1937).

Ting (1936) has indicated in a number of his figures of the maxillae of the Rhynchophora the three tendons which I have just described. McClenahan (1904) also refers to three maxillary tendons in *Balaninus*. Two of these, however, are adductor and abductor attached to the stipes, and not to the cardo, while the third is attached to the base of the lacinia and corresponds to the cranial flexor tendon.

The remaining tendons of the maxilla are those of the palp (figure 5, *mx.p.t.*). Unlike the other tendons these are short and not attached to muscles in the head. In transverse serial sections and in whole mounts only a small extent of tendon can be discovered in the basal region of the limb, becoming anteriorly and posteriorly too diffuse to be referred to by this term. Anteriorly the tendons appear to take their origin from a number of fine strands which are uniformly spread and attached distally to the walls of the three segments of the palp. Posteriorly they merge into a mass of fibrous tissue (figure 5, *deg.*), which has little resemblance to muscle, situated behind the base of the maxilla. It is possible, however, that the fibrous tissue represents the atrophied muscles of the palp, and I feel that the rigidity of the palp remarked on by Ting (1936) is due more to its lack of musculature than to any peculiarity in the mode of articulation of its segments. The palps are thin-walled and presumably retain their shape owing only to the internal pressure of the body fluid, and it would therefore appear improbable that the deep retraction of one segment into another could play any important part in causing the rigidity of the structure as a whole.

(iv) *The labium.* The labium (figures 1, 6, 7 and 8 B, C, D, E, F, *la.*) has been already described as a tongue-shaped structure projecting anteriorly (p. 250). Although this statement is true of the labium as seen in ventral view (figure 1, *la.*), either a lateral view (figure 6 A, *la.*) or sagittal and transverse sections (figures 7, 8) reveals that it is not a flat plate. It is of considerable height, being triangular in transverse section and showing a pronounced dorsal keel. On each side of the keel and a little ventral to its apex arises a row of spine-like setae based upon a shelf-like projection (figure 6 A). These setae occur at the same level as those of the lacinia of the maxilla. More ventrally a distinct groove runs posteriorly and horizontally from the tip of the labium, gradually becoming extinct as it does so. It finally disappears about half-way along the length of the labium. This groove may be seen in figure 6 A, between the terminations of the guide-lines *lig.* and *la.* Reference to the transverse sections (figures 6 B, C, and 8, B, C, D, E, F) at once reveals its meaning. It is caused by the close apposition of an antero-dorsal mass, which can only be interpreted as the ligula (*lig.*), to the dorsal surface of the main body of the labium (*la.*), the two structures being fused together basally without any trace of a suture. The ligula possesses a pronounced dorsal hump near its base, which is well seen in lateral view and marks approximately its posterior termination. Its dorsal keel, however, is confluent with that formed by the apex of the labium. Anteriorly the ligula projects a little in front of the body of the labium, and is therefore visible in antero-ventral view (figure 1, *lig.*).

The ventral surface of the ligula is concave, as is the dorsal surface of the labium, so that a cylindrical cavity exists between the two structures. It cannot, however, be seen externally in lateral view owing to the overlapping of the walls of the ligula by the lateral margins of the labium. The posterior wall of the cavity is formed by the fusion of the ligula with the labium, and on this wall, and therefore lying wholly within the cavity, is inserted a pair of palp-like structures. They arise from a common cylindrical base, and bear minute distal setae. It must be emphasized that they are completely invisible in external view of the labium, and that they can only be revealed by sectioning (figures 6 B, C, D, and 7, *la.p.*). As far as I am aware they have not previously been described, and I suggest that they are the true labial palps (see p. 255). Their position corresponds in general with that of the labial palps of a rostrum-bearing member of the Curculionidae, *Lixus*, illustrated by Williams (1938, figure 98), and with that of the labial palps of *Balaninus*, illustrated by McClenahan (1904). In *Lixus* and *Balaninus* the palps are borne antero-laterally by the

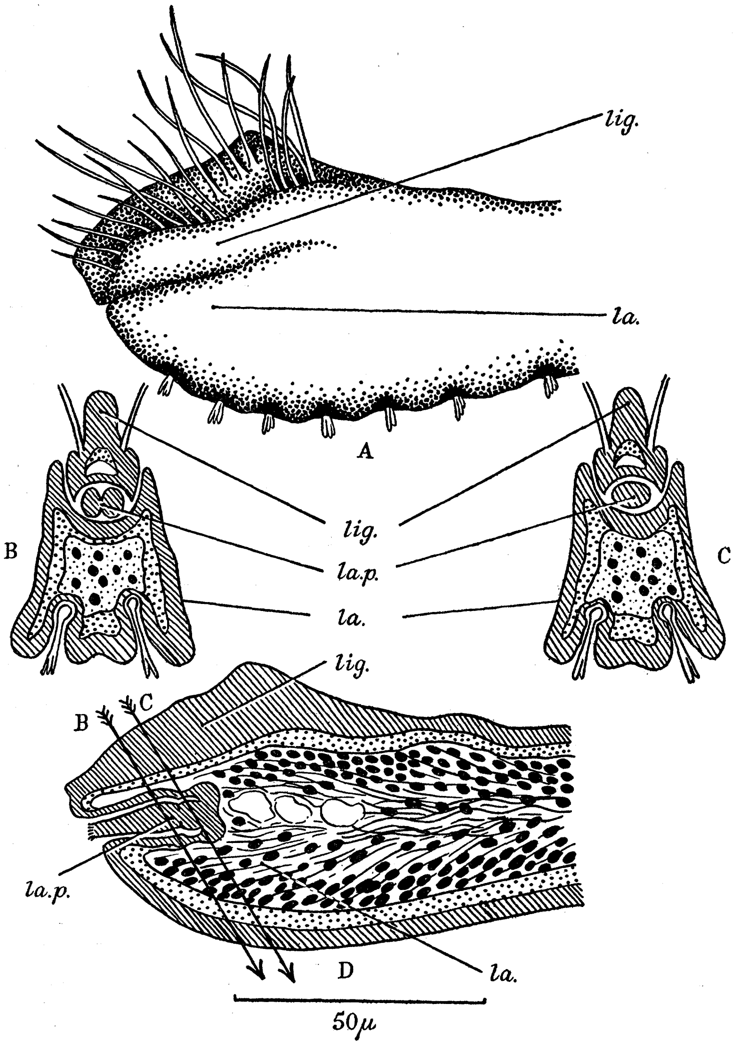

FIGURE 6. The labium and ligula: A, in lateral view from the left; B, in transverse section at the level shown at B in D; C, in transverse section at the level shown in C in D; D, in slightly parasagittal section.

mentum and to some extent between it and the ligula, whereas in *Calandra* they are brought together in the median plane, and withdrawn posteriorly into the space between the labium and the ligula. Ting (1933) states that the Calandrinae are characterized by the absence of labial palps, but later (1936) remarks that in this subfamily they are mere setae or papillae. His description, however, of their location is not very clear, and I am not convinced that his remarks apply to the structures I have just described. I have not been able to discover in the palps any trace of the three segments which they probably once possessed, but in view of their situation and the almost certain reduction that has taken place this is not surprising.

In general the identity and limits of the component parts of the insect labium may be established by a study of its musculature (Snodgrass 1928, 1935; Walker 1931; Das 1937), although the warning delivered by Imms (1937), that these muscles may not retain their original functions and positions of attachment, must be borne in mind. In *Calandra*, however, the rigid fusion of the labium to the pregula, and the masking of the palps by the rigid ligula, causes these structures to play only a passive part in feeding, and it is not therefore to be expected that they should display any well-developed musculature.

Because of this, identification of the areas involved in the labium of *Calandra* is rendered difficult if not impossible. Actually the cavity of the labium is occupied by a mass of somewhat fibrous tissue with many scattered nuclei, in which it is difficult to recognize the limits of the epidermis. It is probable that much of this tissue is to be regarded as atrophied muscle (but see p. 274) like that found, in association with the tendons of the palp, at the base of the maxilla.

It has been remarked that the combined labium and ligula presents anteriorly a triangular appearance in transverse section. Posteriorly, however, in the region of the rather narrower 'neck' of the labium, this appearance is departed from. Ventrally the walls of the labium are more nearly vertical, although the narrow dorsal apex is maintained by the meeting in the median plane of the dorsal portions of the labial walls, which are inclined inwards in roof-like manner. Basally, therefore, the labium has a gable-shaped appearance in transverse section (figure 8 F, *la.*).

Dorsal, that is, morphologically anterior, to the base of the labium, and therefore between mouth and labium, occurs the small lobe of the hypopharynx (figure 7, *hp.*). It is laterally compressed and bears, as already mentioned (p. 257), a number of small setae. Posteriorly the hypopharynx is confluent medially with the floor of the pharynx, which laterally, however, is continuous with the roofs of both labium and pregenae somewhat in front of the level of the posterior ends of the clefts between them. The demarcation of the hypopharynx from the labium is effected by a deep posteriorly directed emargination (see figure 7) which corresponds in position to the salivarium of an orthopterous insect. Behind this emargination a thin median sheet-like extension of the dorsal apex of the labium supports the hypopharynx.

As a result of the 'gable' section of the base of the labium, a groove, corresponding in level with the eaves of the gable, and seen in figure 7 immediately above the head of the tailed arrow, is caused by the meeting of the roof and walls of the labium. This internal groove continues the line of the external groove, seen in figure 6, which marks the separation of the ligula from the labium, and it is perhaps possible, therefore, that what has been referred to as the proximal portion of the roof of the labium in reality represents a more basal portion of the ligula than is indicated in figure 6.

The walls of the labium sweep laterally at the posterior ends of the clefts between the labium and pregenae, and turning forwards become confluent with the inner walls of the pregenae (figure 7). The inverted V-shaped roof of the labium does not terminate at this level, however, but is continued posteriorly and dorsally beneath the hypopharynx (figures 7, 8 G, *la.ex.*) to the floor of the pharynx with which it is fused. It is to be particularly noted that support is thereby given to the pharynx immediately behind the region in which the basal parts of the pharyngeal bracons are fused with the walls of the pharynx (p. 251), a feature which will be seen later (p. 278) to have considerable significance in the functioning of the mouth-parts.

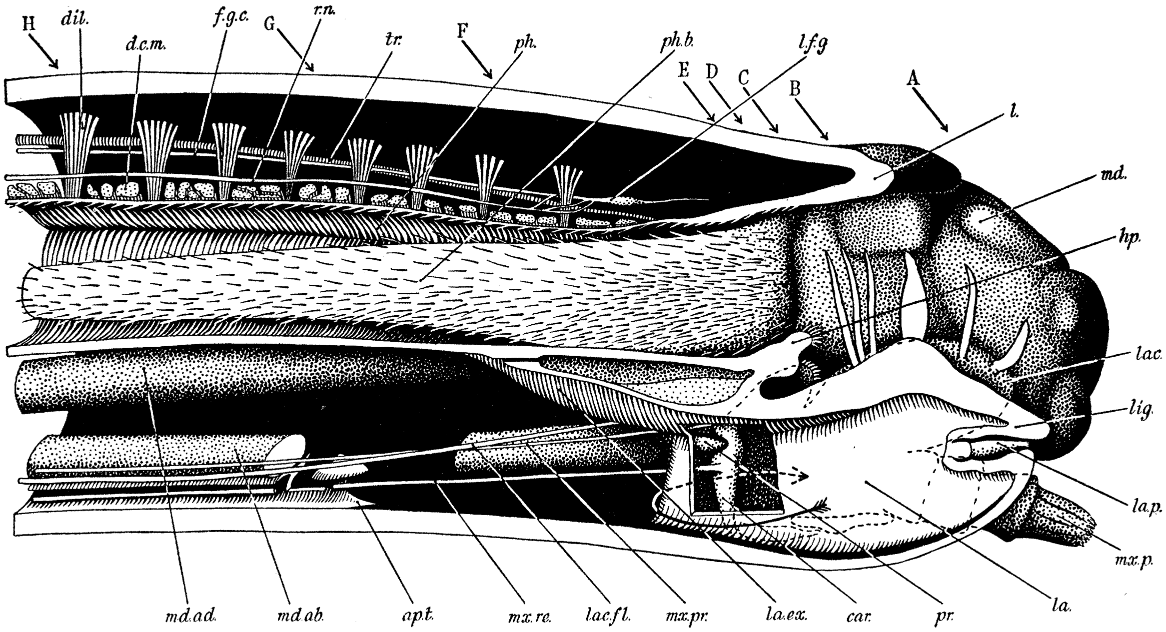

FIGURE 7. The distal portion of the rostrum in sagittal view, based on a reconstruction from transverse and sagittal serial sections. Cut surfaces are left white, and a window has been cut in the left lateral wall of the labium to expose the articulation of the maxilla. To simplify the figure the following structures have been omitted: maxillary setae (with the exception of the stout tooth-like setae), setae of the ligula, setal pits of the integument, the median ventral nerve to the mouth-parts, and the paired ventral tracheae. The left labral nerve, duct of the salivary gland, and the accessory adductor tendon of the mandible are masked by the pharynx. The tailed arrow passes from the cavity of the labium into the cavity of the left pregena. Other arrows indicate the levels of the transverse sections seen in figure 8.

One further point concerning the backward extension of the labial roof remains to be mentioned. It lies a considerable distance beneath the hypopharynx owing to the presence of the deep emargination which separates these structures. As a result, the backward extension of the labial roof lies well beneath the floor of the pharynx, only meeting it some distance behind the hypopharynx. The space intervening between the extension of the labium and the floor of the pharynx is occupied by two thin septa which come together in the median plane. Anteriorly and ventrally (figure 8 F) these septa are closely applied and indistinguishable one from the other, but posteriorly and dorsally (figure 8 G) they diverge so as to leave a V-shaped cavity between them. The area of the apparent single septum is indicated in figure 7 by a uniform hand stipple, and the diverging septa by shaded stippling. The cavity between the septa communicates posteriorly with the haemocoele of the rostrum by a narrow tubular passage through the extension of the labial roof where it fuses with the floor of the pharynx. A fine strand of tissue, possibly a nerve strand, the origin and termination of which I have been unable to discover, penetrates this passage into the space between the septa.

