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.

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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.

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1. Introduction

The present study ensued from the discovery of a new feeding habit in Lepidoptera, i.e. the sucking of blood by puncturing the skin of mammals, found in the Noctuid *Calpe* [= *Calyptra*] *eustrigata* Hmps. in Malaya (BÄNZIGER, 1968). Since the hosts of this unique lepidopterous parasite proved to be Ungulates (water buffalo, sambar deer, Malayan tapir and nilgai antelope) and under experimental conditions also man, the moth can be regarded as a potential vector for infectious diseases and may thus be of veterinary and medical importance. It is therefore most desirable to come to a correct understanding of the piercing mechanism of the moth and this was the primary aim of the present investigation. However, on account of the rarity and difficulty in obtaining *C. eustrigata,* the research was carried out on the closely related fruit-piercing moth *C. thalictri* Bkh., the two species resembling each other so strongly that only the comparison of the genitalia allows their exact determination. Moreover, observations confirmed that the piercing behaviour of the fruit-piercing and the skin-piercing moths is very similar (BÄNZIGER, 1969).

Fruit-piercing moths are well-known in the tropics because of the damage they cause to sweet fruits by piercing them and sucking up the juice, thus causing indirectly their decay. Most of the works on fruit-piercing moths deal with the economic importance, the control measures, the pest and plant relationship, and the bionomics of the moths. Recorded details on the mode and mechanism of

piercing are scarce. DARWIN (1875) and BREITENBACH (1877, 1878, 1882) were the first to advance theories on the method of piercing used by such moths. However, their studies were based only on the morphology of the proboscis of dried specimens of fruit-piercing moths and their assumptions, therefore, had to remain rather theoretical.

Some fourty years later HERING (1926) reported that still no observations on the actual piercing had been made and that even the probability of a piercing act taking place was much discussed. However, he hinted that "the proboscis could be compared with a saw, and that the halves of the proboscis can, to a certain extent, be moved against each other". According to KING & THOMPSON (1958) the Noctuid *Gonodonta nutrix* Cram. pierces oranges by pressing the tip of the proboscis against the fruit and by oscillating the central part of the proboscis to the right and the left. NEUBECKER (1966) distinguished the vertical and rhythmic head movement of a piercing *Sphingomorpha chlorea* Cram. from the vertical and lateral movement of *Serrodes partita* F. So far no integral analysis of the piercing movements and their mechanisms has been issued.

C. thalictri is known as a fruit-piercing moth in Japan (CLAUSEN, 1927; NOMURA & HATTORI, 1967) and has recently been observed attacking different fruits in Switzerland (Bänziger, in preparation). The piercing behaviour of *C. thalictri* (Fig. 1) is corresponding almost exactly to that of *C. eustrigata* (Fig. 2) and it is likely that the piercing mechanisms involved are based on the same principles. The verification of this is planned.

2. Description of the piercing behaviour

For the sake of clarity the piercing behaviour of *C. thalictri* is described first.

After having settled on a fruit, e.g. a grape, the moth palpates the skin. If a point suitable for piercing is found, the proboscis is thrust onto the skin of the fruit (Fig. 3) and the body assumes an angular position. Viewed from the side the proboscis has a slight S-like shape; the tip lies more or less between the protarsi. The clinging movements of the forelegs give an indication of the great efforts involved in pressing the proboscis against the fruit. The proboscis now performs a vibrating action during which the central part of it is bent out laterally, whereas the base and the tip remain in a fixed position (Figs. 4 to 5). Since the frequency of this vibration is higher than the flicker fusion frequency of the human eye, the movement of the proboscis simulates a two dimensional "spindle". The vibration is accompanied by an equally rapid, but nearly imperceptible oscillation of the head. After having pierced the skin of the fruit the proboscis can penetrate the pulp with a relative easiness and sink its whole length into the fruit within a few seconds. Just after the skin has been pierced, the spindle disappears and the proboscis remains straight (Figs. 7 to 9). The oscillations of the head (around the longitudinal axis of the moth) now become slower and very pronounced (Figs. 7 to 8), reminding us of the balance wheel of a watch. If the halves of the proboscis, i.e. the galeae, are marked

and observed with a magnifying glass, it is possible to see that they are displacing very quickly along their longer axis in opposite directions (Figs. 7 to 8). These anti-parallel movements, together with the peculiar armature of the proboscis are responsible for its easy and deep penetration. It is interesting to note that while the proboscis penetrates deeper and deeper into the fruit only the head is lowered whereas the rest of the body maintains its position. This gives the impression that the head pushes the proboscis into the fruit. However, as it will be shown later on, the reverse is true, i.e. the proboscis draws the head towards the fruit.

Having reached a certain depth the proboscis is withdrawn, though usually not completely, and then sinks again into the pulp, forming a new shaft beneath the old one (Figs. 9 to 10). The oscillations of the head and the anti-parallel movements of the galeae take place also during the withdrawal. The piercing act may last from 10 to 30 minutes or longer. The procedure of piercing a soft fruit, such as a peach, may be somewhat modified. The skin of soft fruit is often torn so easily that the spindle effect is much reduced.

Apart from the duration and the intensity of the single movements, the piercing behaviour described corresponds closely to that of the blood-sucking *C. eustrigata.*

3. Functional morphology of the piercing apparatus

3.1. Head and inner mouth-parts

The following description is restricted to those parts of the head and the appendages of *C. thalictri* which are directly involved in piercing, i.e. the maxillae with cardo, stipes and galea and the muscles acting on them (Fig. 11 to 13).

The cardo has the shape of a ventrally convex hemisphere and has two articular extremities linked with the hypostoma of the head and the stipes respectively. No muscles are attached to the cardo whose function, as we shall see, consists mainly in facilitating the movement of the galeae (Figs. 14 to 15).

The very complicated shape of the stipes may be described as consisting of a cylindrical and a more or less flat part. The first has a slit-like aperture opening into the head cavity. Proximally the stipes is linked by a condyle to the cardo and extends a processus into the cavity of the latter (Fig. 13). The distal end of the stipes merges directly into the galea, thus forming a relatively rigid joint in shape of a right angle (Fig. 13). The stipes is linked along the whole of its external edge to
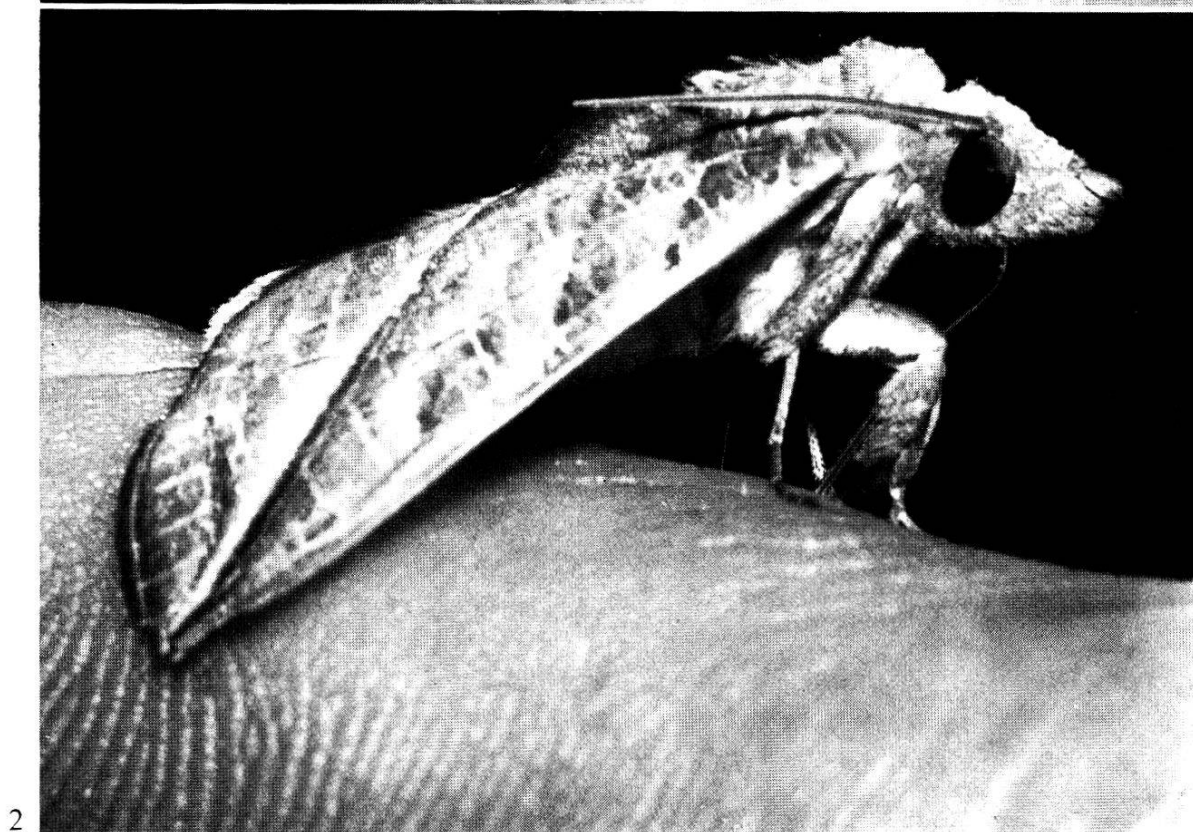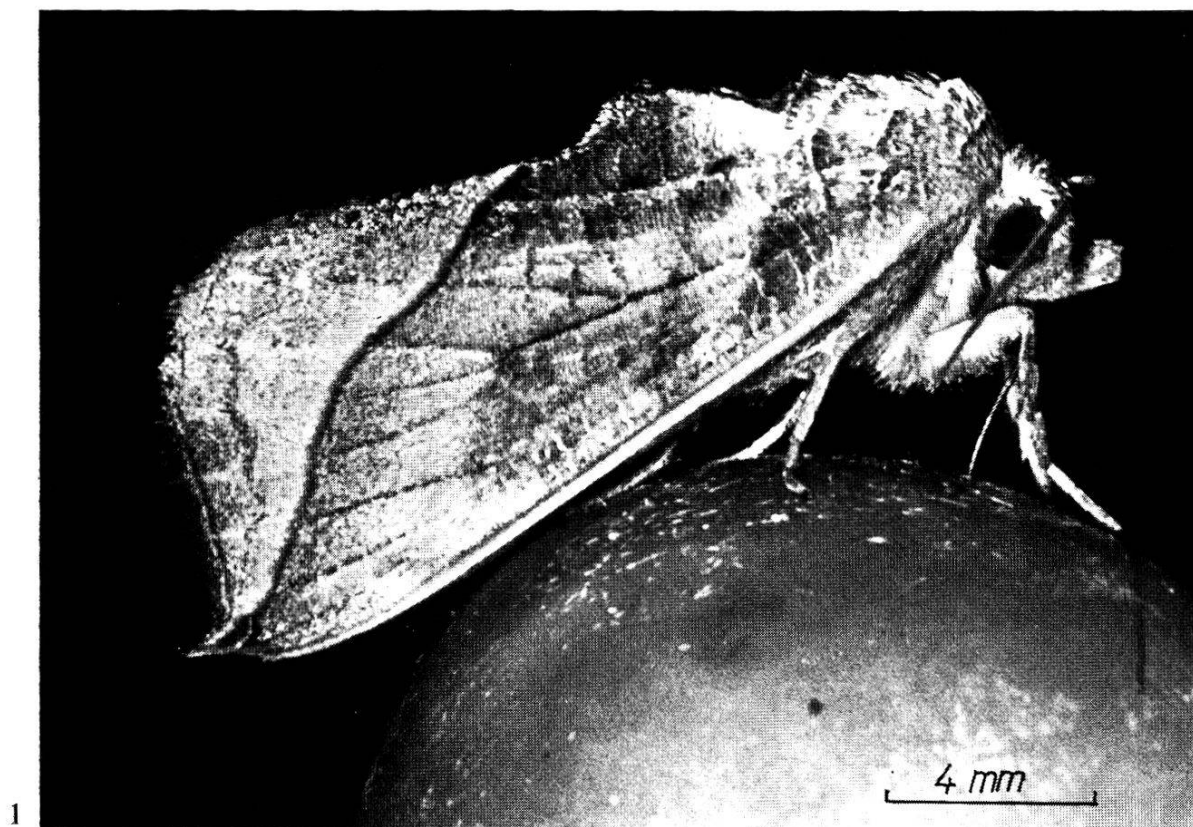
Fig. 1. Calpe thalictri piercing a grape. The different inclination of the wings detracts from the otherwise strong similarity with the species below.

