

## The Feeding Mechanism of the Butterfly *Pieris brassicae* L.

L. E. S. Eastham and Y. E. E. Eassa

*Phil. Trans. R. Soc. Lond. B* 1955 **239**, 1-43  
doi: 10.1098/rstb.1955.0005

### Email alerting service

Receive free email alerts when new articles cite this article - sign up in the box at the top right-hand corner of the article or click [here](#)

To subscribe to *Phil. Trans. R. Soc. Lond. B* go to: <http://rstb.royalsocietypublishing.org/subscriptions>

# THE FEEDING MECHANISM OF THE BUTTERFLY *PIERIS BRASSICAE* L.

BY L. E. S. EASTHAM AND Y. E. E. EASSA

*Department of Zoology, University of Sheffield*

(Communicated by V. B. Wigglesworth, F.R.S.—Received 8 April 1954—Revised 28 July 1954)

## CONTENTS

	PAGE		PAGE
INTRODUCTION	2	THE MUSCLES OF THE HEAD AND PROBOSCIS IN RELATION TO FEEDING	19
MATERIALS AND METHODS	4	The stipital muscles	19
GENERAL STRUCTURE	4	The galea muscles	21
THE MOVEMENTS OF THE PROBOSCIS DURING FEEDING	5	THE NERVOUS SYSTEM IN RELATION TO THE FEEDING MECHANISM	26
THE EXOSKELETON	8	THE SENSILLA OF THE PROBOSCIS	27
The proximal region of the galea	10	THE GLAND CELLS IN THE PROBOSCIS	27
The distal or coilable region of the galea	10	THE SUCKING PUMP	28
The linkage mechanisms of the galeae	15	THE MECHANISM OF THE PROBOSCIS	31
The internal septa of the galea	16	Observations and experiments to test theories on the proboscis mechanism	31
THE MAXILLARY BASAL SCLERITES AND LABIAL PLATE	17	Analysis and conclusions	34
		DISCUSSION	41
		REFERENCES	43

The paper gives a detailed anatomical and functional analysis of the butterfly's proboscis.

The proboscis consists of two maxillary galeae joined ventrally by exocuticular toothed hooks and dorsally by overlapping plates. Between them they form the food tube. The whole is a complex structure in which (i) flexible endocuticle and more rigid exocuticle, (ii) muscles, (iii) an internal skeleton of longitudinal septa, and (iv) haemocoelic turgidity play their part in the process of extension.

Extension of the proboscis is restricted to the sagittal plane. When extended there is always a point of ventral bending at about one-third of the proboscis length. The angle of this bend is variable and the butterfly is enabled thereby to explore different food sources without movement of the body. The transverse section of a coiled proboscis shows a flat dorsal surface which becomes convex in extension.

Contraction of the intrinsic primary oblique muscles of each galea pulls the dorsal and ventral walls towards each other. This sets up an internal pressure in the haemolymph which is maintained by a stipital valve. Because of the preponderance of flexible endocuticle at the junction of the outer walls of the galeae with their inner walls it also causes a transverse dorsal convexity to be imparted to the proboscis.

The inner wall of the galea bounding the food tube consists of transversely placed exocuticular laminae so disposed in a lattice arrangement as to make possible easy movement of the proboscis in the sagittal plane as in coiling and extension, but to prevent lateral movement.

Coiling of the proboscis is due to the elasticity of an exocuticular dorsal longitudinal bar which lies in each galea in the upper wall of the food tube.

Along the proboscis in the dorsal haemolymph there are about one hundred and fifty pairs of large unicellular glands whose secretions are poured into the region of the dorsal linkage. They

serve to lubricate the dorsal plates as they slide over each other in coiling and extension, and possibly to seal up the dorsal part of the food tube when the proboscis is extended.

As a result of examining the proboscis structure and its movements, and from numerous operations involving nerve sections and perforations of the haemocoel, it is concluded that all existing theories on proboscis extension must be rejected. Extension is not caused by inflation, nor by direct muscle action, nor by elasticity of the proboscis wall. Primary intrinsic muscles, under conditions of haemocoelic turgidity maintained by a stipital valve, have effect in producing a transverse dorsal convexity of the proboscis. Extension is a consequence of this dorsal convexity in an elastic system and only indirectly of the contraction of intrinsic muscles. Assisting in the production of this changed shape of the proboscis as seen in transverse section, are (i) the longitudinal internal septa which control the degree of movement of the proboscis walls and (ii) the strong wall of the food tube which acts as a fulcrum on which the movements of the outer galea wall are made.

At the point of ventral bending in the extended proboscis there is a secondary set of intrinsic oblique muscles in each galea which work antagonistically to the primaries and so prevent full extension here.

The pharyngeal sucking pump is described.

#### INTRODUCTION

The different opinions held on the mechanism of extension and coiling of the butterfly's proboscis as expressed in standard works of entomology are excuse enough in themselves for making a fresh approach to the subject.

There are those who regard intrinsic muscles as directly responsible for coiling, e.g. Eltringham (1923), Lameere (1938), Imms (1942), Snodgrass (1935), Schmitt (1938) and Bourgogne (1951), with the corollary that extension is due to blood pressure from the head and/or to elasticity of the proboscis as a whole. On the other hand, Kirbach (1884), Hering (1926), Weber (1933) and Pradhan & Aren (1941) ascribe extension to muscle action and coiling to the elastic properties of the cuticular wall of the proboscis which becomes effective when the muscles relax.

In a third category we find Burmeister (1832) and Portier (1949), who regard some muscles as the cause of coiling and others antagonistic to them as the cause of extension. Reaumur (1734) seems to be the first to express this view, but since he confused the cuticular annulations with ring muscles to which he attributed coiling, he may perhaps be regarded as among those who claimed the intrinsic longitudinal muscles to be the cause of extension. Savigny (1816), in pointing out Reaumur's error, suggested that in the cuticular rings rests the power of the proboscis to coil up.

These conflicting opinions have arisen from faulty or incomplete observations on structure. Even the movements and attitudes of the proboscis during feeding have not been properly recorded. Each explanation so far offered ignores some aspect of structure. But no single morphological feature is adequate to explain proboscis movement. In explanation of this we may anticipate our descriptions on structure and mechanism by stating that the latter is now seen to depend on the cuticular composition of the proboscis wall, on the way in which the two halves of the proboscis are joined together, on the extrinsic and intrinsic musculature and on the stipital valvular mechanism for maintaining turgidity of the haemocoel in each half of the proboscis.

We find that all accounts of the cuticular structure are incorrect or incomplete. For instance, Burgess (1880), Snodgrass (1935), Portier (1949) and Bourgogne (1951) state that the external wall of the proboscis is composed of chitinous annuli between which lies a

thin membrane imparting suppleness. No such thin membrane exists, the cuticle between the annuli being of the same thickness as in those regions where the annuli occur. Weber (1933) does in fact refer to exocuticular rings but does not comment on the substantial intervening thickness of endocuticle. Since exocuticle is relatively rigid as compared with the flexible endocuticle it is clear that these authors are basing their opinions of mechanism on a false structural picture. Pradhan & Aren (1941) also show a differentiation between exo- and endocuticle, but base their theory of mechanism on the greater thickness of the cuticle posteriorly than anteriorly. This difference seems insignificant to us and may well arise from a little obliquity in the cutting of their sections.

As for the musculature, no complete account is to be found, and since in all theories propounded muscle action is invoked either to coil the proboscis (Burgess 1880; Eltringham 1923; Lameere 1938; Imms 1942; Snodgrass 1935; Schmitt 1938; Bourgogne 1951) or to extend it (Kirbach 1884; Hering 1926; Weber 1933; Pradhan & Aren 1941), some error is inevitable and a complete examination is therefore called for.

Burgess (1880), for instance, describes certain basal muscles to which he attributes the withdrawal of the proboscis under the head. These are in fact the elevators of the proboscis base. He also describes two sets of intrinsic muscles arranged in each half of the proboscis as a series of overlapping V's, and we infer from his description that these occur for the full length of the proboscis. Only in one region, however, namely, the 'knee bend' (see p. 6), does this condition occur, and they can be shown to serve there a special purpose. Elsewhere only one set of these muscles occur. He further claims that these muscles serve to coil the proboscis, and he is then left with the problem of extension which he attributes by inference to elasticity of the proboscis wall. Portier (1949), following Burmeister (1832), informs us that the intrinsic muscles have a complex disposition and therefore 'we will not describe them'. In point of fact Burmeister (1832) wrongly describes the intrinsic muscles as arranged in two sets, an upper one for extending and a lower one for coiling the proboscis. This is a travesty of the truth.

Both Schmitt (1938) and Pradhan & Aren (1941) are in some agreement with us on the disposition of extrinsic and intrinsic muscles, but their accounts are incomplete and seem inevitably to have led them to wrong conclusions. Schmitt (1938), for instance, regards intrinsic muscles as effective in coiling, while extrinsic muscles of the stipes are supposed to force blood from the head into the proboscis haemocoel, so causing extension by inflation. With both these propositions we disagree for reasons to be given later.

Pradhan & Aren (1941), following the earlier work of Kirbach (1884), explain extension of the proboscis in terms of each intrinsic muscle working on the proboscis wall as a 'mechanical couple'. The efficiency of this theory depends in their view on the greater thickness and strength of the posterior wall of the proboscis as compared with the anterior wall. We doubt the existence of this difference, either in thickness or in strength.

Elasticity of the proboscis has been variously invoked to explain either coiling (Kirbach 1884; Hering 1926; Weber 1933; Pradhan & Aren 1941) or extension of the proboscis (Lameere 1938; Bourgogne 1951). Yet none of these workers has attempted to discover in which part of the proboscis the elastic properties lie and how in fact these properties express themselves. Without pursuing the point at length it is clear that on the elucidation of this point must rest all other considerations of the effect of the contraction of intrinsic muscles.



If, for instance, it were to be discovered that the elastic properties of the proboscis wall, or some part of it, accounted for extension, then one might fairly expect the intrinsic muscles in some way to cause coiling. If, on the other hand, it is found that elasticity of the proboscis does in fact cause the proboscis to coil up then the way is open to a consideration of the intrinsic muscles as the instigators in some way of the movements leading to extension.

From this welter of conflicting opinions and morphological incompleteness and inaccuracy it is clear that answers have to be found to a number of questions. Does the elastic property of the proboscis cause coiling or uncoiling? Do the intrinsic muscles bring about extension or coiling of the proboscis? Is there any morphological background to the theory that extension is caused by fluid inflation from the head cavity? The fresh approach made in this work has the purpose of answering these questions.

New information on cuticular structure, internal skeleton, musculature and proboscis glands has been produced. As a result of a complete analysis of these structures, of observations on the animal during feeding—of numerous operations involving nerve sections and perforations of the haemocoel—a new theory is offered on the proboscis mechanism for which the senior author (L. E. S. E.) alone is responsible.

#### MATERIALS AND METHODS

Fresh material was fixed in alcoholic Bouin at a temperature of 60° C., the heads being cut from the body to permit of easy penetration of the fixative.

In preparation for cutting, softening of the heads in diaphanol preceded embedding in wax, melting-point 60° C. Sections were cut at a thickness of 7·0 to 10·0  $\mu$ . Stains used were: Mallory's triple stain, Haidenheim's haematoxylin, Delafield's haematoxylin and eosin.

Before operations involving either perforation of the proboscis haemocoel or cutting of nerves, the butterflies were anaesthetized with ether. Perforations of the galea haemocoel were made with finely drawn-out glass needles.

#### GENERAL STRUCTURE

The general form of the mouthparts of a butterfly in relation to the head is well known (figures 1, 2). The reduction of the mandibles to fixed vestiges incorporated into the head capsule, of the labium to a basal plate bearing large palps, and of the maxillae to two long coilable tubes which fit together to form a food tube between them leaving the maxillary palps as minute vestiges, are features referred to in most entomological text-books.

The maxillary galeae are linked together (figure 6) for the whole of their length from tip to base, at which place they are overhung by the labrum (figure 2), and where each basally is joined to the distal end of the stipes. The stipes of the two sides diverge from each other as one passes from their distal to their proximal ends. The space between these divergent stipes is occupied by the triangular labial plate from the posterior lateral angles of which are given off the palps. Proximally to each stipes is attached the cardo of each side.

The cardo, stipes and labial plate fit together so as to form most of the ventral surface of the head, with the hypostoma making up the narrow lateral regions, and the fixed mandi-

bular vestiges the anterior lateral angles, thereof (figure 1). On the front surface of the head capsule are the epicranium, the frons between the antennal bases and the large subquad-rangular clypeus beneath them. To the ventral border of the clypeus is articulated the labrum.

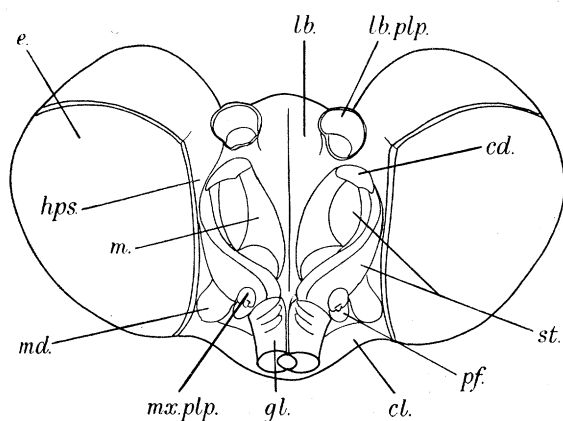


FIGURE 1. Ventral view of head.

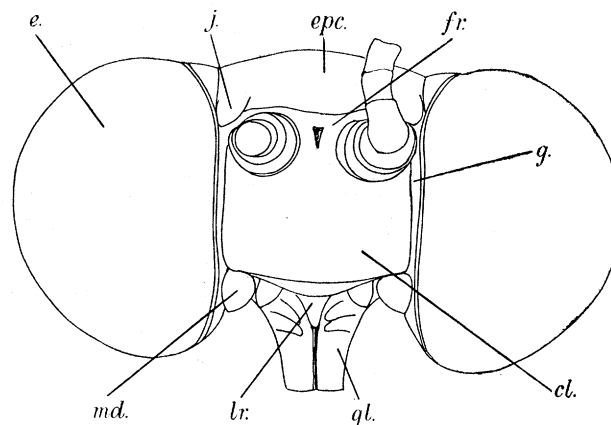


FIGURE 2. Dorsal view of head.

*cd.* cardo; *cl.* clypeus; *e.* eye; *epc.* epicranium; *fr.* frons; *g.* gena; *gl.* galea; *hps.* hypostoma; *j.* jugum; *lb.* labium; *lb.plp.* labial palp; *lr.* labrum; *m.* ventral membrane; *md.* mandible; *mx.plp.* maxillary palp; *pf.* pilifer; *st.* stipes.

#### THE MOVEMENTS OF THE PROBOSCIS DURING FEEDING

The food channel of the proboscis distal to the labrum is tubular. At the level of the labrum, however, the two galeae fail to meet dorsally and thus the tube is reduced to a gutter with the labrum as its roof (figure 3*A*).

At rest the mouth is closed and out of contact with the food tube. The first step, therefore, to the act of feeding is to open the mouth and to raise the proboscis base so as to bring food tube and open mouth into functional relation with each other (figure 4*B*). In the raising of the proboscis base this is made to press upwards on the anterior border of the labrum. The roof of the cibarium is raised and the mouth opened. While this is happening the base of the proboscis is pulled back, an act which brings the open gutter of the food channel still more completely under the labrum. Figures 4*A* and *B* make this point clear.

The proboscis now begins to uncoil and passes rapidly through the phases shown in figure 5*B* (i), (ii) and (iii). These movements involve some further elevation of the proboscis base and of the proximal third of its coilable region. In this way attitudes of actual feeding are attained (figure 5*C*), in which there is always observed the persistence of an obtuse angle in the proboscis at a point *X* (figure 5*B*), about one-third of its length from the base.

The tip may be placed against a moist substratum with its dorsal surface downwards, a 'flamingo' attitude. It may also be turned ventral-surface downwards or the very tip may be placed directly into the food source. All movement is restricted to the sagittal plane. The return to the coiled position is rapid and ends with a final tightening of the coil between the labial palps under the head (figure 5*A*).

The obtuse angle referred to at *X* (figure 5) is a permanent feature of the extended proboscis. We will call it the 'knee bend', and shall have occasion to refer to it in our description of the intrinsic musculature. The 'knee bend' is well seen in a proboscis which

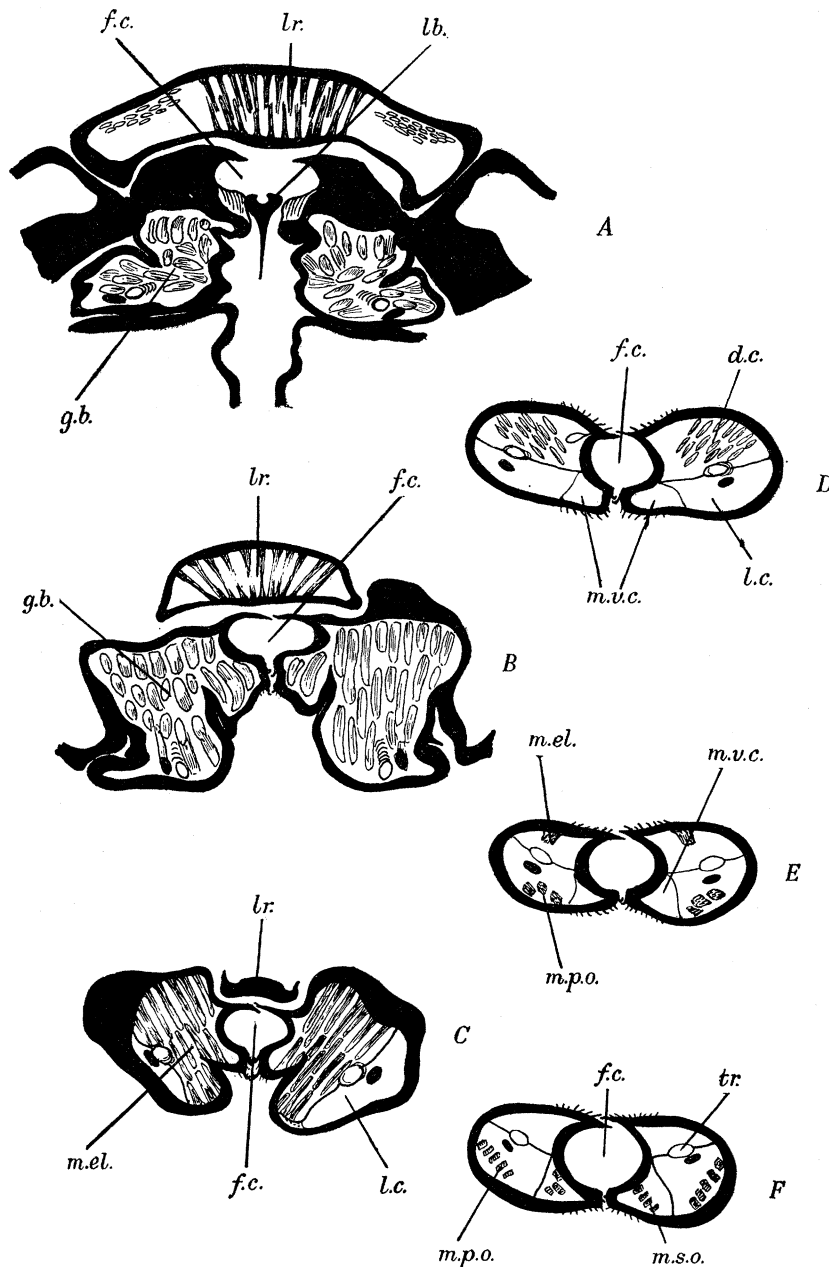


FIGURE 3. Transverse sections, *A*, *B*, *C*, *D*, *E* through basal region of proboscis, and *F* through 'knee bend'. *A*, through base of proboscis under the labrum; *B* and *C*, distal to *A* respectively; *D* and *E*, through proboscis distal to labral region. *d.c.* dorsal chamber; *f.c.* food canal; *g.b.* galea base; *lb.* labium; *l.c.* lateral chamber; *lr.* labrum; *m.el.* elevator muscle; *m.p.o.* primary oblique muscle; *m.s.o.* secondary oblique muscle; *m.v.c.* median ventral chamber; *tr.* trachea.

has been drawn out from the position of rest by a pin inserted into the coil. It is as if some resistance to the straightening action of the pin is offered by the proboscis at this point (figure 5). Having extended the proboscis by this means, removal of the pin results in a

rapid return to the coiled position as if by elasticity of the proboscis wall. Even when the internal musculature has been macerated from within the proboscis, the latter returns to the coiled position.