Although I have for convenience of description referred to the posteriorly directed extension which supports the floor of the pharynx as being merely a continuation of the roof of the labium, I am by no means fully assured that this is necessarily its true nature. I have already referred (p. 261) to the possibility that the basal part of the labial roof may be truly derived from the ligula, and if this is so it is not clear what interpretation must be given to the backward extension. Furthermore, although the extension continues posteriorly the planes of the labial roof, it by no means follows that it is to be regarded as belonging to the labium or ligula. It is interesting to note that in orthopterous insects the paired suspensoria of the hypopharynx, in their simpler form of a single sclerite, articulate distally with the lateral sclerites of the hypopharynx, and proximally end in the stomodaeal wall (Snodgrass 1935, p. 115). The speculation may perhaps be permitted that the extension of *Calandra* under discussion represents the hypopharyngeal suspensoria of a more generalized insect, which in the course of profound modification of the head have taken up a new position and function. Whatever its origin, however, the significance of the extension in the present paper lies in the support it affords to the floor of the pharynx.

Turning now to the articulation of the maxilla, it will have been realized that the cardo (figure 7, *car.*), when seen in lateral view, lies almost vertically in front of the curved rear wall (around which the arrow in figure 7 sweeps) of the cleft which separates the labium from the pregena. From this wall, where it turns forward to become confluent with the lateral wall of the labium, the proarthris (p. 254 and figures 5, 7, *pr.*) arises radially at the level of the 'eaves' of the gable section of the base of the labium. It is therefore directed antero-laterally towards the pregena, so much so, in fact, that were it not for the depression in the wall of the pregena mentioned below, the cardo of the maxilla could not be accommodated at its tip.

Lateral to the base of the proarthris, and therefore immediately posterior to its tip, a window-like aperture in the posterior wall of the labio-pregenal cleft provides access for the maxillary tendons passing to the cardo and lacinia, and also for the nerves and tracheae of the limb. This window extends across the full width of the curved wall, and its lateral margin sweeps forward on to the median wall of the pregena where it terminates in a considerable depression which provides clearance for the sweep of the proximal part of the cardo of the maxilla.

The arthrodial membrane of the maxilla is, of course, attached around the margin of the aperture and sweeps medially around the base of the proarthris.

It is evident, then, that in spite of the weakening of the labio-pregenal wall by the window occurring in it, the proarthris arising from it is situated in a region of considerable mechanical strength, chiefly brought about by the presence of the backward extension of the labial roof and its fusion with the floor of the pharynx. This extension lies in a plane so disposed as to adapt it to resist the pull of the maxillary tendons transmitted through the proarthris.

4. The internal structure of the rostrum

(i) *The tendons of the mouth-parts, and the structures associated with them.* The tubular rostrum encloses only the pharynx, the tendons of the mouth-parts, and the ducts of the salivary glands, together with the nerves and tracheae associated with the mouth-parts and pharynx. The muscles of the mouth-parts and the brain lie completely within the cranium.

The comparatively spacious portion of the haemocoele not occupied by the structures enumerated above is separated into definite blood channels, which will be described in connexion with the stomatogastric nervous system (p. 268).

The tendons of the mouth-parts lie free in the rostrum for some little distance behind the mouth, but more proximally they rest in trough-like guides formed in the upper surfaces of two long, narrow, longitudinally disposed apodemes which rise from the inner surface of the ventral wall of the rostrum and lie one on each side of the sagittal plane.

The form of these apodemes is best appreciated from figures 7 and 8. It will be seen that each consists of a vertical keel-like extension of the integument. Dorsally the keel is expanded transversely, so that the apodeme is T-shaped in section. Towards the apex of the rostrum the outer margin of the transverse portion of the apodeme is upturned, and its inner margin is depressed (figure 8 H, *ap.t.*), but more proximally both margins are upturned, and a median crest separates the dorsal surface into two distinct trough-like concavities (figure 8 I, *ap.t.*) in which the tendons lie. At the extreme posterior ends of the apodemes the vertical keel is swollen and stout, and the apodemes terminate just in front of the anterior tentorial pits.

It will be remembered that, according to the mode of articulation of the mandibles and the points of attachment of their tendons, the mandibular abductor tendon lies in the rostrum lateral and ventral to the mandibular adductor tendon. Owing to the downward curve of the rostrum the former tendon is therefore supported by the extreme anterior end of the apodeme (figures 7, 8 H, *md.ab.*). The adductor tendon, attached to the mandible more dorsally, comes to lie on the apodeme more posteriorly (figures 7, 8 H, *md.ad.*), and it is at this level that the median crest of the apodeme arises so that each tendon lies in its own trough. The abductor tendon preserves its more lateral situation throughout the rostrum, and lies in the outer trough of the apodeme. The accessory adductor tendon of the mandible does not enter into relation with the apodeme, but continues its course posteriorly considerably more dorsally than the tendons just mentioned.

As might be expected from the position of the maxillae, all their tendons lie median, in the distal part of the rostrum, to those of the mandibles. Owing to the twisting of the maxillae described earlier (p. 257) the lacinial flexor tendons lie nearer to the median plane than those of the cardo (figure 8 F, G, H, I, 2, 3 and 4). Posteriorly the three tendons of each maxilla converge and form two vertically disposed groups which lie in the median space between the anterior ends of the apodemes (figure 8 H). More posteriorly still the tendons of each group pass over the margin of the apodeme, and come to lie in a horizontal plane beneath the mandibular adductor tendons in the inner trough of the apodemes (figure 8 I). The lacinial flexor tendon maintains its position on the inner side of the tendons of the cardo, so that, although the group of tendons as a whole is rotated through approximately 90°, there is no twisting of the tendons around each other.

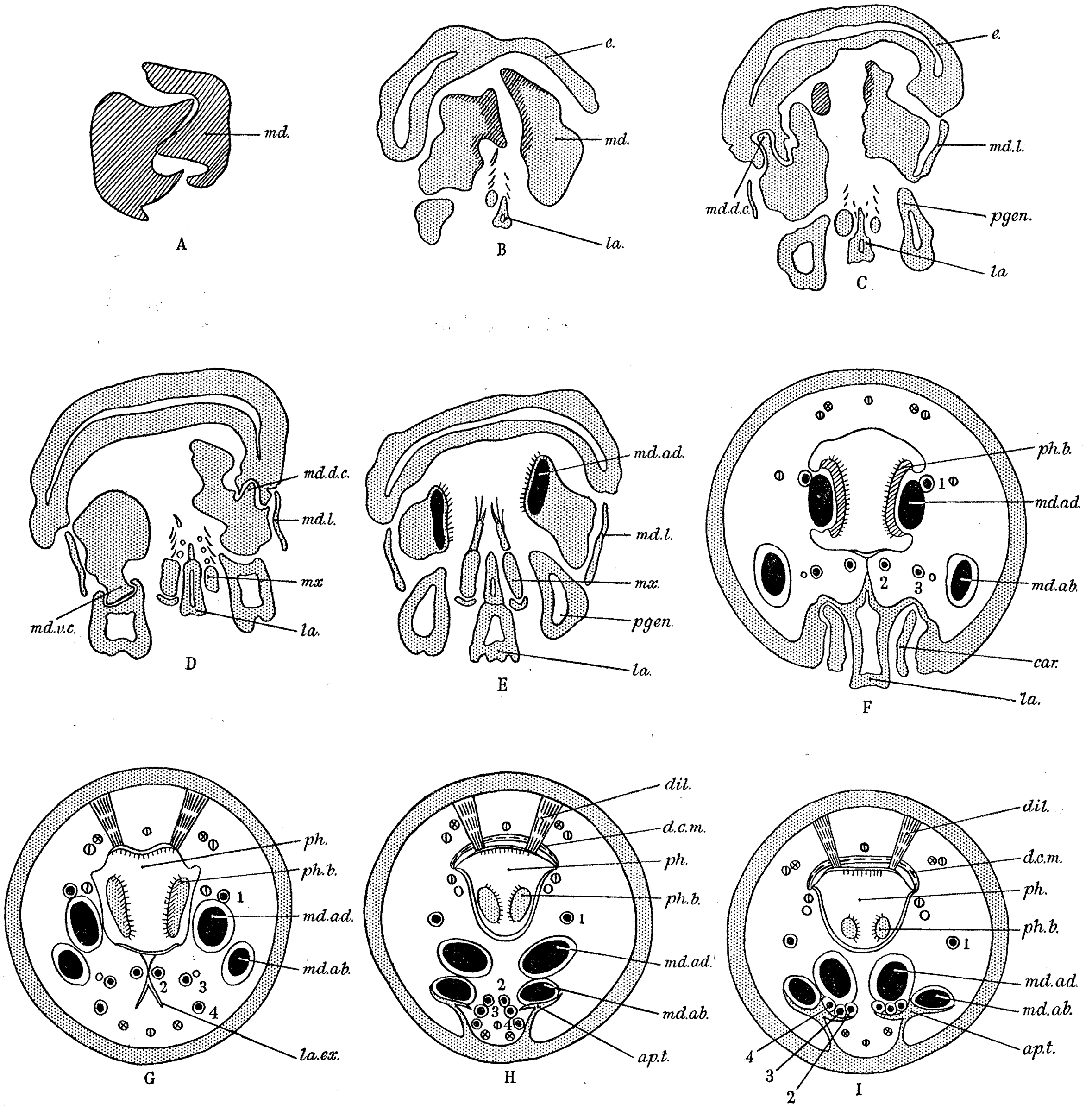

Figure 8. Series of transverse sections at different levels through the rostrum and mouth-parts. The sections are truly transverse towards the base of the rostrum, and are therefore owing to the curvature of the rostrum inclined obliquely backwards in the region of the mouth-parts. Tendons are represented in solid black, tracheae by ⊕, nerves by ⦶, and the ducts of the salivary glands by ○.

Structures suggestive of the supporting apodemes have been described by McClenahan (1904). In discussing the homologies of the mouth-parts and rostrum this author mentions in the late pupa of *Mononychus* the presence of two longitudinal internal ridges separated by one-third of the diameter of the rostrum and extending back to the head, and suggests that they mark internally the lines of fusion of the gular margins with the genae. They therefore should correspond in position with the gular sutures. Hopkins (1911), however, has illustrated the confluence and ultimate convergence in the head of the gular sutures in *Pissodes*, a feature accepted, indeed, as characteristic of Rhynchophora in general. The supporting apodemes which I have described lie truly parallel with each other, and it therefore appears unlikely that McClenahan's suggestion is correct. It is more probable that the apodemes have arisen only in relation to the tendons, and that they are of purely functional significance.

As well as being supported and guided by the apodemes, all the tendons are enclosed in definite tubular sheaths consisting of an inner membrane and an outer irregular epithelial layer. The epithelial layer appears to be most prominent in the late pupae and young imagines, becoming rather difficult to distinguish in older individuals. It often merges with the epithelial layer (an extension of the epidermis) which invests the ventral parts of the apodemes. I am not able to produce evidence as to whether the sheaths are derived from the epithelium of the apodemes or from that of the mouth-parts served by the tendons. But if the tendons are truly apodeme-like ingrowths from the integument of the mouth-parts it would appear not unlikely that the sheaths are produced from local tubular extensions of the epithelium of the limbs which surround the extending tendons. This opinion is supported by the observation that anterior to the supporting apodemes the sheaths are still present, and also by the secondary relation of the tendons to the apodemes.

The sheaths are indicated in figure 8 F, G, H, I as circles surrounding the tendons. In some of the sections strands of connective tissue extend from the sheaths across the haemocoele of the rostrum to the pharynx or rostrum itself, so anchoring them in position. The tendons are freely movable within the sheaths so that the disposition of these parts recalls that of the well-known Bowden cable mechanism. The supporting apodemes are necessary, however, in addition to guide the tendons around the ventrally directed curve of the rostrum.

Another point of considerable functional significance is that the rostrum itself must be very considerably stiffened by the presence of the supporting apodemes, for these are of girder-like cross-section and well adapted to resist forces tending to bend the rostrum.

(ii) *The pharynx*. The true mouth-opening of *Calandra* lies just posterior to the base of the hypopharynx (figure 7, *hp*.). The pharyngeal portion of the fore-gut extends from the mouth throughout the full length of the rostrum to a point just anterior to the tentorium and brain, and, as already stated (p. 250), contains the pharyngeal bracons of the mandibles. It is succeeded by an oesophageal region, of a very different structure, which leads to the crop and proventriculus (p. 279). The pharynx is, of course, lined by a continuation of the integument, and consists essentially of a trough arched over by a thinner roof (figures 7, 8 G, H, I, *ph*.). The anterior end of the trough is firmly fused ventrally to the extension of the roof of the labium (figures 7, 8 G, *la.ex*.) so that the antero-ventral portion of the pharynx is rigidly located in the rostrum. The roof of the pharynx is not uniformly thin. A thickened median tract, armed with recurved aborally directed spines, extends over the whole length of the roof (figure 9, *ph.ex*.), leaving a thin and flexible zone on each side connecting with the outturned dorsal margins of the much thicker ventral portion of the pharynx (figures 7, 8 G, H, I). It will be apparent, therefore, that whereas the floor and main portions of the walls of the pharynx are immovable, the roof is capable of being raised and lowered.