Fig. 2. Blood-sucking moth *Calpe eustrigata* piercing the author's finger.

Fig. 3. Frontal view of *C. thalictri* thrusting the proboscis onto the grape. The erected position of the barbs indicates the high blood-pressure present in the proboscis which is much stiffer in this turgescent state.
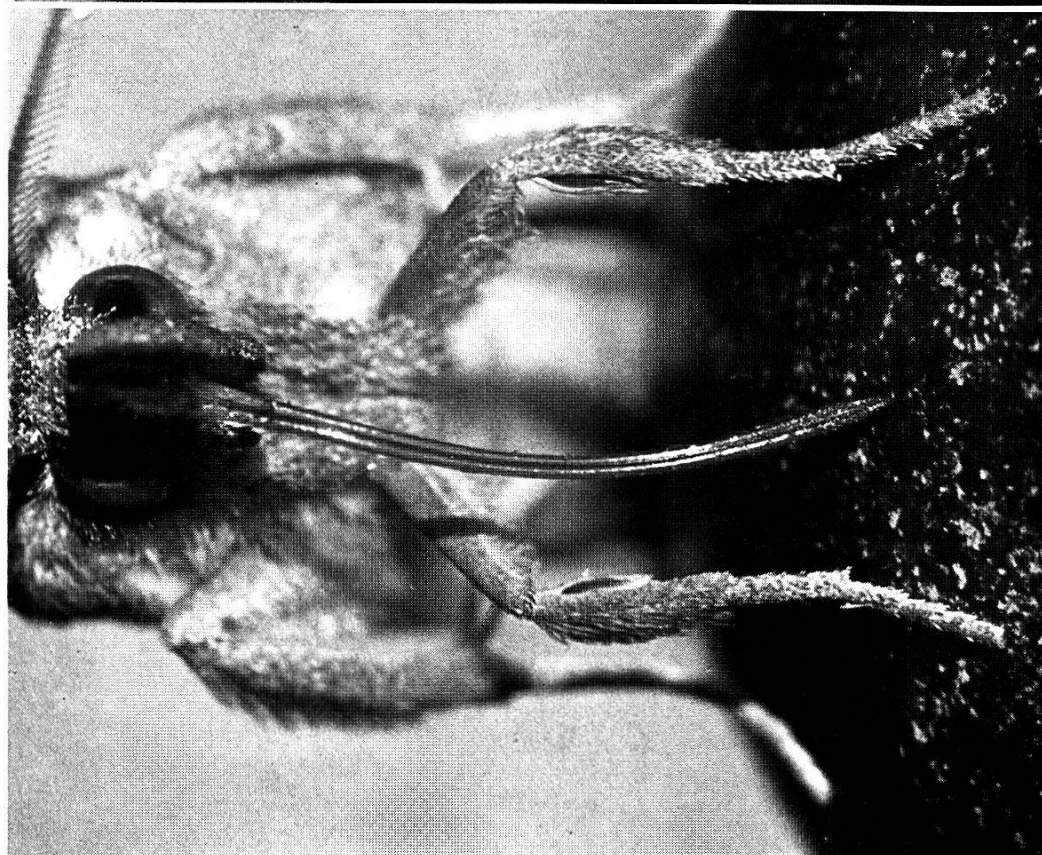
Fig. 4. *C. thalictri* trying to pierce the skin of the grape. The proboscis performs the "spindle" movements. The galea lieing on the outer side of the arcuation is protracted, that of the inner side is retracted (= anti-parallel movements of the galeae), as it can be seen at the end of the proboscis.

Fig. 5. Same as Fig. 4 but galeae displaced in reversed order. (Further explanations on p. 74.)
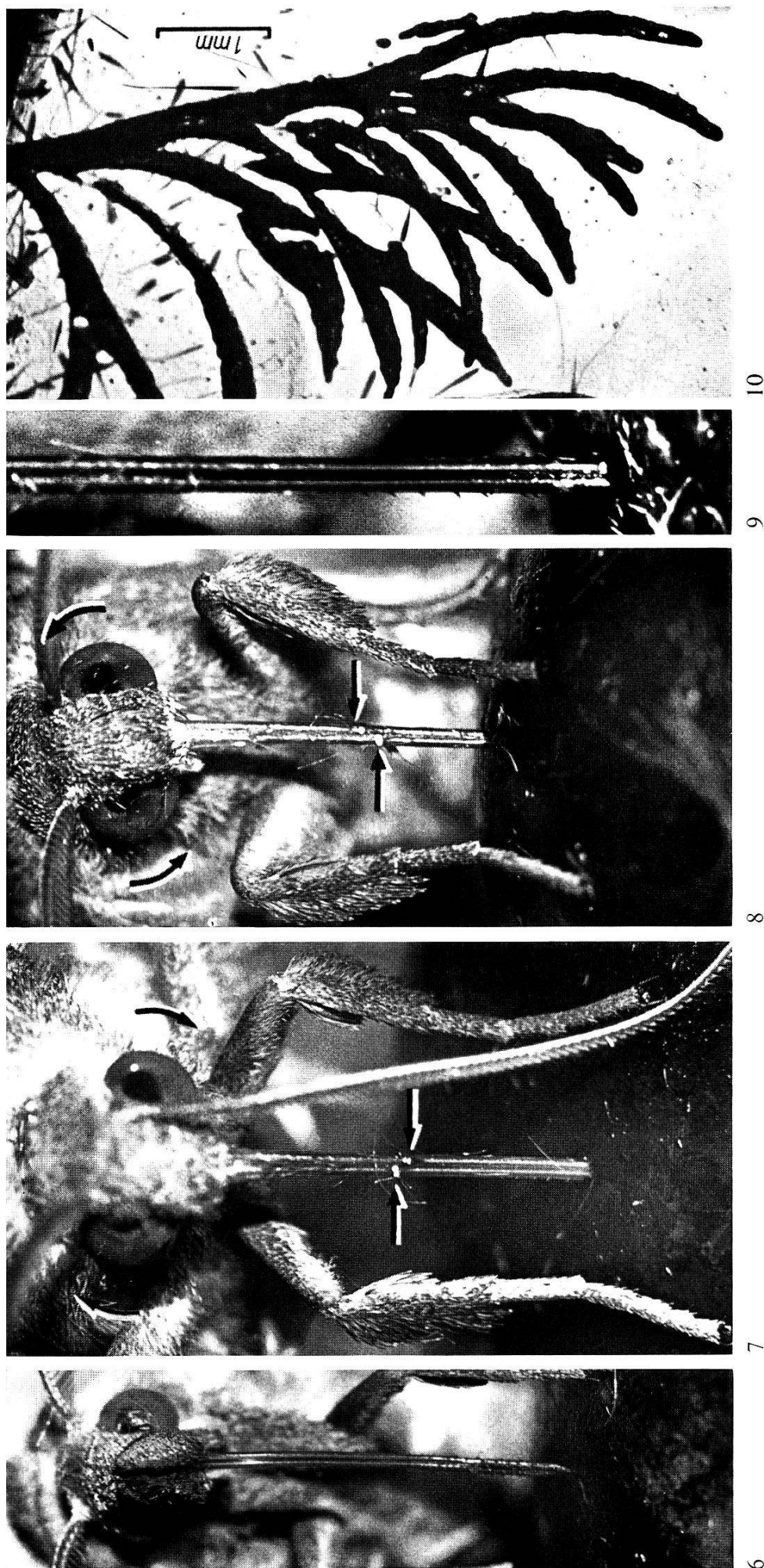
Fig. 6. Same as Figs. 4 and 5 but at phase when the proboscis is straightened by the action of unequal blood-pressure in the two galeae and/or the oblique muscles. Note the markedly displaced state of the galeae.

Fig. 7. The proboscis of *C. thalictri* is penetrating into the pulp of the grape. The anti-parallel displacement of the galeae is shown by the position of the "micro-mirrors" on the proboscis: one galea is retracted and the other protracted. The head is oscillating and is clearly turned. The barbs are erected.

Fig. 8. Same as Fig. 7 but in the phase when both anti-parallel movements and oscillation of the head are reversed.

Fig. 9. Partial withdrawal of the proboscis. Note the erectile barbs which are inclined towards the tip of the proboscis.

Fig. 10. Shafts bored into the agar through a single entrance hole. The branchings are due to repeated partial withdrawals and new penetrations.

the head capsule. This link shows local variations in stiffness. The stiffest part of the joint lies approximately in the centre, so that the movements articulate mainly around this point (Fig. 15).