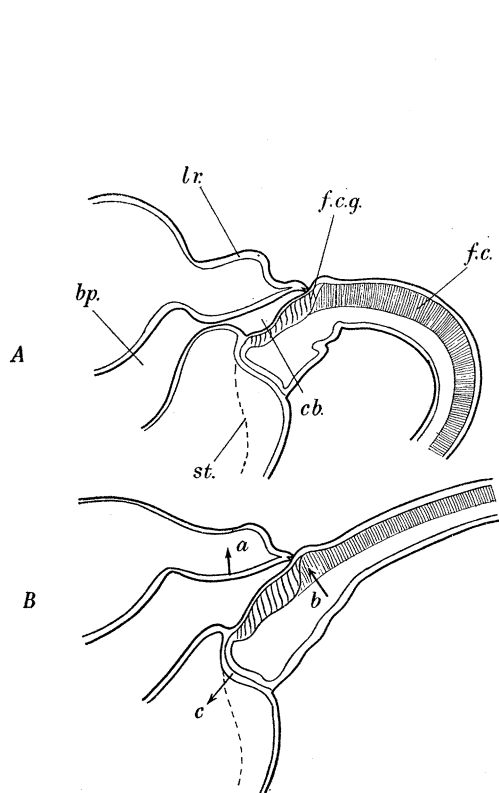


FIGURE 4. Longitudinal vertical sections through front region of head and proximal region of proboscis to show changes between resting condition *A* and feeding position *B*. *bp.* buccopharynx; *cb.* cibarium; *f.c.* food canal; *f.c.g.* food canal as gutter under *lr.* labrum; *st.* stipes. In *B* the arrows indicate the direction of movements of *a* the roof of the cibarium, *b* the proboscis in elevation and *c* in retraction, to bring the proboscis base into relation with the pharynx.

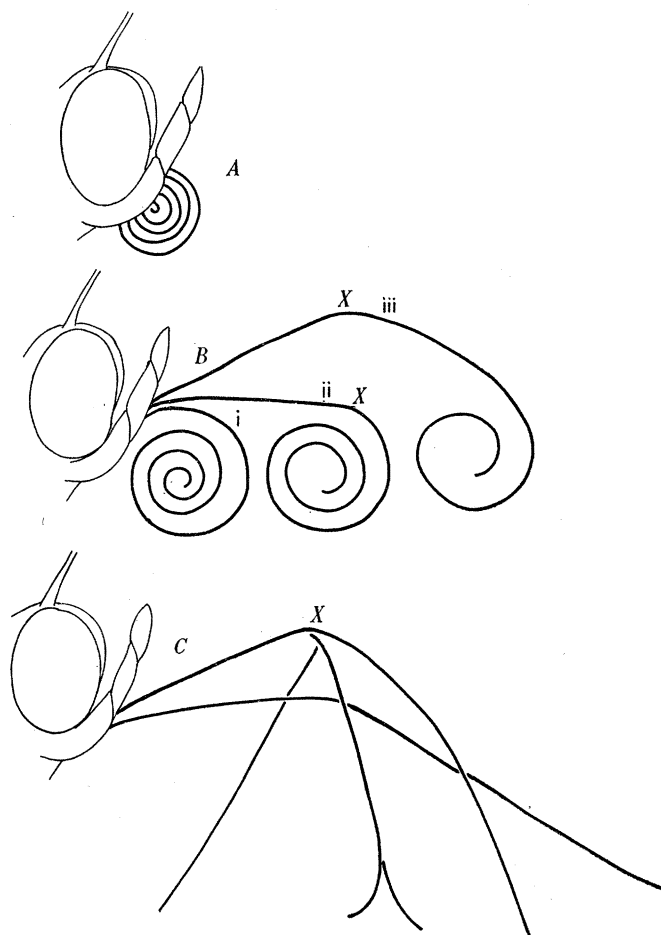


FIGURE 5. Diagram of attitudes adopted by the proboscis before and during feeding. *A*, at rest; *B* (i) base of proboscis elevated, (ii) proximal region uncoiled, (iii) distal region uncoiling; *C*, fully extended with 'knee joint' at *X* with tip of proboscis in five different feeding positions with proximal region relatively fixed.

While the above movements are easily observed, there occur differences in the shape of the proboscis as seen in transverse sections when in the coiled and extended states. These can only be seen with difficulty in the whole proboscis, but they are significant for the theory of mechanism to be offered later. When coiled, for instance, the two halves of the proboscis fit together in such a way that the upper surface of the whole is relatively flat while a deep groove runs along the length of the middle ventral line where the ventral



linkage between the two galeae occurs (figure 6). When the proboscis is extended, however (figure 7), the ventral groove is wider than it is when coiled (figure 6), and the dorsal surface is then seen to be transversely convex.

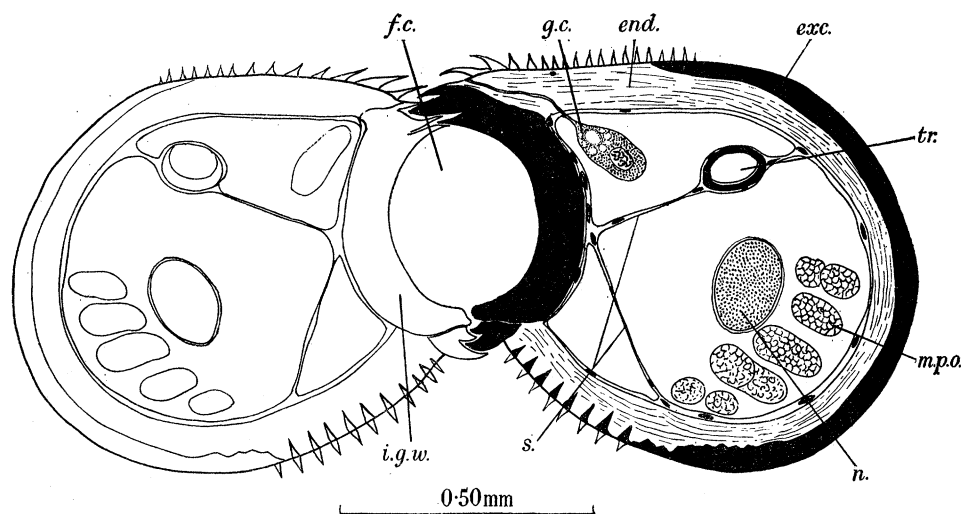


FIGURE 6. Transverse section of the proboscis in proximal region. *end.* endocuticle; *exc.* exocuticle; *f.c.* food canal; *g.c.* gland cell; *i.g.w.* inner galea wall; *m.p.o.* primary oblique muscle; *n.* nerve; *s.* longitudinal septa; *tr.* trachea.

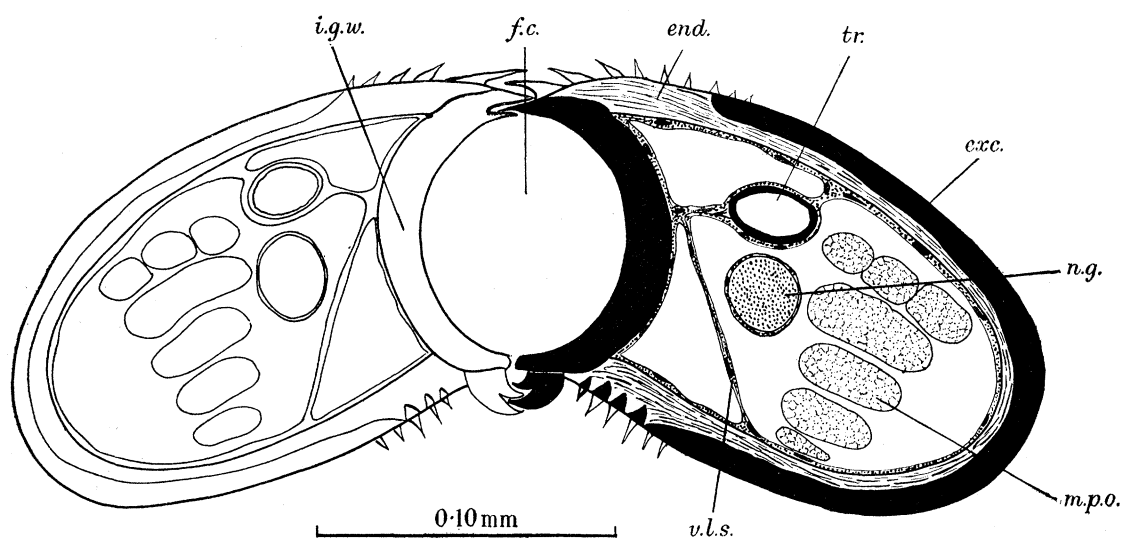


FIGURE 7. Transverse section of the proboscis at about the middle of its length in the extended state. *end.* endocuticle; *exc.* exocuticle; *f.c.* food canal; *i.g.w.* inner wall of galea; *m.p.o.* primary oblique muscle; *n.g.* galea nerve; *tr.* trachea; *v.l.s.* ventral longitudinal septum.

#### THE EXOSKELETON

The proboscis consists of a short basal and a longer distal coilable region (figures 1, 4, 8 and 10). It has a tapering tubular form in which the two halves, the galeae, fit together firmly. The food tube formed by this union is approximately circular in section, and in making its connexion with the cibarium it opens dorsally to form a gutter with the labrum

## ON THE FEEDING MECHANISM OF THE BUTTERFLY

9

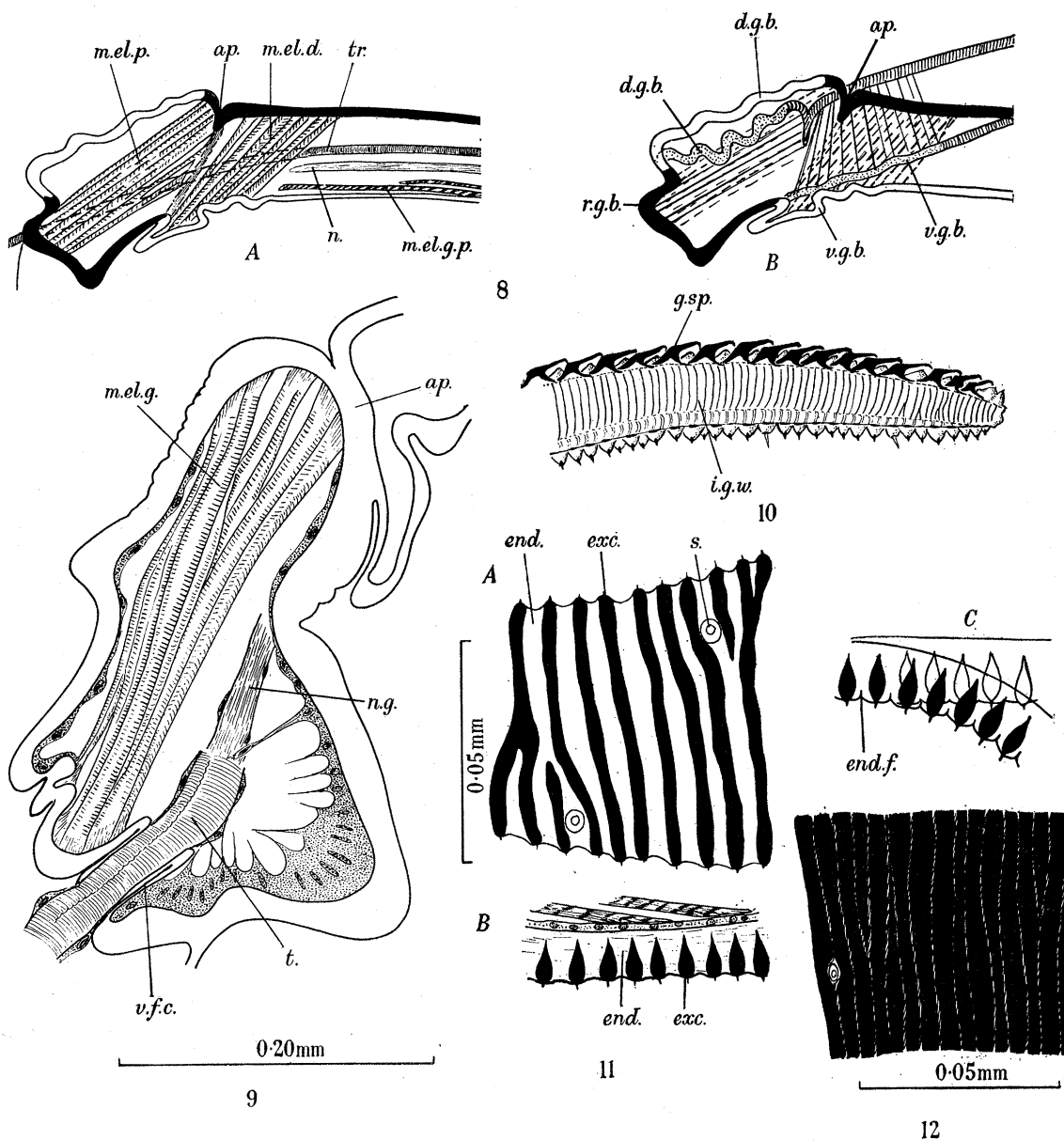


FIGURE 8. Longitudinal sections of galea: *A*, to show basal elevator muscles; *B*, to show action of muscles in elevating the base of the proboscis (semi-diagrammatic). *ap.* apodeme; *d.g.b.* dorsal wall of galea base; *m.el.d.* *m.el.g.p.* proximal elevator muscles of coilable proboscis; distal elevator muscle; *m.el.p.* proximal elevators of proboscis; *n.* nerve; *r.g.b.* rigid wall of galea base; *tr.* trachea; *v.g.b.* ventral wall of galea base.

FIGURE 9. Sagittal section through the base of the galea at the entrance of the galea nerve and trachea. *ap.* apodeme; *m.el.g.* elevator muscle of galea base; *n.g.* galea nerve; *t.* trachea; *v.f.c.* valvular fold of cuticle.

FIGURE 10. Longitudinal section through proboscis tip: *g.sp.* spines on galea wall; *i.g.w.* inner galea wall bounding food canal.

FIGURE 11. Longitudinal sections through the outer galea wall, *A*, tangential; *B*, sagittal; *C*, sagittal in both extended and coiled conditions. *end.* endocuticle; *end.f.* endocuticular fold; *exc.* exocuticle; *s.* sensillum.

FIGURE 12. Longitudinal section through inner galea wall.

as its roof. Figure 3 shows in a series of transverse sections the spatial relations of the galeae to each other as they enter the head. Each galea contains a spacious haemocoel (figure 6), which communicates with the head cavity by way of a slit-like opening in the tubular stipes.

*The proximal region of the galea* (figure 8)

This is short and differs from the proboscis proper in that it does not share in the process of coiling. It is more strongly cuticularized than the distal part and lacks the latter's surface annulations. Its muscular apparatus also is peculiar. A deep transverse cuticular inflexion dorsally marks the division between it and the distal proboscis. This inflexion forms a strong apodeme on which are inserted the elevator muscles of the base of the galea. To it is attached a longitudinal dorsal cuticular bar which lies above the food tube in each galea. As a whole the galea base can be likened to a hollow cylinder open at each end where it communicates in front with the proboscis and behind with the stipes. In both these regions of connexion the cuticle is rigid and mostly exocuticular. Between them (i.e. the wall of the cylinder) it consists of laminated flexible cuticle. This flexible wall is thrown into three more or less transverse folds which accommodate themselves to the changing conditions of the proboscis as it is elevated and lowered (figures 5, 8 and 22).

At the junction of the galea with the stipes the galea nerve and trachea pass from the head into the galea haemocoel of each side (figure 9). Their passage is guarded by a cuticular fold which closely embraces the trachea and nerve as does a collar. This fold serves to protect these delicate structures from compression during proboscis movement. It also serves as a valve, effectively preventing the passage of fluid from the galea to the head should any fluid pressure within the galea be set up.

*The distal or coilable region of the galea*

Except that the galea distal to the basal region tapers towards the tip its structure is fairly uniform from one end to the other. As an exoskeletal structure it can best be considered in terms of (*a*) its outer (antero-dorsal, lateral and post-ventral) wall, (*b*) its median or inner wall, (*c*) its mechanism for linking the two galeae to each other and (*d*) its internal skeleton.

(*a*) The outer wall is about  $12\ \mu$  thick. It bears, particularly dorsally and ventrally, a number of stout exocuticular spines which become more widespread over the surface of the cuticle the nearer the tip of the proboscis is approached (figures 6, 10). Ventrally the spines are simple, but dorsally they are distally turned and hooked, each resting on a bifid base. Doubtless by means of these spines the skins of soft fruits can be pierced.

The thickness of the outer wall is largely taken up with flexible laminated endocuticle, but embedded in this at fairly regular intervals are pigmented, transversely disposed, exocuticular ribs imparting to the proboscis an annulated appearance. These ribs, showing in places anastomoses and branchings, occupy about half the thickness of the cuticle where they occur, and along the proboscis they are separated from each other by regions of surface endocuticle of a width about equal to their own (figure 11).

The exocuticular ribs do not extend across the whole surface of the outer wall. Where the latter meets the inner galea wall (food tube) both dorsally and ventrally little but endocuticle is found (figures 6, 13). Since endocuticle is flexible and exocuticle rigid it follows

that in these antero-dorsal and postero-ventral regions (figure 13) the wall is more flexible than elsewhere, thus making provision for changes in shape during coiling and uncoiling.

