

Functional morphology and movements of the proboscis of Lepidoptera (Insecta)

Harald W. Krenn

Zoologisches Institut, Universität Wien, Althanstrasse 14, A-1090 Wien, Austria

Received March 27, 1990

Summary. The mouthparts of Lepidoptera were investigated in a number of species by morphological and cinematographical methods. Both the galeae (which compose the proboscis) and the basal maxillary components (stipites) were studied in the resting position, in motion, and during feeding. In the resting position the proboscis is coiled so tightly that the surfaces of the consecutive coils are in close contact and the outermost coil touches the ventral side of the head. Cuticular processes of the galeal wall interlock between the coils in this position. In the investigated species they occur on the galeal wall and on the ventral side of the head in varying number and distribution. By the extension of the basal galeal joint, the coiled proboscis is released from its resting position and is elevated continuously. It uncoils in 3–5 steps which effect the entire length simultaneously. Each uncoiling step occurs synchronously with a compression of the stipital tubes on either side of the body. These compression movements pump hemolymph into the galeae. In all investigated Lepidoptera the uncoiled proboscis shows a distinct downward bend at a certain point which is also detectable in anaesthetized or freshly killed animals in some species. This feeding position and the movements of the uncoiled proboscis are similar in all species despite the intrinsic galeal muscles being variously arranged in the galeal lumen in different Lepidoptera. When comparing cross-sections through corresponding regions of coiled and uncoiled proboscises, the curvatures of the dorsal galeal walls remain unchanged. Coiling of the proboscis starts at the tip and progresses to the base. After coiling the proboscis tightly beneath the head, the diameter of the spiral widens due to its elastic properties until the proboscis props itself against the ventral side of the head. This elastic effect combined with the interlocking cuticular processes seems to be responsible for the resting position of the proboscis.

from exposed liquids. From the functional point of view this proboscis is especially remarkable because of its spirally coiled resting position, and its extraordinary length in some species.

The structures of the Lepidopteran mouthparts have been described in a number of species (most important studies are, Berlese 1909; Schmitt 1938; Pradhan and Aren 1941; Eastham and Eassa 1955; Kristensen 1968; Bänzinger 1970; Kristensen and Nielsen 1981). The proboscis consists of the two extremely elongated galeae, each connected with the head by the stipites. General descriptions are given in most entomological textbooks (for example Matsuda 1965). A detailed description of the morphology of the proboscis exists only in a single species (Eastham and Eassa 1955). The only comparative study of the proboscis investigates the cuticle and the structures which link the two galeae (Hepburn 1971). The basal structures of the maxilla, the stipites and its associated muscles, have been compared in various Lepidoptera (Schmitt 1938).

Several partly contradictory interpretations of the mechanism of uncoiling and coiling of the proboscis have been proposed. Increased hemolymph pressure created in the stipites, elasticity of the galeal wall and the musculature within the galeae have variously been thought to cause coiling or uncoiling (for review see Eastham and Eassa 1955; Jones 1977; Smith 1985). Although there is no detailed analysis of the movements of the proboscis, an experimental investigation reveals the principle mechanism. Uncoiling of the proboscis results from the increased hemolymph pressure; coiling is caused by the muscles of the galeae. The elasticity of the galeal wall alone produces a loosely coiled position (Bänzinger 1971). Therefore it is not fully understood how the proboscis keeps its tightly coiled resting position, and what effects the right angle bend in feeding position which has been described in two species (Eastham and Eassa 1955; Vasudeva 1956).

In order to give a comprehensive investigation of the morphology of the proboscis, the present study compares the resting and feeding position as well as the surface and the anatomy of the galeae in a number of Lepi-

A. Introduction

Adult Lepidoptera of the group Glossata, possess a long proboscis to extract nectar from floral tubes as well as

doptera belonging to different families of Glossata. In two selected species the movements of the maxillary structures have been analysed by cinematography.

B. Material and methods

Animals. The investigated species are listed in Table 1. They were collected in the surroundings of Vienna (Austria).

Scanning electron microscopy (SEM). In various species (Table 1) the external structures were examined by SEM. After fixation in Dubosq-Brazil (Romeis 1968; half the formaldehyde being substituted by glutaraldehyde), dehydration with ethanol and acetone, critical point drying, and coating with gold (Hummer JR Technics), the specimens were examined with a Jeol JSM-35CF or with a Cambridge Mk 2a scanning electron microscope. For examination of the proboscis in the resting position rapid cryo-immobilization with dichlorodifluoromethane spray was used.

Light microscopic techniques. The internal structures were investigated by light microscopic serial semithin sections in various species (Table 1). The heads were fixed and dehydrated as described above and embedded in ERL-4206 resin by vacuum impregnation. Semithin sections (1 µm) were made on a Reichert OM-3 microtome with glass knives or a semi-diamond knife (Diatome, Switzerland). The sections were stained with a mixture of 1% azure II and 1% methylene blue in a 1% borax solution.

For comparison of the stipes or the galea at rest and during feeding the animals were fixed with hot Dubosq-Brazil (80° C) and prepared as described above.

Vital staining technique. The hemolymph was stained by application of crystals of methylene blue into the head through holes originat-

Table 1. List of investigated Lepidoptera

Species	Methods of investigation		
Pieridae			
<i>Pieris rapae</i> (Linné, 1758)	SEM	LM	C
<i>Pieris brassicae</i> (Linné, 1758)	SEM	LM	
Nymphalidae			
<i>Inachis io</i> (Linné, 1758)	SEM	LM	
Satyridae			
<i>Maniola jurtina</i> (Linné, 1758)		LM	
<i>Melanargia galathea</i> (Linné, 1758)	SEM		
Lycaenidae			
<i>Polyommatus icarus</i> (Rottemburg, 1775)	SEM	LM	
Hesperiidae			
<i>Ochlodes venata</i> (Bremer and Grey, 1853)	SEM	LM	
Sphingidae			
<i>Macroglossum stellatarum</i> (Linné, 1758)	SEM	LM	
<i>Sphinx ligustri</i> Linné, 1758	SEM	LM	
Noctuidae			
<i>Mamestra brassicae</i> (Linné, 1758)	SEM	LM	C
Pyralidae			
<i>Plodia interpunctella</i> (Hübner, 1813)	SEM	LM	
Yponomeutidae			
<i>Yponomeuta cagnagella</i> (Hübner, 1813)		LM	
Colocephoridae			
<i>Coleophora</i> sp.		LM	

SEM scanning electron microscopy; LM light microscopic semithin sections; C cinefilms

ing from the removal of the labial palpi. This procedure does not impair the function of the proboscis.

Photography and cinematography. Except for *Sphinx ligustri* and *Yponomeuta cagnagella* the movements of the proboscis have been observed in all species in the field or the laboratory. Photographs of the uncoiled proboscis were taken using a 35 mm single lens reflex camera with extension. Photographs of the proboscis' movements were taken from single frames of 16 mm cinefilms (Krenn 1985; Krenn unpublished) which were exposed at 24 frames per second.