SCHMITT (1938) found that the slit-like opening of the stipes can be closed like a valve by the stipital muscles and that by this muscle action the cavity of the stipes is reduced in volume, thus forcing the haemolymph into the galea. The hypothesis by SNODGRASS (1935), who
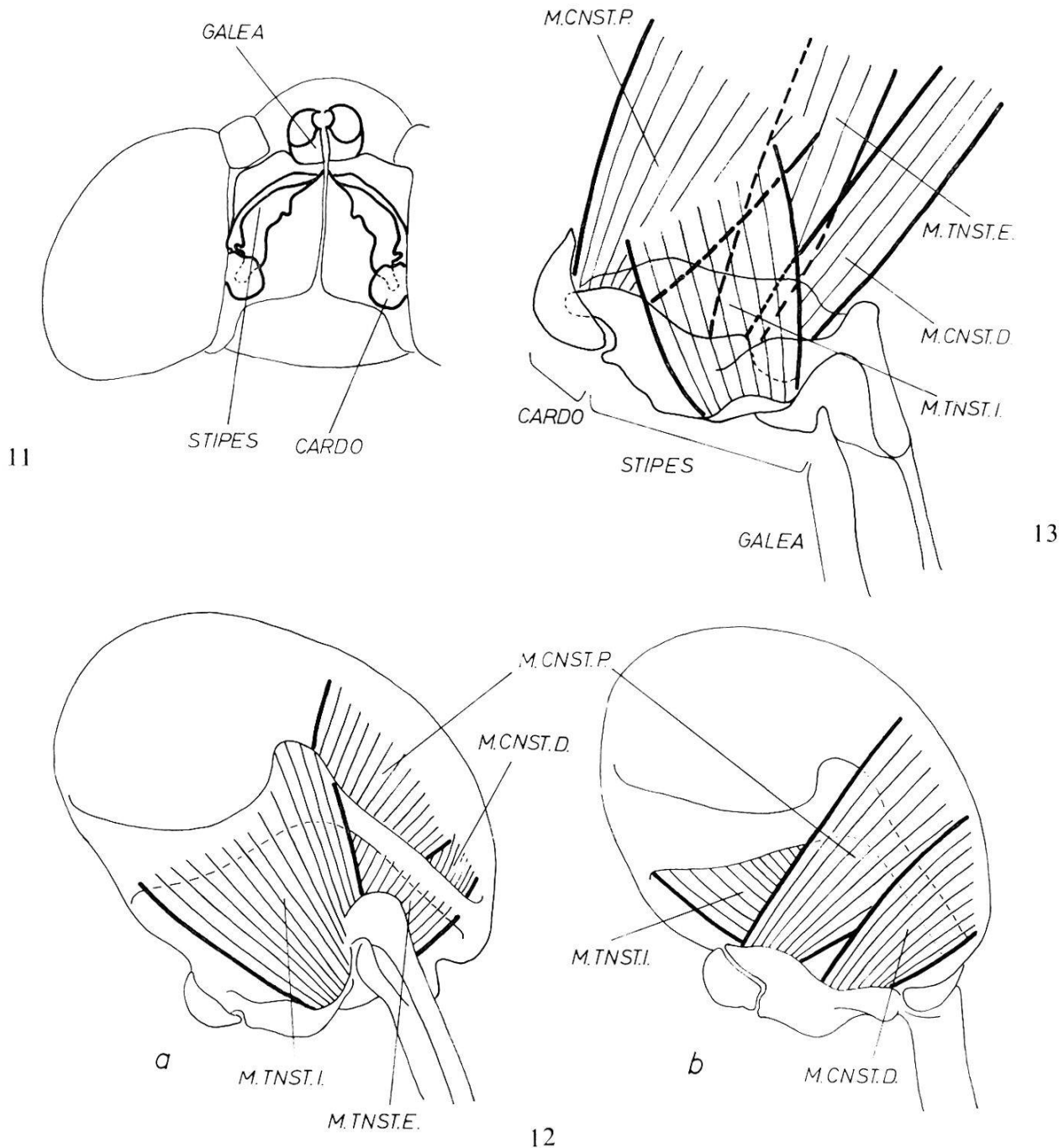
Fig. 11. Ventral view of head.
Fig. 12. Stipital musculature, a) mesal view from inside and b) lateral view.
Fig. 13. Mesal view of left maxilla and muscles attached to stipes.

M.CNST.P. = *musculus craniostipitalis proximalis; M.CNST.D.* = *musculus craniostipitalis distalis; M.TNST.I.* = *musculus tentoriostipitalis internus; M.TNST.E.* = *musculus tentoriostipitalis externus.*

assumed that the proboscis extension in Lepidoptera is possibly brought about by blood-pressure in the haemocoel of the galea, a mechanism similar to that of a toy paper "snake", could thus be confirmed. Coiling is caused mainly by the oblique muscles and to a certain degree by the proboscis' own elasticity. In more recent years new theories on the extension and coiling mechanisms of the lepidopterous proboscis have been advanced (PRADHAM & AREN, 1941; EASTHAM & EASSA, 1955; WIGGLESWORTH, 1964). Because of its importance for the present study, the extension mechanism was the object of a thorough study which proved the correctness of the blood-pressure theory. The results are being published in a separate paper (BÄNZIGER, in the press).

The muscles of the stipes directly responsible for the functioning of the piercing mechanism show an interesting development that to our knowledge, differs from all the stipital muscles studied in Lepidoptera. In the primitive Eriocranidae and Micropterygidae the muscles directly connecting cranium and stipes are few, i.e. one (KRISTENSEN, 1968) and two (HANNEMANN, 1956), respectively. In higheɪ Lepidoptera SCHMITT (1938) found a maximum amount of three stipital muscles, or less in species with reduced mouth-parts. Even in related Noctuids such as *Catocala,* only three muscles occur. We found in *C. thalictri,* as well in *Scolyopteryx libatrix* L., another fruit-piercing moth (BÄNZIGER, 1969), at least 4 muscles[1]. As well as to their number the muscles also differ as to their spacial arrangement from those of the other Lepidoptera (Figs. 12 and 13). The *musculus tentoriostipitalis internus (m.tnst.i.)* is attached to the proximal arm of the tentorium and to the distal apodeme of the stipes, the *musculus tentoriostipitalis externus (m.tnst.e.)* to the distal arm of the tentorium and nearby the valve of the stipes, the *musculus craniostipitalis proximalis (m.cnst.p.)* to the clypeus and to the proximal processus of the stipes, the *musculus craniostipitalis distalis (m.cnst.d.)* to the clypeus (ventro-distally of the *m.cnst.p.*) and nearby the valve of the stipes.

The *m.tnst.i.* and the *m.cnst.p.* are much more developed than the *m.tnst.e.* and the *m.cnst.d.* A contraction of the latter two closes the blood-pressure valve and compresses the stipes, as described by SCHMITT (1938). The *m.tnst.i.* and the *m.cnst.p.* act as galea retractor and protractor respectively. For the sake of clarity these functional terms will be used in this paper. These muscles cause the anti-parallel movement of the galeae by retracting one galea and simultaneously protracting the other and *vice versa.* If, for instance, the right galea is to be protracted, its galea protractor contracts and draws the proximal part of the right stipes together with the swivel-linked cardo towards the rear. Since the stipes has an articulating joint connecting with the head, the distal part

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[1] The *musculus tentoriostipitalis internus* may possibly be considered as consisting of two muscles.
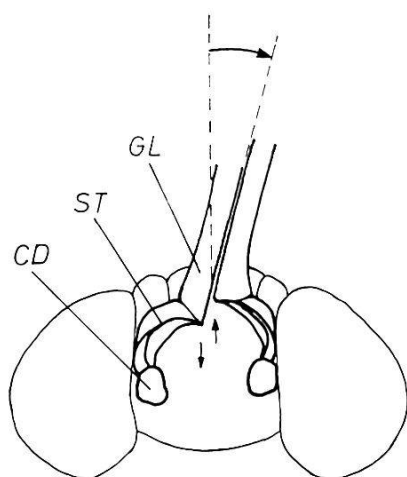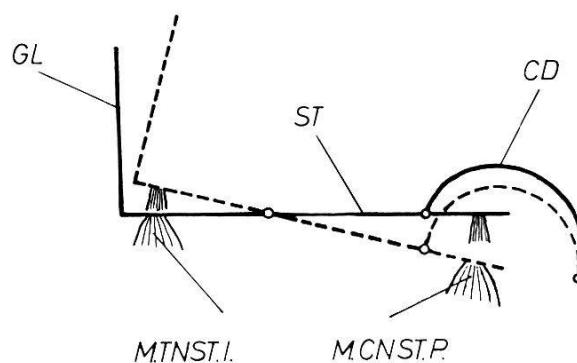
Fig. 14. Ventral view of head with galeae displaced in opposite (anti-parallel) directions and turned aside.

Fig. 15. Anti-parallel galea displacement and turning aside of the galea. (Diagrammatic.)

CD = cardo; *ST* = stipes; *GL* = galea; *M.CNST.P.* = *musculus craniostipitalis proximalis* (galea protractor); *M.TNST.I.* = *musculus tentoriostipitalis internus* (galea retractor).

of the stipes together with the galea will move in the opposite direction, i.e. advance (Fig. 15). In addition to this, the galea will turn laterally to the right (not more than some 15°) on account of the stiff link between stipes and galea (Fig. 14) and the lateral inclination of the stipes. Simultaneously the retractor of the left galea draws the distal part of the stipes together with the galea towards the rear. The left galea turns also to the right, again because of the stiff link between galea and stipes (Fig. 14). The extent of the anti-parallel displacement of the galeae amounts to 3 to 4% of the total length of the proboscis, i.e. the right galea advances 0.2 mm and the left recedes 0.2 mm. The effect is equivalent to an elongation of the proboscis of 0.2 mm. The lateral turning of the proboscis as a secondary effect of the anti-parallel displacement of the galeae is of great importance when the moth tries to pierce the skin of the fruit.