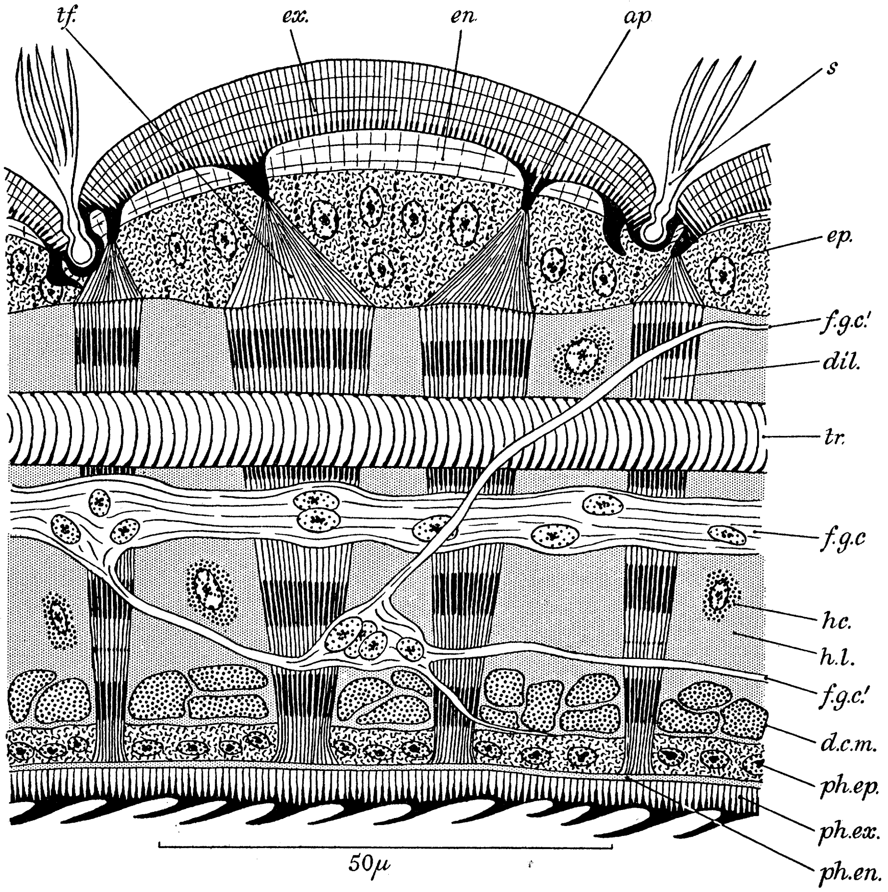

FIGURE 9. Part of a parasagittal section through the rostrum about mid-way along its length, showing the pharyngeal musculature and the frontal ganglion connective.

The musculature of the pharynx is restricted to the flexible roof, and is so arranged as to cause the movements just mentioned. Dilator muscles (figures 7, 8 H, I and 9, 10, *dil.*) are serially disposed more or less regularly in pairs, and are attached to the roof of the pharynx at the level of the lateral margins of the thickened median strip. Each dilator muscle is inclined obliquely outwards as it passes upwards to its insertion on the rostral wall, which is carried out through the medium of tonofibrillae (figure 9, *tf.*) passing through the epidermis of the rostrum (figure 9, *ep.*) to a small peg-shaped apodeme (figure 9, *ap.*). In conformity with the arrangement of the muscles the apodemes are disposed in two longitudinal rows placed beneath the inner pair of the four lines of punctures borne dorsally by the rostrum. Each puncture is occupied by a scale-like divided seta (figure 9, *s.*).

The apodemes of the dilator muscles are of interest in that they appear in my sections to consist only of extensions of the exocuticular layer of the integument which project through the endocuticle, but it is of course possible that an exceedingly thin layer of the endocuticle passes over the inner face of the apodeme.

I have been unable to discover tonofibrillae in the insertions of the dilator muscles on the roof of the pharynx, but here the epithelium is thin and compressed beneath the incomplete circular muscles of the pharynx.

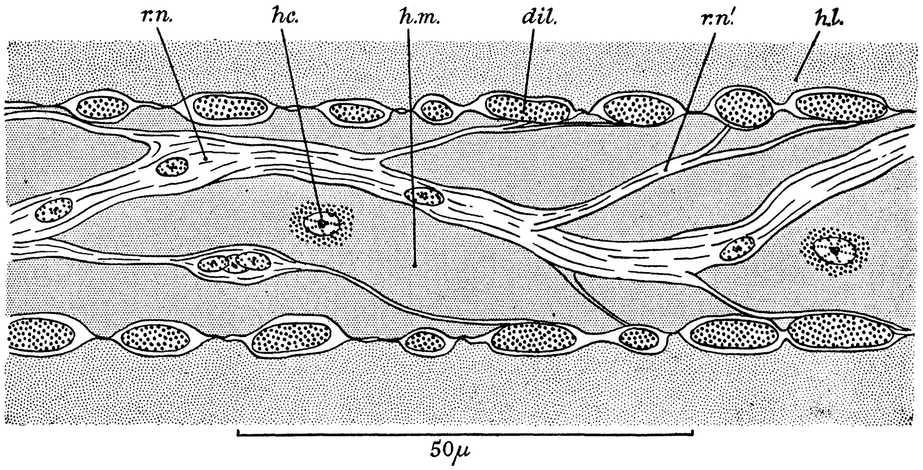

FIGURE 10. Part of a frontal section through the rostrum at the level of the recurrent nerve, showing part of the pharyngeal musculature and the arrangement of the blood channels.

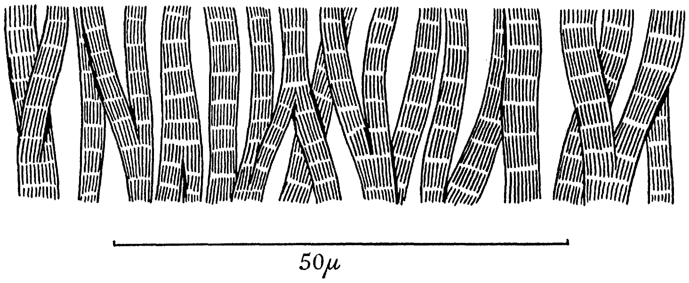

FIGURE 11. Part of a frontal section through the rostrum, ventral to that shown in figure 10, passing through the circular muscles of the pharynx and showing their irregular arrangement.

It is possible that the longitudinal extent of the series of pharyngeal dilator muscles gives some indication of the homologies of the regions involved in the roof of the rostrum. Snodgrass (1935, p. 119) states that: 'The frons gives attachment to the muscles of the labrum (figure 60, *mlra*, *mlrp*.) and to stomodaeal dilators lying posterior to the frontal ganglion (figure 115).' Since the dilator muscles of the stomodaeum of *Calandra* are restricted to that portion of it which can be described as the pharynx, and which occupies the full length of the rostrum, it would appear that the whole of the roof of the rostrum is of frontal origin.

This conclusion is in agreement with the findings of McClenahan (1904), who, from a study of the development of the rostrum in *Balaninus* and *Mononychus*, was able to state that the rostrum was composed of the frons, genae and gula.

The circular muscles of the pharynx, unlike the dilator muscles, are somewhat irregularly arranged. They are incomplete and extend transversely only over the roof of the pharynx where they form a meshwork of strands running mainly parallel with each other (figure 11). The dilator muscles make their attachment to the roof of the pharynx through gaps between the circular muscles (figure 9, *d.c.m.*). At each of their ends the circular muscles are inserted on the outturned margin of the thickened trough-like floor of the pharynx (figure 8 H, I, *d.c.m.*).

It will be evident that the antagonistic action of these two components of the pharyngeal musculature must result in the elevation and depression of the roof of the pharynx.

The description which I have given of the pharynx of *Calandra* agrees in general with that given by McClenahan (1904) for *Mononychus*. It is to be noticed, however, that McClenahan indicates in a sagittal half of the rostrum illustrated in figure 14 the presence of spines on the floor of the rostrum as well as on the roof. In a transverse section illustrated in figure 17, however, no such ventral spines are apparent, and no spines have been found in this situation in *Calandra*. Both Ting (1933) and Murray & Tiegs (1935) refer to the pharynx as the oesophagus, in spite of the fact that Ting mentions the 'oesophagus' as possessing backwardly directed spines, and Murray & Tiegs illustrate the pharyngeal dilator muscles.

(iii) *The nerves and tracheae of the rostrum, and the ducts of the salivary glands*. Dorsal to the pharynx a median longitudinal blood channel (figure 10, *h.m.*) is separated from the remainder of the haemocoele by laterally disposed membranous walls. Each wall is double, its two layers enveloping the dilator muscles of the pharynx but being elsewhere closely applied to each other (figure 10). In origin the median blood channel appears to be a continuation of the aorta, which passes through the circumoesophageal nerve ring above the gut and beneath the brain (figure 12, *ao.*). In figure 8 G, H, I, the median blood channel lies between the right and left series of pharyngeal dilator muscles, and it will be seen by reference to figure 8 F that it is confluent anteriorly with the remainder of the haemocoele, conveniently referred to as the lateral haemocoele of the rostrum, lying lateral and ventral to it (figure 10, *h.l.*).

Haemocytes (figures 9, 10, *hc.*) are readily recognizable in these blood channels, which in the sections are filled with coagulated and characteristically staining blood.

The nerves of the rostrum, belonging mainly to the stomatogastric portion of the visceral nervous system, must be described in relation to these three compartments, lateral and median, of the rostral haemocoele.

Murray & Tiegs (1935) have very briefly described the stomatogastric nervous system of both the larva and imago of *C. oryzae*. They state (p. 471) that the larval system 'comprises three ganglia, unpaired and lying above the oesophagus. The first (frontal ganglion) is the largest; it sends a nerve to the labrum, other nerves to the oesophagus and to the oesophageal dilator muscles. The second ganglion (hypocerebral ganglion) is more elongate. The recurrent nerve joining the two is only very short. The third ganglion (ventricular) lies just in front of the mid-gut, to which it sends branches. Connexion with the brain is established by a pair of fine nerves passing forwards to the hypocerebral ganglion.'

As a result of the development of the rostrum at metamorphosis the stomatogastric ganglia become more widely spaced. 'The frontal ganglion is at the tip of the rostrum; the hypocerebral ganglion is elongate and lies just in front of the brain, so that the recurrent nerve is now very long. The ventricular ganglion lies just in front of the crop. In the imago it shows quite a definite connexion with the tritocerebrum behind.'

Further references to the stomatogastric system are made in describing the nervous system generally, but as a whole the account given by these authors is confusing and inaccurate, and must be examined critically.

Apart from the recurrent nerve, the nerves of the stomatogastric system receive only very inadequate mention. It is true that a labro-frontal nerve is mentioned in the text (pp. 470, 473), but it is not specifically indicated in the figures concerned (text-figures 1, 2 and 6). No mention is made of a frontal connective branch of this nerve, and, although a labral branch is figured in both larva and imago it is not described in the text. An element of confusion is introduced by the mention in the larva of a pair of fine nerves passing forwards from the tritocerebrum to the hypocerebral ganglion, whereas in the imago only the ventricular ganglion is mentioned as having connexion with the brain.

Further comparison of the figures given by Murray & Tiegs with their account does nothing to resolve these difficulties, but on the contrary introduces fresh complexities. On p. 469 these authors state that in the larva the 'three cerebral nerves (text-fig. 6) (ocellar, antennal and labro-frontal), moreover, emerge as a single trunk from the tip of the brain (text-fig. 1)'. Indicated in text-fig. 1 are certainly three nerves arising close together from the brain. Two of them, however, are designated respectively the frontal (*not* labro-frontal) and ocellar, while the third, according to its distribution, appears to be the labral, although the terminations of the guide-lines concerned are obscure. Above the recurrent nerve the aorta is shown extending anteriorly to the hypocerebral ganglion, and crossing the tip of the ocellar nerve an elongated structure has some appearance of being continuous with it. As far as can be ascertained, however, this structure is indicated as being the antennal nerve. If this is so, then it does not originate, in this figure, from the brain in company with the ocellar and labro-frontal nerves as stated in the passage quoted above. If it is not the antennal nerve, then this nerve does not appear to be represented in the figure.

Text-fig. 6, also referred to in the above passage, shows *four* nerves arising together from the brain. These are the frontal, ocellar, antennal and labral nerves. No separation of a single labro-frontal nerve into frontal ganglion connective and labral branches (assuming for the present that the 'frontal nerve' of the figure represents a frontal connective branch), which would justify the statement that *three* nerves arise together, is indicated.

The 'frontal nerve' of Murray & Tiegs passes upwards from the brain to the antero-dorsal wall of the head (text-figs. 1, 2), whereas that commonly so named in the stomatogastric nervous systems of insects generally extends anteriorly from the frontal ganglion, this ganglion being connected with the brain by the frontal ganglion connective branches of the labro-frontal nerves (Snodgrass 1926, p. 15 and fig. 6; Weber 1933, fig. 256 C). Whatever the homology of the 'frontal nerve' referred to by Murray & Tiegs, it is neither the true frontal nerve nor the frontal ganglion connective.

Turning now to the labral nerves, these, although indicated in the imago by Murray & Tiegs in text-fig. 2 as paired nerves arising antero-laterally from the brain in company with the antennal and 'frontal nerves', are seen in the rostrum to lie dorsal to the recurrent nerve between the right and left series of pharyngeal dilator muscles (referred to by Murray & Tiegs as oesophageal dilators). The interpretation is therefore suggested that the labral nerves lie with the recurrent nerve in the median blood channel which I have already mentioned (p. 268). In point of fact, however, only the recurrent nerve is found in this portion of the haemocoele, the labral nerves lying in the lateral portions of the rostral haemocoele (p. 271).