C. Results

I. Resting and feeding position

Figure 1 shows the Lepidopteran mouthparts in the resting position. The proboscis is coiled in a tight spiral beneath the head (Figs. 1, 4a). The number of coils varies from 3.5 to 7 coils in the investigated species (Table 2). The dorsal and the ventral galeal walls of the consecutive coils are in close contact with each other throughout the entire length. The outermost coil rests against the labium on the ventral side of the head. In some species the labium forms a groove between the labial palpi, which is especially deep in the investigated Sphingidae. In these species the coiled proboscis lies in this U-shaped groove of the labium (Fig. 5a, b). The short basal galeal joint which links each galea to the stipes forms a right angle in the resting position.

The stipes consists of a flat medial part and a tubular lateral part which is made of flexible cuticle on its lateral side. In the resting position the stipital tube is expanded and its rigid medial side is in a longitudinal position (Figs. 1, 3b).

In the feeding position the uncoiled proboscis forms a downward bend in a specific region in all examined species. The region proximal to this bend is extended


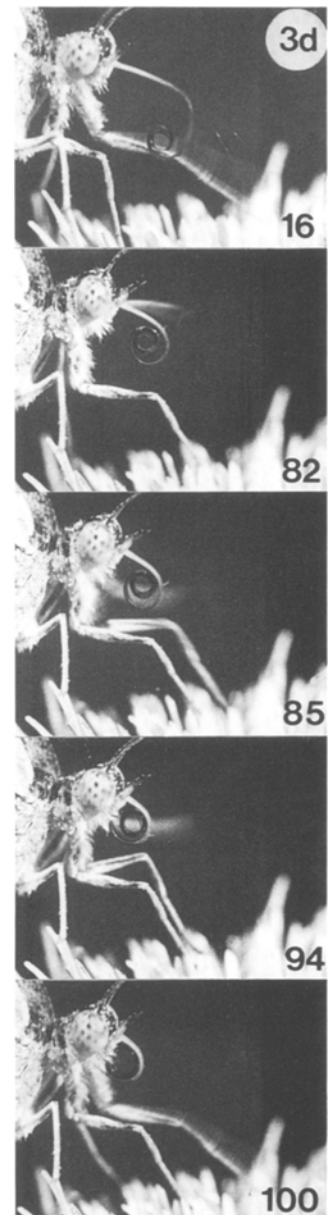
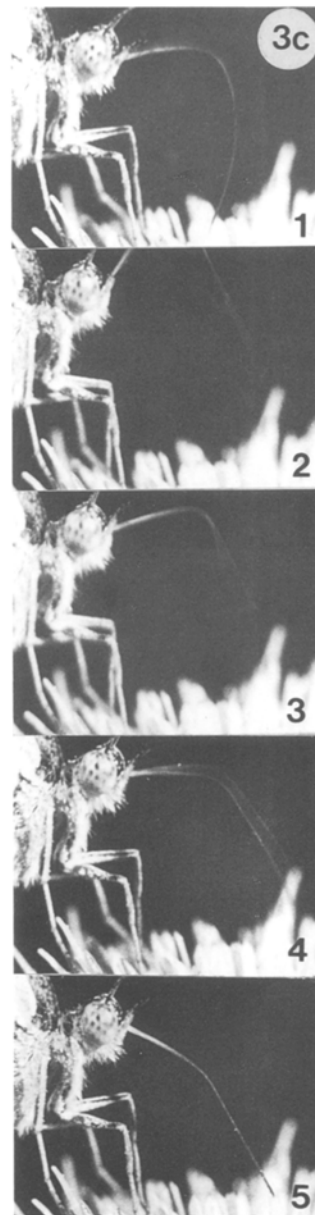
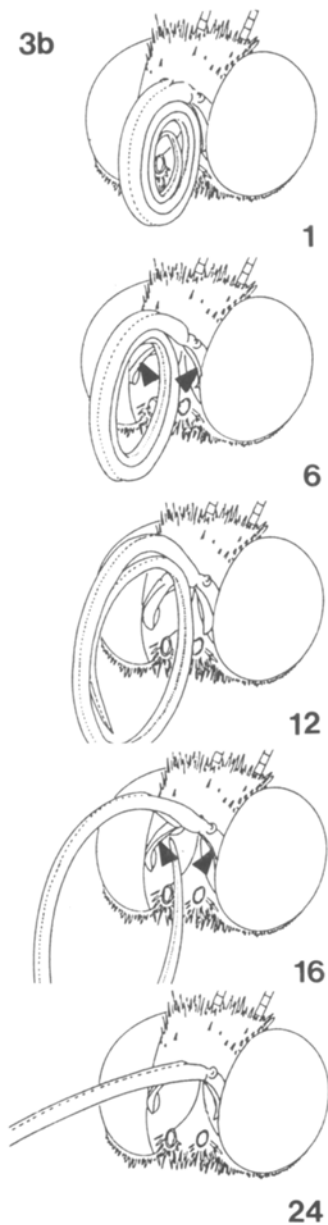
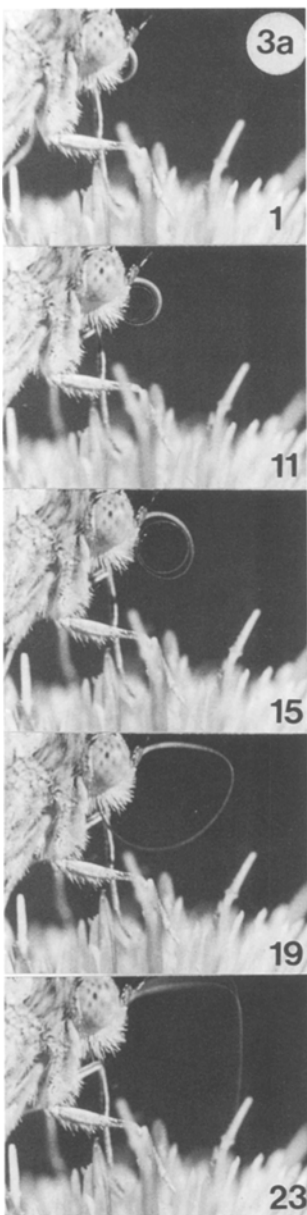
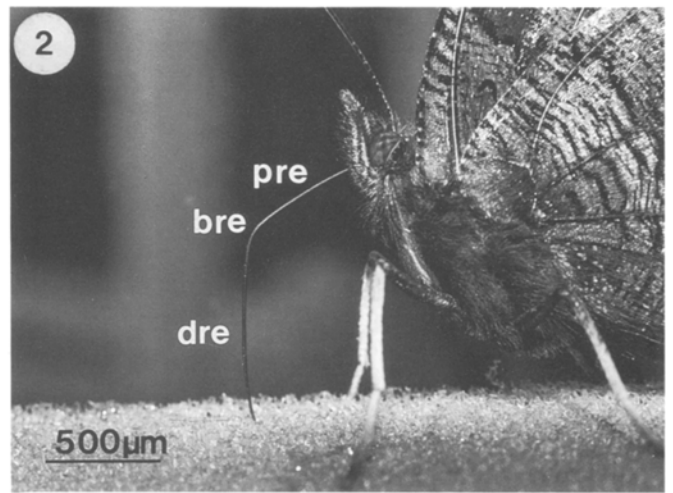
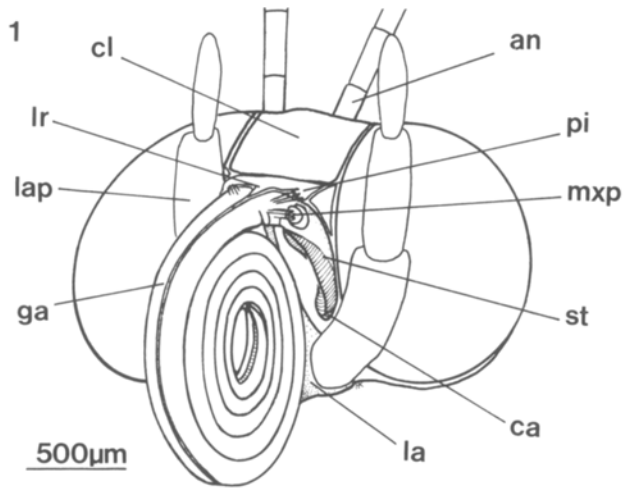