3.2. The proboscis

In nectar-sucking and non-piercing fruit-sucking moths the proboscis tapers gradually from the base towards the tip (Fig. 16 d, e). In *C. thalictri, C. eustrigata* and *S. libatrix,* however, only an almost imperceptible tapering of the proboscis occurs from the base approximately to the middle of the length, after which the proboscis thickens again almost imperceptibly towards about $^1/_{12}$ of its length from the tip, where a sudden, nearly triangular pointing is noticed (Fig. 16 a to c).
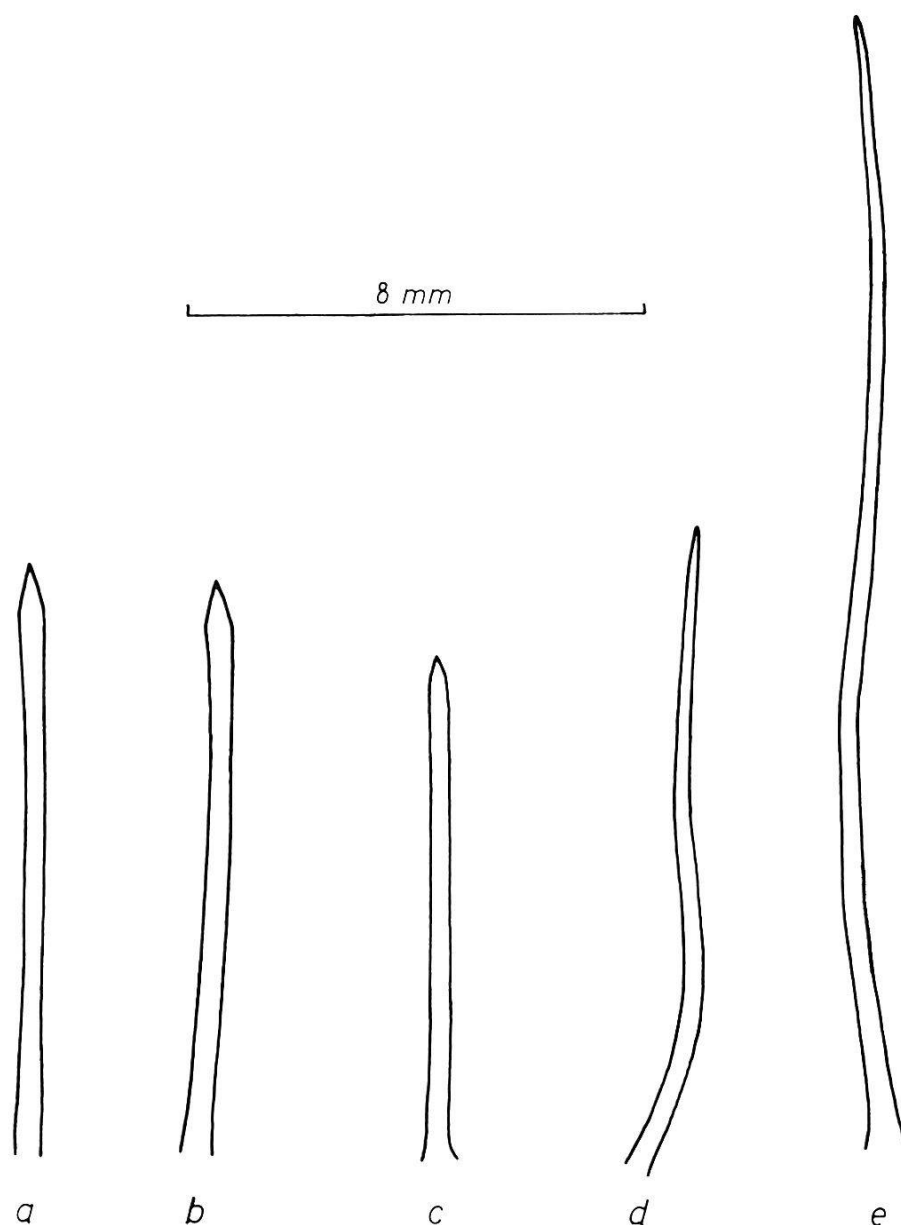
Fig. 16. Dimensions of proboscis of some noctuid moths. a) *Calpe thalictri* (fruit-piercing); b) *C. eustrigata* (skin-piercing blood-sucking); c) *Scolyopteryx libatrix* (fruit-piercing); d) *Lygephila craccae* (non-piercing fruit-sucking); e) *Autographa gamma* (nectar-sucking).

The proboscis is formed by the two grooved galeae which enclose the food canal of the proboscis (Fig. 17). The galeae are held together dorsally and ventrally by two rows of interlocking processi (RÉAUMUR, 1734; BREITENBACH, 1882; EASTHAM & EASSA, 1955). This kind of link does not prevent the anti-parallel movement of the galeae, this being an important prerequisite enabling the moths to pierce. The transverse section of the galea has the shape of a full crescent. The inner walls of the galeae, i.e. the lining of the food canal, consist of exocuticula (Fig. 17), the outer walls of endocuticula with annuli of exocuticula embedded in them. This combination of relatively soft endocuticula and stiffer exocuticula gives the proboscis the necessary suppleness for coiling and at the same time a certain degree of stability.

17   GL.HC.   NV.   TR.   F.C.   S.O.M.   P.O.M.

18
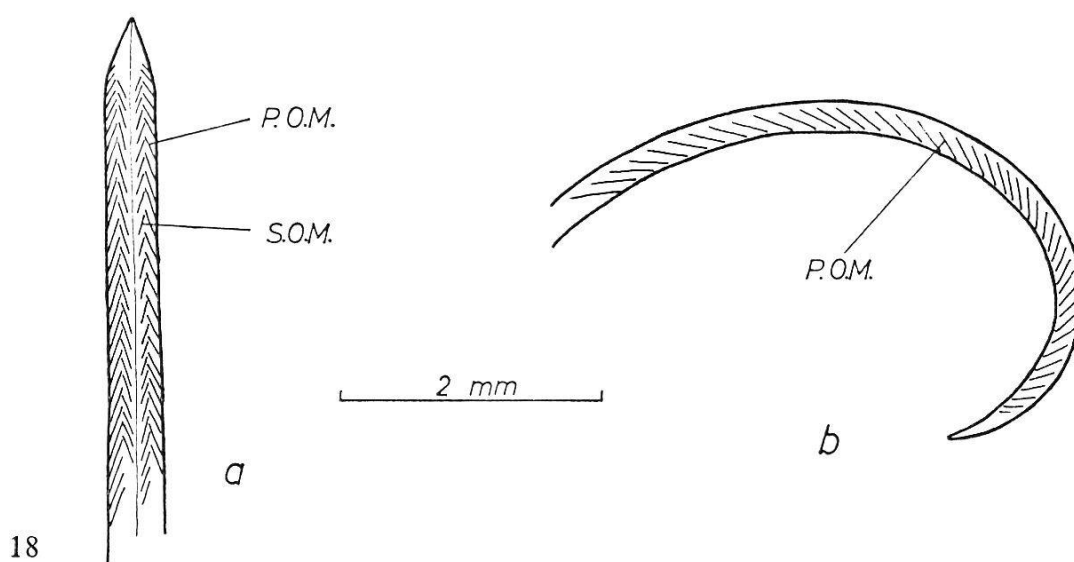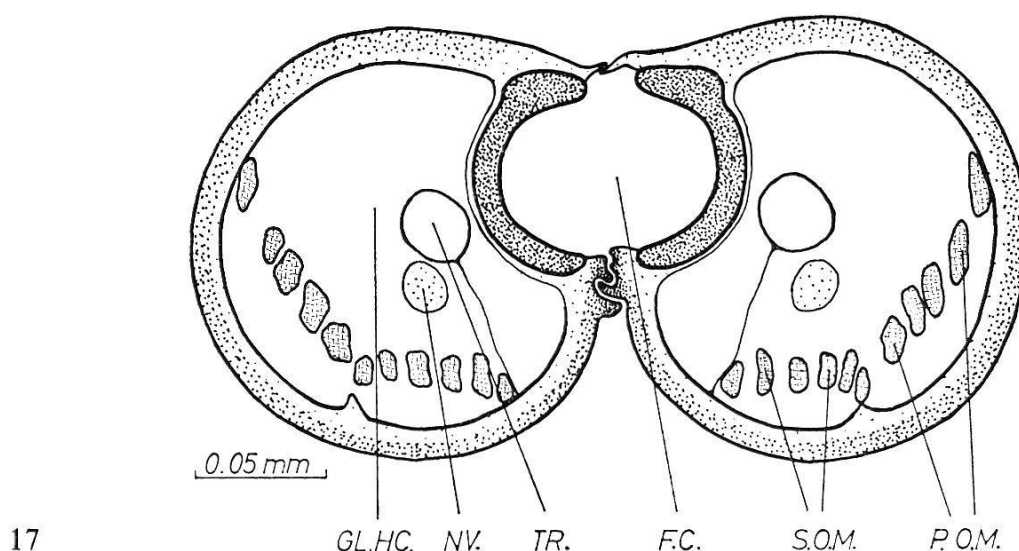
Fig. 17. Transverse section of proboscis.

Fig. 18. Longitudinal sections of median and distal region of proboscis showing the galea musculature a) from above and b) from the side.

F.C. = food canal; *GL.HC.* = galea haemocoel; *NV.* = nerve; *P.O.M.* = primary oblique muscle; *S.O.M.* = secondary oblique muscle; *TR.* = trachea.

Each galea of *C. thalictri* has two sets of muscles which occur throughout the whole length of the proboscis (Figs. 17 and 18). The muscles of the first set, the primary oblique muscles after EASTHAM & EASSA (1955), are oriented in a proximal-distal manner from the dorso-lateral wall to the medio-ventral wall. The second set, the secondary oblique muscles, are oriented in a proximal-distal manner from the inner part of the ventral wall to the middle of the ventral wall. In *Pieris brassicae* L. only a few secondary oblique muscles are found in a very restricted area causing there the "knee bend" as described by EASTHAM & EASSA (1955).

C. thalictri, S. libatrix, and to a much lesser degree *P. brassicae,* can uncoil their proboscis to such an extent that full extension is surpassed and the proboscis is turned upwards and backwards. We will term this movement hyper-uncoiling.