The flexibility of the endocuticle, particularly between the exocuticular ribs, is well seen by comparing sagittal sections of the proboscis in the coiled and extended positions (figure 11 C). In the coiled position the endocuticle is reflected inwards into surface foldings between the exocuticular ribs. Such foldings open out when the proboscis is uncoiled and

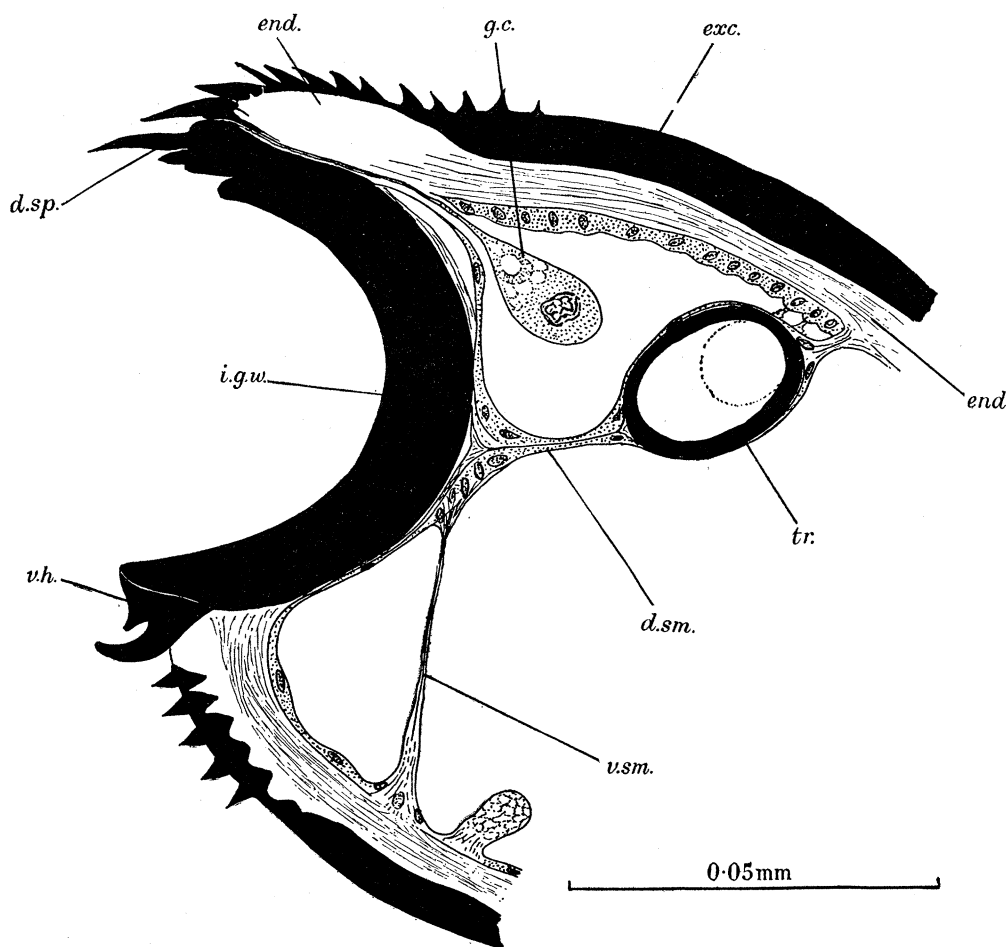
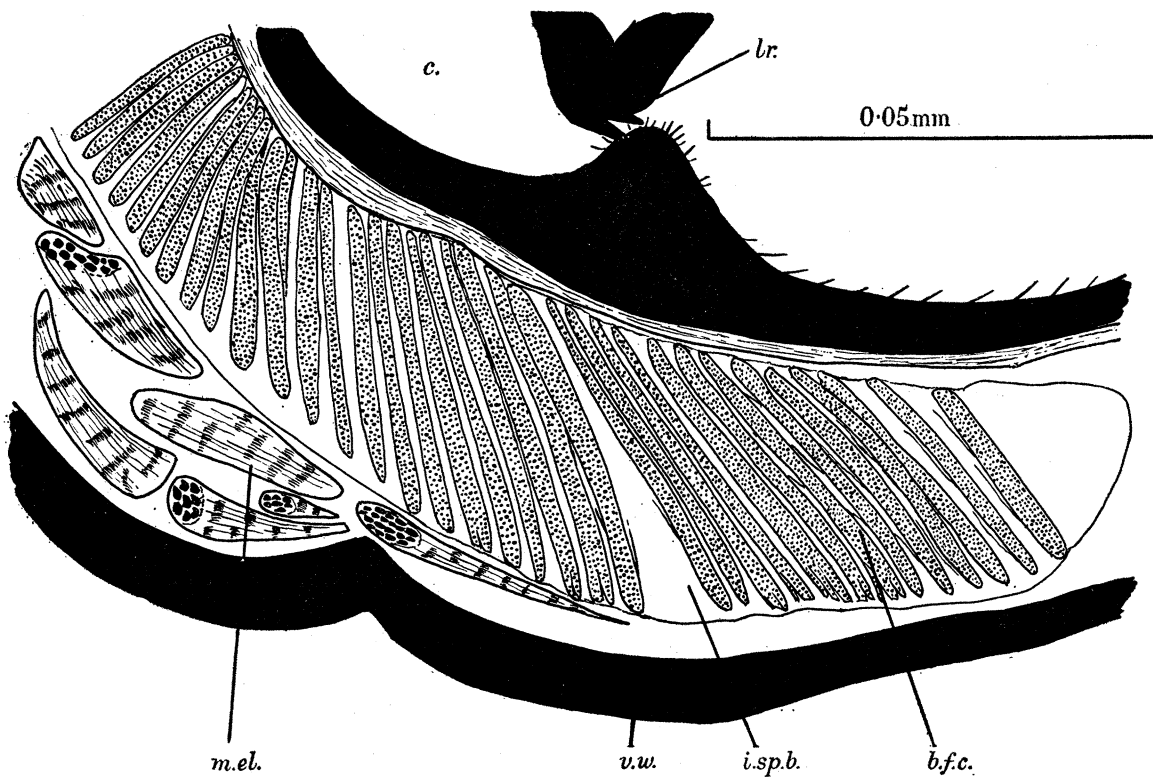


FIGURE 13. Transverse section through galea in median region. *d.sm.* dorsal septum; *d.sp.* dorsal spine; *end.* endocuticle; *exc.* exocuticle; *g.c.* gland cell; *i.g.w.* inner galea wall; *tr.* trachea; *v.h.* ventral hook; *v.sm.* ventral septum.

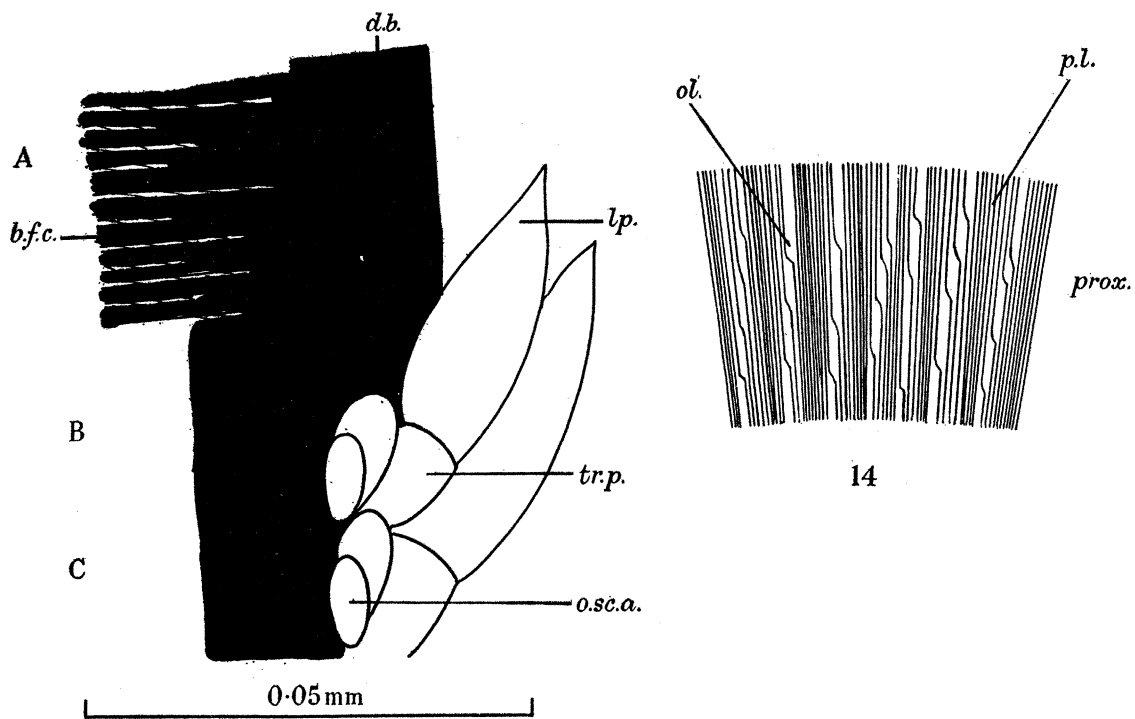
thus demonstrate the ability of the cuticle to accommodate itself to the movements of the proboscis in the vertical plane.

(b) The median wall of the galea is about  $15 \mu$  thick and consists of exocuticle to endocuticle in the proportion of about 10:1 (figure 13). It is therefore more rigid than the outer wall. To it are attached the structures by which the two galeae are joined together. Its composition, as will shortly be seen, is such that a circular section of the food tube is maintained in both coiled and extended conditions. On close examination the median wall is seen to consist of a series of exocuticular laminae placed transversely to the food tube. These are arranged in a large series of bars, within which the laminae are so closely packed against each other that their presence cannot easily be detected except where the





15



16

14

FIGURES 14 to 16



wall is perforated by a sensillum, or where, through a fault in cutting sections, the laminar constitution of a bar is disclosed.

Between neighbouring closely packed regions or bars, the laminae pass across the intervening spaces in an oblique manner, as is shown in figures 12, 14 and 16. As seen in vertical longitudinal sections, the laminae connecting one bar to another pass upwards and distally to the bar next in front (figure 12). As seen in horizontal longitudinal sections, connecting laminae between bars pass from within outwards to the bar next in front (figure 17). The arrangement of laminae on one side of the food tube, therefore, is the mirror image of that on the other. These arrangements are absolutely regular, and on them depend the ability of the food-tube wall to accommodate itself to the changes in coiling and uncoiling undergone by the proboscis. On them also depends the restriction of the proboscis to movement in the vertical plane only.

In figure 17 a horizontal section through the region of ventral linkage, the proximal part of the section is uppermost in the drawing. Examination of this will demonstrate that should an attempt be made to bend the proboscis to one side distal to a fixed point, the laminae of one side will go into a state of tension and thus restrict, or even prevent, that lateral bending. For instance, a bending movement of the proboscis in the direction of the arrow at *B*, point *A* being fixed, will put all the laminae on the right side into a state of compression and those on the left into a state of tension. These latter must therefore resist the lateral bending force and tend to keep the proboscis in the sagittal plane. The inner wall of the galea thus has a lattice structure which restricts movement of the proboscis to the vertical plane, providing by this same means free coiling movements in that same plane. A somewhat similar cuticular device has been described by Slifer (1950) in the tarsal arolium of *Melanoplus differentialis*, where it serves to accommodate the tarsus to the varying degrees of pressure to which the foot is subjected.

The median laminated bars, here described, are associated dorsally and ventrally with the structures which link the two galeae together. Ventrally, alternate bars end in a swelling, and to each swelling is articulated a curved toothed hook, the full series of which form the ventral linking apparatus (figures 6, 17). Dorsally they all become fused into a dorsal longitudinal elastic bar which runs in each galea as a continuous structure for the whole length of the proboscis (figures 16, 19). Before fusing into this they become fused in pairs,

---

*Legends to Figures 14–16*

FIGURE 14. Longitudinal section through inner wall of galea to show its laminated structure; diagrammatic. *ol.* and *p.l.* regions of open spaced and close packed lamina respectively; *prox.* proximal end of section.

FIGURE 15. Vertical longitudinal section through base of galea to show greater separation between the bars in wall of food canal and the gradual disappearance of laminae connecting the bars with each other.

FIGURE 16. Horizontal section through dorsal linkage region through three levels. *B*, at the level of the dorsal longitudinal bar; *A*, at the level where the latter receives the inner galea wall bars; and *C* at the level of the dorsal linkage proper. *b.f.c.* bar in wall of food canal; *c.* cibarium; *d.b.* dorsal longitudinal bar of galea; *i.sp.b.* interspace between the bars; *l.p.* lance-shaped plate; *lr.* labrum; *m.el.* elevator muscles of galea base; *o.sc.a.* oval scleritic area; *tr.p.* triangular process; *v.w.* ventral wall of galea.

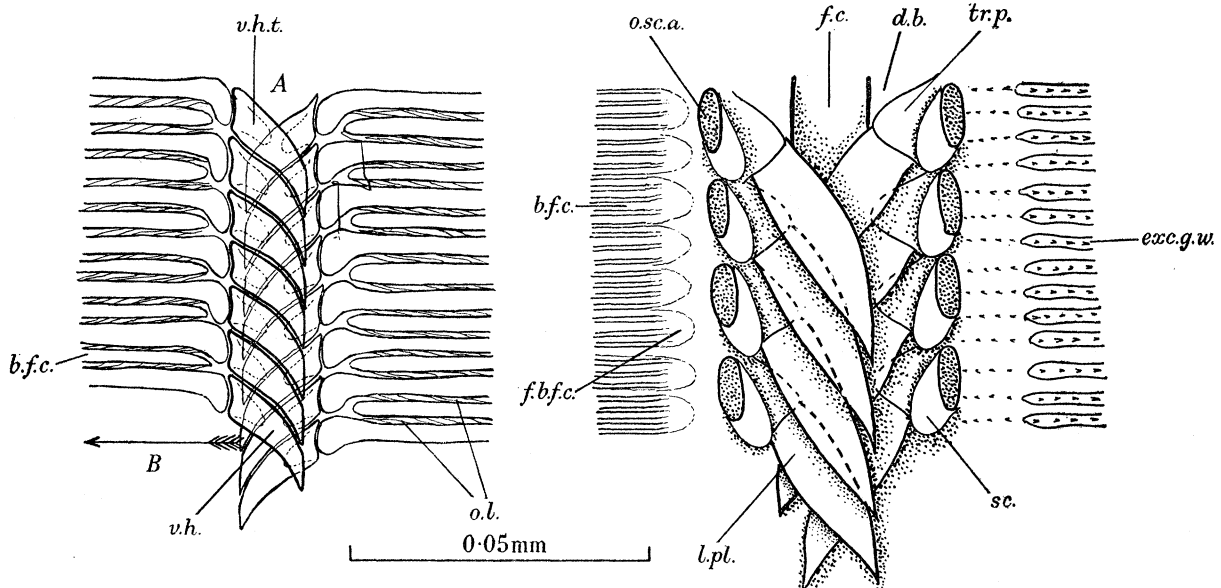


FIGURE 17

FIGURE 18

FIGURE 17. Horizontal longitudinal section through ventral linkage mechanism. For explanation of *A* and arrow *B* see text.

FIGURE 18. Composite horizontal section through dorsal linkage region at several depths indicating on the left spatial relations with the inner wall of the galea, on the right with the outer wall of the galea. *b.f.c.* bars in wall of food canal; *d.b.* dorsal bar; *exc.g.w.* external galea wall; *f.b.f.c.* fused bars at upper region of food canal; *f.c.* food canal; *l.pl.* lance-shaped plates; *o.l.* open spaced laminae between bars in wall of food canal; *o.s.c.a.* oval scleritic area; *sc.* scale; *tr.p.* triangular process; *v.h.* ventral hook; *v.h.t.* tooth of ventral hook (dotted outline).

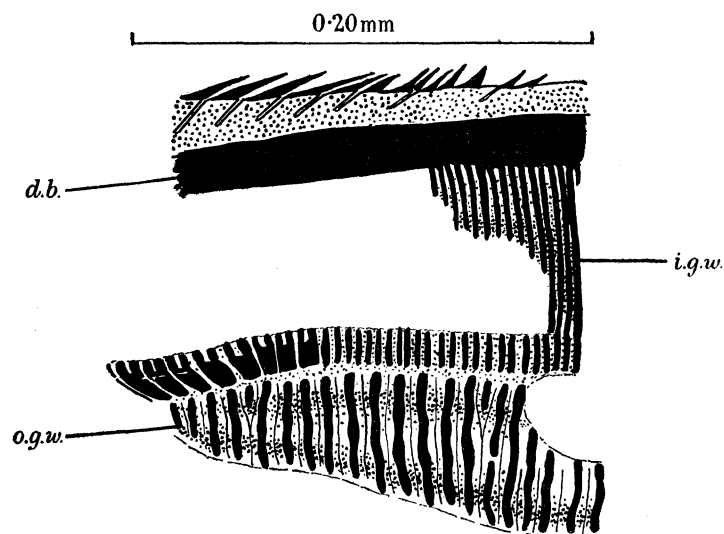


FIGURE 19. Vertical longitudinal section through the proboscis in the region of the dorsal cuticular bar. *d.b.* dorsal bar of food canal; *i.g.w.* inner wall of galea; *o.g.w.* outer wall of galea.

neighbouring larger sections again fusing together so as to form themselves eventually into the dorsal continuous bar. There is evidence, provided later, that in this dorsal bar rests those elastic properties on which depend the ability of the proboscis to come to the coiled position when at rest.

In the region of the cibarium where the food tube becomes an open gutter (figure 3*A*) there are no exocuticular annulations on the outer wall, but the barred structure of the median wall of the galea persists (figure 15). These bars, however, become more clearly separated from each other in a homogeneous matrix which is probably endocuticle. The deeper within the cibarium that one goes, the less frequently are found the laminar connexions between neighbouring bars. This is a region where coiling does not occur and the absence of the lattice structure here is referable to this fact.

*The linkage mechanisms of the galeae* (figures 17, 18)

Immediately after the adult emerges and while the cuticle is still soft the two separate galeae are brought together. They are then linked firmly together to form the proboscis.

The two galeae are linked together by two different mechanisms, dorsal and ventral. Since the proboscis is coiled when at rest and extended to a relatively straight form when feeding, it will be appreciated that movement from the position of rest to the extended position must affect antero-dorsal and postero-ventral surfaces of the proboscis differently. The ventral (concave when coiled) border has to be extended or stretched and the dorsal (convex when coiled) border has to be brought under compression. The reverse processes occur in coiling. The different mechanisms on the dorsal and ventral sides partly depend on these facts.

Ventral linkage is effected by a series of closely applied, curved, toothed hooks which lock into each other from the two sides. These hooks are exocuticular and very rigid. Each hook is firmly fixed by its broad base to the lower swollen end of a median bar (figures 6, 14 and 17). The hooks of a side fit closely against each other, curving towards the opposite side as well as distally (figure 17). They fit so closely that no space is left between them, even as seen under the oil-immersion lens. On the broad base of each hook and ventral to it is an incurved tooth pointing in the same direction as the hook itself (figures 6, 13 and 17).

The hooks of one side interlock with those of the other, so that the points of the hooks of one side fit into the recesses between the hooks and their incurved teeth of the other. The fact that the hooks in their interlocking are directed distally makes possible the sliding movements which they must perform during movement of the proboscis as a whole. Their curved form and that of their teeth determines the relatively rigid adherence between them from side to side—a firmness which is doubtless contributed to by the rigidity of the walls of the food channel to which they are fixed.

Dorsal linkage is not so firm and rigid as is the ventral. It is effected by a series of overlapping distally directed lance-shaped plates of cuticle. These on either side overlap each other like the tiles on a roof from the base of the proboscis to the tip. When the two galeae are applied to each other the lance-shaped plates of one side overlap those of the other side. In so doing they effectively bridge the gap between the dorsal longitudinal bars of the two galeae. The manner of their attachment to the longitudinal bar of the galea is complex (figure 18).

Placed dorsally on the surface of each longitudinal bar a little distance from its median border there is a longitudinal series of oval scleritic areas of such a size that each coincides with about four median wall bars, leaving a space between any two equal to about half this distance. Attached to each of these on its median side and directed distally and across towards the opposite side is an oval thin scleritic scale. Beneath this, and also firmly united with the first-mentioned oval scleritic area, is a broad triangular process (figure 18), whose base lies on the oval area, with its blunt apex pointing towards the opposite side. To the distally facing side of this triangular process is articulated the straight base of the lance-shaped plate which overlaps the one next distal to it. Being directed distally but obliquely to the opposite side each plate also overlaps a corresponding plate of that opposite side.

It will be seen that the dorsal linkage mechanism is much looser than is the ventral. Whereas the ventral mechanism clamps one side to the other while still allowing movement, the dorsal mechanism appears to do little more than provide a closed roof to the food canal. By virtue of the close application of the overlapping plates, however, considerable changes of attitude may be brought about in the proboscis without unsealing the dorsal wall of the food canal.