Fig. 1. Schematic ventral view of the head of *Pieris rapae*, mouthparts in resting position. The highly modified maxilla consists of cardo, stipes, one-segmented maxillary palpus and elongated galea composing the proboscis. The stipes represents a tube consisting of rigid cuticle medially (*hatched*) and membranous cuticle laterally. The triangular labium bears the three-segmented labial palpi on the posterior end

Fig. 2. *Inachis io* (photography). Proboscis in uncoiled position during food uptake showing the bend region at about one third of the proboscis' length

Fig. 3a-d. *Pieris rapae*. Movements of the mouthparts (pictures and drawings taken from single frames of a 16 mm cinefilm, frame-numbers are given at 24 pictures per minute): **a** Stepwise uncoiling of the proboscis synchronously in all regions. **b** Stipes compressions (indicated by arrowheads) synchronously with uncoiling steps. **c** Movements of the uncoiled proboscis: elevation of the proboscis, bending and unbending of the bend region. **d** Coiling progresses from the tip to the base



horizontally. Distally from the bend the proboscis is in an almost vertical position (Fig. 2). The tip can be bent in all directions. In *Mamestra brassicae*, *Plodia interpunctella*, and *Polyommatus icarus* the distal region retains a slight curvature so that the bend region appears rounded. In *Pieris rapae* (Fig. 3c), *Inachis io* (Fig. 2), *Ochlodes venata*, *Maniola jurtina*, and *Macroglossum stellatarum* the bend region is very conspicuous. It was also detectable in freshly killed or anaesthetized animals when the proboscis was extended by the aid of tweezers. After this artificial extension, the proboscis returned into a loosely coiled position showing fewer coils than in the resting position (Table 2).

II. Movements of the mouthparts

During the very rapid uncoiling process two patterns of movement are detectable, a continuous elevation of the proboscis and several separate uncoiling movements (Fig. 3a, b). Uncoiling starts with the extension of the basal galeal joint which moves the coiled proboscis upward (Fig. 3a). During this continuous elevation the proboscis uncoils in 3–5 distinct steps. With each of these short movements all regions of the entire proboscis uncoil simultaneously. During uncoiling of the last coil the proboscis is at its maximum elevation and the galeal joint is extended at about 180°. Each uncoiling step occurs synchronously with one compression movement of both stipites. The medial side of each stipital tube moves in a laterad direction and compresses the tube longitudinally. In the compressed position the medial side of the tubular part is in an oblique position (Fig. 3b).

The movements of the uncoiled proboscis consist of extension and flexion of the basal galeal joint and the bend region. Their combination leads to upward and downward motions of the whole proboscis together with forward and backward movements of the extended distal region of the proboscis (Fig. 3c). Towards the tip the proboscis is more flexible and can be curved forward or backward. The movements of the tip are not only restricted to those in the sagittal plane. In the uncoiled position of the proboscis, the stipites are more or less compressed. Further compression movements result in an extension of the bend region, whereby the proximal and distal region meet at an obtuse angle. In this way the proboscis can be extended completely and the bend is nearly undetectable. When the bend region reaches its maximum curvature, the proximal region and the distal region meet at an acute angle and the tip is beneath the thorax. In some species (e.g., *Mamestra brassicae*) the whole head also moves up and down.

The coiling process (Fig. 3d) starts at the tip and proceeds on towards the base of the proboscis. First the tip and the distal region are coiled in several narrow coils while the proximal region stays rectilinear. Afterwards the bend region is coiled while the whole proboscis is sometimes elevated; this is followed by coiling of the proximal region. When butterflies stop the coiling process in this position, the proboscis unspirals without

compressions of the stipites until the outermost coil touches the ventral side of the head. This position shows fewer coils with a greater diameter compared with the tightly coiled position (Fig. 3d). It can be observed when the animal interrupts feeding for a short time. The cinematography shows that further coiling cycles, starting at the tip and proceeding to the base, end in the tightly coiled position. This last stage of the coiling process is characterized by alternating compressions of the stipites. A stipites compression on one side of the body leads to a laterad movement of the coiled proboscis in the opposite direction. After complete coiling of the proboscis, there is a slight countermovement detectable. The proboscis unspirals whereby the coils slide over each other until they are in close contact and the outermost coil touches the ventral side of the head.

III. External structures

The cuticle of the galeae, the labium, and the ventral membrane of the head bear spine-like cuticular processes (Figs. 4–8). In the resting position they interlock between the consecutive coils (Fig. 6b). With the exception of Sphingidae, these cuticular processes have been found in all species investigated, however, their number and distribution over the galeae varies (Table 2). Several species have numerous processes on the dorsal, lateral, and ventral galeal walls which are more hair-like in the proximal region and become shorter and more spine-like distally (Fig. 6a, b). In others the cuticular processes appear only on the dorsal and/or ventral side of the galeae (Fig. 8). They are particularly numerous on the ventral side of the proximal region and disappear distally (e.g., *Ochlodes venata*). In some species the cuticle is sculptured in areas where no processes exist (Fig. 8). Only the galeae of *Macroglossum stellatarum* and *Sphinx ligustri* do not have any cuticular processes. Apart from the sensillae, the surfaces of their galeae are completely smooth (Fig. 7).

However, in all investigated Lepidoptera the labium and the membranous cuticle between the labium and the stipites bear similar cuticular structures (Figs. 4b, 5b, Table 2).

IV. Expanded and compressed stipites

In *Pieris rapae* and *Mamestra brassicae* the stipites were examined in expanded and compressed positions. Cross-sections through the stipites at rest show a wide lumen. The stipital lamella, which is formed by the interior side of the tubular part, does not close the connection to the head (Fig. 9a). Cross-sections during compression movements show that the stipital tube is folded longitudinally. The opening to the head is closed (Fig. 9b). Compared with the expanded position, the cross-sectional area is reduced by more than 70% in *Pieris rapae*.