Unlike *P. brassicae,* both *C. thalictri* and *S. libatrix* are capable of curving their proboscis laterally. There are two possible agents for such a movement: blood-pressure and/or muscle action. It can be shown by experiment that, if in a proboscis the blood-pressure of one galea is higher than that of the other, the lateral and ventral walls of the first are more dilated, causing the proboscis to curve laterally and somewhat upwards. However, the degree of this induced lateral curvature is always less than that normally performed by the moth. An additional action of the oblique muscles is therefore not improbable. The simultaneous action of both sets of muscles produces normal coiling in all three species investigated. This has been proved by electric stimulation causing all muscles to contract simultaneously. Unfortunately, it was not possible to stimulate only one set of muscles – either primary or secondary – and thus study the effect of each set alone. Since *P. brassicae* cannot bend the proboscis laterally and since the secondary oblique muscles are almost entirely lacking in this species, it seems likely that the additional lateral curvature in *C. thalictri* and *S. libatrix* is caused by the secondary muscles. However, the orientation of the primary muscles does not appear to be less favourable in causing the lateral movement. We therefore cannot ascertain whether the first or the second set of muscles or a combination of blood-pressure with one of the two sets of muscles is finally responsible for this movement.

3.3. The armature of the proboscis

One of the most interesting and important features of the proboscis of the fruit-piercing moths is the armature. KÜNCKEL (1875), DARWIN (1875), READ (1878) and especially BREITENBACH (1877, 1878, 1882) studying mainly the proboscis of the fruit-piercing species *Othreis fullonia* Cl. and *Achaea lienardi* Bsd. distinguished different structures which they called in turn: hooks, barbs, teeth, spines, hairs etc. MÜLLER (1877) interpreted them as gustatory papillae, whereas GUYÉNOT (1912) ascribed a tactile function to them. FRINGS & FRINGS (1956) proved the presence of chemoreceptors on the proboscis of a number of non-piercing Lepidoptera. TAYLOR (1957) described setae, bristles, teeth and papillae of proboscides in the most important lepidopterous families. NEUBECKER (1966) found that the tip of the proboscis of some fruit-piercing species is sharp and reinforced, whereas in others it is

Fig. 19. Distal part of proboscis and armature of some noctuid moths. a) *Calpe thalictri* (fruit-piercing); b) *C. eustrigata* (skin-piercing blood-sucking); c) *Scolyopteryx libatrix* (fruit-piercing); d) *Lygephila craccae* (non-piercing fruit-sucking); e) *Autographa gamma* (nectar-sucking).

blunt and not reinforced. The first species are able to pierce a grape, the latter are not, probably because the blunt proboscis can find no hold on the smooth skin of a grape (NEUBECKER, 1966).

In this study of *C. thalictri, C. eustrigata* and *S. libatrix,* three morphologically and functionally different types of formations were found besides a small number of sensillae which shall not be described in detail.

The first type will be called tearing hooks. They have the shape of a somewhat squat hook whose point is curved backwards towards the
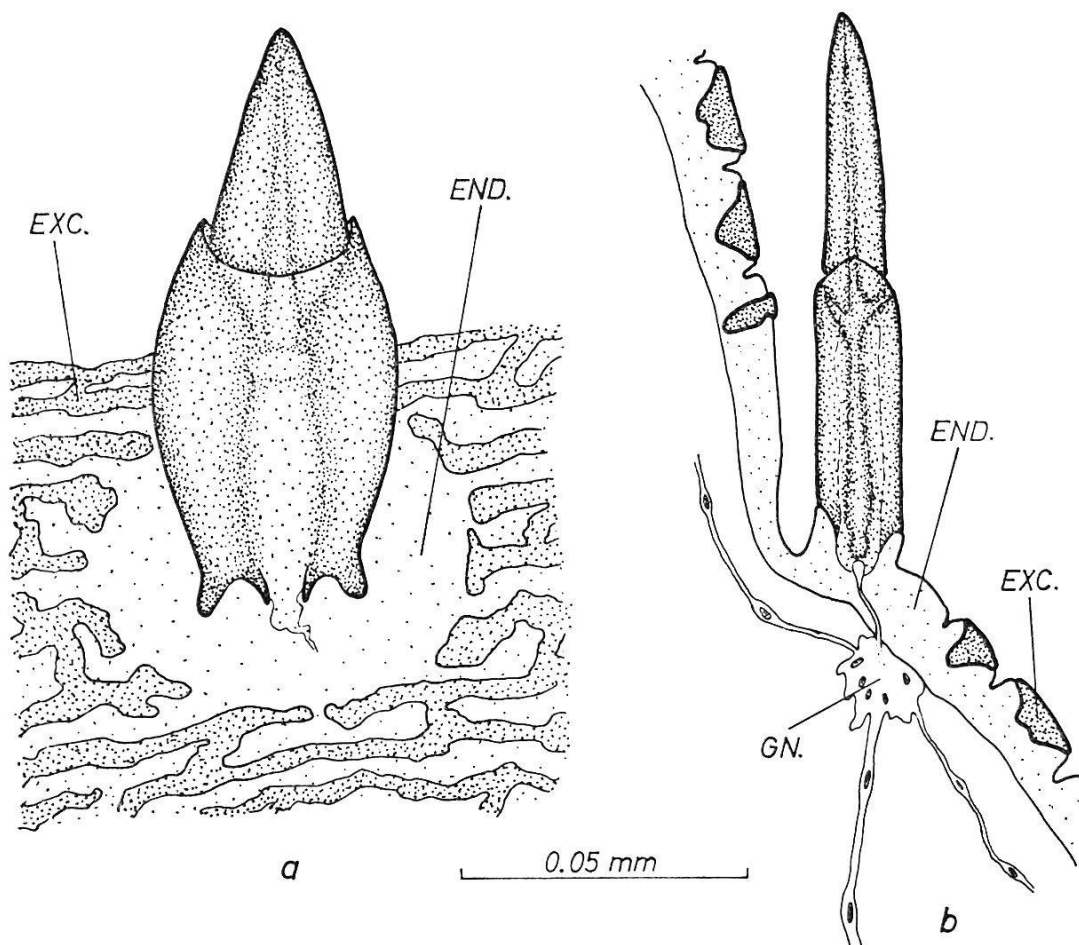
Fig. 20. Erectile barb from the lateral external galea wall, a) seen from the flat side and b) in lateral view. *END.* = endocuticula; *EXC.* = exocuticula; *GN.* = ganglion.

head. More than 25 of them are arranged around the tip of the proboscis (Figs. 19 a, b and 24). They are fixed rather firmly to the proboscis. Their main task is to tear open the skin of fruits.

The second type, the erectile barbs, are shaped like pointed blades (Fig. 20). They consist of two parts, a flat cylindroid socket and a dagger-shaped processus. The socket of the erectile barbs near the food canal bears long spine-like processes (Fig. 22). The erectile barbs are innervated (Fig. 20 b); but it is not yet known whether they are

DISTAL SIDE

BLOOD

PRESSURE

PROXIMAL SIDE
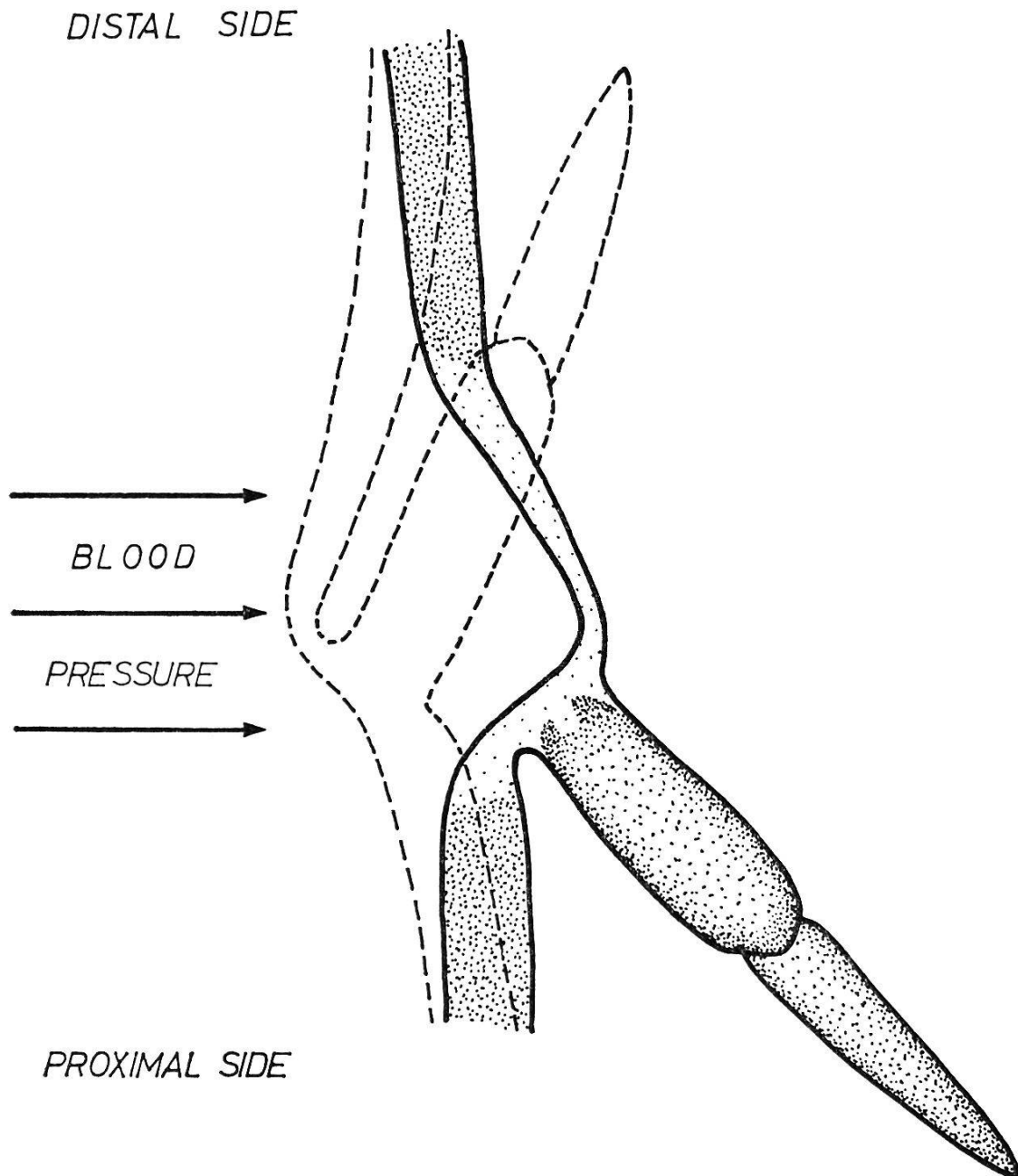
Fig. 21. Mechanism of erection of erectile barb: full drawing = situation at high blood-pressure; pointed lines = situation at low pressure.

sensitive to mechanical and/or chemical stimuli. They number well over 150 and are disposed mainly dorsally and ventrally on the distal half of the proboscis but not around the tip (Figs. 19 a, b, c and 25). It was found that the barbs can be actively erected by blood-pressure – a fact which makes them unique in the insect world. The wall of the galea around the joint of the erectile barb consists of endocuticula. It is therefore more flexible than the rest of the wall (Fig. 20 a, b). The elastic area is asymmetrically depressed. The barb originates at the proximal part of the depression and inclines forward towards the tip of the proboscis when at rest. If the blood-pressure in the galea is increased by the compression of the stipes, the elastic cavity bulges out

(Fig. 21). Thus the barb becomes erected on a protrusion and is then inclined in the opposite direction, i.e. backwards. After the blood-pressure has decreased, the return to the resting position is ensured by the elasticity of the galea wall. Since no muscles are attached to the barbs their erection is solely caused by blood-pressure.