In giving an account, therefore, of the structures lying within the rostrum of *Calandra*, it is necessary to pay detailed attention to the stomatogastric portion of the nervous system. It should be borne in mind that the following description results from the examination of series of transverse, frontal and sagittal sections, whereas that given by Murray & Tiegs may be based, in part at least, on the information derived from dissections, for these authors state (p. 406) that while serial sections were used in detailed histological examinations, hand dissections proved invaluable for 'the grosser anatomical features'. This possible difference between the methods of examination adopted, and the difference between the species examined, may well account for some of the discrepancies between the two accounts.

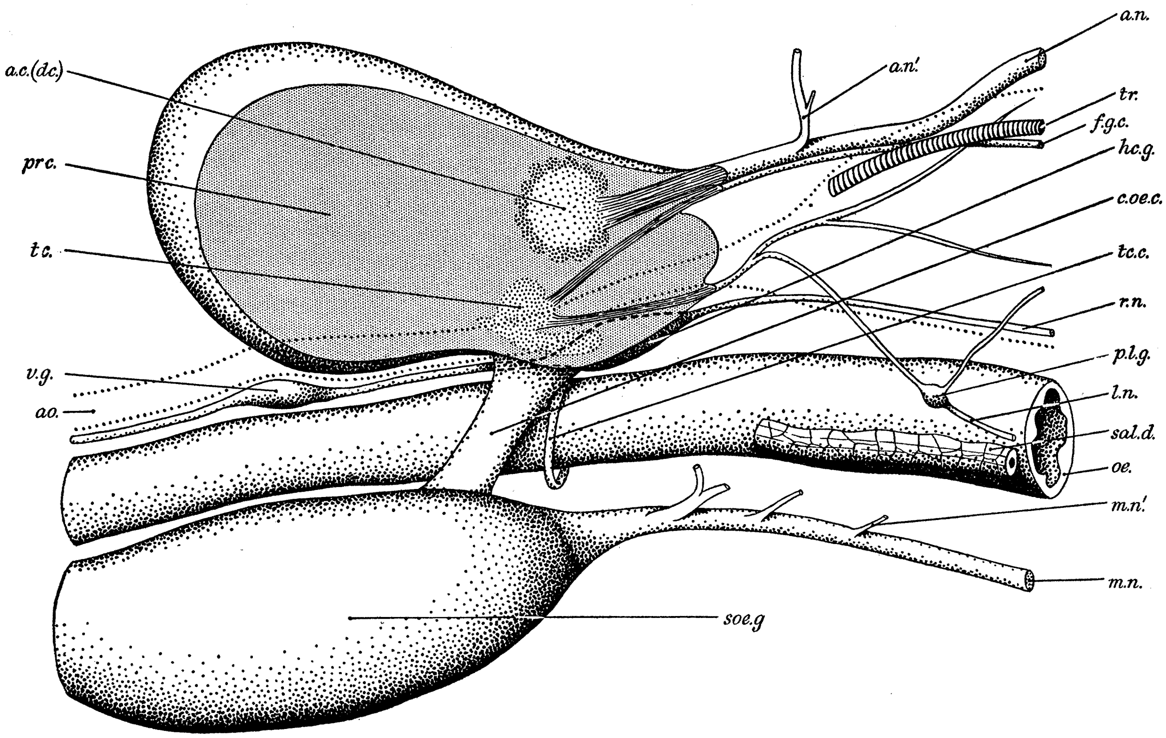

Figure 12. The brain and suboesophageal ganglion seen in lateral view from the right to show the origin of the nerves of the rostrum. A parasagittal slice, bearing the roots of the right optic nerves, has been removed so as to expose the fibre tracts of the antennal and labral nerves and the frontal ganglion connective. Details of the protocerebrum are omitted. With the exception of the oesophagus, aorta, and recurrent nerve, only the structures of the right side are shown.

The brain of *Calandra* is flexed and rotated postero-dorsally, so that the protocerebrum (figure 12, *prc.*), which forms the main mass of the brain, lies dorsal and posterior to the deutocerebrum and tritocerebrum (figure 12, *dc.* and *tc.*). The deutocerebrum forms the antero-dorsal margin of the brain, and the tritocerebral lobes project ventrally beneath it. The circumoesophageal connectives (figure 12, *c.oe.c.*) passing from the tritocerebral lobes to the suboesophageal ganglion (figure 12, *soe.g.*) are short, and the tritocerebral commissure (figure 12, *tc.c.*) arises close to and anterior to the origin of the circumoesophageal connectives from the brain.

The antero-lateral regions of the lateral lobes of the protocerebrum give rise to the optic nerve fibres (not seen in figure 12), while the remaining three pairs of cerebral nerves arise from the deutocerebrum and tritocerebrum. Anteriorly a pair of stout nerves is given off by the deutocerebral lobes; these are the antennal nerves (figure 12, *a.n.*), the fibres of which may be seen in parasagittal sections to arise from the antennal centres (figure 12, *a.c.*). The olfactory glomeruli surrounding the antennal centres are conspicuous. The antennal nerves pass forwards for some distance parallel with each other, and then are inclined sharply antero-dorsally and diverge from each other. They thus enter the bases of the antennae from a postero-dorsal aspect. Branches given off dorsally from the antennal nerves (figure 12, *a.n.′*) before their entry into the antennae may be composed of motor fibres, but although they penetrate into the antennal muscles which lie posterior to the bases of the antennae I have not observed with certainty a connexion between these branches and the muscles.

In close apposition ventrally to the antennal nerves, and apparently arising with them from the deutocerebrum, occurs a pair of more slender nerves (figure 12, *f.g.c.*). At the level at which the antennal nerves sweep sharply dorsally these more ventral nerves preserve their forward course and pass into the rostrum, where they come into close relation on each side with a tracheal branch (figure 12, *tr.*). In spite of their relation to the antennal nerves the nerves under discussion are not of deutocerebral origin. Their fibres are seen in parasagittal sections to arise from the tritocerebrum and to sweep upwards and forwards through the mass of the deutocerebrum close to the antennal centres, with the result that they emerge from the brain close beneath the antennal nerves (figure 12). From their site of origin and their relation in the rostrum to the remaining cerebral nerves I have identified them as the frontal ganglion connectives.

The third pair of cerebral nerves arises directly from the tritocerebrum, their fibres originating close to those of the frontal ganglion connectives and issuing from the brain considerably beneath and a little median to the antennal nerves. A ventral branch from each nerve takes a ventral sweep and passes down the rostrum, in company with the duct of the salivary gland, as the labral nerve (figure 12, *l.n.*). Dorsal twigs are given off to the muscles of the posterior region of the pharynx. In the region where the labral nerve enters the neighbourhood of the duct of the salivary gland it bears a small ganglionic swelling which may be termed the posterior labral ganglion. From it a nerve branch passes dorsally to the region of the base of the antenna.

It will be seen that this account conflicts with that given by Murray & Tiegs, in which it is stated (pp. 470, 473) that a combined labro-frontal nerve arises independently of the antennal nerve. I have not succeeded in discovering the 'frontal nerve' illustrated in the imago by these authors in text-fig. 2.

Both the frontal ganglion connectives and the labral nerves come to lie in the lateral compartments of the rostral haemocoele already mentioned (p. 268), and extend parallel with each other almost to the extreme tip of the rostrum. The frontal ganglion connective is found in the basal part of the rostrum at a horizontal level midway between the roof of the pharynx and that of the rostrum (figure 9, *f.g.c.*), and retains for its full length the close relation with the tracheal branch already mentioned (figures 12, 13, *tr.*). The relation between nerve and trachea is not entirely constant, the two often being slightly twisted around each other. Branches from the frontal ganglion connective (figure 9, *f.g.c.'*) are given off to the outer ends of the incomplete circular muscles of the pharynx and to the pharyngeal dilator muscles.

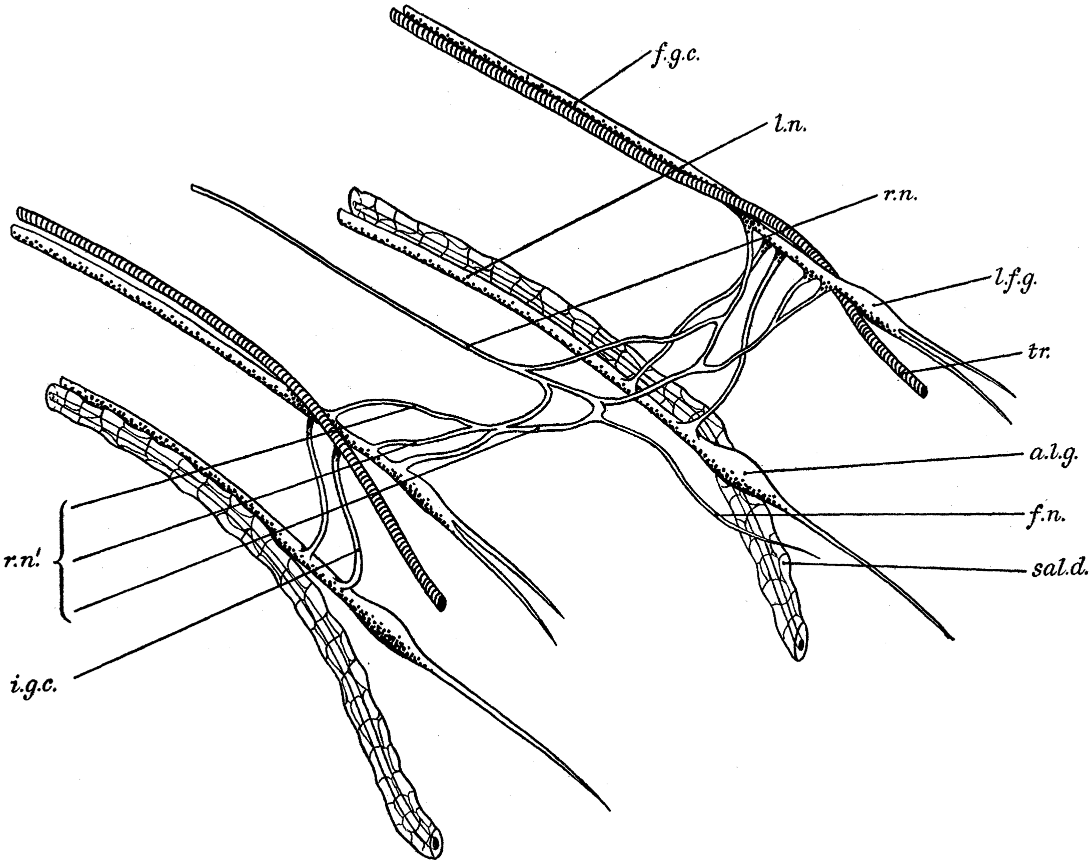

FIGURE 13. The stomatogastric nerves of the anterior end of the rostrum seen in antero-lateral view from above.

The labral nerve traverses the rostrum in company with the duct of the salivary gland (figures 12, 13, *sal.d.*). Towards the tip of the rostrum, as seen in figure 13, the salivary duct takes a more ventral course in passing towards its external aperture, and so diverges from the labral nerve. The labral nerve occupies a slightly more median position in the rostrum than does the frontal ganglion connective. It lies close to the pharynx just beneath the outturned margin of the thickened trough which forms its floor and walls, that is, just beneath the insertions of the dorsal circular muscles. The relation of frontal ganglion connectives and labral nerves may be seen from figure 13 and from the transverse sections illustrated in figure 8.

At the tip of the rostrum I have been unable, after careful examination of transverse, sagittal and frontal sections, to discover the median frontal ganglion described (p. 472) and illustrated (text-fig. 2) by Murray & Tiegs as occupying this position in *C. oryzae*. As seen in my preparations both the frontal ganglion connectives and the labral nerves bear distally small ganglionic swellings, so that a dorsal pair of lateral frontal ganglia (figure 13, *l.f.g.*) and a more ventral pair of anterior labral ganglia (figure 13, *a.l.g.*) may be identified. Fine nerve branches extend forwards from these ganglia. Those from the lateral frontal ganglia extend to the antero-dorsal margin of the epistoma, and those from the anterior labral ganglia penetrate to the bases of the mandibles. It is possible that, like the degeneration of the wings, the loss of the median frontal ganglion and its replacement by paired lateral ganglia may be taken as evidence that *C. granaria* is morphologically less primitive than *C. oryzae*.

Between the frontal ganglion connectives and the labral nerves connexion is established on each side by a small number of nerve strands immediately posterior to the lateral frontal and the labral ganglia. These may be referred to as the interganglionic connectives (figure 13, *i.g.c.*).

In addition to these two pairs of nerves, the frontal ganglion connectives and the labral nerves, lying in the lateral compartments of the rostral haemocoele, a fifth nerve traverses the rostrum. This, however, lies in the median compartment of the haemocoele, and is the recurrent nerve (figures 10, 12, 13, *r.n.*). Anteriorly it gives off a number of branches (figure 13, *r.n.′*) which form a delicate plexus and pass into the frontal ganglion connectives just posterior to the lateral frontal ganglia, that is, in the region which also receives the interganglionic connectives. It will be realized that this plexus occupies the position of the median frontal ganglion described by Murray & Tiegs. In spite of the absence of a median frontal ganglion, however, the designation of frontal ganglion connectives is justifiably applied to those nerves in virtue of their relation to the recurrent nerve.

A fine nerve strand extends forward from the plexus towards the labral region of the epistoma (figure 13, *f.n.*) and may be taken to represent the true frontal nerve.

Posteriorly the recurrent nerve enters the hypocerebral ganglion (figure 12, *hc.g.*), and through it makes connexion with the ventricular ganglion (figure 12, *v.g.*).