The pumping effect of these compressions was detectable after staining of the hemolymph in the head. Each compression forces hemolymph from the stipites

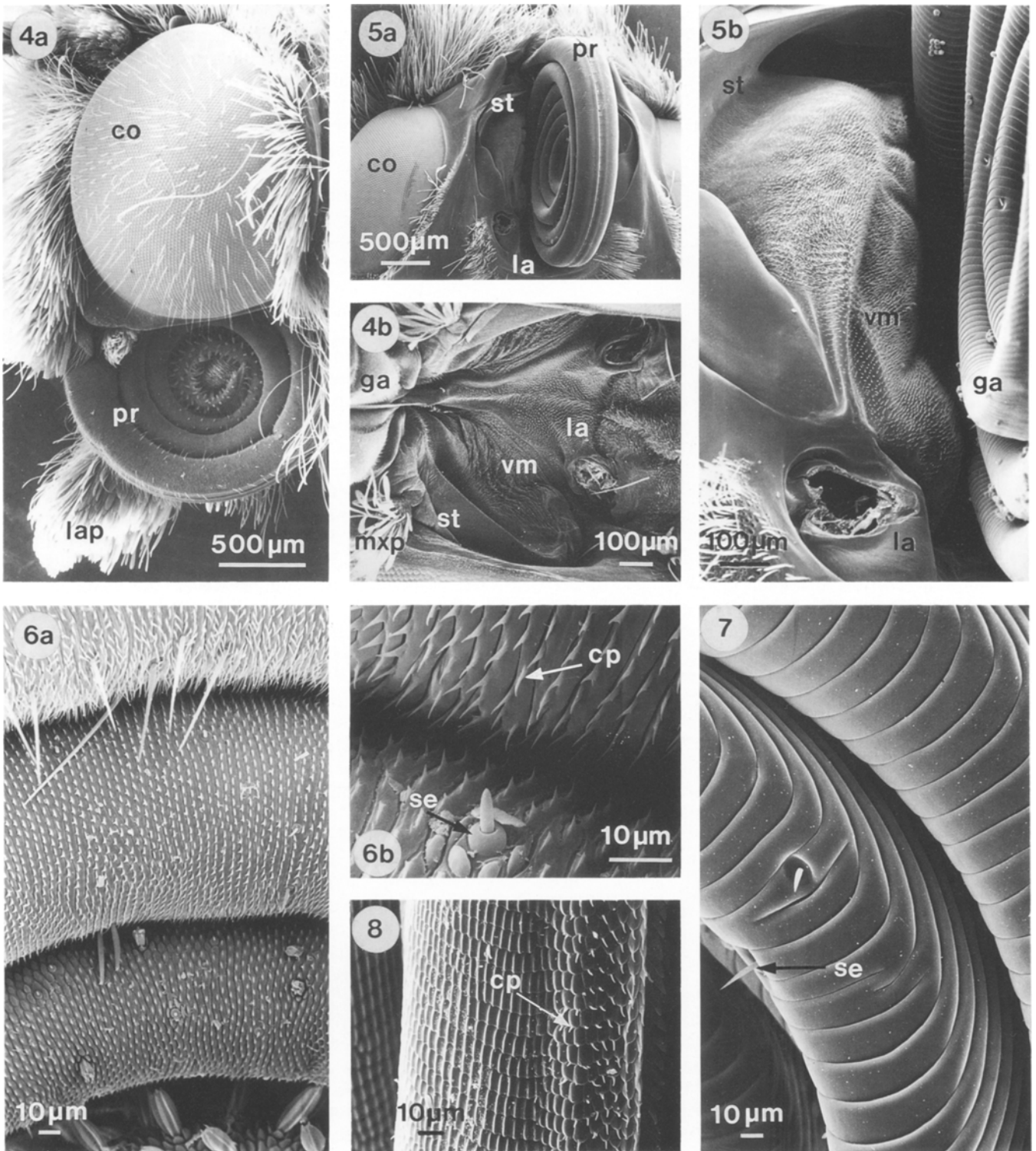


Fig. 4a, b. Head of *Mamestra brassicae* (SEM): **a** Lateral view; proboscis coiled in resting position (left labial palpus removed). **b** Ventral view; labium and ventral membrane bear cuticular processes (both labial palpi removed)

Fig. 5a, b. Ventral view of the head of *Macroglossum stellatarum* (SEM, both labial palpi removed): **a** Coiled proboscis rests in U-shaped groove of the labium. **b** Enlargement of **a**, ventral membrane bears cuticular processes

Fig. 6a, b. Lateral view of the proboscis of *Mamestra brassicae* in resting position (SEM): **a** The galeal wall bears numerous cuticu-

lar processes; the coils are in close contact with each other. **b** Enlargement of **a**, cuticular processes interlock between the coils

Fig. 7. Lateral view of the proboscis of *Macroglossum stellatarum* (SEM); no cuticular processes on the galeal wall

Fig. 8. Dorsal view of the proboscis of *Ochloides venata* (SEM); cuticular processes on the dorsal wall of the galea, the rest of the surface shows sculptured cuticle

Table 2. Tightly and loosely coiled position of the proboscis and distribution of the cuticular processes in various Lepidoptera ($n=5$)

Species	Number of coils		Cuticular processes on galeae	Cuticular processes on ventral side of the head
	Tightly coiled	Loosely coiled		
<i>Pieris rapae</i>	4.5	2.5	++	++
<i>Inachis io</i>	5.5	2.5	+	nd
<i>Melanargia galathea</i>	4.5	nd	+	nd
<i>Polyommatus icarus</i>	5	1.5	+	++
<i>Ochlodes venata</i>	5	3.5	+	++
<i>Mamestra brassicae</i>	3.5	1.5	++	++
<i>Macroglossum stellatarum</i>	7	3.5	0	+
<i>Sphinx ligustri</i>	nd	nd	0	+
<i>Plodia interpunctella</i>	3.5	2.5	++	++
<i>Yponomeuta cagnagella</i>	nd	nd	++	nd
<i>Coleophora</i> sp.	5.5	nd	++	nd

++ on the whole surface; + dorsal and ventral side of the proximal galea, or only on the ventral membrane; 0 not at all; nd not determined in this species

into the galea. During expansion the lumen of the stipes refills with hemolymph from the head.

V. Contours of coiled and uncoiled proboscis

In *Pieris rapae* and *Pieris brassicae* cross-sections through the coiled proboscis show that the dorsal walls of the galeae are flatter in the proximal region than in the distal region where they are more convex (Fig. 10a–c). A cross-section in the uncoiled position shows the same convexity of the dorsal galeal wall, when compared with the corresponding section through the same region in the coiled position.

VI. Muscles of the proboscis

In all investigated Lepidoptera each galea contains a nerve, a trachea, one or two longitudinal septa, and numerous muscles (Figs. 10–12). The lumen of the basal galeal joint contains the basal galeal muscle which runs from the proximal end of the galea to the dorsal wall at the start of the proximal region. Distally the lateral and ventral areas of the galea contain the intrinsic galeal muscles. According to Eastham and Eassa (1955) the muscles which are in the lateral area are called primary oblique galeal muscles and the muscles which run ventro-medially are called secondary oblique galeal muscles. However, in some species the intrinsic galeal muscles cannot be classified into primary or secondary oblique muscles because they all run nearly longitudinally along the ventral wall. The investigated species show different arrangements of their galeal muscles in the various regions of the proboscis (Table 3). The cross-sections in Fig. 12a–e give examples of the different arrangements.