The erection of the barbs can be observed under the stereomicroscope simply by squeezing with a forceps a living or dead proboscis

0.05 mm

L. DENT.

R. SP.

22   23
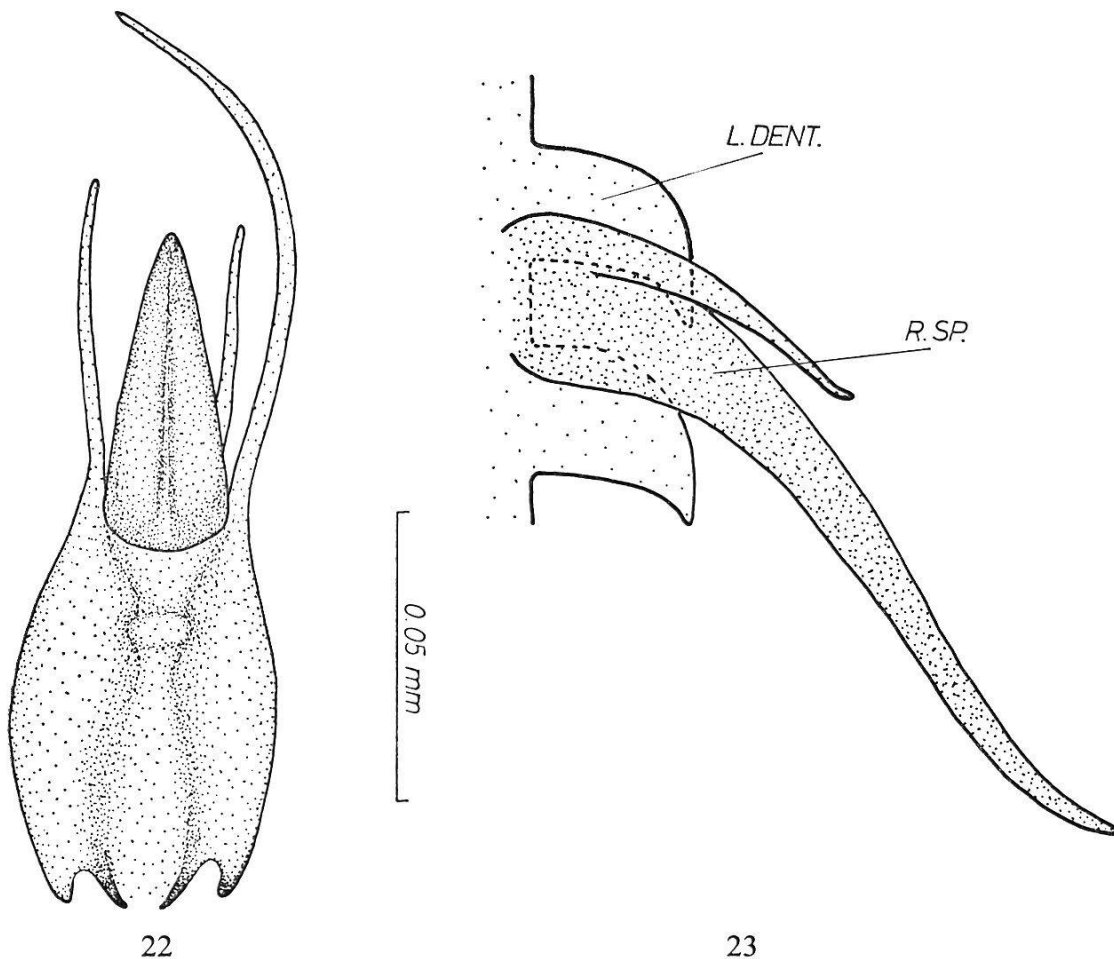
Fig. 22. Erectile barb with processi from the region of the opening of the food canal.

Fig. 23. Rasping spine *(R.SP.)* and linking denticles *(L.DENT.).*

in its extended state. This condition is necessary because the barbs can be erected only after the proboscis has been extended, which is also true when the moth is alive. Evidently the erection of the barbs needs a higher pressure than the stretching of the proboscis. A proboscis can be artificially extended by preventing the reflux of the blood contained in the galeae by tying off the proboscis at its base and by forcing the blood towards the tip by some additional knots tied distally from the first one. The squeezing of such a proboscis increases the blood-pressure and causes the barbs to erect. It is interesting to note that all barbs become erected almost at the same moment. This has

also been observed on the proboscis of moths puncturing fruit under natural conditions.

The further analysis of the mechanism of this erection shows that the barb is in a labile state when it reaches the vertical position. As the blood-pressure increases and the cavity is pushed towards the outside, the cuticle of the flexible area is subjected to an ever increasing longitudinal stress until the moment when it becomes flat. After that the stress diminishes. Thus a further increase in the pressure produces a sudden bulging out of the cuticle and at the same time the abrupt erection of the barb.

The third type, the rasping spines (Fig. 23), has no function directly responsible for the piercing. Their shape, disposition and manner of attachment suggest that their main task is to lacerate the pulp cells.

24   25
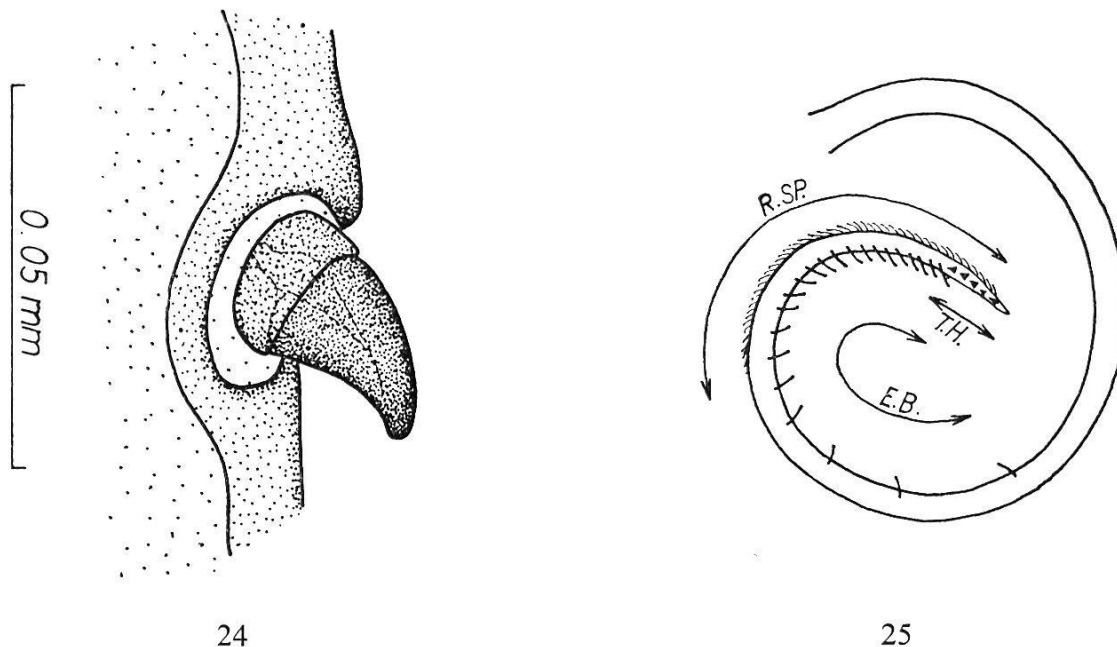
Fig. 24. Tearing hook from the region of the proboscis' tip.

Fig. 25. Lateral view of the proboscis, showing the distribution of the three structures of the armature. (Diagrammatic.) *E.B.* = erectile barbs; *R. SP.* = rasping spines; *T.H.* = tearing hooks.

They are spine-like in shape with a slender processus arising at their base. Unlike the erectile barbs they are firmly fixed and situated in two rows along the entrance to the food canal (Fig. 27). The rasping spines are oriented obliquely backwards and towards the spines of the opposite row, so that they become interlaced with each other (Figs. 26 and 27). This increases their stability and that of the link between the two galeae.

Figs. 26 and 27 depict the disposition of the rasping spines, the erectile barbs with processi and the linking denticles, the latter being involved, more proximally, in the linking of the two galeae. Fig. 25