#### *The internal septa of the galea*

Consideration of the cuticular structure of the galea in relation to the movements of the proboscis would be incomplete without a description of its internal skeleton.

The base of the galea adjoining the cibarium has its haemolymph space largely filled with muscles, together with a nerve and a trachea (figure 3*A, B*). As one passes farther distally these intrinsic muscles (the elevators of the galea base) come to occupy the inner dorsal half of the blood space (figure 3*C*). It is here that there comes into the picture a longitudinal septum. This septum, as seen in transverse section, passes diagonally across the galea from its inner ventral to its outer dorsal wall. The trachea which passes the full length of the proboscis now lies in this septum, (figure 3*C*), and the galea nerve in the blood space beneath it.

Passing still farther distally the intrinsic muscles of the galea are found to occupy a still more dorsal position, and the space ventral to the septum becomes further divided by another more or less vertical longitudinal septum (figures 3*D, 7*). We have now passed from the galea base into its coilable region and there are now three chambers into which the blood space has been divided. These are: a dorsal, in which the last parts of the basal elevator muscles of the galea are seen; a lateral, in which lie the galea nerve and the oblique muscles of the galea; and a median ventral chamber (figure 3*E*). The partitions dividing the whole blood space pass in this form from one end of the proboscis to the other (figures 6, 7). Their arrangement is constant and they appear to be relatively unstretchable. A close examination of their structure reveals that they are exoskeletal and consist of thin in-turnings of the cuticular walls of the galea (figure 13).

It will be shown later that the internal septa of the galea help to determine the shape of the galea when under the impress of the contraction of its intrinsic muscles.

At the extreme tip of the proboscis there are no longitudinal septa, the three compartments becoming confluent here.



## THE MAXILLARY BASAL SCLERITES AND LABIAL PLATE (figure 1)

The relations between these sclerites and the head on the one hand and the proboscis on the other have been described.

The stipes is a complex sclerite. To its anterior border is fitted the galea base and just lateral to this attachment, the short sensory maxillary palp. To its posterior border is attached a small curved sclerite, the cardo.

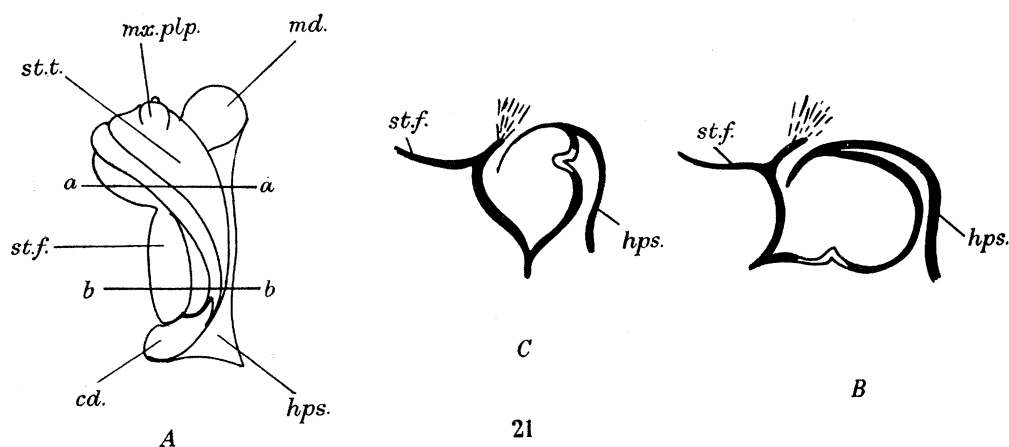
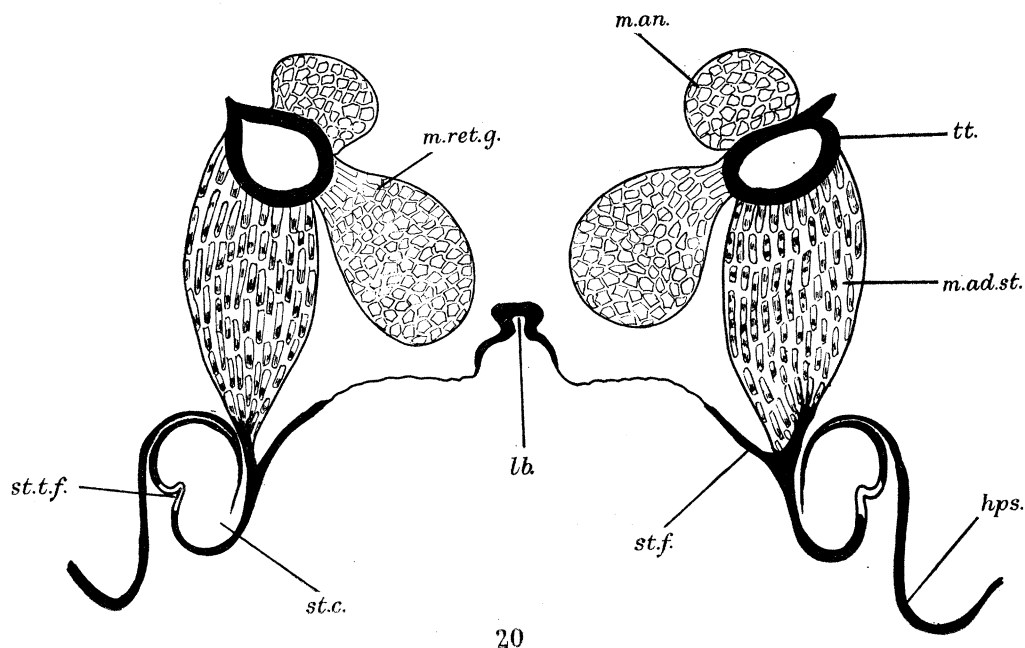


FIGURE 20. Transverse section through the lower region of the head to show the stipital valve and its muscles.

FIGURE 21. The stipes as seen in surface view and in sections, *A*, whole mount; *B* and *C*, transverse sections through levels *aa* and *bb* respectively. *cd.* cardo; *hps.* hypostoma; *lb.* labium; *m.ad.st.* stipital adductor muscle; *m.an.* antennary muscle; *md.* mandible; *m.ret.g.* retractor muscle of galea; *mx.plp.* maxillary palp; *st.c.* stipital cavity; *st.f.* flat part of stipes; *st.t.* tubular stipes; *st.t.f.* flexible wall of tubular stipes; *tt.* tentorium.



The stipes in its outer region has the form of a tube placed more or less in the antero-posterior axis of the head. Its contained blood space is continuous with that of the galea in front and that of the head cavity above it. The complexity of its form, as seen in surface view, can be gleaned from figures 20 and 21. It consists essentially of a plate, the median part of which is flat, its lateral part being rolled in upon itself to form a tube containing haemolymph. The cavity of this tubular part communicates by a slit-like opening above with the

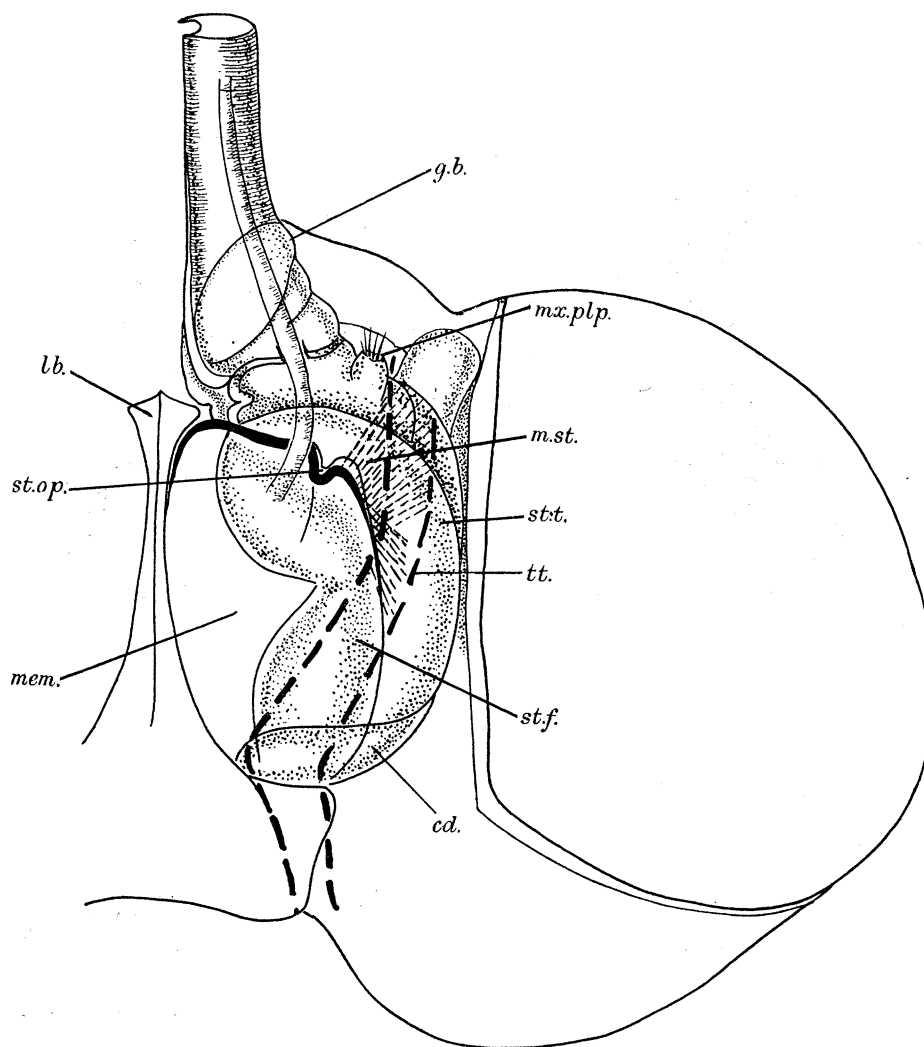


FIGURE 22. Whole mount of head to show by transparency the stipital opening and its controlling muscles. *cd.* cardo; *g.b.* galea base; *lb.* labium; *mem.* membranous floor of cranium; *m.st.* stipital muscle; *mx.plp.* maxillary palp; *st.f.* flat part of stipes; *st.op.* opening of stipes to cranium; *st.t.* tubular part of stipes; *tt.* tentorium (double interrupted line).

blood space of the head. If we trace the course of this sclerite from its median to its lateral border we pass first along its flat part. At the lateral edge of this flat part an apodeme projects obliquely upwards into the head cavity to receive the insertions of the stipital adductor muscles from the tentorium. The stipes now turns sharply ventral-wards and then curves outwards to the side. Before it reaches the hypostoma, however, it again turns upwards and mesially towards the stipital apodeme to enclose in a tubular space part of the cephalic haemolymph. The sclerite then turns lateral-wards again to join the hypostoma at

its side. The fold of the stipes which thus turns inwards to form a tube applies itself against the stipital apodeme at the edge of the flat part so as to form a flap valve which guards the exit from the tube to the head cavity (figure 20).

Along the wall of the tubular part, ventrally in front but becoming lateral in the posterior regions, is a groove of flexible cuticle. This might be expected to accommodate itself to changes in fluid pressure within the stipital and galea tube. Figure 21 shows the stipes in surface and transverse sectional views.

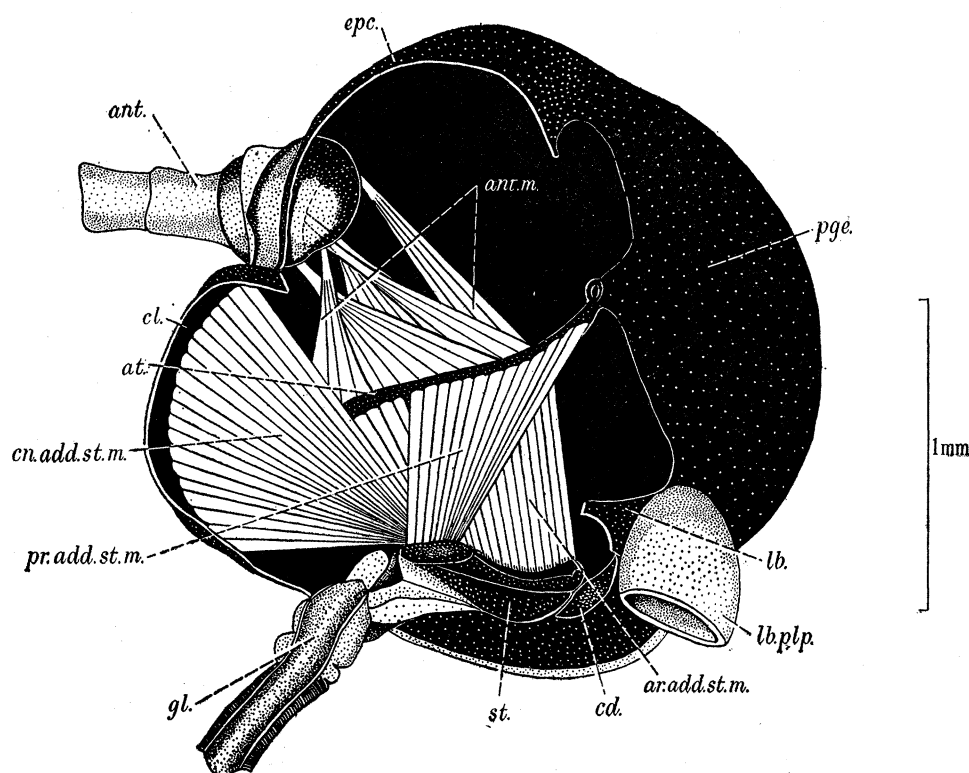


Figure 23. Right side of head as seen from within. *ant.* antenna; *ant.m.* antennary muscles; *ar.add.st.m.* anterior stipital adductor muscle; *at.* anterior arm of tentorium; *cd.* cardo; *cl.* clypeus; *cn.add.st.m.* cranial adductor muscle of stipes; *epc.* epicranium; *gl.* galea; *lb.* labium; *lb.plp.* labial palp; *pge.* post-gena; *pr.add.st.m.* posterior tentorial stipital adductor muscle; *st.* stipes.

#### THE MUSCLES OF THE HEAD AND PROBOSCIS IN RELATION TO FEEDING

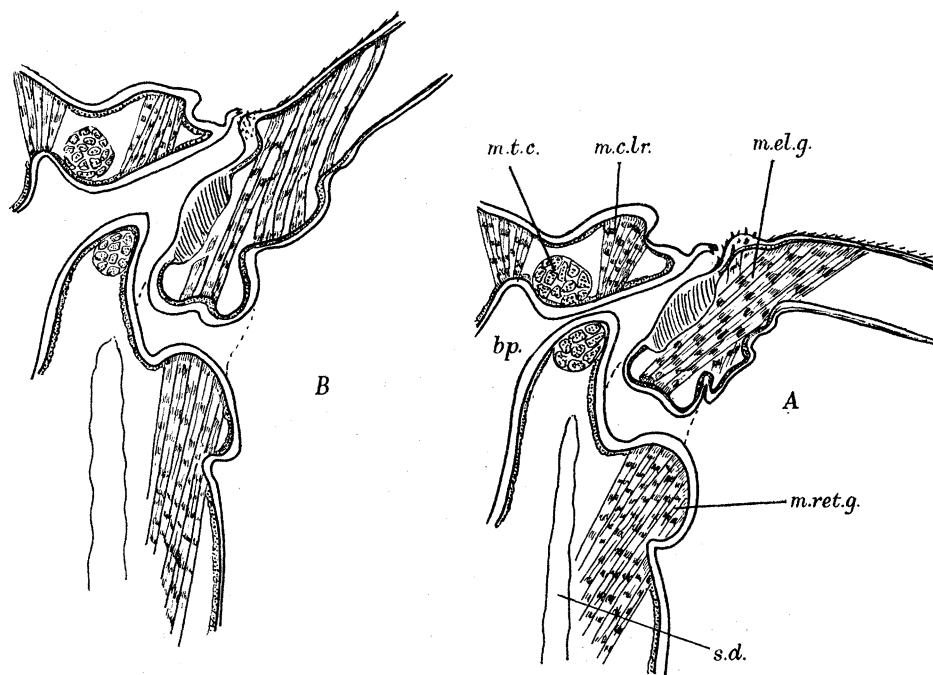
This musculature involves, in addition to that of the proboscis and the sucking pump, muscles with their insertions on the stipes and their origins either on the head capsule or on the anterior arm of the tentorium.

The tentorial arm at each side passes above the level of the stipes, between the occiput behind and the mandible in front. It curves to the side as it reaches its anterior point of attachment and thus its anterior part lies somewhat lateral to the stipes (figures 20, 22 and 23).

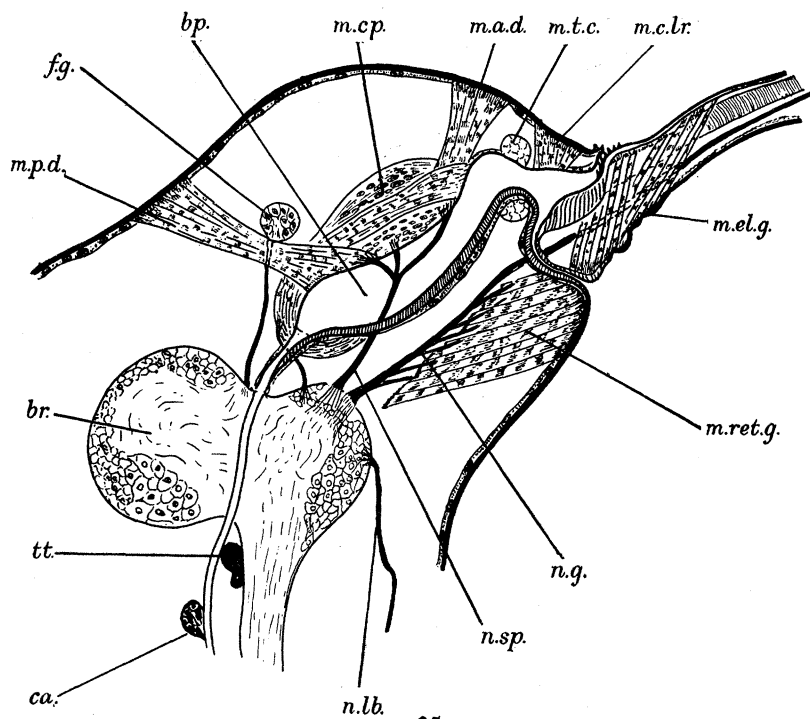
#### *The stipital muscles* (figure 23)

There are three stipital muscles with insertions on the stipital apodeme:

- (i) The cranial adductor muscle, *cn.add.st.m.*, has its origin on the gena and clypeus.
- (ii) The anterior tentorial muscle, *ar.add.st.m.*, originates on the inner and outer faces



24



25

FIGURE 24. Median longitudinal section through mouth and base of proboscis. *A*, mouth closed, proboscis coiled; *B*, mouth open, proboscis raised.

FIGURE 25. Median longitudinal section of head. *bp.* bucco-pharynx; *br.* brain; *ca.* corpus allatum; *fg.* frontal ganglion; *m.a.d.* and *m.p.d.* anterior and posterior dilator muscles; *m.c.l.r.* labral compressor muscle; *m.cp.* compressor muscle of sucking pump; *m.el.g.* elevator muscles of galea; *m.ret.g.* retractor muscle of galea; *m.t.c.* transverse sphincter of cibarium; *n.g.* galea nerve; *n.lb.* labial nerve; *n.sp.* sucking pump nerve; *s.d.* salivary duct; *tt.* tentorium.

of the anterior part of the tentorial arm and its insertion lies on the posterior part of the stipital apodeme.