In the distal portion of the rostrum the recurrent nerve pursues a quite irregular course. For some little distance behind the anterior plexus it lies more or less parallel with but at a lower level than the frontal ganglion connectives (figure 12, *r.n.*). It then passes nearer to the roof of the pharynx, and comes to lie on the dorsal circular muscle layer, following a sinuous course (figure 10, *r.n.*). Branches are given off to the dilator muscles of the pharynx (figure 10, *r.n.′*), and, as far as can be ascertained, to the dorsal circular muscles. More posteriorly, in the proximal region of the rostrum, the recurrent nerve is straight and follows a direct course back to the hypocerebral ganglion. Above the posterior region of the pharynx and above the oesophagus it gives off only a few small branches.

The hypocerebral ganglion (figure 12, *hc.g.*) is lodged beneath the anterior region of the brain in the cleft between the downwardly projecting tritocerebral lobes, to which it is closely apposed. In the views obtained from transverse and frontal sections fibres from each tritocerebral lobe may be clearly seen to pass into the ganglion. The recurrent nerve continues beneath the brain and the aorta to the ventricular ganglion (figure 12, *v.g.*), nerves from which innervate the crop and proventriculus.

Nerves passing into the rostrum arise also from the suboesophageal ganglion. A pair of nerves, one from each lobe of the ganglion (figure 12, *m.n.*), extends anteriorly, and just before entering the rostrum gives off branches to the muscles of the mouth-parts (figure

12, *m.n.'*). It may be presumed that these branches are composed mainly of motor fibres, while those fibres forming the rostral continuation of the nerve are responsible for the sensory innervation of the mouth-parts themselves.

After traversing the rostrum for some distance the nerves to the mouth-parts come together to form a single, somewhat diffuse nerve, which lies near the ventral wall of the rostrum in the median space between the apodemes supporting the tendons of the mouth-parts (figure 8 G, H, I). It extends anteriorly as far as the base of the labium, where it bears a small ganglionic swelling. Fibrous tissue already mentioned (p. 260) as occupying the cavity of the labium may contain fibres from this ganglion. Other fibre bundles may be seen with difficulty to pass into the bases of the maxillae and mandibles.

This mode of innervation of the mouth-parts is clearly correlated with the great specialization of the head of *Calandra*, and may be contrasted with that obtaining in the more generalized insect, wherein paired nerves extend from the suboesophageal ganglion to the mandibles, maxillae and labium.

It will be appreciated, then, from the foregoing account, that the innervation of the rostrum and its associated structures is considerably more complex than is indicated by Murray & Tiegs. It is not claimed, however, that the present account is in any way complete; my preparations show great numbers of fine nerve strands which have not been followed out in detail.

The dorsal pair of tracheal branches (figures 7, 9, 12 and 13, *tr.*) of the rostrum has already been adequately mentioned in describing the course of the frontal ganglion connectives. In addition, however, a second pair of tracheae lies with the ventral nerve to the mouth-parts in the median space between the supporting apodemes of the rostral tendons (figure 8 G, H, I). Both these pairs of tracheae give off numerous branches, some of which, on account of their size and the fact that they continue parallel with their parent trunk, suggest when seen only in transverse section that more than two pairs of tracheae pass down the rostrum. The tracheae, not only of the rostrum but of the body generally, are characterized by the possession of fine hair-like processes projecting from the taenidia into the lumen (see Wigglesworth 1939, p. 182).

The dorsal and ventral tracheae of the rostrum are figured by Murray & Tiegs (1935, text-fig. 10).

The coiled 'salivary' glands of *Calandra* are closely applied to the lateral surfaces of the crop (p. 280), and their ducts pass forward lateral to the brain to enter the rostrum. As already mentioned in describing the stomatogastric nervous system they lie lateral to the pharynx in company with the labral nerves, and diverge anteriorly from these nerves as they approach their external apertures.

The external aperture of each duct lies laterally, in front of the base of the maxilla and immediately posterior to the ventral condyle of the mandible. It is therefore situated on the dorsal surface of the base of the pregena where it is joined by the floor of the pharynx.

It is clear, then, that as Murray & Tiegs (1935) have pointed out, the salivary glands of *Calandra* are true maxillary glands.

The detailed structure of the ducts of the glands may be most conveniently described in giving an account of the secretory portion of the glands (p. 280).

5. The movements and functions of the mouth-parts, and the transport of food along the pharynx

As already described (p. 253), the axis of rotation of each mandible of *Calandra* lies obliquely to all three planes, transverse, sagittal and frontal, of the rostrum. From the ventral condyle, articulating with the pregena, it slopes upwards, forwards and outwards to the dorsal condyle received by the epistoma and lies at an angle of about 30° to the almost plane median surface of the mandible itself, the anterior surface of which bears the mandibular teeth. The median surface of the mandible stands almost vertically and in a slightly parasagittal plane when the mandibles are drawn into close apposition. As seen in anterior view, therefore, the ventrally situated recurved apical tooth of the left mandible lies in front of, but arises from an area of the mandible lateral to, the axis of rotation. The subapical tooth above it also lies anteriorly, but less laterally, to the axis, while the median tooth stands immediately in front of it. The remaining mandibular tooth, the molar, is found considerably median to the axis since its situation is dorso-median while that of the dorsal condyle, determining the slope of the axis, articulates with the epistoma dorso-laterally.

The oblique disposition of its axis of rotation plays a part of paramount importance in determining the mode of functioning of the mandible, as it determines the inclination of the arcs of movement swept by the individual teeth. It will be convenient to consider the movement of abduction of the left mandible, starting from its position of rest when it is in median apposition to the right mandible. This movement is produced by the contraction of the mandibular abductor muscle in the head, and is transmitted to the mandible by the abductor tendon, which is attached to the mandible antero-laterally to the ventral condyle. Its pull therefore rotates the mandible laterally. Rotation takes place through about 90°, terminating when the site of attachment of the abductor tendon on the rotating mandible reaches an ineffective position postero-lateral to the ventral condyle. The flexible lateral plate of the mandible passes beneath the ventro-lateral wall of the rostrum, while the mandible occupies and overlaps externally the cleft between the pregena and the epistoma. On the completion of full rotation the mandible comes to rest in such a position that its median surface is exposed to the exterior and now faces antero-ventrally.

The paths swept by the mandibular teeth can now be traced. The apical tooth, owing to its starting point lying both in front of and lateral to the axis of rotation, sweeps laterally, posteriorly, and, to start with, slightly ventrally with respect to the rostrum. Its postero-lateral movement is continued throughout its arc of rotation, but owing to the inclination of the mandibular axis the ventral movement of the tooth passes into a dorsal one in the latter part of the arc.

The movement performed by the subapical tooth is very similar to that of the apical tooth, but, since it starts from a point disposed less laterally to the axis of rotation both its posterior and dorsal components are less pronounced.

The median tooth, however, lies immediately anterior to the axis of rotation, with the result that, sweeping laterally with the motion of the mandible, it also moves ventrally in the first part of its range. Towards the end of its range of movement it passes almost horizontally backwards.

In contrast to the teeth more ventral to it, the molar tooth of the mandible begins its arc of movement by passing forwards with only a slight ventro-lateral deflexion from its situation median to the axis of rotation. As its movement progresses, however, its ventro-lateral deflexion becomes more pronounced, while its anteriorly directed component diminishes. The molar teeth of the mandible are thereby drawn completely away from each other.

The reversal of these arcs of movement is effected by the pull of the adductor tendon inserted on the median side of the dorsal condyle of the mandible. It has interesting consequences. At the beginning of adduction the median surface of the mandible faces antero-ventrally, and the median tooth lies anterior and dorsal to the subapical and apical teeth. On adduction, then, it is the median tooth which comes first into contact with the grain, being followed in turn by the subapical and apical teeth passing forwards and inwards behind it. As already described (p. 250) the apical tooth is sharp and recurved, and is, from its appearance, a more effective cutting agent than the teeth which precede it. Since it cuts last, the food it detaches must to a large extent remain in the excavation in the grain. On the next abduction of the mandibles this food will be little disturbed by the rounded backs of the teeth passing through and over it. As the mandibles come together for the second time, however, the median tooth, being the first to encounter the detached food, will tend to sweep it inwards and backwards into the pre-oral cavity. Such a mechanism of food collection would account for the fact that the most effective cutting tooth is the last to come into contact with the grain.

Food collection is probably further facilitated by the asymmetry of the mandibles. Among Crustacea it has been shown (Cannon & Manton 1927) that this plays a large part in food transference, and in *Calandra* also it is probable that food is passed in a zigzag manner between the teeth of right and left mandibles until it reaches the molar teeth. Furthermore, the asymmetry of the mandibles has the obvious result of allowing the mandibles to come completely together on apposition.

The movements and functions of the right mandible are similar to those of the left, with the exception that here the subapical tooth is the prominent cutting tooth.

It is difficult to obtain by direct observation any information on the actual cutting of the grain by the individual mandibular teeth, but as far as I can deduce from their action, it is due to the fact that, although they are curved inwards and slightly upwards, their curves do not coincide with those of their arcs of movement. The curved long axis of each tooth slopes a little more anteriorly and dorsally than does its arc of rotation, so that the tooth performs a scythe-like sweep, its sharp ventral margin passing at an obtuse angle over the surface of the grain. It therefore cuts in a manner like that of the blade of a plane, but as a result of the friable nature of the food continuous shavings are not produced.

It has been stated that the molar teeth of the mandibles work mainly in an antero-posterior direction, and the pharyngeal bracons, therefore, attached close behind these teeth, are necessarily caused to move to and fro in the pharynx.

In general, therefore, it may be said of the mandibles of *Calandra* that the angle of inclination of their axes of rotation is such as to impart to each tooth movement in a direction and to an extent appropriate to its shape and function.

The movements of the molar teeth and pharyngeal bracons will be discussed in greater detail after describing the functions of the maxillae.

The movements of the maxillae of *Calandra* have already been mentioned in describing the structure of the limb, and it remains only to indicate the purpose of these movements and the manner in which they are correlated with those of the mandibles.

When the mandibles are closed and at rest, the maxillae are found also to be at rest, with only the massive marginal sclerites of the cardo, stipes and galea visible in the clefts between the labium and the pregenae. The palps are carried in an antero-ventrally directed attitude, the right palp resting in the small notch on the margin of the right mandible between the reduced apical and the much larger subapical tooth (see figure 1). The laciniae rest against the sloping sides of the labium, and their teeth and setae are enclosed between the apposed mandibles.

For the most part the mandibles move simultaneously, and as they move apart on abduction the maxillae are brought forward so that their stout lacinial teeth and spines reach the mandibular teeth and remove from them accumulations of ground food particles. The posteriorly directed curvature of the lacinial armature enhances the efficiency of this action. On the retraction of the maxillae the laciniae are drawn back to the level of the labium and the collected food is carried into the pre-oral cavity.

It will be recalled that the labium possesses its own setal armature in the form of two rows of longitudinally disposed setae which stand vertically one on each side of its dorsal apex, and that the teeth of the laciniae of the maxillae lie between these and the finer lacinial setae. Food collected from the mandibles by the lacinial teeth is therefore bounded by lateral retaining walls of closely arranged setae, and it is probable that during the movements of the maxillae it is worked progressively backwards to the molar region of the mandibles between these walls. Its lateral escape on to the anterior biting region of the mandibles is thereby prevented. It is interesting to note that the labial setae, terminating posteriorly at the level of the dorsal hump of the labium, also terminate at the level of the molar region of the mandibles. Furthermore, although on retraction of the maxilla the posterior lacinial setae lie well behind this level, on protraction they correspond with it.

During the collection of food by the maxillae and its transference to the molar teeth of the mandibles some trituration almost certainly takes place, but this must be of little consequence compared with that carried out by the mandibles themselves. The maxillae are primarily concerned with food transference.

At this point it is necessary to refer to the secretion of the maxillary glands. The openings of these glands near the bases of the maxillae have been described (p. 274), and it is clear that movements of the maxillae are capable of distributing the secretion over the whole mouth region. Although not present copiously on the mouth-parts, and perhaps not of great importance in digestion, its presence must enable food to adhere more readily to the mouth-parts and so add to the efficiency of the mechanism of food collection and transference.

Food particles, then, may reach the molar regions of the mandibles either by the action of the asymmetrical mandibular teeth or through the intervention of the maxillae.

Apart from the symmetrical movements of abduction and adduction of the mandibles, performed by both of these structures working together, irregular and asymmetrical movements also take place. These asymmetrical movements are of great significance in the functioning of the molar regions and pharyngeal bracons. Often one mandible may be seen to suspend its movements completely for a considerable period while its fellow functions actively, or both mandibles may continue their movements although out of phase with each other and with different periodicities. At these times the molar regions of the mandibles, moving mainly antero-posteriorly, are also moving relatively to each other. The result therefore is a great increase in their triturating capacity. In addition, this relative movement must result in food being worked progressively posteriorly into the effective field of action of the bases of the pharyngeal bracons, a process which is assisted by the laciniae of the maxillae working independently of those appendages as a whole. By the pull of the cranial flexor tendons of the maxillae (p. 257) the lacinial teeth are passed backwards between the molar teeth of the mandibles and so bring food to the bases of the bracons.

It will be recalled that the bases of the bracons are armed medially with closely set spines grouped in a triangular area. Moving in sympathy with the mandibles, the bracons must possess on their own account some powers of trituration, but their prime function is that of food transport. This has been recognized by McClenahan (1904) and by Ting (1933). Aggregations of food particles, moistened by the secretion of the maxillary glands, accumulate in the manner described between the bases of the bracons. As these structures move anteriorly, their aborally directed spines pass ineffectively over the food mass. As they return, however, the spines enable them to move the food aborally, and by repetition of their movements the bracons are therefore responsible for the progressive transport of food along the pharynx.