DISTAL SIDE

PROXIMAL SIDE

26   27
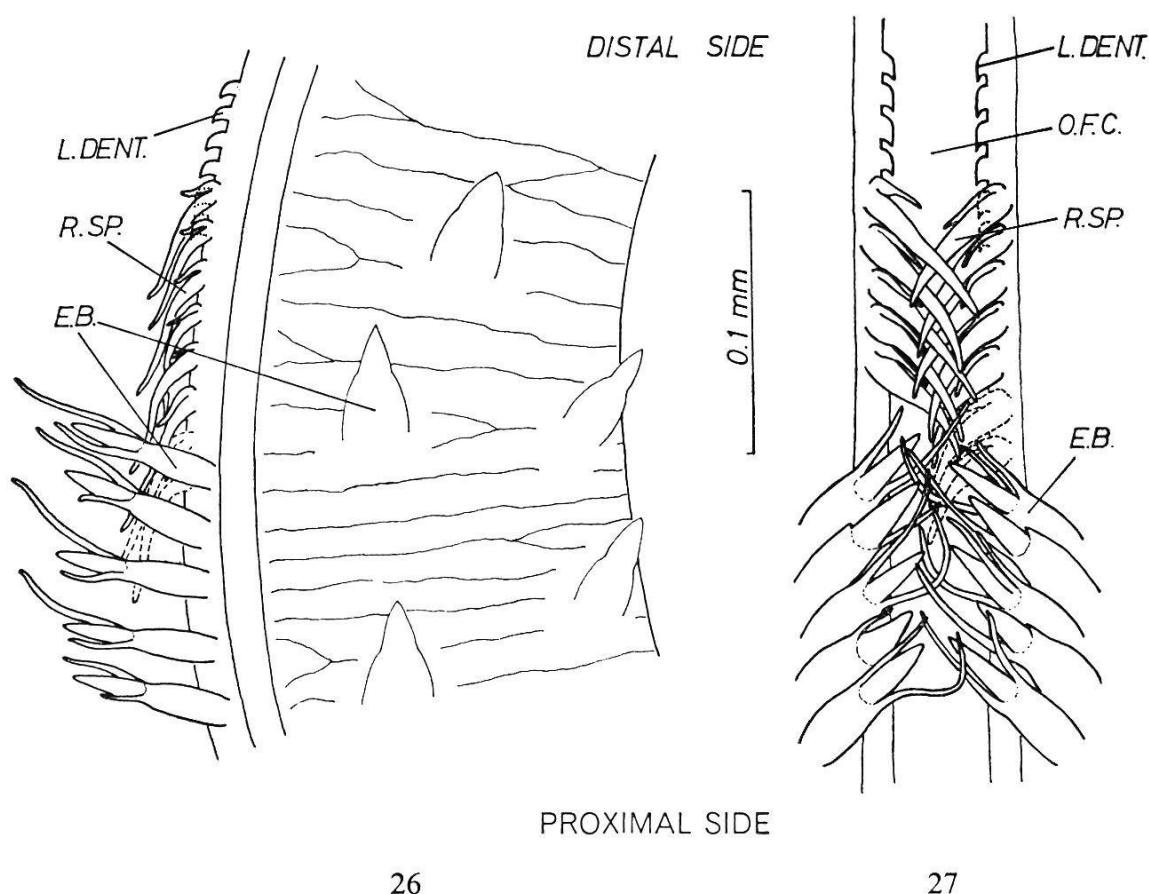
Fig. 26. Armature along the entrance to the food canal as seen in lateral view.

Fig. 27. Same as Fig. 26 seen from above (denticles, spines and barbs are in reality superposed, but for reasons of clarity they are shown in contiguity only).

E.B. = erectile barb; *L.DENT.* = linking denticle; *O.F.C.* = opening of food canal; *R.SP.* = rasping spine.

shows the distribution of the tearing hooks, erectile barbs and rasping spines.

The armature of the proboscis of the blood-sucking moth *C. eustrigata* (Fig. 19 b) presents no substantial differences when compared with that of *C. thalictri*. In the blood-sucking species the tip is more sclerotized, the tearing hooks are stronger and the erectile barbs remarkably elongated. The proboscis of the fruit-piercing *S. libatrix* (Fig. 19 c), on the other hand, is weaker than that of *C. thalictri* and has no typical tearing hooks. The function of these is assumed by a number of crenatures at the lateral edge near the tip of the proboscis. The erectile barbs are well developed and have long dagger-shaped processi.

A great number of other Noctuidae, which feed on the juice flowing out from over-ripe fruit or lick the pulp of fruit whose skin has been split or damaged otherwise (BÄNZIGER, 1969), have no tearing hooks and no erectile barbs on their proboscis. As may be seen in a typical example of a non-piercing fruit-sucking moth, such as *Lygephila crac-*

cae F. (Fig. 19 d), the structures on the proboscis consist of bristle-like sensillae which are not firmly fixed and cannot be erected. Consequently they are suitable neither for gripping nor tearing. The rasping spines are present, and it may not be impossible for such moths to rasp away the superficial cells of the pulp with these structures and thus obtain more sap. However, to prove this a special study will have to be carried out.

The simplest armature of the proboscis in Noctuids seems to occur in nectar-sucking species, e.g. *Autographa gamma* L. (Fig. 19 e). Only a very few hairs are present on their proboscides.

4. The piercing mechanism

4.1. First phase: the perforation of the skin

For the study of the very rapid movements a stroboscope was used and over 1000 flashlight photomacrographs were taken.

The piercing turned out to be composed of two separate phases, viz. perforation of the skin and penetration into the pulp. The photographs of the first phase show that besides the previously mentioned movements (i.e. spindle formation and reduced oscillations of the head) further features occur, normally invisible to the naked eye, not only because of the minute size of the object, but also on account of the rapidity with which the movements are performed: (i) the anti-parallel movements of the galeae, previously observed only during the second phase, (ii) the raised position of the erectile barbs which are oriented backward towards the head and (iii) the nearly vertical position of the tarsi. The frequency of the movement of the proboscis causing the spindle effect amounts to 16–19 cycles per second.

First the clearer facts shall be interpreted. The raised position of the tarsi (Fig. 5) gives evidence of the force employed to thrust the proboscis onto the fruit. The upright position of the erectile barbs (Fig. 3) shows that the haemocoel of the galeae is under high pressure. This turgescence confers on the proboscis as a whole the highest possible rigidity, which permits a better transmission of the stresses acting on it. At the same time, the teeth are ready to come into action as soon as the skin has been perforated.

The greatly reduced oscillations of the head are, in the first phase, only a passive compensatory reaction in answer to the lateral bending of the proboscis. The amplitude of the oscillations of the head is much too slight to be able to cause the bending. During the first phase the head is pulled firmly against the thorax in order to guarantee the effectiveness of the thrusting force of the head and the forming of the spindle.

What causes the formation of the spindle? The analysis of all the photographs taken shows clearly that in the bent state the galeae are definitely displaced in an anti-parallel sense, i.e. the galea lying on the outer side of the arcuation is always longer (protracted) than that on the inner side (retracted) (Figs. 4 and 5). The mechanism of the anti-parallel displacement with its secondary effect of turning aside the galeae has been explained on pp. 62 to 63 and Figs. 14 and 15. If these facts are considered the formation of the spindle is readily understandable. When the anti-parallel displacement induces the base of the proboscis to turn to one side, the tip of the proboscis which is thrust against the fruit cannot follow in that direction, consequently the proboscis will arcuate. Although it seems likely that the action of the oblique muscles and/or the unequal blood-pressure in the two galeae (discussed on p. 66) contribute to the bending of the proboscis, this has not been proved. Presumably, the spindle phenomenon allows the moth to bring particular effects of stress upon the surface of the fruit. Since the bent proboscis is longer than the secant line formed by it, it must produce an increasing pressure on the fruit when it is straightened, provided the distance between the head of the moth and the surface of the fruit is kept constant. Since this happens 30–40 times per second (twice per cycle), the skin of the fruit is strained by a rapid vibrating force, comparable to that of a pneumatic hammer. Although the efficacy of that force is reduced by the elasticity of the fruit's skin, this drawback is counterbalanced by the concentration of the force on an extremely small area. The minutely pointed tip of the proboscis measures not more than 80 μ^2. After the moth has tried to pierce the skin on a certain spot for about 10 seconds, the skin of that place, if not already torn open, has undergone some 350 thrusts.

Fig. 6 shows the galeae displaced in anti-parallel sense and the proboscis straight. This feature captured in several photographs can be explained only if we assume that the proboscis is straightened by a separate force, namely that of the unequal blood-pressure and/or the action of the oblique muscles. Thus the stress effect is remarkably enhanced, because in the displaced status the proboscis is longer and the tip of one galea only concentrates the whole stress on an even smaller area.

The objection that the movements simulating the spindle may result from yielding reactions of the proboscis due to an overwhelming stress from the head does not seem to be justified. First, a yielding of the proboscis would not cause it to bend laterally, but backwards or forwards since this is the line of least resistance. Second, the fact that the bending ensues alternatively to the right and to the left with high frequency and constant amplitude, is not compatible with the unpredictable occurrence of failure to withstand the thrust of the head.

It can be argued that the bending movements could bring the tearing hooks in contact with the skin which they would grip or scratch until a hole is made. In fact, this action of the proboscis cannot be excluded in the case of fruit with soft or rugose skin, such as peaches or oranges, and probably it is of some importance when the blood-sucking *C. eustrigata* pierces the skin of mammals, using the pores at the insertion point of the hairs as starting point (BÄNZIGER, 1968). However, the bending degree of the proboscis is not sufficient to bring the tearing hooks in contact with the skin of a grape. This fact indicates that such an action of the tearing hooks is not necessary for the primary perforation of the fruit's skin, although it may be helpful.

In all cases, however, the tearing hooks come to act after a little hole has been made. They rip the fruit's skin rapidly open to the needed size, i.e. the diameter of the proboscis. Normally less than one second is sufficient for this procedure, after which the second phase begins.

The sequence of the movements and forces at work during the first phase, illustrated in Fig. 28, thus are:

a) The moth clings firmly to the fruit. The proboscis, made stiff by high blood-pressure in the galeae is thrusted by the head against the fruit.

b) By the action of the protractor and the retractor muscles the galeae are displaced in anti-parallel directions, e.g. the right one protracted and the left retracted.

c) This movement causes (on account of morphological reasons) the proboscis to bend to the right. This arcuation is probably enhanced by a further mechanism (high blood-pressure in the right galea and/or contraction of the oblique muscles in the left).

d) The movement back to the straight position is achieved by this mechanism only, whereby the galeae remain in the displaced state until the proboscis is more or less straight, thus producing a stress effect upon the fruit (proboscis with displaced galeae is longer; stress per area is double with a single galea; straight proboscis is longer than the secant line of a bent proboscis).

e) The galeae are brought back to the normal undisplaced state, then the proboscis is bent to the other side by the mechanism mentioned. Because of their rapidity (16–19 cycles per second) the movements simulate a spindle; they are performed until a little hole is made. The rigid tearing hooks come into action and tear the skin open to the diameter of the proboscis.