The inclinations of the galeal muscles, which all insert tangentially on the ventral galeal wall, were established from longitudinal sections in coiled galeae. In *Mamestra brassicae* and *Pieris rapae* the angle between the primary oblique galeal muscles and the galeal axis is about 15° in the proximal region. It increases to more than 35° in the bend and decreases again to 15° – 20° in the distal region and the tip (Fig. 11). The inclination of the secondary oblique galeal muscles is less than 15° .

D. Discussion

I. Resting position

The spirally coiled resting position of the Lepidopteran proboscis is unique in insects. It has generally been assumed that the elasticity of the cuticle coils the proboscis passively and is also responsible for the resting position (Eastham and Eassa 1955; Hepburn 1971). Experiments indicated that the galeal muscles coil the proboscis. However, neither they, nor the elasticity, is responsible for maintaining the tightly coiled resting position (Bänzinger 1971). In lachryphagous moths, it has been proposed that spine-like cuticular structures on the galeal surface maintain the resting position (Bänzinger 1973).

The present investigation shows that cuticular processes are not exclusively characteristic for the galeae of these specialized Lepidoptera. With the exception of Sphingidae, they occur in all investigated species at least in galeal areas which touch each other in the coiled position. In all investigated species, including Sphingidae, similar cuticular structures have been found on the ventral side of the head. As shown by SEM the cuticular processes are interlocked between the single coils, sticking together like the bristles of two brushes in the resting position of the proboscis. After complete coiling, the spiral of the proboscis widens passively. The coiled proboscis props itself beneath the head because its elastic properties tend to uncoil it into a loosely coiled position. In this way the cuticular processes are interlocked and prevent further uncoiling. Even when the butterfly did not coil the proboscis tightly, this combination of spring-loaded proboscis and interlocking cuticular processes can maintain the resting position without muscle action.

Cuticular processes also appear on the lateral walls in some species (e.g., *Pieris rapae*, *Mamestra brassicae*). There, they could give additional support by interlocking with the setae of the labial palpi which embrace the coiled proboscis on either side. When comparing the length of the proboscis and the distribution of the cuticular processes in different species, it could be expected that species with a very long proboscis have more cuticular processes. The opposite is true in the investigated species. The proboscis of *Macroglossum stellatarum* has approximately double the length of the proboscis in *Pieris rapae* (11.2 mm long), and in *Sphinx ligustri* it is more than 39 mm long (Nilsson 1989), however, both Sphingidae do not have any cuticular processes on the galeal surface. However, the ventral membrane of the head also shows cuticular processes in these spe-

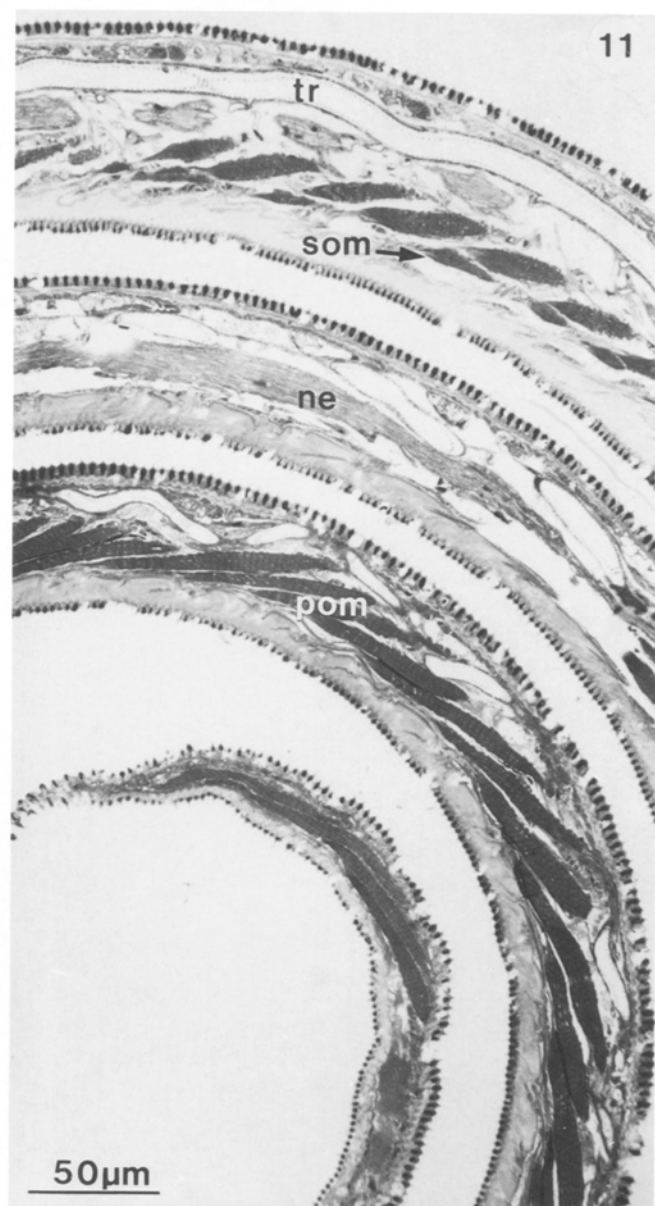
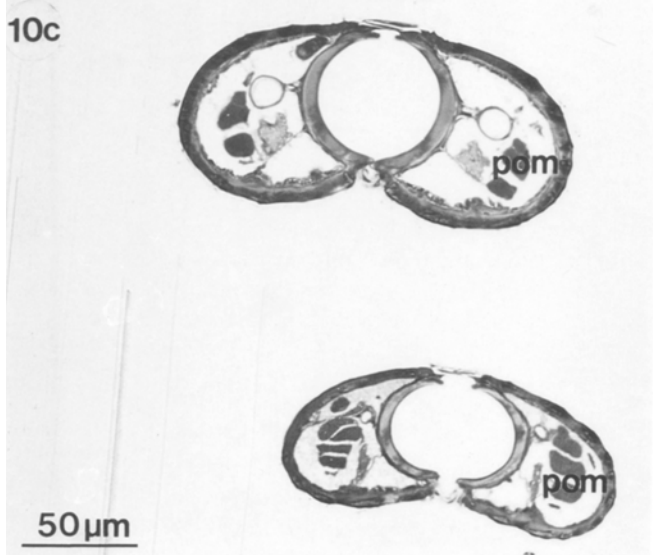
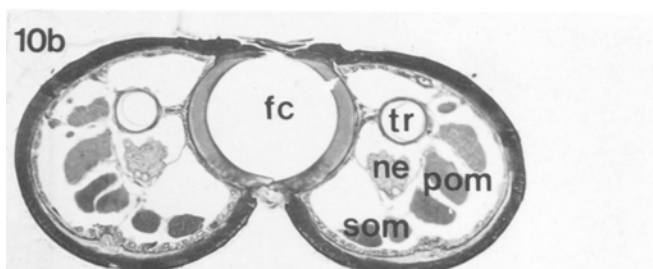
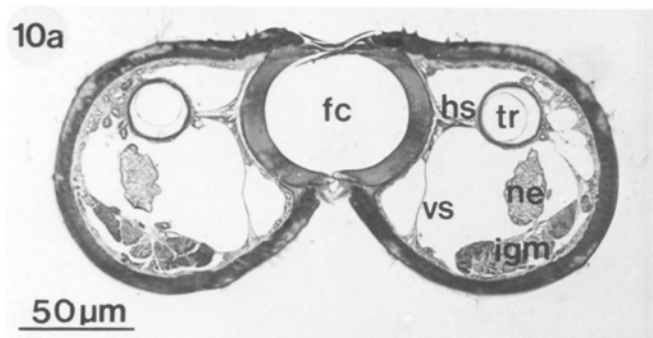
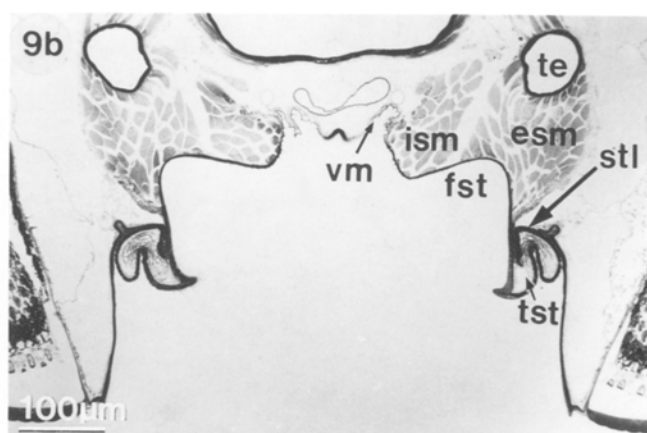
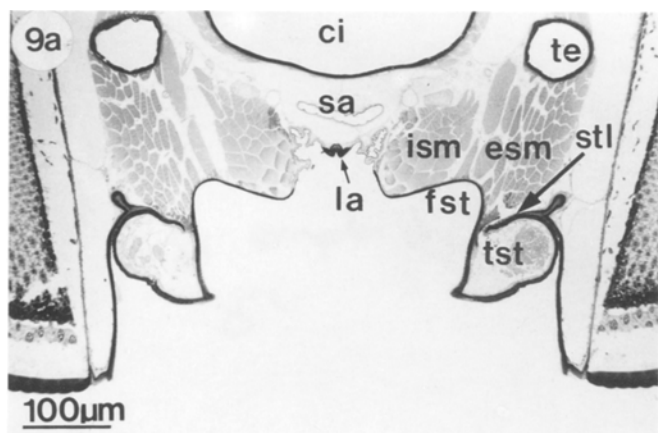