In this process of food transport the roof of the pharynx must play a part of considerable importance. It will be remembered that a median tract of the pharyngeal roof is armed with aborally directed spines, and it is clear that a depression of the roof, brought about by the contraction of its incomplete circular muscles, will cause food masses to be gripped securely in the reduced lumen of the pharynx. The bracons, smoothly tapered towards their tips, will slide freely through and over the food on their forward movement. Relaxation of the circular muscles and elevation of the roof of the pharynx by the action of its dilator muscles frees the food in readiness for its further transport by the imminent backward movement of the bracons. Although I have been unable to devise any method of discovering by direct observation whether the movements of pharynx and mandibles are correlated in the manner I have suggested, I have no doubt that they are, since this appears to be the only explanation of the peculiarities of the structures encountered. No other mode of food transport, such as peristaltic action, is possible in view of the restricted musculature of the pharynx.

The significance of the rigid fusion anteriorly of the floor of the pharynx with the backward extension of the labial roof, and the flexibility of the walls of the pharynx in this region are now apparent. The flexibility of the walls allows of free movement of the bracons, while the rigid abutment of the floor prevents any possibility of disturbance of the pharynx as a whole caused by this movement. The structural features of this portion of the pharynx are precisely adapted to the presence and function of the bracons.

In the next section of this paper the structure of the oesophagus, crop, and proventriculus will be described, and followed by a discussion on the passage of food through these parts of the fore-gut.

6. The morphology of the post-pharyngeal region of the fore-gut

Descriptions and illustrations of the gross appearance of the alimentary canal of *Calandra granaria* (Müller 1928) and that of *C. oryzae* (Murray & Tiegs 1935) are already available. It is therefore unnecessary to give a further general illustration, and the following account is intended to amplify the descriptions of the fore-gut given by these authors.

(i) *The oesophagus*. The oesophagus of *Calandra* is a simple tube extending from the termination of the pharynx at the base of the rostrum to the sac-like crop which lies in the prothorax. It is, of course, subcerebral in position, and is encircled by the circum-oesophageal connectives. In passing beneath the brain it lies also beneath the aorta and passes over the transverse bar of the tentorium. In gross external view no reliable structural peculiarities serve to define the termination of the oesophagus at its junction with the crop, although in the arrangement of their musculature and in the presence of spines within the crop these two regions of the stomodaeum are clearly distinct.

As usually seen in transverse section the epithelium of the oesophagus is thrown into deep longitudinal furrows, while its intima is thin and delicate compared with that of the ventral portion of the pharynx. Unlike the pharynx the oesophagus is completely enveloped by continuous circular muscles, dilator or longitudinal muscles being absent. The transition from the structure of the pharynx to that of the oesophagus is abrupt, but is quite simply accomplished by the loss of the dorsal dilator muscles, the extension ventrally of the dorsal circular muscles, and the great diminution in thickness of the intima.

Posteriorly the oesophagus becomes progressively dilated, and merges into the crop.

(ii) *The crop*. The large crop may be conveniently regarded as a simple modification and dilation of the oesophagus. The internal furrows of the oesophageal epithelium are continued into the crop where, while still remaining longitudinally disposed, they are less deep and more irregular in arrangement. Furrows may be seen to become confluent or to diverge from each other. It is apparent that the presence of the furrows allows of considerable expansion of the crop by the accumulation in it of food, and in preparations from a number of specimens the extent of the furrowing may be seen to vary with the degree of dilation of the crop.

Internally the crop is armed with slender backwardly directed spines which arise almost without exception from the crests between the furrows of the crop epithelium. This disposition of the spines, however, does not produce any appearance of a linear pattern, for their distance apart, measured in an antero-posterior direction, corresponds in general with the distance between the furrows. The spines appear therefore to be uniformly scattered, with the exception that they are more numerous and longer posteriorly than they are anteriorly.

In referring to the oesophagus it was stated that its musculature differed from that of the crop. Whereas the musculature of the oesophagus consists of a single sheet of circular muscles, that of the crop is formed by a double coat of oblique circular muscles. The superficial layer of this double coat contains fibres which are inclined backwards at an angle of about 30° to the transverse plane, while the fibres of the inner layer are inclined forwards to a similar extent. No longitudinal muscles of the crop have been discovered.

Nerve fibres from the ventricular ganglion are readily seen to penetrate into the muscle layers of the crop.

As mentioned earlier (p. 274) the coiled tubes of the maxillary glands are closely applied to the lateral walls of the crop, and may be conveniently described at this stage. Each gland consists of an irregularly coiled continuous tube of simple structure. The almost straight ducts passing forwards down the rostrum to their openings near the bases of the maxillae (p. 274) have the same basic structure as the glands themselves. The slight difference in appearance that exists between the coiled gland and its straight duct is due to the difference in size of the cells which constitute these two portions of the tube. The lumen of the glandular region is encircled by only a few columnar cells which are necessarily much narrower distally than they are basally. The nuclei of these cells are situated basally, and are slightly elongated in the direction of the length of the tube. A fine chitinous intima, staining a deep red with Mallory's triple stain, lines the gland and is continuous throughout the duct to its external opening. The epithelium of the duct of the gland, in contrast to that of the gland itself, is composed of flattened cells with small nuclei which are greatly elongated and lie parallel with the wall of the duct.

Müller (1928) describes the situation on the walls of the crop of the coiled portions of the glands of *C. granaria*, but does not mention the ducts and their external openings. In fact, it is implicit in his account that the glands discharge directly into the crop, for he says: 'On the outer walls of the crop (fig. 13) are situated numerous long closely coiled glandular tubes. It is probable that they produce an amylolytic enzyme which converts the finely divided corn in the crop into sugar.' Not only, however, do the glands have no direct functional connexion with the crop in the imago, as made clear for *C. oryzae* by Murray & Tiegs (1935) and for *C. granaria* in this paper, but in development also they are completely dissociated from it. In the larva of *C. oryzae* they arise as ectodermal ingrowths (Tiegs & Murray 1938), and in metamorphosis they redevelop as 'two thick hollow straight columns of actively dividing cells, which slowly extend up the rostrum', and only on or about the fifth day of pupation enter the thorax (Murray & Tiegs 1935).

(iii) *The proventriculus*. The proventriculus of *C. granaria* has been already described by Müller (1928), but unfortunately his account is difficult to follow and is lacking in detail. It is therefore inadequate for the purpose of discussing the precise mode of operation of this portion of the fore-gut, but it is interesting to observe that in spite of the deficiencies of his account, and offering no substantial evidence in support of his views, this author has defined the function of the proventriculus as constituting a sieve rather than a masticating apparatus. This is in direct opposition to the opinion of Ting (1933), who states that food is masticated in the 'gastric mill'. I agree fully with the opinion of Müller, and am able to give it strong morphological support.

The barrel-shaped proventriculus is interposed in typical manner between the crop and the mid-gut. Its size varies with the degree of contraction of the powerful sphincter muscle (figures 16, 17 and 18, *sph.*) which surrounds it and brings into operation the rows of backwardly inclined triangular chitinous plates which line it. These plates are, of course, elaborations of the chitinous intima of this portion of the fore-gut, and are readily seen by opening the proventriculus mid-dorsally (figures 14, 17, *sv.p.*). They are set transversely to the axis of the fore-gut and are regularly disposed in eight double rows, each double row containing about sixty pairs of plates and constituting what Müller (1928) has referred to by the term 'Kauapparat'. Murray & Tiegs (1935), without giving a detailed description of the proventriculus of *C. oryzae*, have referred to the occurrence in it of some sixty plates in each row. The rows of plates are regularly arranged around the inner circumference of the proventriculus.

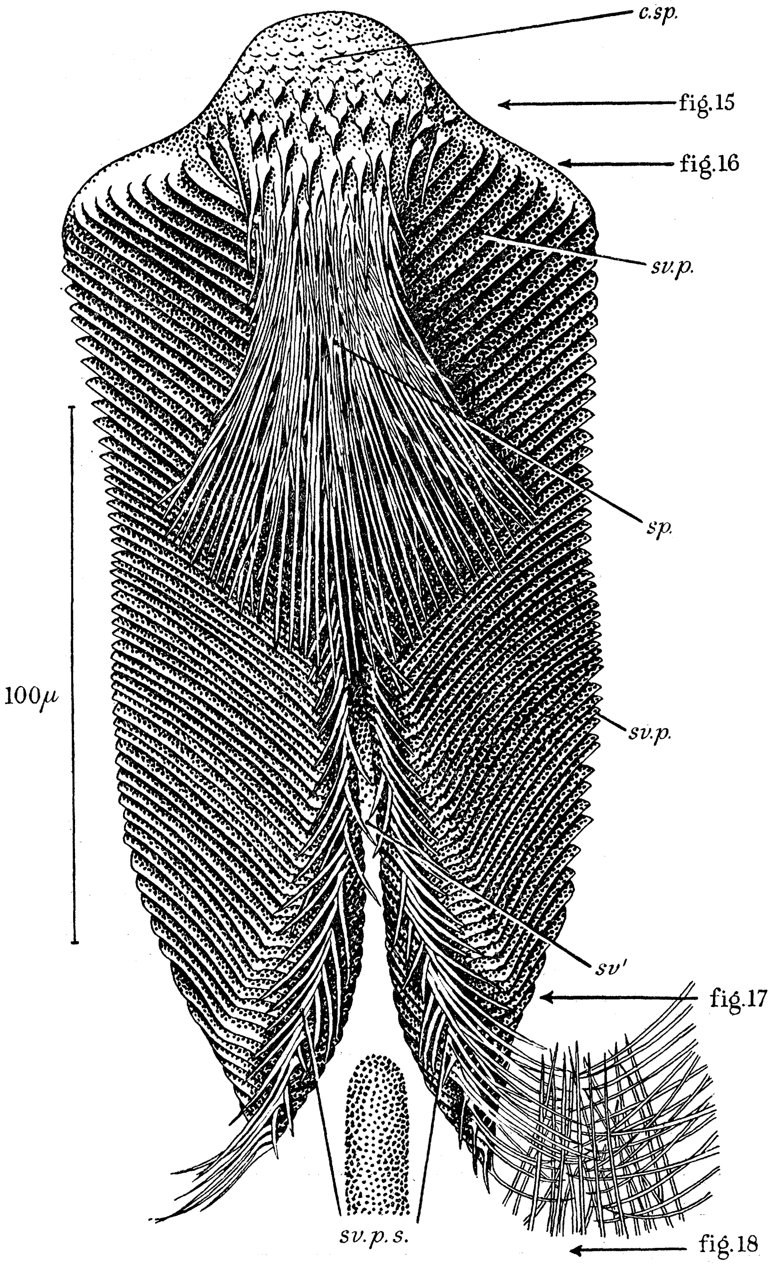

FIGURE 14. One of the eight pairs of series of plates constituting the proventriculus, seen from within after opening the proventriculus longitudinally. The wall of the proventriculus is not shown. The levels of the transverse sections shown in figures 15, 16, 17 and 18 are indicated by arrows.

Müller (1928) refers to the grooved ('geriffelten') surface of the proventricular plates, but I am not clear as to what precisely he is describing. Owing to the backward inclination of the plates, several of each row are seen in both optical and actual transverse sections, and the appearance is given of a single plate transversely ridged (figure 17). In addition, however, each plate is faintly striated in the direction of its length, and the meaning of this is not fully apparent. There is some slight evidence to suggest that each plate is formed by the fusion of transverse rows of setae: transverse sections through the plates well below the bases of the apical setae still show closely apposed and partially fused chitinous cylinders, giving an impression of the fusion of setae. The grooving noted by Müller may refer to such a structure of the plates. On the other hand, a striated appearance may well be produced in the plates by the existence in them of trabeculae like those often seen in the integument of Coleoptera in general (Snodgrass 1935) and of *Calandra* itself.

Anteriorly the plates approximate very closely to the form of a right-angled triangle, the vertical sides of the plates of one row being apposed to the corresponding sides of the plates of the accompanying row. The apices of the plates almost meet, therefore, in the centres of the double rows. More posteriorly, however, the shape of the plates approaches that of an isosceles triangle, without actually attaining to it, so that the apices of the plates stand farther apart. Furthermore, the bases of the posterior plates are shorter than those of the anterior ones (figure 14), thus accentuating the separation of the rows of apices. The lines formed by the series of apices of the plates therefore diverge strongly in passing posteriorly (figure 14).

At this point it is convenient to anticipate to a slight extent the description of the mode of functioning of the proventriculus which will be given later, and for the purpose of establishing points of reference to speak of the longitudinal gap enclosed by the double rows of plates as forming an exit from the sieve (figures 14, 17, *sv.′*) constituted by the proventriculus. In a corresponding manner the gap between adjacent double rows of plates (figure 17, *sv.*) may be spoken of as giving entrance to the sieve.

Apically the plates of the proventriculus bear setae (figures 14, 17) which are continued, in diminishing order of size, down the margins of the plates facing the entrances to the sieve. They disappear completely at the level of a slight irregularity in the margin of each plate not far from the apex. This irregularity may be clearly seen in the foreshortened view of the plates obtained in figure 14. A similar arrangement of setae is found on the plates of *C. oryzae*, which have been compared with those of *C. granaria*, but in this species a stout apically directed spine replaces the slight marginal irregularity of *C. granaria*.

Owing to the shape of the individual plates, and the fact that the lumen of the proventriculus narrows posteriorly, the entrance gaps to the sieve diminish posteriorly (figure 20, *sv.*). As a result of the divergence of the apices of the plates already mentioned, however, the exit gaps expand posteriorly (figure 20, *sv.′*). The apical setae of the plates emphasize this condition by being curved away from the exit gaps posteriorly and arching over the rear of the entrance gaps, where they interlock with the setae of the adjacent double row of plates (figure 14). Moreover, numerous setae arise from the wall of the proventriculus at the extreme posterior ends of the entrance gaps, and interlock with the apical setae of the plates (figure 14). These setae are mentioned by Müller. The entrance gaps to the sieve are therefore closed posteriorly by a dense felt-work of setae.