(iii) The posterior tentorial muscle, *pr.add.st.m.*, has its origin on the inner face of the posterior part of the tentorial arm and its insertion on the anterior half of the stipital apodeme. It thus crosses the last-mentioned muscle in its path.

It is these muscles which, by pulling on the stipital apodeme, close the aperture between the stipital and head cavities (figure 20).

#### *The galea muscles*

(a) Retractor muscles (figures 24, 25, 26, *m.ret.g.*). These have their origin on the anterior tentorial arm and their insertions on the galea cuticle at the junction between the stipes and galea. They draw the base of the proboscis backwards and bring the food canal more fully into the cibarial region (figure 4).

(b) Elevator muscles (figures 8, 24, 25, and 26). These raise the basal region of the proboscis as a preliminary to feeding. They are arranged in two groups, proximals and distals. The proximal elevators have their origin in the rigid cuticle of the galea base (figure 8), passing upwards to their insertion on the dorsal apodeme. The more ventral fibres run parallel to the proboscis; those more dorsally placed diverge to the side before reaching their insertions (figure 26).

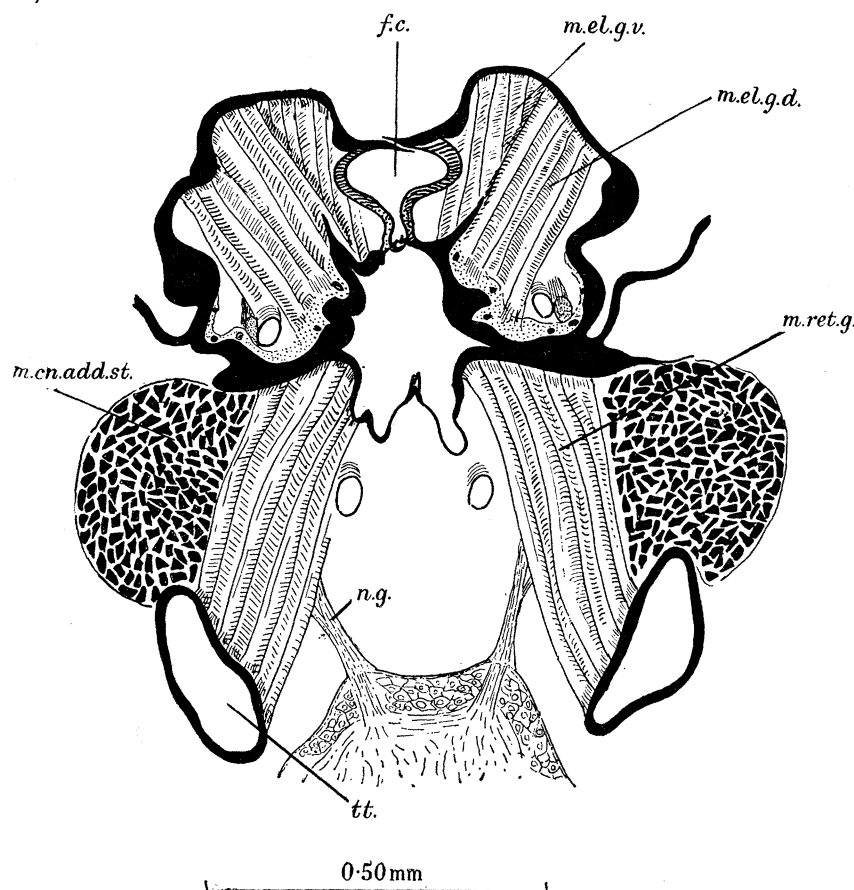
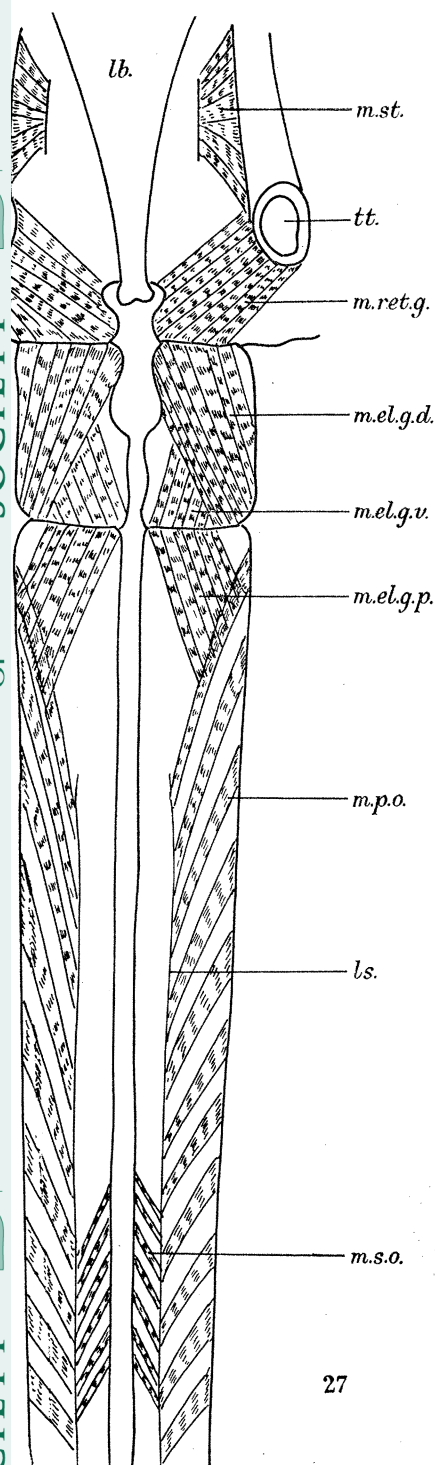
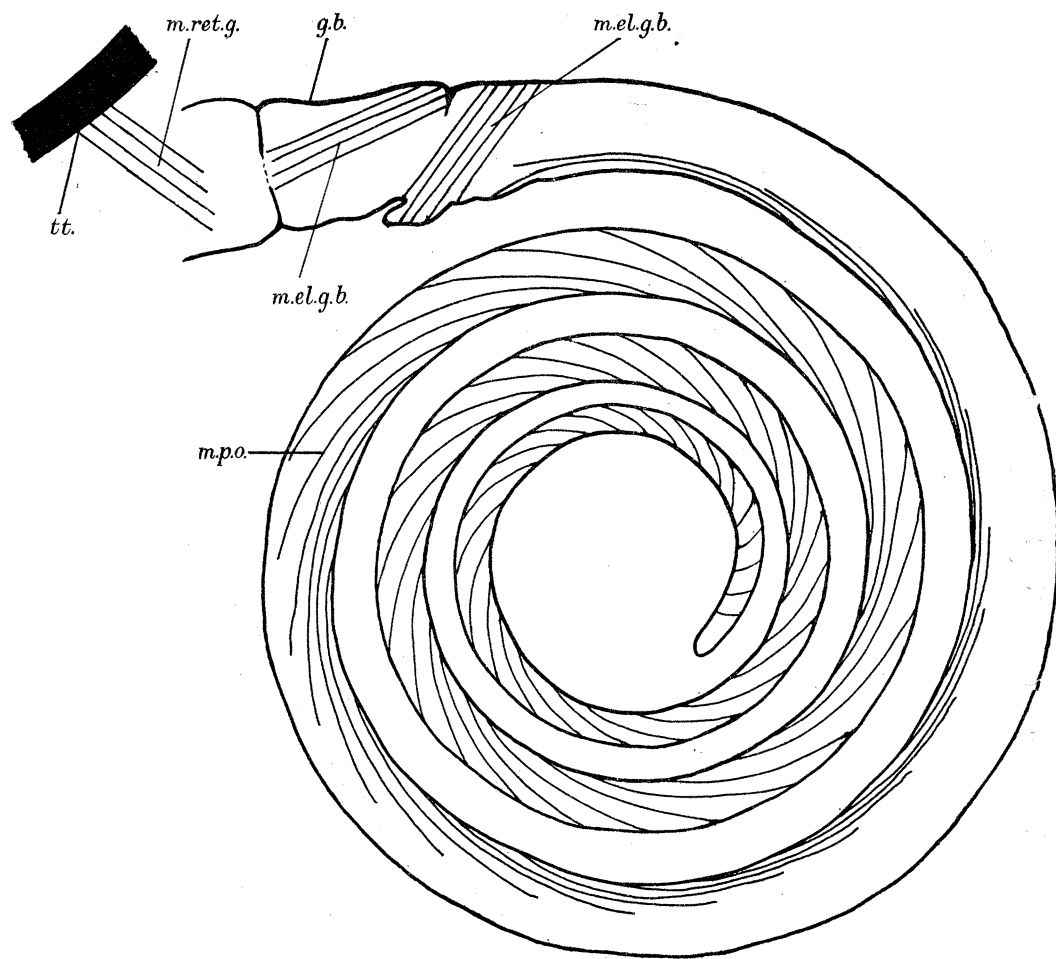


FIGURE 26. Horizontal section through the anterior head region. *f.c.* food canal; *m.cn.add.st.* cranio-stipital adductor muscle; *m.el.g.d.* and *m.el.g.v.* dorsal and ventral elevator muscles of galea base; *m.ret.g.* retractor muscle of galea; *n.g.* galea nerve; *tt.* tentorium.





27



28

FIGURE 27. Diagram of proboscis musculature (fore-shortened) as seen from above.

FIGURE 28. Diagram of proboscis musculature as seen from the side. *g.b.* galea base; *lb.* labium; *l.s.* longitudinal septum; *m.el.g.b.* elevator muscles of the galea base; *m.el.g.d.* and *m.el.g.v.* dorsal and ventral elevator muscles; *m.el.g.p.* proximal elevators of proboscis; *m.p.o.* primary oblique muscles; *m.ret.g.* retractor muscles; *m.s.o.* secondary oblique muscles; *m.st.* stipital muscle; *tt.* tentorium.



The distal elevators (figure 8) originate on the dorsal apodeme as well as on the dorsal surface of the proboscis distal to this. They pass in a proximal direction and downwards on to the flexible ventral wall of the galea base. Reference to figure 8 makes clear their action in working on the flexible wall of the galea base so as to raise its distal apodemal region.

*The proximal elevator muscles of the proboscis (figure 27, m.el.g.p.)*

The basal elevator muscles just mentioned give place to the primary oblique muscles next to be described. There is, however, in the proximal region of the coilable proboscis just distal to the galea base, a set of ventral oblique muscles which appear as an extension of the basal elevators. They have their origins on the distal part of the floor of the galea base and diverge outwards and distally towards their insertions on the outer parts of the floor of the latero-ventral chamber of the galea haemocoel. From their disposition they should serve to elevate this region of the proboscis and account for those small movements made by the proboscis when it is beginning to be elevated and also when it is being coiled up to the position of rest. We will call them the proximal elevator muscles of the galea (figures 8A, 27).

*The primary oblique muscles of the galea (figures 27, 28, 29, 30 and 31)*

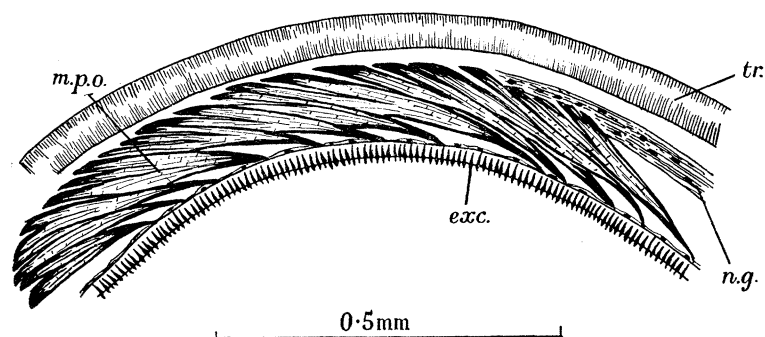
These muscles occupy the lateral haemocoel of the proboscis throughout its coilable length. In the more proximal region they overlap the distal elevator muscles already mentioned (figures 27, 28). In all regions their origins are proximal and lateral to their insertions which are distal and medio-ventral.

Typically, as, for instance, about the middle of the length of the proboscis, each muscle has its origin in a broad base attached to the outer wall of the galea about half-way up its side. From this origin the muscle tapers to a single point insertion on the ventral wall of the lateral chamber of the galea close to the inner septum bounding the lateral chamber (figure 29). As seen in side view each muscle is wedge-shaped. Its broad origin occupies a length of the proboscis wall equal to that taken up by about six annulations of the cuticle. Its distally and ventrally placed insertion is attached to a single exocuticular annulation.

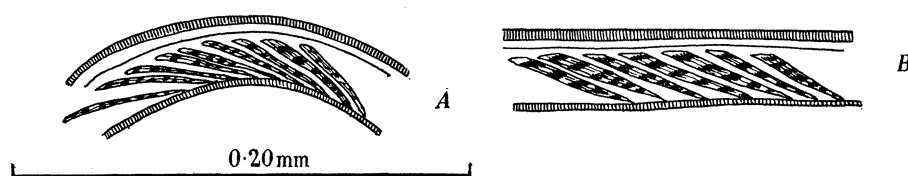
It follows from this that the muscle is oblique in both longitudinal and transverse senses: (a) in passing from a higher point of origin to a lower insertion distal to that origin and (b) in passing from the outer to the ventral wall and so transversely across the proboscis. Each muscle at its broad origin is incised, so giving divided points of origin separated by what appear to be small tendinous strands (figure 29). In the coiled state these muscles are relaxed and each in its course conforms to the curvature of the proboscis. In the extended condition of the proboscis the muscles are contracted and straight (figure 30).

Proximally these oblique muscles are longer and run a more longitudinal course than in the more distal regions (figure 28). Thus it is found that as we pass distally along the proboscis, the origins become successively placed more laterally and higher up the side. With this change in position of origin, they become progressively shorter and stouter and more transverse in their direction the nearer the tip of the proboscis is approached. At the extreme end of the proboscis where there are no longitudinal septa the oblique muscles are almost directly transverse passing in the dorso-ventral direction. As seen in vertical

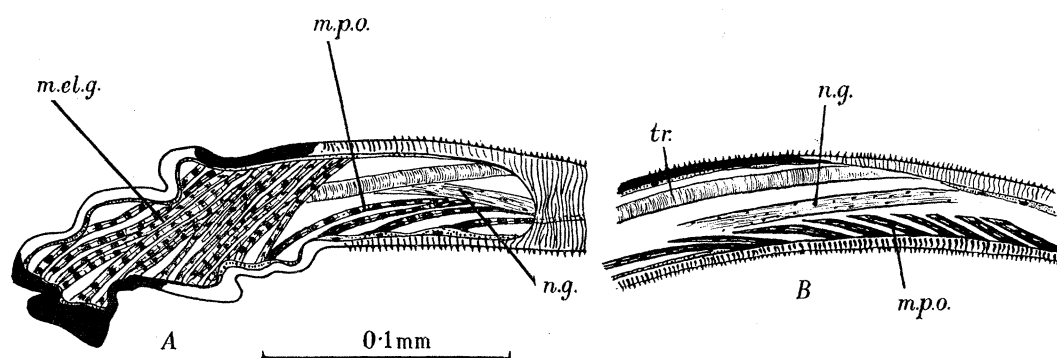
longitudinal sections, there is little or no space between any of these muscles. Reference to figures 7, 29, 31, 32 and 33 indicates the wealth of this musculature, a wealth which is difficult to reconcile with the view expressed in certain quarters that it is these muscles that effect the coiling of the proboscis, a process which we will show is brought about by its elastic properties. The muscles serve to draw dorsal and ventral galea walls towards each other.



29



30



31

FIGURE 29. Vertical longitudinal section through oblique muscles in outer coil of proboscis.

FIGURE 30. Vertical longitudinal sections through similar parts of the proboscis in *A*, coiled state and *B*, extended state.

FIGURE 31. Vertical longitudinal sections, *A*, through proximal region, and *B*, through a slightly more distal region of the proboscis. *exc.* exocuticular spines in ventral wall; *m.el.g.* elevator muscles; *m.p.o.* primary oblique muscles; *n.g.* galea nerve; *tr.* trachea.

#### *The secondary oblique muscles*

When the butterfly extends its proboscis, at a point about one-third of its length from its base, there is always maintained an angle varying from about 70 to 120° (figure 5). This angle we have called the 'knee bend'. It is here, and only here, that there occurs a secondary

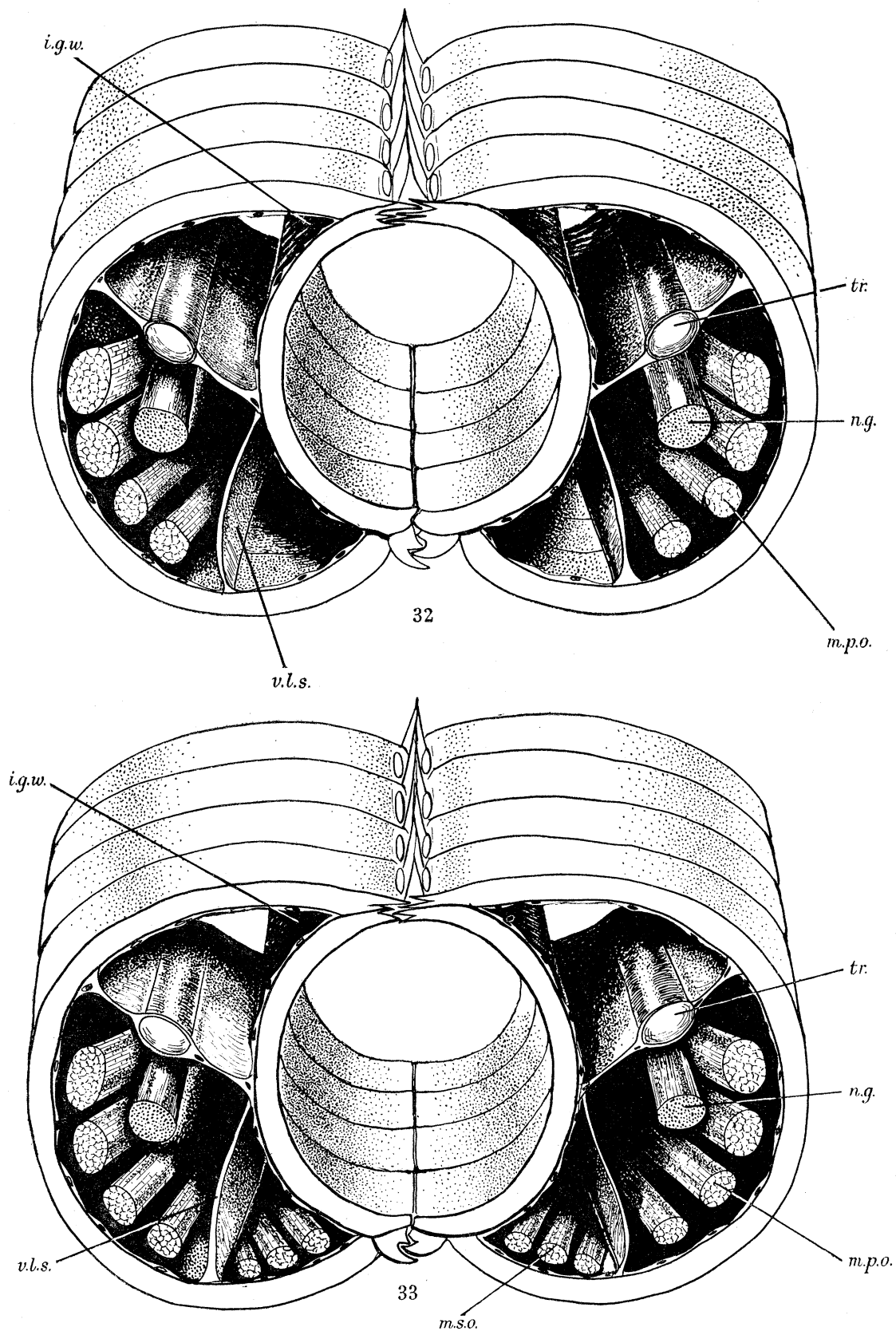


FIGURE 32. Thick section of proboscis, taken distal to the 'knee bend' (figure 5), and viewed from the proximal end.