Fig. 9a, b. Head of *Pieris rapae* (semithin section): **a** Cross-section with expanded position of stipites. **b** Cross-section with compressed position of stipites

Fig. 10a–c. Cross-sections of the proboscis of *Pieris rapae* in loosely coiled position showing semithin sections of: **a** The proximal region; **b** the bend region; **c** two sections of the distal region

Fig. 11. Longitudinal semithin section of the coiled proboscis of *Pieris rapae*. Primary oblique galeal muscles insert tangentially on the ventral wall, even at the tip

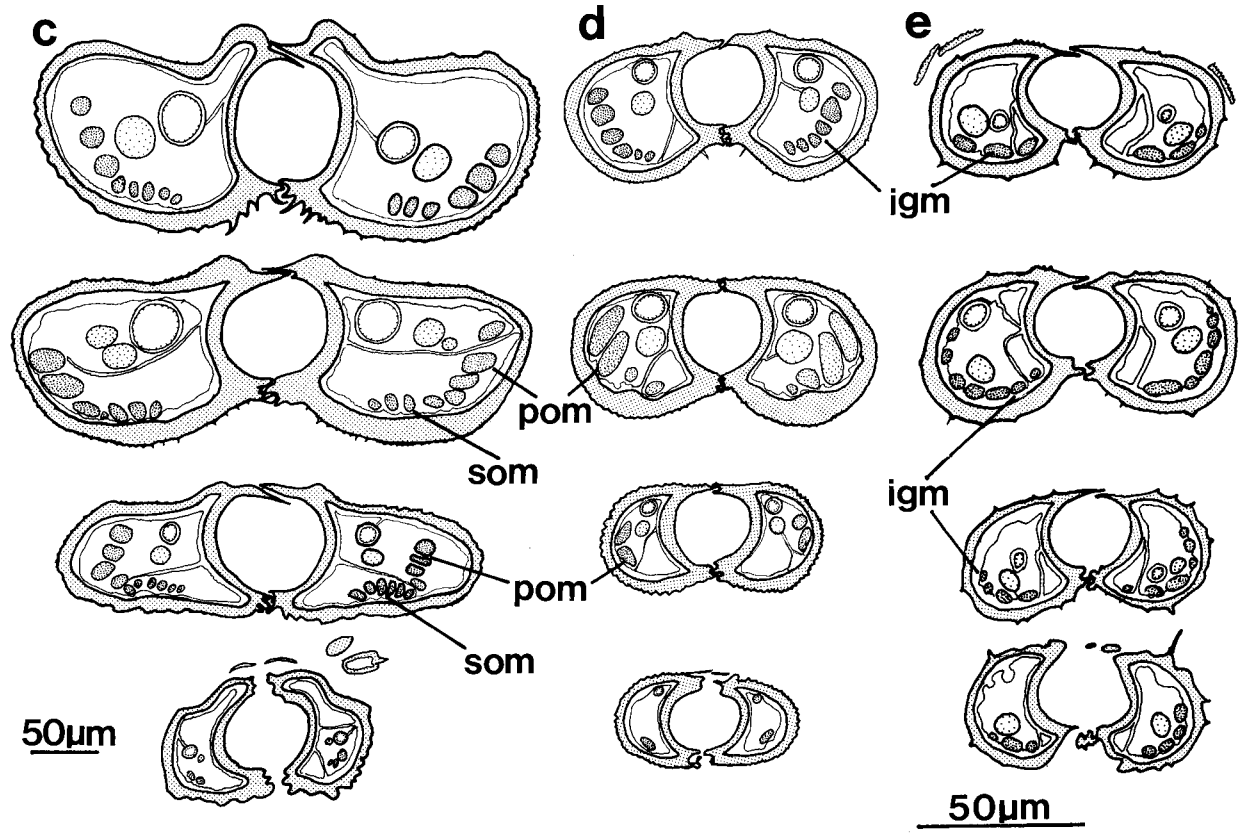
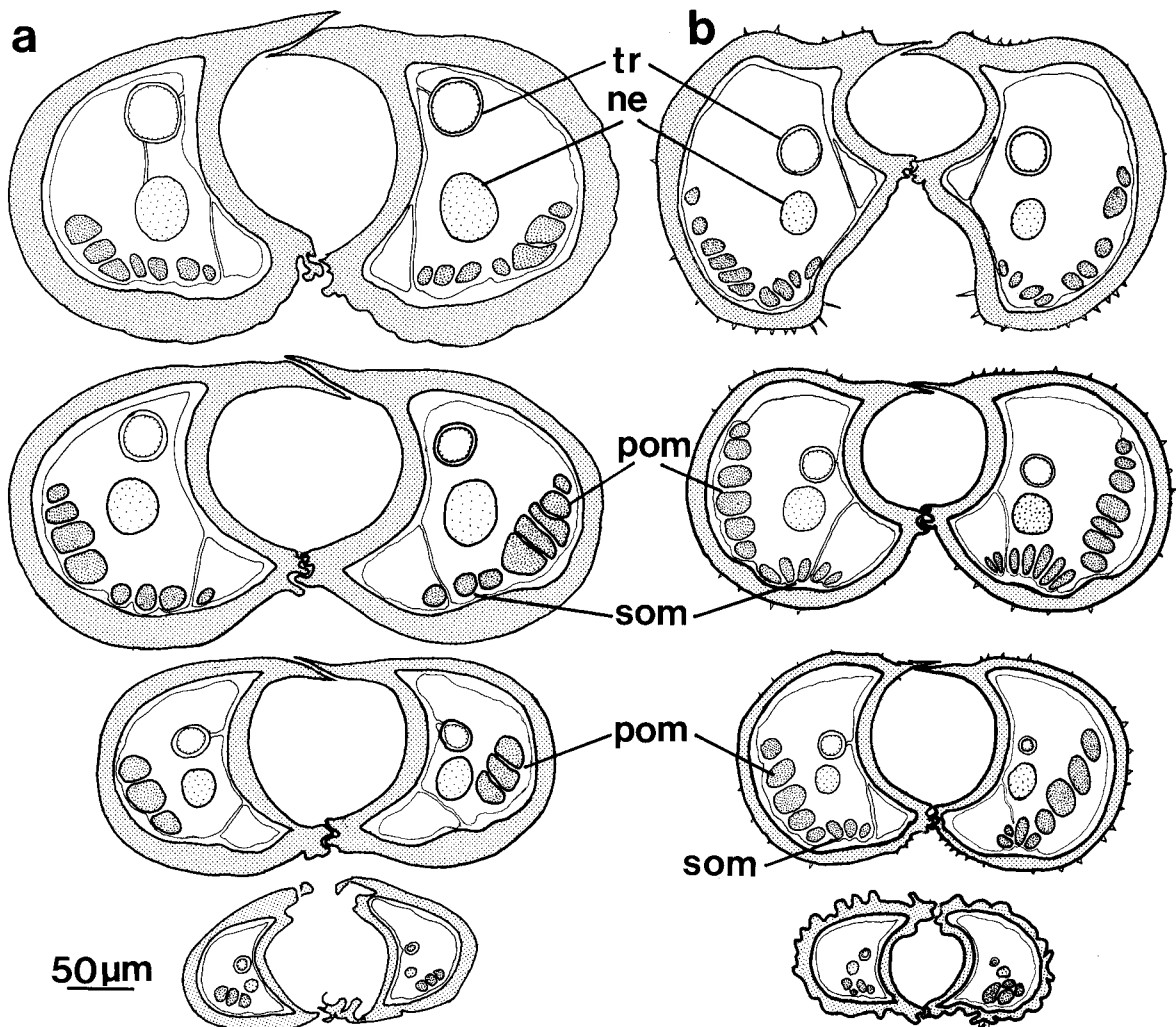