Anteriorly the exit gaps from the sieve apparatus are closed owing to the fact that each double row of plates takes its origin anteriorly in a prominent cushion-like swelling at the level of the junction between the crop and proventriculus. There are therefore eight of these cushions (figures 14, 15 and 16, *c.sp.*) disposed regularly around the entrance to the proventriculus. Each cushion bears a characteristic armature. Anteriorly it consists only of slight denticle-like prominences (figure 14), but more posteriorly these prominences are produced into definite short spines (figures 14, 15). More posteriorly still the spines are greatly elongated, so that projecting from the rear of each cushion occurs a dense mass of

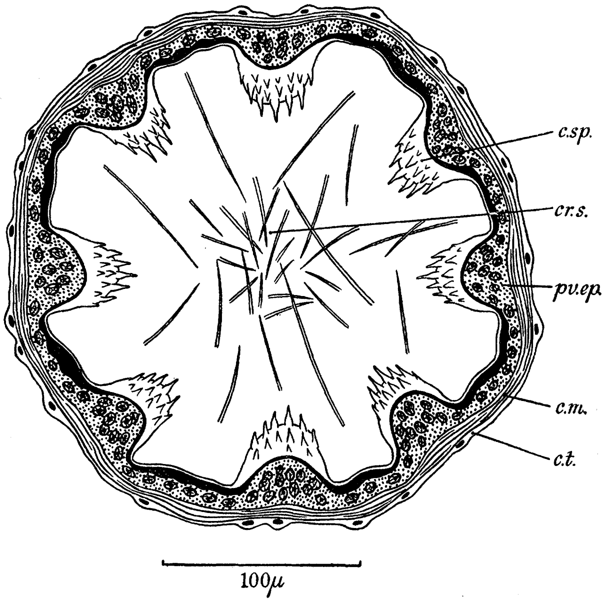

Figure 15. Transverse section through the anterior end of the proventriculus just at its junction with the crop.

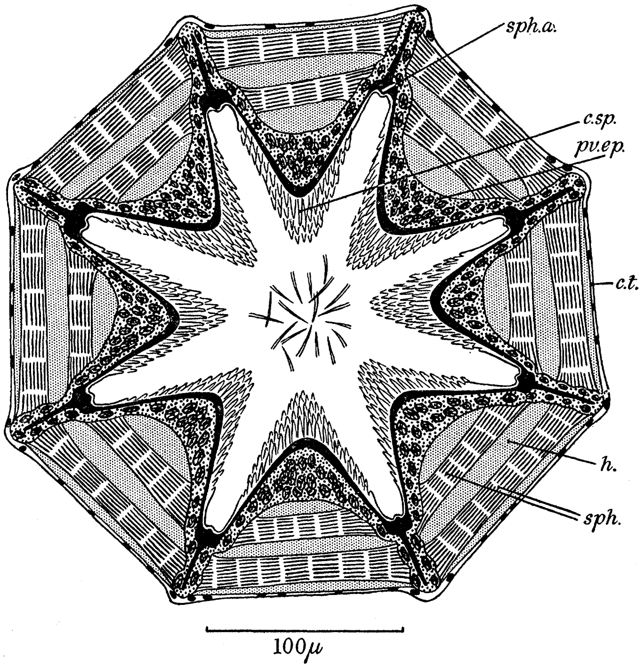

Figure 16. Transverse section through the anterior end of the proventriculus, a little posterior to that shown in figure 15.

bristle-like spines. The longest of these spines extends as far back as the middle of the length of the rows of plates, and the bundle of spines as a whole is spread fan-wise (figure 14, *sp.*) and lies at an angle of about 60° to the surface of the rows of plates.

This pattern of the armature of the proventriculus may be compared with that found in other Rhynchophora. Lindemann (1876) has described and illustrated the proventricular armature of a number of Rhynchophora, and has proposed the use of these structures as an aid to classification. Nüsslin (1913) also gives figures of the proventriculus of a number of bark-beetles, and it appears from a comparison of these two groups of figures with the condition found in *Calandra* that in general the bark-beetles possess a more massive and complex armature. In these latter Rhynchophora the apical setae of the posterior plates are often compacted together into curved club-like masses; the anterior cushion with its denticles and spines is very extensive; and the bristle-like spines extending backwards from the cushion are massive and blade-like. It would appear probable, then, that the proventriculus of the bark-beetles may be a triturating structure either in addition to, or instead of, a filter apparatus.* It is interesting to observe, however, that in these beetles the marginal irregularity of the plates noted in *Calandra* is again clearly evident, appearing to be a constant feature of the proventricular armature.

It has been stated that the plates of the proventriculus are elaborations of the chitinous intima of this specialized region of the fore-gut. The general intima lining the proventriculus may be regarded as forming an octagonal tube, the surfaces of which are strongly curved towards its lumen. Each double row of plates arises from the convex inner surface of a wall of the tube (figure 17) so that the apices of the plates converge towards the axis of the tube. At the base of each exit gap (figure 17, *sv.′*), that is along the centre of each wall of the proventriculus, a longitudinal furrow (figure 19, *pv.f.c.*) is clearly apparent in transverse sections. The integument involved in these furrows appears to be thinner than that elsewhere. The furrows are of vital importance in allowing of the movements of the proventricular wall as the sphincter muscles contract and relax.

The angles of the octagonal tube are produced into well-marked sheet-like longitudinal apodemes (figures 16, 17, *sph.a.*) which offer surfaces of attachment to the sphincter muscles (figures 16, 17, 18 and 19, *sph.*).

The staining reactions of the intima of the proventriculus as seen in transverse sections are interesting. The plates themselves stain a brilliant red, characteristic in general of the exocuticle, with Mallory's triple stain, while the general intima forming the walls of the tube takes on a blue coloration typical of the endocuticle. Each apodeme of the sphincter muscles, however, displays a central lamina, staining blue with Mallory and presumably of endocuticular origin (figure 19, *ap.en.*), which projects centrifugally apparently entirely free distally from its enveloping sheath of exocuticle (figure 19, *ap.ex.*). The reactions of the cuticle to Mallory, however, are occasionally very capricious, and it may be well not to take too much account of the appearance just described. If, on the other hand, the apodemes have truly the structure that their appearance suggests, then it is highly probable that this structure concerns the flexion of the proventriculus along the well-defined lines of the apodemes.

Beneath the intima of the proventriculus its epithelium (figures 15, 16, 17 and 18, *pv.ep.*) is strongly developed. It necessarily envelops the proventriculus, including its

* An account of the proventriculus of the bark-beetle *Ips radiatae* has been given by Eaton (1942) while this paper was in the press. This author holds the view that in *Ips* the proventriculus is, in its anterior region, a grinding apparatus, and posteriorly a filter.

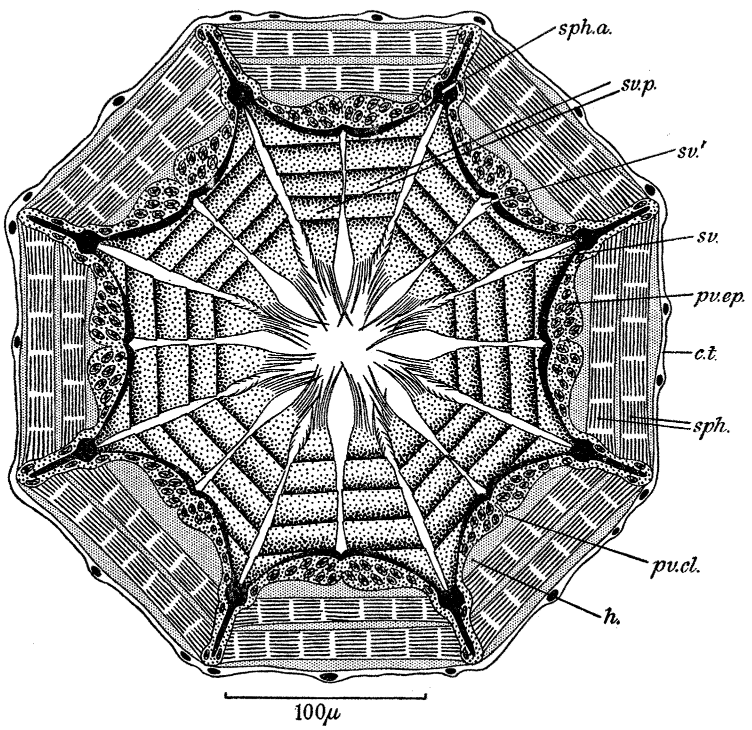

FIGURE 17. Transverse section through the proventriculus towards its posterior end.

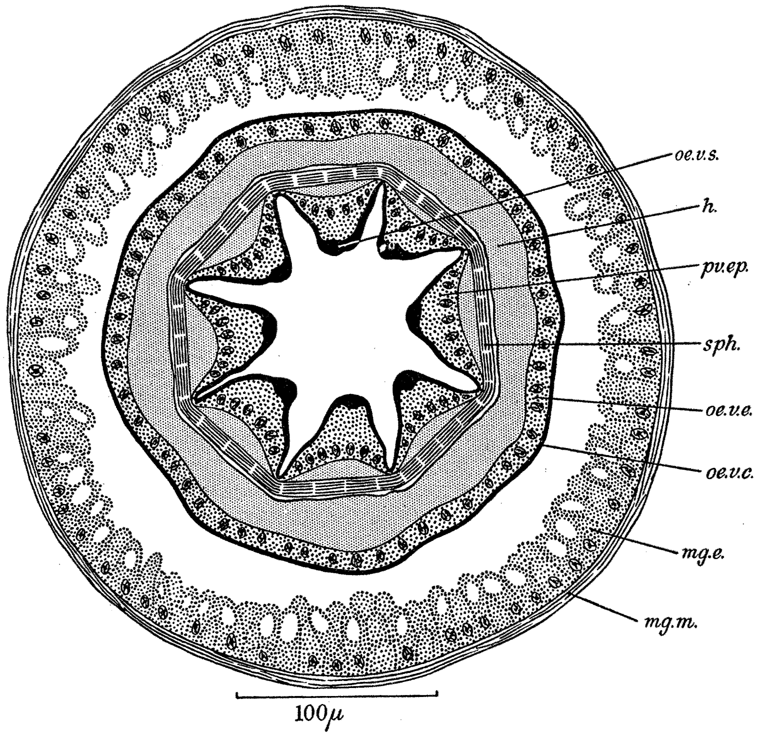

FIGURE 18. Transverse section through the junction of the fore-gut and mid-gut, showing the oesophageal valve.

apodemes, completely, but it is not of uniform thickness. Underlying the longitudinal furrows beneath the exit gaps from the sieve the epithelium is deeply cleft (figures 17, *pv.cl.*, and 19). According to the state of contraction or relaxation of the particular proventriculus under examination this cleft may be either open or closed. At the sides of the cleft the epithelium is very thick, but becomes progressively thinner in passing towards the apodemes.

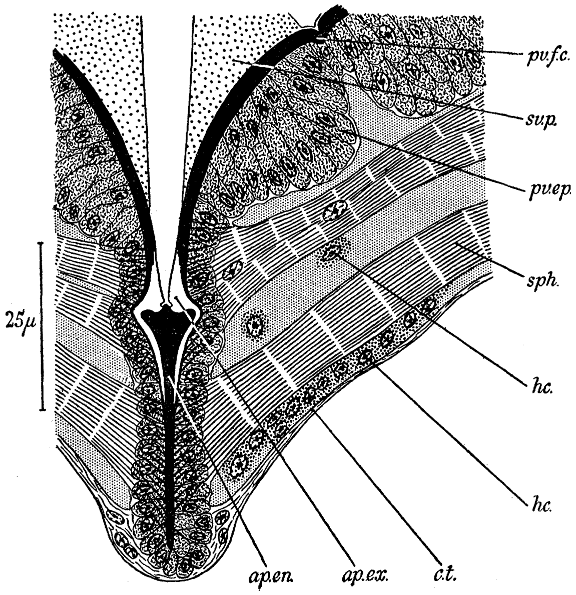

FIGURE 19. Part of the transverse section seen in figure 17, enlarged to show the details of the sphincter muscles and their apodemes.

The sphincter muscles of the proventriculus form by no means a continuous sheet. In transverse sections both inner and outer sphincter muscles are clearly recognizable (figures 16, 17, *sph.*) throughout most of the length of the organ, and it is furthermore apparent that these muscles are not continuous around its circumference, being interrupted by the apodemes on which they are inserted by means of tonofibrillae passing through the epithelium of the intima. In superficial view or longitudinal section it is seen that a large number of individual muscles makes up both inner and outer groups. These muscles all pass transversely across the wall of the proventriculus from apodeme to apodeme. It is evident that the sphincter muscles result from an elaboration of the simpler circular component of the fore-gut musculature, for at the front and rear of the proventriculus they merge into a continuous single sheet of circular muscle (figures 15, *c.m.*, and 18, *sph.*). The combined contractions of the sphincter muscles are clearly capable of compressing the proventriculus, but as will be seen later the dissociation of the muscles into circumferential segments has functional implications.

Completely enveloping the proventriculus and constituting its most superficial component, a thin sheet of tissue resembling connective tissue also encloses a blood space (figures 16, 17 and 18, *h.*).* The sphincter muscles and proventricular epithelium are therefore bathed by blood, in which are recognizable numerous haemocytes (figure 19, *hc.*).

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* Eaton (1942) has described the superficial layer of circular muscle in *Ips radiatae* as occupying precisely this position, and passing continuously over the tips of the apodemes. After renewed examination of my sections I am still of the opinion that the outermost layer is composed of connective tissue.

Behind the proventriculus a typical oesophageal valve projects as a double annular fold into the mid-gut (figure 18). Internally the valve is deeply furrowed, the furrows being actually the angles between the posterior continuations of the eight strongly curved walls of the proventriculus. Longitudinal thickenings of these walls give rise to chitinous rods (figure 18, *oe.v.s.*) which support the valve. The anterior tip of one of these rods is seen between the guide-lines *sv.p.s.* in figure 14.