FIGURE 33. Thick section of proboscis, in the region of 'knee bend' (figure 5), and viewed from the proximal end (diagrammatic). *i.g.w.* inner wall of galea; *m.p.o.* primary oblique muscles; *m.s.o.* secondary oblique muscles; *n.g.* galea nerve; *tr.* trachea; *v.l.s.* ventral longitudinal septum (diagrammatic).



set of oblique muscles (figure 33). These exist along with the primary muscles and occupy the median ventral chamber of the galea. As seen in coronal sections they converge towards the insertions of the primary muscles and thus form with these a series of overlapping V's, the apices of which point distally along the proboscis (figure 34). Each muscle takes its origin on the ventral wall of the galea just lateral to the place of ventral linkage at the junction between outer and inner walls of the galea. Each passes distally and laterally to its narrow tendinous insertion on the ventral wall of the galea close to the septum separating the median ventral and lateral compartments. In view of the place of origin as described, it follows that the secondary muscles lie in the horizontal plane. The significance of this will be noted when the mechanism is under discussion.

There are nine or ten such muscles, and the angle they make with the longitudinal axis of the proboscis is the same as that made by the primary oblique muscles in the same region, viz. about 30°.

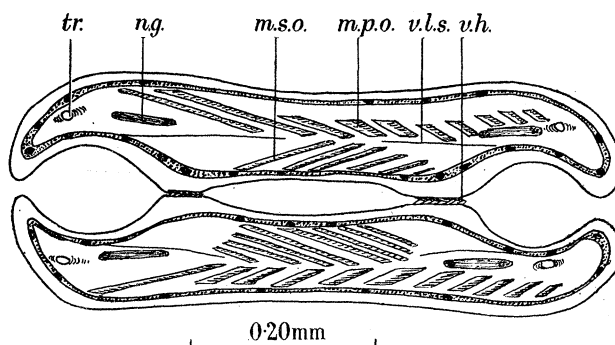


FIGURE 34. Coronal section of proboscis at the 'knee bend'. *m.p.o.* primary oblique muscles; *m.s.o.* secondary oblique muscles; *n.g.* galea nerve; *tr.* trachea; *v.h.* ventral linkage hooks; *v.l.s.* ventral longitudinal septum.

The secondary muscles are more slender than are the primaries in their region; they occupy the same length of the proboscis as do six primaries. Figure 33 shows in stereogram the arrangement of both primary and secondary oblique muscles.

#### THE NERVOUS SYSTEM IN RELATION TO THE FEEDING MECHANISM

As might be expected, the withdrawal of the mandible from active use and its incorporation as an immovable structure into the wall of the head capsule has resulted in the disappearance of the mandibular nerve. The maxillary nerve, on the other hand, is large. It emerges ventrally at each side from the anterior surface of the suboesophageal ganglion (figures 25, 26). It passes directly forwards giving off branches to the retractor muscles of the proboscis base as well as to the stipital muscles. Its main branch, however, passes into the basal joints of the proboscis and so to the galea haemocoel in which it continues to the proboscis tip (figures 6, 32 and 33), supplying in its course the intrinsic muscles of the proboscis. The labial nerve also emerges ventrally from the suboesophageal ganglion and passes backwards to the labial palps.

From points at each side on the anterior face of the suboesophageal ganglion above the origin of the maxillary nerve at each side, there arise two nerves one above the other

(figure 25). The ventral, and larger, of these two passes above the maxillary nerve and embracing the lateral wall of the sucking pump, innervates the muscles of this organ. The more dorsal nerve passes directly over the postero-dorsal wall of the sucking pump to innervate the muscles there.

#### THE SENSILLA OF THE PROBOSCIS

In addition to the many spines which occur on the surface of the proboscis (figure 10), there is also a sparse distribution of trichoid sensilla. In the wall of the food canal there are also two pairs of modified trichoid sensilla, one pair near the base of the proboscis, the other at about half-way along its length. Similar sensilla were reported by Kirbach (1884).

Each of the sensilla (figure 35) is found at the junction of the two longitudinal septa with the inner wall of the proboscis. The inner cuticular wall is perforated by a cylindrical extension of the neighbouring hypodermis to form a sheath to a central extension of the sense cell. The termination of this latter coincides with the outer end of the extruded

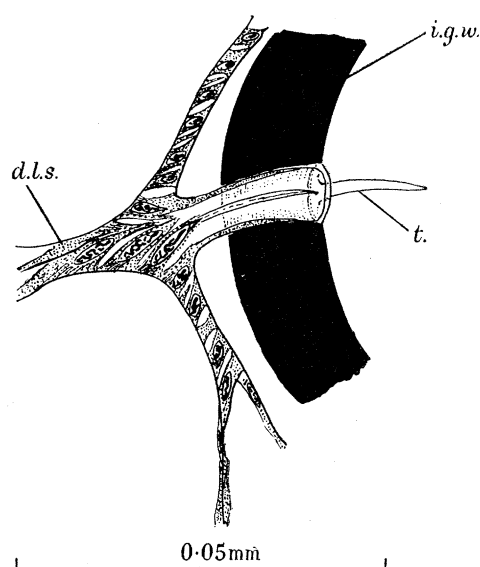


FIGURE 35. Longitudinal section through trichoid sensillum penetrating the inner wall of the food canal.

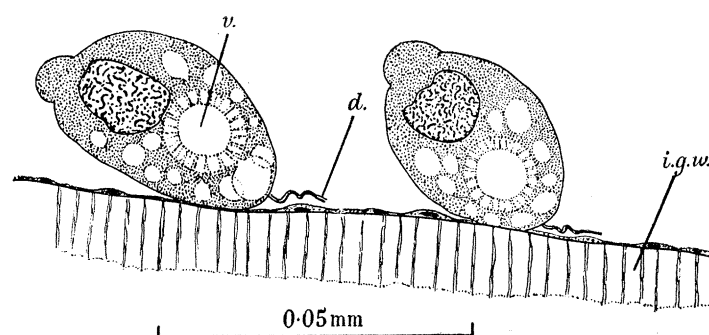


FIGURE 36. Horizontal longitudinal section of proboscis with two gland cells. *d.* duct; *d.l.s.* dorsal longitudinal septum; *i.g.w.* inner galea wall; *t.* trichium; *v.* vacuole.

cylinder of hypodermal protoplasm over which is a thin cap or sheet. From this latter there extends towards and into the food canal the trichium. This whole organ is regarded as a trichoid sensillum only modified by the thickness of the cuticular wall with which it is associated. What the function of these sensilla may be is not clear. They do not appear to be concerned with proboscis movement.

#### THE GLAND CELLS IN THE PROBOSCIS

Situated in the antero-dorsal angle of the haemocoel of each galea is a series of large unicellular glands (figure 6). Each cell is roughly pear-shaped with the narrow part directed distally towards the junction between the inner and outer walls of the galea in the



dorsal region. These cells are uninucleate, the large granular nucleus occupying the swollen part of the cell. The narrow extension of the cell ends in a fine duct which passes through the cuticular wall of the proboscis to open between the overlapping plates by which the two galeae join each other dorsally. Between the nucleus and the emerging duct is a large spherical vacuole whose perimeter is bounded by a protoplasmic fringe perforated by numerous radiating canals (figures 6, 36). In the surrounding protoplasm of the cell are numerous smaller spherical vacuoles which feed the large central one just mentioned. The larger subsidiary or feeding vacuoles can in convenient instances be seen to be connected with the central vacuole each by a fine canal. That a connexion exists between the central vacuole and the duct seems reasonably certain.

Since the ducts open into the dorsal union of the two galeae we suggest that their secretion is used to seal up the gaps between these plates so forming thereby a complete tube up which the fluid can be drawn by the sucking action of the pharyngeal pump. They may also serve to lubricate the plates as they slide over each other during proboscis extension. They lie in a position where they will be subjected to pressure when the proboscis is extended. Any pressure brought to bear on them must cause the contained vacuole of each cell to pour its contents out through its duct and so presumably come into action to seal the duct at the time of feeding. It seems possible even that physical pressure on the cells may be effected not only by way of the haemolymph but by the inner and upper dorsal walls of the galea surrounding the cells being brought together (figure 13). The distribution of these cells along the proboscis is in not quite regular pairs. Altogether there are about one hundred and fifty pairs of them in a proboscis. We have found no reference to the occurrence of gland cells similar to these in any member of the Lepidoptera.

#### THE SUCKING PUMP (figures 37 and 38)

The sucking pump is treated as a separate unit since its mechanism is quite distinct from that of the extension and coiling of the proboscis. It is a complex structure, opening in front by a narrow aperture where it receives the food channel from between the galeae and by a similar small opening into the oesophagus behind. It consists of a strongly cuticularized floor and a flexible roof, and into its floor is fused the hypopharynx, no longer distinguishable as a separate region. This being so, the sucking pump is both cibarial and buccopharyngeal.

The floor of the pump consists of a subquadrangular sclerite whose front border is strengthened to form a strong ridge. Each lateral end of this ridge is firmly fused to the gena just above the mandible at its own side. From each such region of fusion a hypopharyngeal ridge runs backwards in the sclerotized pharyngeal floor and towards the middle line. There they merge into the floor of the pump at the sides of a median trough-like depression (figure 38). The opening of the salivary duct lies beneath the anterior ridge.

The floor of the salivary duct at its opening is sclerotized, its roof flexible and membranous. On its roof in the middle line are inserted a pair of salivary dilator muscles whose origins lie on the hypopharyngeal ridge at each side (figure 38). The contraction of these muscles brings about the opening of the salivary duct.

In contrast with its cuticular floor, the roof of the sucking pump is membranous and

flexible. Into its upper wall is incorporated a complex musculature by the contraction of which the sucking pump is brought into operation. The sclerotized floor of the pump being fixed, movements of its membranous roof make possible those changes in volume necessary for the intake of the copious fluids on which the butterfly feeds.

That this first part of the alimentary tract in the adult is of greater capacity than it is in the larva is due to the fusion of the hypopharynx (cibarial part) with the buccopharyngeal region behind it.

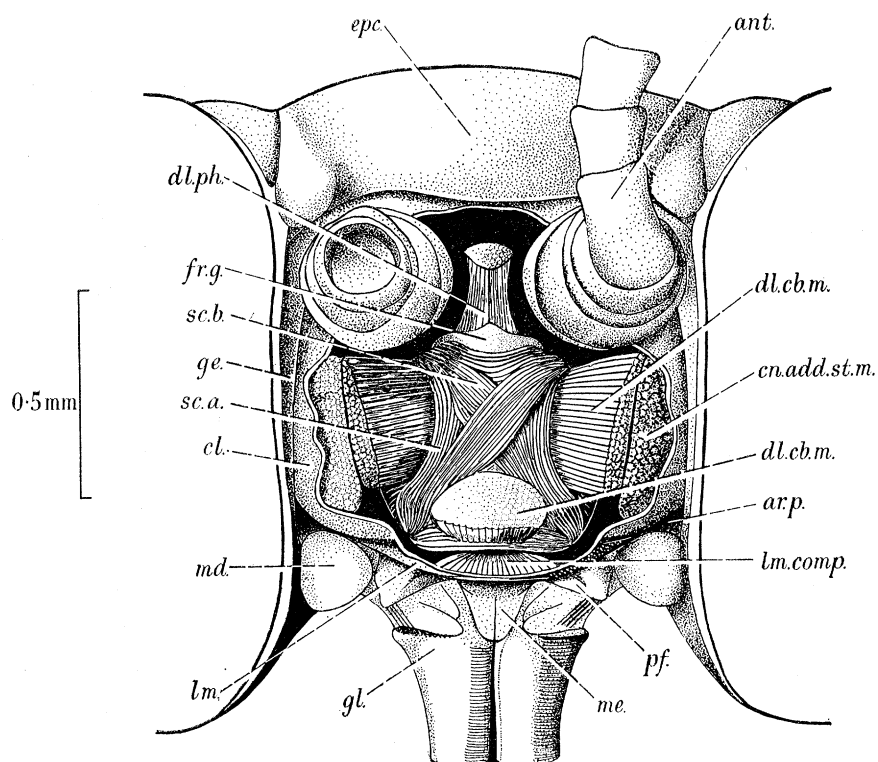


FIGURE 37. Dissection of the musculature of the sucking pump. *ant.* antenna; *ar.p.* anterior tentorial pit; *cl.* clypeus; *cn.add.st.m.* cranio-stipital adductor; *dl.cb.m.* dilatator muscles of cibarium; *dl.ph.* pharyngeal dilator; *epc.* epicranium; *fr.g.* frontal ganglion; *ge.* gena; *gl.* galea; *lm.* labrum; *lm.comp.* labral compressor; *md.* mandible; *me.* median labral extension; *pf.* pilifer; *sc.a.* lateral compressors; *sc.b.* cruciform compressors.

The muscles of the pump, though complex, can be considered under three headings: (a) the muscles controlling the entrance and exit of fluid; (b) the compressors; (c) the dilators.

(a) The labral compressor muscles open the passage under the labrum from the proboscis to the cibarium. These, passing from the outer to the inner wall of the labrum, by their contraction enlarge the entrance passage to the pump (figures 24, 25). Immediately posterior to these muscles, both above and below the cibarial space, there are transverse muscles (*m.t.c.*) (figures 24, 25) inserted on the cibarial wall. The contraction of these muscles closes the entrance from the proboscis to the sucking pump as does a sphincter. Posterior to the frontal ganglion (figure 25), a band of muscle fibres passes from the posterior part of the hypopharyngeal ridge of one side, up the side of the pump and transversely

over its dorsal surface and so down to the hypopharyngeal ridge of the other side. This serves as a posterior sphincter capable of closing the oesophageal exit.

(b) The compressor muscles of the pump are arranged in three layers. A first layer has its fibres running longitudinally over the whole of the dorsal wall between the anterior and the posterior sphincters. Dorsal to these are to be found two further more laterally placed bands of longitudinal muscles with similar origins and insertions (figure 37, *sc.a.*).

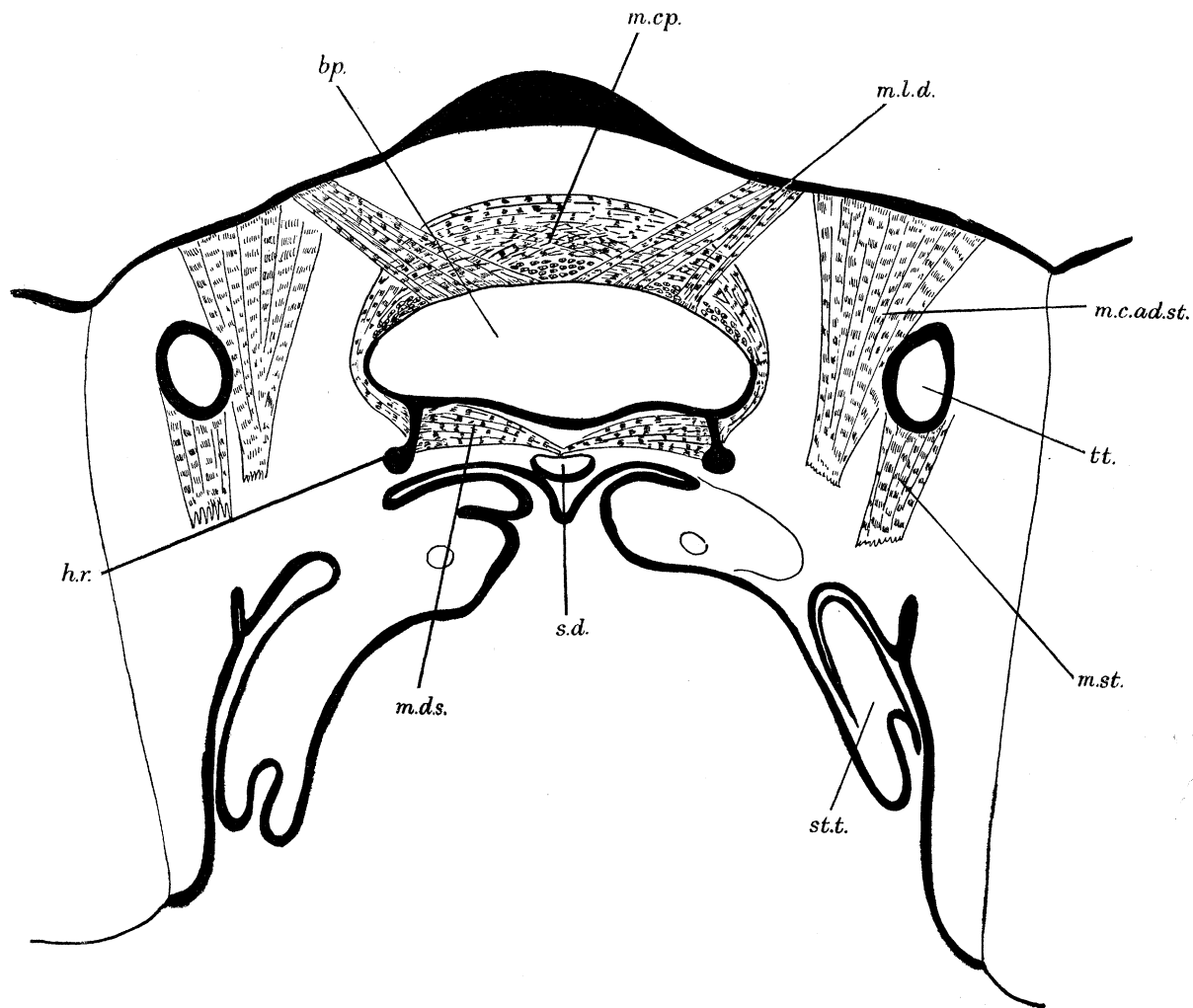


FIGURE 38. Transverse section through sucking pump. *bp.* bucco-pharynx; *h.r.* hypopharyngeal ridge; *m.c.ad.st.* cranio-stipital adductor muscles; *m.cp.* compressor muscles; *m.d.s.* dilator muscle of salivary duct; *m.l.d.* lateral dilator muscle; *m.st.* stipital muscle; *s.d.* salivary duct; *st.t.* tubular stipes; *tt.* tentorium.

Two other prominent muscle bands run diagonally from each front corner of the pump to the posterior angle of the opposite side, the muscle bands of one side passing over those of the other (figure 37) to form a cruciform system. These also have their origins and insertions on the hypopharyngeal ridge and the anterior transverse ridge of the pump floor respectively.

The frontal ganglion (figure 25)—an important landmark in this region—lies dorsal to the pump in its posterior region. In front of it a few transverse muscle fibres pass dorsally

over the sucking pump—being attached to the hypopharyngeal region beneath at either side. Behind it, on the other hand, are the transverse muscles of the posterior sphincter muscle.

(c) The dilator muscles (figures 25, 37 and 38) consist essentially of three pairs of muscles, two of which, the anterior cibarial and the posterior pharyngeal dilators, have lost their paired nature (figure 37). The anterior cibarial dilator takes its origin on the inner clypeal wall (figure 25), with its insertion on the dorsal wall of the pump in the angle between the two anterior arms of the cruciform muscle. The lateral cibarial dilator muscles form a pair whose origins are on the lateral parts of the clypeus with insertions on the roof of the pump beneath the lateral longitudinal muscles (figure 38). The pharyngeal dilator (figures 25, 37) is a single muscle with its origin in the middle of the clypeus. It passes to its insertion on the postero-dorsal surface of the sucking pump posterior to the frontal ganglion.