Table 3. Arrangements of intrinsic galeal muscles within various regions of the proboscis in different Lepidoptera

Species	Regions of the proboscis		
	Proximal	Bend	Distal
<i>Pieris rapae</i>	igm	pom, som	pom
<i>Inachis io</i>	pom, som	pom, som	pom, som
<i>Maniola jurtina</i>	igm	pom, som	pom
<i>Polyommatus icarus</i>	igm	pom	pom
<i>Ochlodes venata</i>	igm	pom	pom
<i>Mamestra brassicae</i>	pom, som	pom, som	pom, som
<i>Macroglossum stellatarum</i>	pom, som	pom, som	pom
<i>Sphinx ligustri</i>	pom, som	pom, som	pom
<i>Plodia interpunctella</i>	igm	pom, som	pom, som
<i>Yponomeuta cagnagella</i>	igm	igm	igm
<i>Coleophora</i> sp.	igm	igm	igm

cies. It seems that they fix the coiled proboscis in the U-shaped labium (Fig. 5b).

II. Movements of the proboscis

Although there are several interpretations of the mechanism of the proboscis there is only one description of its movements. According to this, the uncoiling process runs successively from the base to the tip, and the coiling process runs in the same pattern of movement starting at the tip (Eastham and Eassa 1955). The present cinematographic analysis shows a different pattern for uncoiling. The proboscis uncoils in several steps in all regions simultaneously, in coincidence with compression movements of both stipites.

Bänzinger (1971) noticed movements of the stipites during uncoiling and interpreted them as pumping actions which force hemolymph into the galeae. Staining experiments show that in fact each compression forces hemolymph from the head into the attached galea. The valve function of the stipital lamella (Schmitt 1938) prevents a back flow between the single compressions. Therefore the effect of the compression movements accumulates until the necessary pressure for full extension of the proboscis is reached. Increased internal pressure acts in the entire galea simultaneously. This explains the simultaneous uncoiling of all regions of the proboscis. The alternating compression movements of the stipites during the last phase of the coiling process do not lead to uncoiling, but cause sideways movements of the coiled proboscis. The functional significance of these movements remains uncertain. Perhaps they ensure interlocking of the cuticular processes between the coils.

Fig. 12a–e. Cross-sections of various regions of the proboscis in: **a** *Macroglossum stellatarum*; **b** *Mamestra brassicae*; **c** *Inachis io*; **d** *Ochlodes venata*; **e** *Coleophora* sp. Schematic drawings from semithin sections show: the first row the proximal region, the second row the bend region, the third row the distal region, and the fourth row the tip region

In consideration of the valve function of the stipites the increased internal pressure has to be released during the coiling process by active opening of the stipites. The functional analysis of the stipital muscles in skin-piercing moths shows that, contrary to the other stipital muscles, the interior tentorio-stipital muscle cannot compress the stipites (Bänzinger 1970). Its point of insertion indicates that it could open the stipital valve to allow back-flow of the hemolymph into the head.

According to the functional mechanism proposed by Eastham and Eassa (1955), the uncoiled position is caused by the more convex shape of the dorsal galeal wall which is a result of the action of the primary oblique galeal muscles. In their paper the authors use illustrations of cross-sections to show the transverse bending of the dorsal wall in the extended position compared with the flattened dorsal wall of the coiled proboscis. However, they incorrectly compared cross-sections of the distal region with cross-sections of the proximal region of the proboscis. The present study demonstrates that the shape of cross-sections changes from proximal to distal (Figs. 10, 12). The comparison of cross-sections through corresponding regions indicates no change in curvature of the dorsal galeal wall in the coiled and uncoiled position. According to Eastham and Eassa (1955), the dorsal wall has to be bent transversely also at the tip, therefore the primary oblique galeal muscles should run in a dorso-ventral direction in this region. Longitudinal sections in *Pieris rapae* and *Mamestra brassicae* prove that there are no dorso-ventral muscles throughout the galeae, even in the tip.

All investigated species show similar foraging movements. They seem to be especially useful for probing among tubular corollae, and enable the animals to forage inflorescences (e.g., thistles) rapidly, without moving the whole body. Extension of the bend region results from further increase of the internal pressure due to simultaneous compression movements of both stipites. Sideways movements of the tip can be explained by compressions of only one stipite. The flexion of the bend region seems to be a result of the elasticity but an interaction with the intrinsic galeal muscles cannot be ruled out.