A blood space (figure 18, *h.*), continuous with that surrounding the anterior part of the proventriculus, is enclosed between the double walls of the valve, and in this space a single continuous sheet of muscle (figure 18, *sph.*) encircles the inner wall of the valve.

7. The function of the crop and proventriculus

The precise mode of operation of the crop and proventriculus may now be discussed. The pharyngeal bracons have been specified as the active agents in the transport of food along the pharynx, and to a large extent food passes along the oesophagus also by the impetus received from food following but still in the pharynx. It is difficult to state whether the circular muscles of the oesophagus enable this portion of the fore-gut to aid the passage of food by simple peristaltic movements, or whether the oesophagus functions in a merely passive manner as a simple connecting tube between the pharynx and crop. What is certain is that the contraction of the circular muscles of the oesophagus, in the absence of a localized sphincter at the anterior end of the crop, is capable of preventing the escape orally of food from the crop.

Food particles accumulate in the crop and greatly distend it. They appear there to be intimately mixed with a fluid and to undergo at least considerable digestion. The oblique circular muscles of the crop are capable of causing the necessary kneading movements, and the spines are effective in mixing food and fluid. As will be seen later, the fluid found in the crop must be derived from the mid-gut.

The remarks made by Plateau (1876) in his classical work on digestion in insects apply in full force to *Calandra*. He says: ‘When digestion in the crop is complete, its contents are subjected to a strong pressure by the walls of this organ which carry out peristaltic contractions, sliding or filtering a little at a time through the valvular apparatus (the gizzard of other authors), guided by the ridges and their chitinous projections.

‘The valvular apparatus is by no means a triturating apparatus accessory to the mouth-parts, for in carnivorous Coleoptera and locusts where it shows a typical structure, the animal or vegetable matter which has passed through it is found, after its passage, in masses of the same size and shape as before.’

Further, this author insists that on morphological grounds alone the proventriculus even of beetles like *Dytiscus* cannot be an effective triturating apparatus. ‘Examination of the so-called teeth of the gizzard of the Dytiscidae shows that they are too weak for the functions attributed to them. Their margins are provided with numerous hairs which, while they are able to guide food material in an appropriate direction, would suffer greatly in true mastication.’

Conclusions attained by various authors with regard to the function of the proventriculus have been summarized by Wigglesworth (1939), who quotes evidence that in some cases at least the proventriculus may be a masticating apparatus. But the proof of this in isolated instances in no way invalidates the application of Plateau's statements to *Calandra*.

All the morphological features exhibited by the proventriculus of *Calandra* are capable of explanation on the grounds that the organ functions by retaining minute particles in the crop while they undergo digestion, yet at the same time allowing the access to them of digestive fluid from the mid-gut.

It will be evident that when the proventricular sphincter muscles are contracted the apical setae of the series of triangular plates will converge centrally. Furthermore, and equally important, the long spines borne by the cushions at the anterior end of the proventriculus will be tightly pressed together and lie back on the plates. The lumen of the organ is by these means effectively blocked. The only passage between the crop and the mid-gut is by way of the longitudinal entrance gaps to the sieve plates, transversely through the narrow spaces between the plates themselves, and so by way of the longitudinal exit gaps from the sieve to the mid-gut. Food particles found in the crop are, however, too large to pass through the narrow spaces between the sieve plates, which are about 2μ wide. They are therefore necessarily retained in the crop. The principle involved in the retention of food particles by the proventriculus is precisely that of 'edge filtration' applied in some commercial processes of filtering.

Although the closure of the lumen of the proventriculus by the contraction of its sphincter prevents the passage of food, no obstacle is offered to the flow of fluid under the influence of mid-gut contraction forwards into the crop along paths such as that indicated by the arrows in figure 20. That the fluid found in the crop is actually derived from the mid-gut, and not from the salivary glands, appears to be clearly indicated on the one hand by the lack of a copious salivary secretion, and on the other by the very elaboration of the proventriculus itself. Were the fluid of the crop not of mid-gut origin a simple occluding sphincter between mid-gut and crop would be functionally adequate. The softening and partial digestion of the powdered grain in the crop gives rise to a pasty 'mehlbrei' (Müller 1928) which ultimately on the relaxation of the proventricular sphincter muscles is squeezed through the proventriculus into the mid-gut.

The description of the proventriculus and its mode of operation as a sieve which I have given refers to the contracted organ, but it is possible to suggest what occurs when the sphincter muscles are relaxed and the organ is distended by the passage of food.

First, the strongly curved sides of the octagonal tube will tend to be straightened, flexion taking place most particularly along the line of the furrow in each wall (figure 19, *pv.f.c.*) but also along the lines of the apodemes of the muscles. This will result in the closer approximation of the constituent series of the double rows of plates: that is, in the diminution of the exit gaps from the sieve, with a corresponding increase in the extent of the entrance gaps. Whether straightening of the walls of the proventriculus takes place to such an extent that the parallel plates interdigitate I am not able to state, nor am I able to state with certainty whether the total increase in diameter of the proventriculus may be accounted for by this straightening. Interdigitation of the numerous and closely set plates appears somewhat improbable, and I incline to the view that in addition to straightening some stretching of the intima of the above-mentioned furrow and its underlying epithelium takes place. (Some little indication of this is given by one series of transverse sections.)

Stretching of the intima in the furrow would, of course, tend to increase the size of the exit gaps and so counteract the tendency to closure of these gaps by the straightening of the proventricular walls.

It is improbable that all the muscles of the proventriculus necessarily function together either in contraction or in relaxation. On the contrary it may be that the meaning of the dissociation of the sphincter muscles into independent segments is that asymmetrical movements of the proventriculus are thereby facilitated. Irregular changes in size of the channels through the sieve, or of its lumen, would result in a powerful kneading of the mehlbrei as it passes through into the mid-gut.

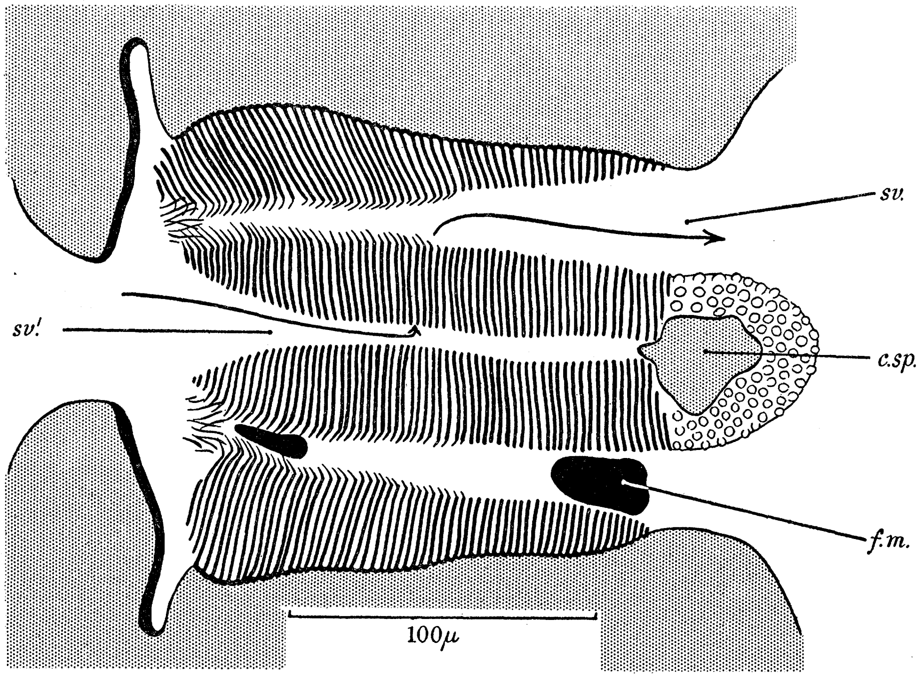

FIGURE 20. Diagram based on a photograph of a frontal section through the lower half of the proventriculus. The tapering entrance and exit channels of the sieve are clearly apparent, and two masses of partially digested and agglutinated food are shown trapped in one of the entrance channels. The arrow indicates the path along which fluid is driven from the mid-gut forwards into the proventriculus.

It is interesting to note that in one series of frontal sections the food extruded into the mid-gut is cut into a considerable number of parallel closely apposed longitudinal ribbons or columns, clearly distinct through their being stained differentially to some extent with Mallory. I conclude that this can only have resulted in the following way. When the sphincter muscles relax and the compression of the crop drives the semi-liquid food into the mid-gut, the groups of bristle-like setae from being closely pressed on to the series of plates are allowed to spring to a semi-erect position. Apically they collectively form by their crossing and intermeshing a grid which partially at any rate occupies the lumen of the proventriculus. Food forced through this grid, if semi-solid rather than semi-liquid, might retain in the mid-gut the individual strands into which it is cut.

Briefly, then, the operation of the proventriculus forms one event in a regular cycle of movements involving the crop, proventriculus, and mid-gut. While the proventriculus is contracted the crop fills with food, and the mid-gut contracts so as to drive digestive fluid through the sieve into the crop. On the completion of those processes of softening and digestion of the food which take place in the crop, the proventriculus and mid-gut are relaxed, and contraction of the crop drives food posteriorly into the mid-gut. The crop is then relaxed, the proventriculus contracted, and the cycle repeated.

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Abbreviations used in the figures

a.c. antennal centre; *a.l.g.* anterior labral ganglion; *a.n.* antennal nerve; *a.n.'* branch of antennal nerve; *ao.* aorta; *ap.* apodeme of pharyngeal dilator muscle; *ap.en.* endocuticle of sphincter apodeme; *ap.ex.* exocuticle of sphincter apodeme; *ap.t.* apodeme supporting tendons; *b.s.* basal setae of maxilla; *car.* cardo of maxilla; *c.m.* circular muscle of proventriculus; *c.oe.c.* circumoesophageal connective; *cr.s.* crop setae; *c.sp.* cushion armed with spines; *c.t.* connective tissue; *dc.* deutocerebrum; *d.c.m.* dorsal circular muscle of pharynx; *deg.* degenerate muscle of maxillary palp; *dil.* dilator muscle of pharynx; *d.s.* dorsal sclerite of maxilla; *e.* epistoma; *en.* endocuticle of roof of rostrum; *ep.* epidermis of roof of rostrum; *ex.* exocuticle of roof of rostrum; *f.g.c.* frontal ganglion connective; *f.g.c.′* branch of frontal ganglion connective; *f.m.* food mass; *f.n.* frontal nerve; *gal.* galea of maxilla; *h.* haemocoele; *hc.* haemocyte; *hc.g.* hypocerebral ganglion; *h.l.* lateral portion of rostral haemocoele; *h.m.* median portion of rostral haemocoele; *hp.* hypopharynx; *i.g.c.* interganglionic connective; *l.* labrum; *la.* labium; *lac.* lacinia of maxilla; *lac.fl.* lacinial flexor tendon; *lac.s.*1, *lac.s.*2, first and second lacinial sclerites; *la.ex.* backward extension of base of labium; *l.f.g.* lateral frontal ganglion; *la.p.* labial palp; *lig.* ligula; *l.n.* labral nerve; *md.* mandible; *md.ab.* abductor tendon of mandible; *md.ad.* adductor tendon of mandible; *md.ad.′* accessory adductor tendon of mandible; *md.ap.* apical tooth of mandible; *md.d.c.* dorsal condyle of mandible; *md.l.* lateral plate of mandible; *md.me.* median tooth of mandible; *md.mo.* molar tooth of mandible; *md.sa.* sub-apical tooth of mandible; *md.v.c.* ventral condyle of mandible; *mg.e.* mid-gut epithelium; *mg.m.* mid-gut muscle coat; *m.n.* nerve to mouth-parts; *m.n.′* branch of nerve to mouth-parts; *mx.* maxilla; *mx.p.* maxillary palp; *mx.pr.* promotor tendon of maxilla; *mx.p.t.* tendon of maxillary palp; *mx.re.* remotor tendon of maxilla; *oe.* oesophagus; *oe.v.c.* cuticle of oesophageal valve; *oe.v.e.* epithelium of oesophageal valve; *oe.v.s.* ‘skeleton’ of oesophageal valve; *pgen.* pregena; *pgul.* pregula; *ph.* pharynx; *ph.b.* pharyngeal bracon; *ph.en.* endocuticle of pharynx; *ph.ep.* pharyngeal epithelium; *ph.ex.* exocuticle of pharynx; *p.l.g.* posterior labral ganglion; *pr.* proarthris; *prc.* protocerebrum; *pv.cl.* cleft in epithelium of proventriculus; *pv.ep.* epithelium of proventriculus; *pv.f.c.* flexible cuticle of proventriculus; *r.n.* recurrent nerve; *r.n.′* branch of recurrent nerve; *s.* seta; *sal.d.* duct of salivary gland; *soe.g.* suboesophageal ganglion; *sp.* bristle-like spines of proventriculus; *sph.* sphincter muscle of proventriculus; *sph.a.* apodeme of sphincter of proventriculus; *st.* stipes of the maxilla; *sv.* entrance to sieve; *sv.′* exit from sieve; *sv.p.* sieve plate; *sv.p.s.* apical setae of sieve plate; *tc.* tritocerebrum; *tc.c.* tritocerebral commissure; *tf.* tonofibrillae; *tr.* trachea; *v.g.* ventricular ganglion; *v.s.*1, *v.s.*2 first and second ventral sclerites of the maxilla; 1, tendon of accessory mandibular adductor muscle; 2, tendon of maxillary cranial flexor muscle; 3, tendon of maxillary promotor muscle; 4, tendon of maxillary remotor muscle.