The effect of the contraction of the several muscles during the intake of food and its subsequent passage into the alimentary canal is clear from their insertions and origins. For the intake of fluid from the proboscis the anterior sphincter muscles must be relaxed and the posterior sphincter contracted, thus opening the sucking pump in front and closing it behind. The three dilators contracting in turn from before backwards then raise the roof of the pump and, in enlarging its cavity, suck into it the fluid from the proboscis.

If, now, the anterior sphincter muscles contract and the posterior ones relax, the cavity of the sucking pump becomes closed in front and open behind.

Contraction of the complex transverse longitudinal and cruciform compressor muscles coupled with relaxation of the dilators must now diminish the cavity of the sucking pump, so forcing the contained fluid backwards into the oesophagus.

#### THE MECHANISM OF THE PROBOSCIS

On the basis of the structures described we may now examine the questions posed by the several opinions reviewed in the introduction.

##### *Observations and experiments to test theories on the proboscis mechanism*

(a) In view of the theory that blood forced from the head into the proboscis causes proboscis extension, observations were made on butterflies, the proboscides of which had been cut across. After such treatment the basal region could be elevated as a preliminary to feeding, but full extension of the proboscis seemed impossible. A considerable degree of muscular twitching, as evinced by raising and lowering the stipes, took place, and with these movements haemolymph was seen to pulse out of the cut ends of the galeae. It would appear from this that, whether or not blood is pumped into the proboscis to cause its extension, a closed haemocoel of the proboscis is a prerequisite for full extension. The power to elevate the base of the proboscis is not, however, impaired by the above treatment. Elevation of the basal region, therefore, may fairly be attributable to muscle action alone.

It has been shown that the proboscis haemocoel is in communication with that of the head by way of the internal slit-like opening of the stipes. It is through this that Schmitt (1938) thought that the haemolymph was forced from the head to the proboscis to cause



its extension. Should it be normally possible for this to happen, perforation of the head cavity should equally prevent its occurrence. With this in view, the ventral wall of the head capsule was perforated in the region of the labial plate without injury to the suboesophageal nerve mass. This operation appeared in no way to impair the capacity of the butterfly to extend the proboscis. Since such a perforation would render ineffective any mechanism for forcing fluid from the head into the proboscis there would seem, in the absence of any visible mechanism for the movement of blood fluid to the proboscis, no reason for regarding the opening between the head cavity and the stipes as serving the purpose suggested by Schmitt (1938).

To put the latter's theory to a further test a fine cannula was inserted into the head cavity of a butterfly, and by means of gentle pressure from a rubber bulb, fluid was forced

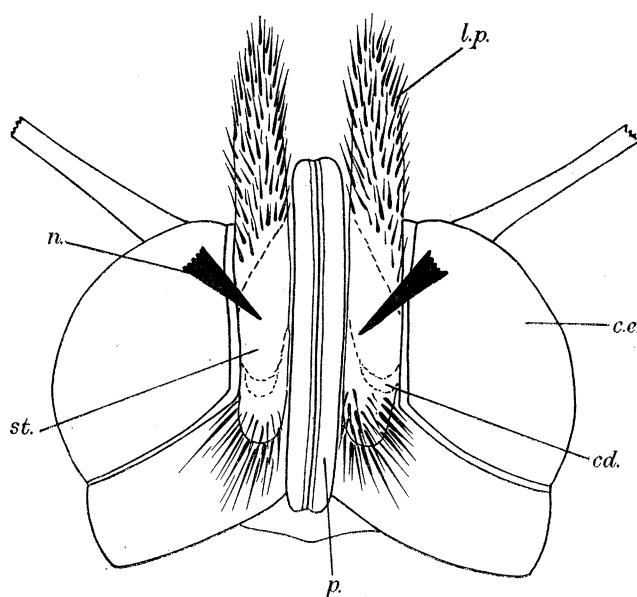


FIGURE 39. Diagram of ventral surface of head to show positions of perforations into the stipital tube. *cd.* cardo; *c.e.* compound eye; *l.p.* labial palp; *p.* proboscis; *n.* needle; *st.* stipital tube.

into the head. No extension of the proboscis occurred but the introduced fluid, taking the path of least resistance, was forced into the thorax, causing the wings to be depressed as a result of the arching of the thoracic terga.

By inserting the cannula into the stipital cavity, however, it was possible to inflate the proboscis, showing that the stipital valve served to prevent back-flow of blood from the proboscis haemocoel to the head. It is assumed, therefore, that the stipital aperture is so constructed as to form a closed haemocoel in the proboscis rather than to serve as a passage for fluid under pressure from the head.

We may then tentatively assume that in some way a closed proboscis haemocoel is necessary for extension.

To test this on further specimens each stipital tube was perforated after anaesthesia (figure 39). After recovery, even though the butterflies had been without food for 24 h, only partial extension of the proboscis, similar to that shown in figure 5*B* (i), occurred. That the proboscis did not uncoil fully under these circumstances is no proof that it could

not do so. But when on similarly operated specimens the perforations were closed by smearing them with celloidin, the proboscis did in fact become fully extended. The inference that perforation of the stipes had made full extension of the proboscis impossible seems good.

The point was put to a further test as follows: By inserting a fine glass needle between the two galeae at their bases the proboscis was divided into its two component halves without injury—the butterfly having been kept without food for about 20 h. The stipital tube of the right side was then perforated. After recovery from the ether the butterfly extended the galea of the left (unoperated) side as in feeding, while that of the right (operated) side remained coiled, and except for slight lifting movements at the base, was motionless.

The closing of the wound by celloidin in the right stipes returned to the galea of this side its original power of extension, and the two galeae could then be extended as in feeding except that they remained separate from each other and tended to diverge in so doing. A similar experiment was carried out, perforating the left stipes and leaving the right untouched, with corresponding results.

There is confirmation, therefore, of the view that for full extension of the proboscis a prerequisite is the formation of a closed haemocoel in both galeae—which is effected by the muscle-controlled valve of the stipital aperture.

The purpose served by this feature will be better understood when further treatment is accorded to the musculature.

(*b*) Having by these experiments rejected the 'inflation' theory, it is necessary to see whether the intrinsic muscles coil or uncoil the proboscis. That they are not concerned in coiling would appear to be proved by the ability of the proboscis to coil by its own elasticity. Histological study has shown the existence of a dorsal continuous cuticular bar in each galea into which the inner and outer walls of the galea are fused. That this is the responsible agent in elastic coiling was proved by removing from the living butterfly the two galeae in turn. Each galea was then divided into two halves, dorsal and ventral, by stripping each half from the other along the line of the food canal. When this was done the dorsal half containing the dorsal bar immediately coiled into a tight spiral, the ventral half, devoid of elasticity, having remained loosely outstretched.

We cannot therefore doubt the thesis that the proboscis is brought to rest in the coiled state by its own elastic properties, and that these rest in the dorsal longitudinal bar. The views of Lameere (1938) and Bourgogne (1951) that elasticity causes extension are therefore rejected.

(*c*) Is there any proof that the intrinsic muscles bring about uncoiling or extension? It was felt that should destruction of the nerve supply prevent uncoiling a reasonable solution to the problem would have been found. By dissection of the head and by serial sections, the precise course of the galea nerve was determined. This course is shown in figures 25 and 26. By inserting a fine scalpel through the ventral flexible membrane of the head between the labium and the stipes (figure 1, *m*), it is possible to sever the nerve of either side between its exit from the suboesophageal nerve mass and its entrance into the galea (figure 26). In one specimen after anaesthesia, the two galeae were separated from each other. The scalpel was inserted so as to cut the galea nerve of the animal's right side, leaving the left side intact. On recovery the two galeae remained separated from each other and

the one on the left (unoperated) side became extended with a slight turning to the left side, while on the right (operated) side the galea remained loosely coiled.

A corresponding treatment of another butterfly was given, leaving the right side untouched and the left side with its galea nerve cut. In this instance, after recovery, the right galea extended as in feeding, though with a little turning to the right side, the left galea remaining loosely coiled, as in figure 5*B* (i).

To prove in these cases that the nerve in question had in fact been cut, the head of each specimen was fixed and sectioned. Examinations of these sections showed in the first case an intact nerve on the left, and a cut nerve on the right side. In the second case the reverse state of affairs was found. In short, our experiments lead us to the view that extension is caused by intrinsic muscles stimulated by the galea nerve, but only under conditions in which the haemocoel of each galea forms a closed system, i.e. a fluid-filled tube in which the muscles pulling on the galea walls can act. The views of Kirbach (1884), Hering (1926), Weber (1933) and Pradhan & Aren (1941) are therefore unsatisfactory in that they claim that muscles irrespective of blood pressure cause extension. Our experiments also lead us to conclude that the theory of blood inflation of the galea is without foundation.

#### *Analysis and conclusions*

We may now consider how the oblique muscles bring about the changed form of the proboscis as seen in transverse section from the coiled to the extended state and then proceed to the further point as to why such a change is associated with extension.

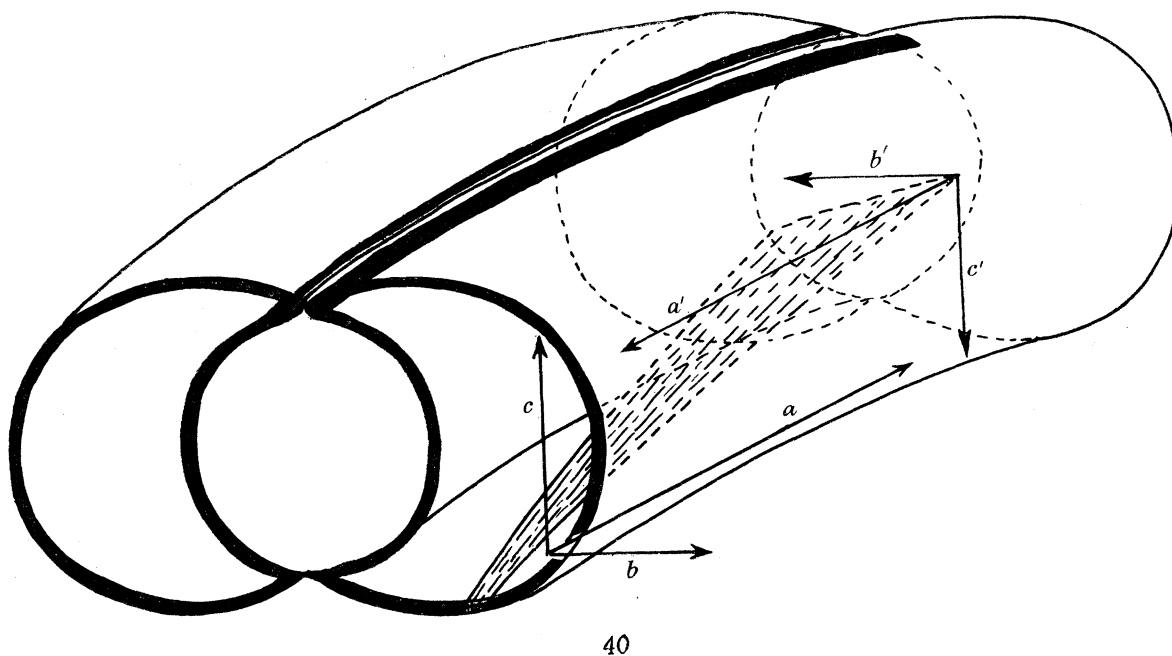
Let us simplify the matter by considering the effect of a contraction of a single diagonal (oblique) muscle at about the middle of the length of the proboscis. Its origin is half-way up the inner surface of the outer wall of the galea, i.e. in an 'equatorial' position as seen in transverse section. The insertion distal to its origin is mid-ventral and lies close to the junction of the ventral septum with the galea wall. The length of the muscle when contracted is such that it lies at an angle of about 35° with the ventral wall of the galea.

That the muscle is contracted when the proboscis is extended, and not when it is coiled, is shown clearly in figure 30. The effect of this contraction is to pull dorsal and ventral surfaces of the galea closer together, and in so doing to change the transverse sectional configuration of the proboscis.

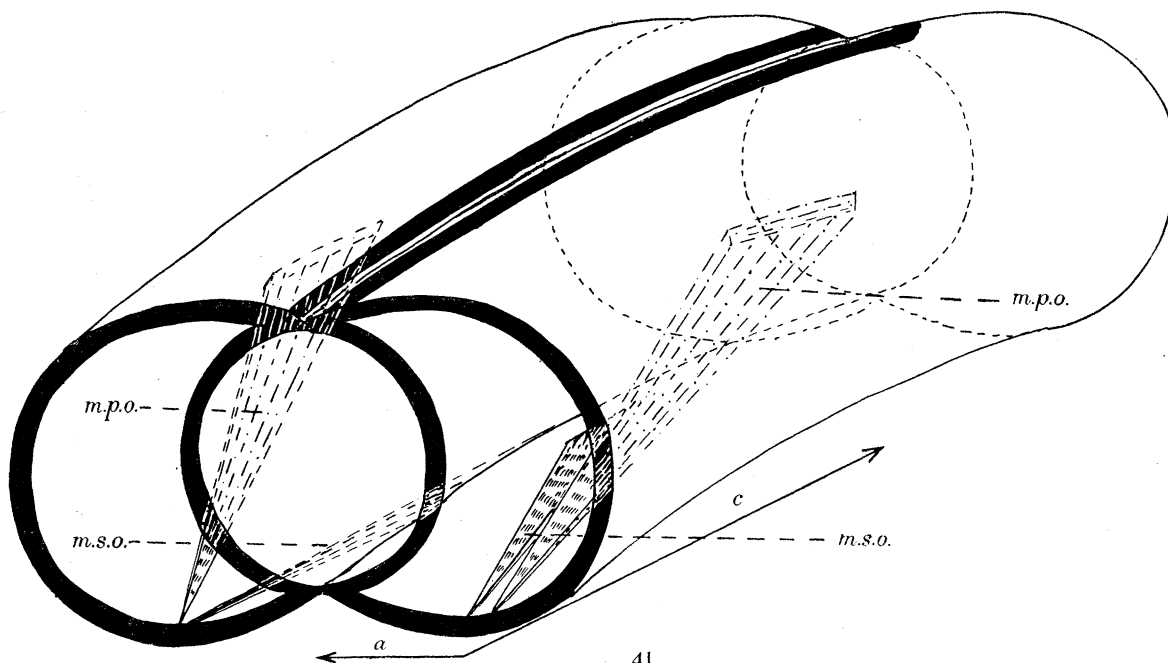
When the proboscis is coiled the ventral groove between the two galeae is flanked by the well-rounded contours of the galeae (figure 6). From this ventral region each galea wall passes in a nearly circular curve to the dorsal surface. Here the whole dorsal surface formed by the union of the two galeae is flat (figure 6). When extended, however, the ventral groove between the two galeae is shallower and wider (figure 7), and the dorsal surface of each galea is depressed in relation to the dorsal linkage line so as to leave this latter as a ridge raised above the level of the galea surface to each side of it. This change has been brought about by the pulling together of the dorsal and ventral walls of the galeae, and in process of that change the outer wall of each galea has been thrust outwards beyond the confines of its original nearly circular curvature (figure 7).

The thesis offered is that the change of form here described is itself responsible for extension. In explanation of the effect of the oblique muscles we can analyse the force

exerted by a single contracting muscle at its insertion into its three components: (*a*) horizontal longitudinal, (*b*) horizontal transverse and (*c*) vertical transverse (figure 40). The relative effects of these components are partly determined by the angle at which the



40



41

FIGURE 40. Diagram of a section of the coiled proboscis to show components of force exerted by a primary oblique muscle (left side).

FIGURE 41. Diagram of a section of the coiled proboscis with both primary and secondary muscles and showing components of force of the latter. For explanation see text. *m.p.o.* and *m.s.o.* primary and secondary oblique muscles respectively.



muscle lies in the proboscis haemocoel. Thus, other things being equal, the greater the angle with the horizontal the muscle makes, the more important will be the vertical transverse component ( $c$ ). Or, the smaller this angle, the more important will become the horizontal longitudinal component ( $a$ ).

We can readily see, however, that component ( $a$ ) tends to coil the proboscis on the fixed basal point of the head. Component ( $b$ ) pulls across the proboscis against the fixed point of the ventral linkage of the two galeae. Component ( $c$ ) must pull upper and lower walls of the proboscis towards each other. In so doing, it works counter to component ( $a$ ), for its effect, as will be shown later, is to bring about the very change of transverse configuration which is responsible for extension.

If we assume that contraction of the muscle moves the galea wall at both its origin and its insertion, components of force at the origin of the muscle will exist corresponding to those at the insertion just described (figure 40).

These components of force are ( $a'$ ) horizontal longitudinal, ( $b'$ ) horizontal transverse and ( $c'$ ) vertical transverse. Reference to figure 40 shows that component ( $a'$ ) will assist in coiling the proboscis by thrusting along the length of the dorsal elastic bar, already coiled at rest. Component ( $b'$ ) neutralizes component ( $b$ ) at the insertion end of the muscle. Force ( $c'$ ), however, by pulling downwards on the dorso-lateral wall of the galea clearly reinforces the effect of force ( $c$ ) so as to bring upper and lower walls closer together.

The relative effects of these components are also partly determined by the material on which they work, viz. the proboscis wall, the most important features of which are shown in figure 6.

First might be mentioned the ventral linkage which permits of no lateral movement of the linked parts on each other. Secondly, we have the dorsal elastic bar at the junction of the dorsal wall of the galea with its inner wall. Thirdly, there are the exocuticular annulations lying transversely in the galea wall separated from each other by laminated flexible endocuticle. Fourthly, there are the dorsal and ventral flexible endocuticular parts of the galea wall separating the exocuticular annulations from the wall of the food canal. Fifthly, since the flexible dorsal region just mentioned is more extensive than the ventral (figures 6, 7 and 14), there is a greater effect by the oblique muscles in pulling the dorsal outer wall downwards than in pulling the ventral wall upwards. This largely accounts for the dorsal transverse convexity shown in figure 7. Sixthly, we have the exocuticular laminated walls of the food canal, so constructed as to permit little or no lateral movement of the proboscis as a whole, as well as to preserve, at all times, in both coiled and extended conditions of the proboscis, its transverse circular form.

The rigid form of the food canal provides the fulcrum on which component ( $b$ ) can work. The dorsal elastic bar assists component ( $a$ ) in its attempt to maintain the coiled condition, as also does force ( $a'$ ). The exocuticular annulations—more or less circular in the coiled resting condition of the proboscis—resist components ( $c$ ) and ( $c'$ ). The flexible endocuticular regions, both dorsally and ventrally, provide regions along the proboscis length which can accommodate the proboscis to those forces which tend to bend the exocuticular annulations, and to bring dorsal and ventral walls of the proboscis closer together (figures 6, 7). That the proboscis undergoes the changes in transverse configuration in extension is clear from observation. That this change is coupled with contraction of the oblique muscles is

also clear. We therefore conclude that the balance of these conflicting components of force in relation to the peculiar properties of the wall of the proboscis is of such an order that component (*c*) (vertical-transverse), aided by component (*b*) (horizontal transverse), has a stronger effect than the resisting component (*a*) (horizontal longitudinal), with the result that the above-described change of form is brought about (figure 7).

While the account given may be adequate for explaining some aspects of the change in form of the proboscis, as seen in transverse section, by the approximation of dorsal and ventral walls of the proboscis, other factors must be considered which appear to determine more securely the regularity of the change of form.