III. Galeal muscles

There is no doubt that the intrinsic galeal muscles are responsible for coiling the proboscis (Bänzinger 1971). The reason why there are different muscle sets in many species, however, is less obvious. The present morphological comparison demonstrates that the experimental investigation on the mechanism of the proboscis (Bänzinger 1971) was carried out in Lepidoptera with different arrangements of primary and secondary oblique galeal muscles. However, Bänzinger's results were the same in all species. Therefore, the arrangement of muscles has obviously no bearing on the fundamental mechanism of coiling and uncoiling.

The right angle "knee bend" in the uncoiled position was attributed to an antagonistic arrangement of prima-

ry and secondary oblique galeal muscles in this region (Eastham and Eassa 1955; Vasudeva 1956). Although different muscle arrangements occur in the investigated species, there were only slight differences in length and radius of the bend. In some species no secondary oblique galeal muscles are present at all while in others this set of muscles occurs in the whole galea. Anaesthetized butterflies showed likewise the bend region after their proboscis was uncoiled with the aid of tweezers. These facts suggest that the bend is formed passively, obviously by the galeal cuticle regardless of the arrangement of the galeal muscles in this region.

In only one group of the Glossata, the Eriocraniidae, the galeae do not contain any muscles, although the proboscis is perfectly functional (Kristensen 1968). The investigation of several non-ditrysian Glossata shows that they possess only one or a few longitudinal galeal muscles (Kristensen and Nielsen 1981). In two presently investigated species (*Yponomeuta cagnagella* and *Coleophora* sp.) there are numerous muscles but they cannot be differentiated into distinct sets. Further examinations of various ditrysian Lepidoptera would show the phylogenetical pathways that led from simple longitudinal muscles to the variously arranged oblique galeal muscles and might elucidate their functional role.

IV. Conclusions with regard to the mechanism of the proboscis

Based on the hemolymph pressure hypothesis (Schmitt 1938; Bänzinger 1971) the present investigation leads to an improved explanation of the mechanism of the Lepidopteran proboscis.

Uncoiling is a result of the step-by-step increase of the hemolymph pressure in the galeae created by compression movements of the stipites. The uncoiled position and its passively formed bend region is maintained by the valve function of the stipites. The elasticity of the cuticle tends to recoil an extended proboscis in a loosely coiled position but tends to uncoil a tightly coiled proboscis from its resting position. After the proboscis was coiled beneath the head by its musculature, this elastic effect props the coiled proboscis under the head. In this position the cuticular processes interlock between the coils and keep the coiled position without further muscle action.

This interpretation gives a reason for the step-by-step uncoiling process, it explains the "knee bend" irrespective of the arrangements of the galeal muscles, and explains how the proboscis is kept in resting position without muscle action.

Acknowledgements. I thank Miss H. Grillitsch for assistance in preparing the illustrations, Mr. C. Matznetter for help with the typewriting, Miss V. Ribarich and Mr. N. De Courcy for correcting the translation and, for instance, Dr. G. Pass for stimulation of this study and for critical reading.

Abbreviations

<i>an</i>	antenna	<i>mxp</i>	maxillary palpus
<i>bre</i>	bend region	<i>ne</i>	nerve
<i>ca</i>	cardo	<i>pi</i>	pilifer
<i>ci</i>	cibarium	<i>pom</i>	primary oblique galeal muscles
<i>cl</i>	clypeus	<i>pr</i>	proboscis
<i>co</i>	complex eye	<i>pre</i>	proximal region
<i>cp</i>	cuticular process	<i>sa</i>	salivarium
<i>dre</i>	distal region	<i>se</i>	sensillum
<i>esm</i>	external tentorio-stipital muscle	<i>som</i>	secondary oblique galeal muscles
<i>fc</i>	food canal	<i>st</i>	stipes
<i>fst</i>	flat part of the stipes	<i>stl</i>	stipital lamella
<i>ga</i>	galea	<i>te</i>	tentorium
<i>hs</i>	horizontal septum	<i>tr</i>	trachea
<i>igm</i>	intrinsic galeal muscles	<i>tst</i>	tubular part of the stipes
<i>ism</i>	internal tentorio-stipital muscle	<i>vm</i>	ventral membrane
<i>la</i>	labium	<i>vs</i>	vertical septum
<i>lap</i>	labial palpus		
<i>lr</i>	labrum		

References

- Bänzinger H (1970) The Piercing Mechanism of the Fruit-piercing Moth *Calpe (Calyptra) thalictri* Bkh. (Noctuidae) with Reference to the Skin-piercing Blood-sucking Moth *C. eustrigata* Hmps. Acta Trop 27/1:53–88
- Bänzinger H (1971) Extension and Coiling of the lepidopterous Proboscis – a new Interpretation of the Blood-pressure Theory. Mitt Schweiz Entomol Ges 43/3–4:225–239
- Bänzinger H (1973) Biologie der lacriphagen Lepidopteren in Thailand and Malaya. Rev Suisse Zool 79/4/63:1381–1469
- Berlese A (1909) Gli Insetti 1. Società Editrice Libreria, Milano, pp 446–457
- Eastham LES, Eassa YEE (1955) The feeding mechanism of the butterfly *Pieris brassicae* L. Philos Trans R Soc Lond B Biol Sci 239:1–43
- Hepburn HR (1971) Proboscis extension and recoil in Lepidoptera. J Insect Physiol 17:637–656
- Jones JC (1977) The Circulatory System of Insects. Thomas CC (ed) Springfield, Illinois, USA pp 89–90
- Krenn H (1985) *Artogeia (Pieris) rapae* L. (Pier.) – Rüsselbewegungen und Nahrungsaufnahme. Film C 1819 des ÖWF Wien (Österreichisches Bundesinstitut für den wissenschaftlichen Film)
- Kristensen NP (1968) The Anatomy of the Head and the Alimentary Canal of Adult Eriocraniidae (Lep., Dacnonypha). Entomol Medd 36:239–292
- Kristensen NP, Nielsen ES (1981) Intrinsic proboscis musculature in non-ditrysian Lepidoptera – Glossata: Structure and phylogenetic significance. Entomol Scand Suppl 15:299–304
- Matsuda R (1965) Morphology and evolution of the insect head. Mem Am Ent Inst 4:215–221
- Nilsson AL (1989) The evolution of flowers with deep corolla tubes. Nature 334:147–149
- Pradhan S, Aren NS (1941) Anatomy and musculature of the mouthparts of *Scirpophaga nivella* (Pyr.), with a discussion on the coiling and uncoiling mechanisms of the proboscis in Lepidoptera. Indian J Entomol 3/2:179–195
- Romeis B (1968) Mikroskopische Technik. 16th edn München, Wien, Oldenburg
- Schmitt JB (1938) The feeding mechanism of adult Lepidoptera. Smithsonian Misc Collect 97/4:1–28
- Smith JJB (1985) Feeding Mechanisms. In: Kerkut GA, Gilbert LI (eds) Comprehensive Insect Physiology, Biochemistry and Pharmacology. Vol 4. Pergamon Press, Oxford New York Toronto Sydney Paris Frankfurt, pp 64–67
- Vasudeva S (1956) Studies on the Morphology of the Common Lemon Butterfly *Papilio demoleus* L. J Zool Soc India 8/2:211–234