First may be mentioned the longitudinal septa which pass from one end to the other of the coiled part of the proboscis. These endoskeletal septa, as far as can be determined, are unstretchable and appear to act as firm 'guy ropes' controlling the flexible outer galea

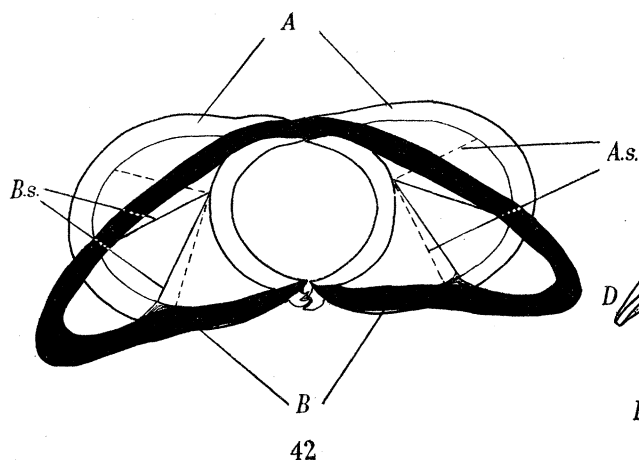


FIGURE 42. Diagram of superimposed transverse sections of the proboscis in, *A* coiled (unshaded) and *B* extended (shaded) conditions. *A.s.* and *B.s.* longitudinal septa.

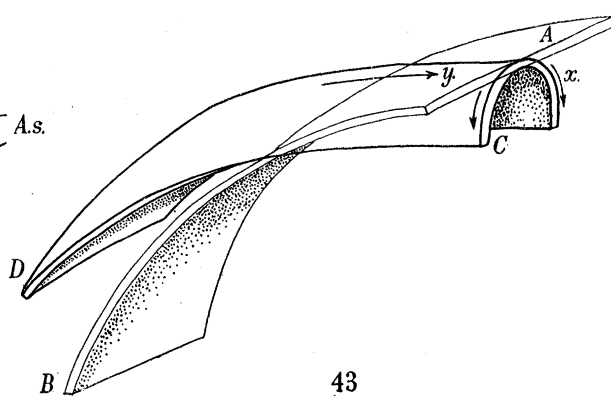


FIGURE 43. Diagram to illustrate the effect of applying a force of lateral compression across a longitudinally curved elastic strip. For explanation see text.

wall in its movements relative to the fixed inner wall. They are capable of radial movement from their common axis of attachment on the inner wall of the galea (figure 6), but are apparently able to maintain a constant transverse dimension under conditions of proboscis coiling or extension. They may be said, therefore, to keep under some control the movements of the galea wall brought about by muscle contraction referred to above (figure 42).

Finally, there is the more difficult problem of the reason for the need for a maintained internal fluid pressure during extension. We may employ here the simple analogy of a closed rubber tube only partly filled with fluid. Lateral pressure applied to the wall of such a tube has little or no effect except on the place where it is applied. Impart greater initial turgidity, to the tube by adding more fluid, however, and pressure applied at any part of its wall becomes effective on other parts of the tube wall distant from the place of pressure application, the effect being transmitted along the tube under these turgid conditions by the contained fluid.

In the case of the proboscis, perforated either by section across it, or by making a hole in the stipital tube, turgidity is lost and contraction of the intrinsic muscles only results in driving fluid out of the tube with little or no uniform effect on the tube wall.

In the intact animal the closure of the galea tube by the muscles working the stipital valve prevents loss of blood from the galea tube when the oblique muscles draw the upper and lower walls of the galea towards each other. The tube thus receives the necessary turgidity, now making effective the contraction of the intrinsic muscles in producing a uniform effect on the galea wall—which effect is the one already described (figure 42).

If muscle contraction causes a change in form of the proboscis as seen in transverse section, giving to it a transverse convexity on the dorsal side, we may now ask the further question: whether this change of form is not itself responsible for the uncoiling? For instance, a coiled steel rule, when coiled in its case, is flat in section, but when it is drawn out it assumes a curved transverse section, convex on one side and concave on the other, and in this state attains the condition of extension. In this case the rule has to be forced into its case, and bending of it can only occur when its transverse curvature is flattened out. The condition of rest is one of extension and force has to be applied to coil it up, the rule having been manufactured with these properties.

We might reverse the situation by procuring an elastic coiled strip, e.g. of xylonite, so made that it assumes the coiled position when at rest (figure 43*A, B*). In this state its transverse section is flat. If now the lateral borders of the strip are pressed down the coil begins to straighten out as in figure 43*C, D*. In exerting pressure on the upper surface of the strip at its sides this upper surface is put into a state of tension from side to side and the under-surface into a state of compression. Having regard to the elastic properties of the material of which the strip is composed the lateral tension  $x$ , imposed on its upper surface increases its lateral dimension, an increase which takes effect at the expense  $y$ , of its longitudinal dimension. The longitudinal axis therefore diminishes sufficiently to convert the coiled or curved state into the straight or extended state (figure 43). Lateral tension brought about by transverse curvature thus results in extension.

Herein lies the explanation of the extension of the butterfly's proboscis. When coiled the proboscis has a flat dorsal surface, and an equatorial line drawn across it transversely divides it into upper and lower halves more or less similar to each other. When extended the proboscis dorsal surface becomes arched as the upper and lower walls of each galea become pulled towards each other. We are inferring that as the muscles bring about this change of form the whole dorsal surface is subjected to a state of tension across it, which, as in the case of the elastic coiled strip in our analogy, results in a shortening of the whole of the dorsal longitudinal axis. This shortening has as its further result the straightening out of the hitherto coiled system. It appears probable that in this straightening, the dorsal longitudinal bars play an important part in responding to the effects of lateral tension here described. The forces described as bringing about these changes of form would seem to put the dorsal linkage under some stress, tending to pull each galea away from its partner in the dorsal line. That this does not take place is undoubtedly due to the firmness of the ventral linkage and the ability of the inner walls of the galeae forming the food tube to maintain themselves in the circular tubular form in both coiled and extended states. We may fairly assume, however, that some slight withdrawal of the overlapping plates of the



dorsal linkage from each other may take place. In so far as it happens at all the food tube would leak along this line during feeding. This is often observed to occur in fact, and it may be assumed that, provided the interruption of the food tube is not too serious, feeding can take place. In any event, in view of the rather loose dorsal association of the two galeae with each other, it might be suggested that the secretion of the galea glands already described will serve: (*a*) to lubricate the dorsal plates as they slide over each other during coiling and extension, and (*b*) to seal up the minute gaps between these plates at the times they tend to be drawn apart. It is interesting to note that from the mechanical point of view the compression of the galea haemocoel by the oblique muscles might well cause the gland cells to pour out their secretions into the dorsal linkage—this occurring just at the moment of extension when their secretions would serve to seal up the gaps in this region.

Since the proboscis tapers to the tip the energy required to bring about the necessary change of form to cause extension must be greater as the tip is approached. This is reflected in the increased strength of the oblique musculature towards the tip of the proboscis, and in its more directly dorso-ventral direction. Figures 6 and 7, when compared, will illustrate both these points, the latter section having been taken more distally than the former. It has been found, in fact, that at the very tip of the proboscis the oblique muscles have become almost directly dorso-ventral and they have such size that they nearly fill the haemocoel in this region.

On occasions during feeding the tip of the proboscis, which normally coils downwards, is seen to coil upwards in the opposite direction. This fact, surprising as it may seem, would appear to be due to the discontinuity of the longitudinal septa at the tip of the proboscis, and the resulting absence of their controlling influence on proboscis movement, and in part due also to the dorso-ventral direction in which the oblique muscles pass in this region.

In our description of the attitudes adopted by the proboscis during feeding, attention was drawn to a persistent point of bending—the ‘knee bend’. We may regard this region as one where the process of extension is resisted.

Careful examination has revealed no significant difference in the cuticular structure of the proboscis in this region neither in thickness nor in quality. There is a significant difference in the musculature, however, to which reference has been made. Additional oblique musculature, which we have called ‘secondary’, lies in the median ventral compartment of the galea here (figures 33, 34).

These secondary muscles, as seen from above, form with their corresponding primaries a series of overlapping V's, the apices of which are formed by their closely applied insertions. The angles these two sets of muscles make with the longitudinal axis of the proboscis are the same. When viewed transversely, however, the secondary muscles lie in the horizontal plane. In other words, the vertical transverse component of force for them is negligible (figure 41). Their horizontal transverse component is directed inwards, i.e. in the opposite direction to the corresponding component of the primary muscles (figure 40), and thus these two components neutralize each other. We are then left with the effective horizontal longitudinal component, the result of whose operation, we have seen, is to resist extension. Hence the horizontal longitudinal force effected by the primary oblique muscles which tends to coil the proboscis is in this region of the ‘knee bend’ reinforced by the



secondaries. We may thus explain the existence here of the 'knee bend' where full extension is resisted.

That a single galea can be fully extended as in our experiments may appear at first to involve a principle different from that invoked when both galeae are joined together. If, however, we compare figure 6 (coiled) with figure 7 (extended) it can be seen that each half of the proboscis is separately endowed with a curvature which is greater dorsally when extended than when coiled. The single galea in its extension seems, therefore, to be employing forces similar to those operating for the proboscis as a whole. In the complete proboscis it was envisaged that the primary oblique muscles must tend to pull the two galeae apart—being prevented from doing so by the strong ventral linkage. When the two galeae are separated from each other we should therefore expect that in their extension

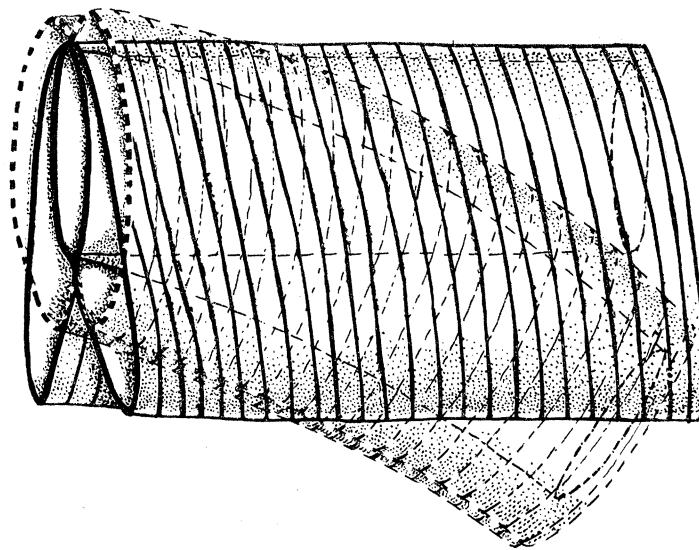


FIGURE 44. Diagram of a short length of proboscis in coiled (broken lines) and extended (complete lines) conditions.

they would diverge from each other. That this is in fact observed gives further support to our thesis. Though we contend that full extension is effected in the manner so described the ability of the oblique muscles to bring about local elevation of the proboscis as described by Kirbach (1884) must not be ignored. The partial extension of the proboscis after stipital perforation suggests the partial truth of Kirbach's contention in this respect.

The theory offered implies a condition of tension across the transverse axes of the longitudinal septa. It is interesting to note that in the structure of the dorsal septum is embedded the main galea trachea. Its cuticular walls (figures 6, 13) are very thick—probably serving to resist the external pressure to which they become subjected when the oblique muscles contract.

We may now briefly indicate the events which occur when the proboscis moves to the feeding position. The retractor muscles of the galea base pull this latter back under the head and so draw this region of the proboscis, where the food canal is in the form of a gutter, more deeply under the labrum.

The elevator muscles of the galea base raise the proboscis base as a preliminary to uncoiling.

Within each galea haemocoel the intrinsic muscles draw upper and lower galea walls towards each other, so setting up an internal pressure which is maintained by the closure of the stipital valve worked by the stipital muscles.

The result of the drawing together of the upper and lower galea walls is to endow the proboscis as a whole with a dorsal keel, which condition—because of the elastic properties of the cuticle—can only be maintained with the proboscis in the extended position. Extension therefore occurs *pari passu* with the above events. This is indicated diagrammatically for a small length of the proboscis in figure 44. In returning to the position of rest all these muscle systems relax, blood pressure is released and the haemolymph can flow freely between the head and the galea, and by virtue of the elastic properties of the dorsal bar in each galea the proboscis returns to the tightly coiled position under the head.

#### DISCUSSION

The problems involved in the movements of the proboscis have included those of endocuticular flexibility and exocuticular elasticity and rigidity. They also concern muscles which by their contraction move the cuticle, the direction and extent of whose movements depends on the flexibility or rigidity just mentioned. Related to these features is the further one of muscles being, by virtue of the bending power and elasticity of the cuticle, one step removed from the ultimate effect produced by them.

Movement of the proboscis in its coiling and uncoiling is apparently simple—as simple as the coiling of a watch spring. The matter is, however, made complex because two parts—the maxillary galeae—go to form the proboscis. Not only has it to coil and uncoil, but it must form between its components a food tube sufficiently circular in section to permit of the unobstructed flow of fluid through it during feeding. Linkage between the two galeae is important therefore. Since these linkages are median, both dorsal and ventral, and since, further, the proboscis only coils in the vertical plane, it is to be expected that firmness of union embodying some freedom of movement must be ensured for coiling and uncoiling to be possible. In either of these movements it seems clear that forces of a different nature will bear on the two regions of linkage, ventral and dorsal (concave and convex). Ventrally the linkage provides the rigid attachment between the two galeae. Dorsally the union is effected by a series of overlapping cuticular plates. Here movement during coiling and uncoiling is of a greater order than ventrally, and the overlapping plates must be envisaged as sliding over each other during coiling and uncoiling, being lubricated, no doubt, by the secretions of some three hundred unicellular glands with which the proboscis is provided. But since the proboscis wall is a continuous structure there arises the question as to how it accommodates itself to the proboscis movements. This power to accommodate itself to coiling and uncoiling rests in the endocuticle which alternates along the length of the proboscis with transverse exocuticular ribs and which becomes thrown into minute transverse folds ventrally when coiled. The flexibility of the proboscis wall finds expression at the instance of an exocuticular elastic bar lying in the dorsal region of each galea which brings the proboscis to the coiled resting state without expenditure of energy. The flexibility just mentioned also finds expression at the instance of an internal musculature, the effect of which is not to uncoil the proboscis directly, but to bring about a change of form of such a nature that the coiled state must give way to the uncoiled or

extended state. The ultimate effect of uncoiling is, therefore, one step removed from the muscles which initiate the action, a feature which is not uncommon in exoskeletons, as, for instance, in wing movement of insects which results from tergal changes of shape induced by muscle contraction.

The open food tube is maintained at all times with a circular section—a fact which implies considerable rigidity of structure of its walls. One might fairly ask why this should have been designed to have a circular section when coiled at rest, for clearly the open channel serves no purpose when the animal is not feeding. Its maintained circular form is, of course, dependent on its rigidity, and the question might be put in terms of rigidity rather than openness of channel. What purpose then is served by the rigidity of the walls of the food tube? The answer is two-fold. First, it incorporates within its dorsal wall the longitudinal exocuticular elastic bar by which the proboscis is coiled without expenditure of energy. Secondly, it provides the strong fulcrum on which the outer wall of the galea can be flexed by the contracting oblique muscles so as to bring about the changed shape already referred to.

But the power of the proboscis as a whole to coil and uncoil easily must not be sacrificed to this rigidity. This ease of coiling is provided by the almost unique lattice structure of the wall of the food tube, so designed as to make coiling and uncoiling in the vertical plane easily possible, but also so designed as to restrict these movements to the vertical plane. It is not difficult to see that, should appreciable bending to either the right or to the left side be possible while uncoiled, the regularity of form on which this uncoiled state depends could not easily be maintained. Indeed, that this regularity of form is necessary is indicated by the existence of internal skeletal septa whose function is to control the shape of the outer cuticular wall of the galea when under the influence of contracting muscles. It is further indicated by the fact that turgidity of the galea haemocoel must be of such an order that the muscles within it produce a uniform effect from one end of the proboscis to the other.

Simple uncoiling, as here discussed, would result in full extension to the straight state. That this is not the case is due to the existence of a region where uncoiling is resisted—the 'knee bend'. The existence of a special set of muscles antagonistic to the primary oblique muscles in this region provides us with another example of the importance of cuticular flexibility, for they may be said to restore in this small length of the proboscis the transverse configuration of the coiled or semi-coiled state. By this simple device a great efficiency is conferred on the butterfly, making possible the easy exploitation of the nectaries of flowers with the minimum movement of the body as a whole, in much the same way that the fisherman casts his line to various parts of a stream without himself changing his standing position.

The analysis attempted here is qualitative, and it may be for others to apply quantitative methods in its further elucidation. From the facts described in relation to the suggested theory we can see, however, something of the importance to the butterfly of the precise disposition of the cuticular, muscular and glandular components of its proboscis.

We thank the many colleagues who by discussion have helped towards the completion of this paper. In particular should be mentioned Mr F. W. Adams, whom we thank for his suggestion of the analogy to the coiled steel ruler. It is also a pleasure to thank

## ON THE FEEDING MECHANISM OF THE BUTTERFLY

43

Professor V. B. Wigglesworth, F.R.S. for his kindness in providing non-diapausing pupae during the winter from which a regular supply of butterflies were reared, and Mr J. Hancock for his help both in breeding winter butterflies and in cutting numerous sections on which many of the results here recorded have depended.

## REFERENCES

- Bourgogne, J. 1951 *Traité de Zoologie*, **10**, no. 1, p. 174. Paris: Masson.
- Burgess, E. 1880 The structure and action of a butterfly's trunk. *Amer. Nat.* **14**, no. 5, p. 313.
- Burmeister, H. 1832 *Handbuch der Entomologie*, **1**. Berlin: G. Reimer.
- Eltringham, H. 1923 *Butterfly lore*. London: Clarendon Press.
- Hering, M. 1926 *Biologie der Schmetterlinge*. Berlin: Springer.
- Imms, A. D. 1942 *Outlines of Entomology*. London: Methuen.
- Kirbach, P. 1884 Über die Mundwerkzeuge der Schmetterlinge. *Arch. Naturgesch.* **50**, 78.
- Lameere, A. 1938 *Précis de Zoologie*, **5**. Brussels: Université de Bruxelles. Institut Zoologique Forley-Rousseau.
- Portier, P. 1949 *La biologie des Lépidoptères*. Encyclopédie Entomologique A. **23**. Paris: Paul Lechevalier.
- Pradhan, S. & Aren, N. S. 1941 The anatomy and musculature of the mouth parts of *Scirpophaga nivella* (Pyralidae) with a discussion on the coiling and uncoiling mechanisms of the proboscis of Lepidoptera. *Indian J. Ent.* **3**, 179–195.
- Reaumur, M. de 1734 *Mémoires pour servir à l'Histoire des Insects*, **1**. Paris: L'Imprimerie Royale.
- Savigny, J. D. 1816 Mémoires sur les animaux sans vertèbres. Part I. Mem. 1–2. Théorie des organes de la bouche des Crustacés et des Insects. *Insecta, Linn.* Paris: Deterville.
- Schmitt, J. B. 1938 The feeding mechanisms of adult Lepidoptera. *Smithson Misc. Coll.* **97**, no. 4, pp. 1–28.
- Slifer, E. H. 1950 Vulnerable areas on the surface of the tarsus and pretarsus of the grasshopper *Melanoplus differentialis* (Acrididae, Orthoptera); with special reference to the arolium. *Ann. ent. Soc. Amer.* **43**, no. 2, pp. 173–188.
- Snodgrass, R. E. 1935 *Principles of insect morphology*. New York: McGraw-Hill.
- Weber, H. 1933 *Lehrbuch der Entomologie*. Jena: Fischer.