4.2. Second phase: the penetration into the pulp

As soon as the tearing hooks have opened a hole large enough to permit the proboscis to penetrate into the pulp, another piercing mechanism begins to work. Measurements with the stroboscope indicate a much slower frequency in the anti-parallel movements of the galeae than during the previous phase, i.e. 7–8 cycles per second. The frequency tends to decrease when the proboscis is very deeply inserted
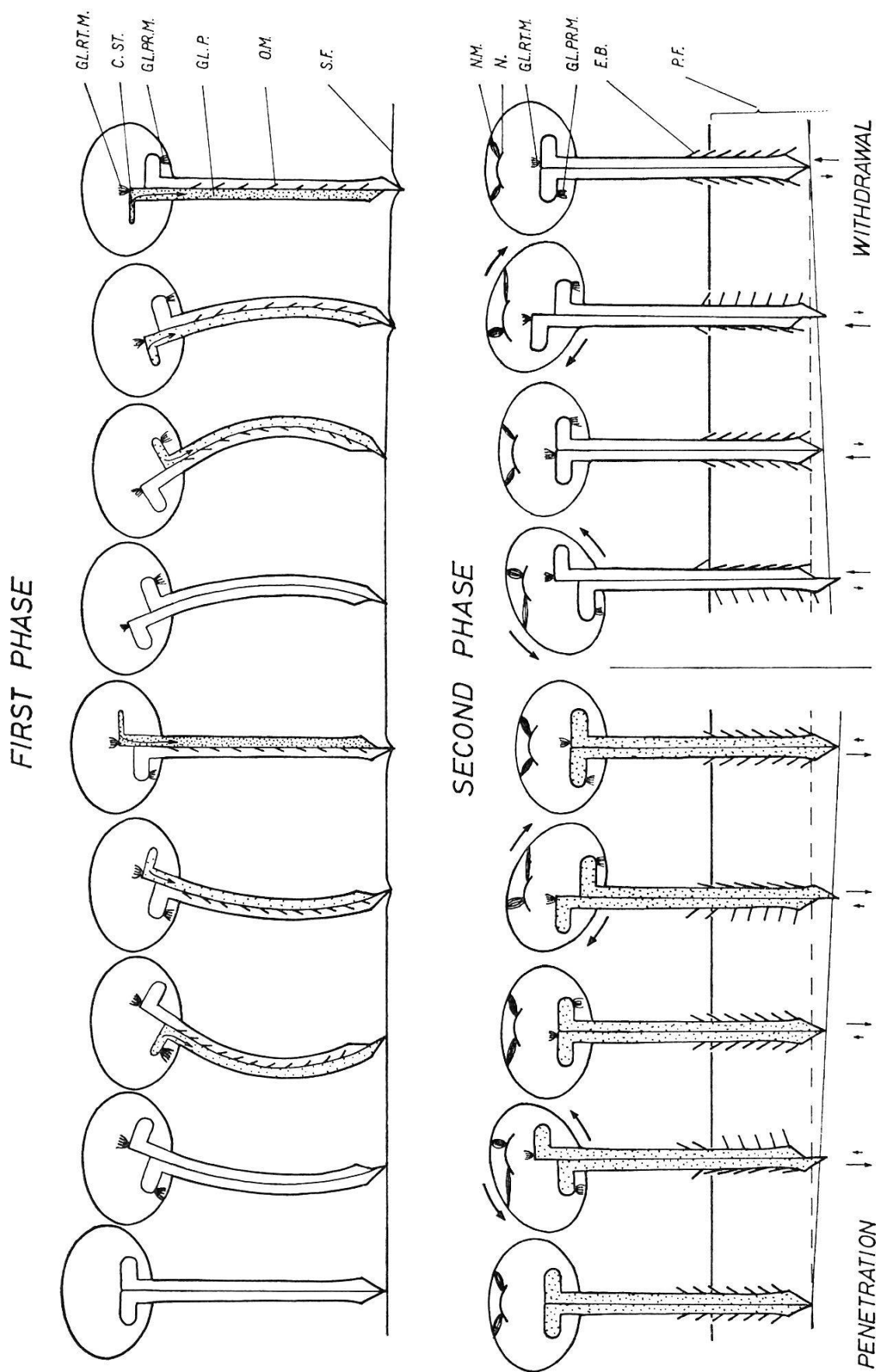
Fig. 28. Piercing process during the first phase (perforation of the skin) and second phase (penetration into the pulp). (Diagrammatic; explanations on pp. 75 and 79). *C.ST.* = compressed stipes; *E.B.* = erectile barb; *GL.PR.M.* = galea protractor muscle; *GL.RT.M.* = galea retractor muscle; *GL.P.* = galea under pressure; *N.* = neck; *N.M.* = neck musculature; *P.F.* = pulp of the fruit; *S.F.* = skin of the fruit; *O.M.* = oblique muscle.

in the pulp. The oscillations of the head, now very pronounced, are synchronized with the anti-parallel movements, which can be seen distinctly in Figs. 7 to 8 by the relative position of the "micro-mirrors" made of aluminum foil glued onto each galea, both at the same distance from the proboscis base. The main piercing effect during the second phase is achieved by the anti-parallel movement caused by the protractor and retractor muscles, in the way it has already been explained on pp. 62–63. The secondary effect of the lateral bending of the proboscis, which in the first phase simulates the spindle, is now a handicap, since the proboscis can no more freely swing after it has been inserted into the fruit. The anti-parallel movements would therefore be impeded, if the lateral bending was not counteracted by the very pronounced oscillations of the head. Thus, when the right galea is retracted and the left one protracted, the proboscis, instead of bending to the left, remains straight because the head turns in levorotatory sense and by this neutralizes the undesired bending (Figs. 7 to 8). The causative correlation between the head oscillations and the suppression of the spindle formation could be verified by an experiment, where the head was prevented from oscillating by the gentle touch of a forceps. Whenever the head was forced to a standstill, the not inserted part of the proboscis was bending laterally back and forth, as during the first phase, though much slower.

The oscillations of the head are not a passive compensatory reaction due to a forced suppression of the spindle formation, but an active movement preventing it. In fact the moth occasionally oscillates the head too strongly and instead of avoiding the formation of a spindle produces one with inversed phase. Apparently the oscillation is caused by the moth's neck musculature. The pronounced oscillations also improve the anti-parallel movements because the turning head pushes the protracted galea somewhat deeper into the fruit and pulls the retracted galea out of it.

The action of the erectile barbs was studied with moths which were induced to pierce sweetened agar. The proboscides were observed and photographed by transillumination. To avoid discontinuity of light refraction the agar layer was kept only a few millimeters thick. Different concentrations (2% and 6%) were used in order to check whether the consistency of the medium has an influence on the working of the barbs. The results were compared also with observations on the piercing of transilluminated white grapes – a more natural medium than agar.

The mechanism which erects the barbs has been explained on pp. 68 to 71. As depicted in Fig. 3, the erectile barbs are raised and inclined backwards already during the first phase and are thus ready to come into action when they enter the fruit. The working of the erectile barbs

reminds us somewhat of a harpoon with movable hooks as used by skin divers, but brought to a higher perfection thanks to the great angle of traverse of the barbs covering some 170° and their remote control by blood-pressure. These details of construction enable the proboscis to penetrate into the pulp and withdraw from it with the greatest ease. By a single average push due to the anti-parallel movement one galea (e.g. the right one) pierces the pulp with a group of 15–25 erectile barbs which, after the anti-parallel movement is reversed, are caught by the pulp. Thus the barbs are pushed forward more and more as the galea withdraws, but the force exerted by the resistance of the pulp is counteracted by the permanent blood-pressure in the galea which tends to keep the barbs in a position of backward inclination. The two conflicting forces will cause the galea to come to a standstill or at least retard the recession. At the same time the other galea is forced to advance beyond the right galea on account of the anti-parallel movement. This action is repeated alternately by both galeae until a certain depth is reached, after which the proboscis is withdrawn and then re-inserted. These movements, shown in the Fig. 29 a to d, could also be observed under the stereomicroscope.

The efficacy of the mechanism of penetration was tested with a simple balance especially made for this purpose. A moth was induced to climb on the balance which was regulated in such a way that the moth was distinctly lighter than the counterweight. The moth was then permitted to pierce a piece of agar which was situated below the pan of the balance. The agar had no direct contact with any part of the balance. As the proboscis progressively penetrated the agar, the instant came when the pan carrying the moth was drawn towards the agar, indicating that the proboscis was drawing the moth (and with it the pan of the balance) downwards, i.e. against the force exerted by the counterweight. The experiment shows that the proboscis, as soon as a sufficient number of erectile barbs is in contact with the agar, does not penetrate by means of a downward thrust conveyed from the legs to the proboscis by the body of the moth but by virtue of the anti-parallel movements alone. In fact, because of the backward inclination of the barbs, the galeae can more easily advance than recede. (This effect reminds one of that children's game, in which a person lets an ear of barley climb up inside its sleeve by moving the arm.) Care was taken to make sure that this effect was not caused by an upward motion of the head – which may occasionally happen – for this would only prove that the proboscis was well-anchored in the fruit. It was possible to observe clearly how, at the moment when the balance tipped over and during the subsequent period until the withdrawal, the proboscis, together with the head, constantly sank towards the agar. The tipping over of the balance is not due to weight increase by food intake either,

since after the experiment the moth was still lighter than the counter-weight.

The withdrawal of the proboscis is based on the same mechanism. However, the blood-pressure is decreased during this process, causing the erectile barbs to orient towards the tip of the proboscis (Figs. 9 and 29 d). Thus the anti-parallel movement of the galeae leads to a retraction of the proboscis, since now the protracting galea is braked by the pulp, whereas the retracting galea finds no resistance. The withdrawal of the proboscis proceeds much quicker than the penetration, because the proboscis can move in the shaft rasped out during the previous penetration and because the legs can be propped against the fruit and thus develop a drawing force which is greater than the thrusting force used for penetration.

The pulp of a mature grape is tougher than a 2% agar gel, but not as tough as a 6% agar gel. The consistency of a grape, however, is much less homogeneous because of its cellular structure. Despite this differences, the working of the barbs is the same in both concentrations of agar and in the grape.

For penetration into the pulp the tearing hooks are of minor importance on account of their squat shape, unexposed location and immovability.

The firmly fixed, acuminated rasping spines seem designed to lacerate the cells during the frequent upward and downward movements of the proboscis. Their disposition along the slit-like opening of the food canal, through which the food is imbibed, increases their efficiency, since the released sap together with cell fragments can readily flow into the food canal. The extremely interlaced disposition of the rasping spines suggests that they function also as a filter in order to prevent a possible obstruction of the food canal by large pulp fragments.

The sequence of the movements and forces at work during the second phase, illustrated in Fig. 28, thus are:

a) Through the hole of the skin one galea is pushed into the fruit by the anti-parallel movement assisted by the thrusting force of the head. At the same time the muscles of the neck turn the head eliminating by this the now obstructing bending of the proboscis.

b) All movements are inverted and as the galea is induced to recede the erectile barbs grip the pulp (high blood-pressure in the galea tends to keep them inclined backward) preventing full retraction. The other galea advances by the anti-parallel movement beyond the anchored galea as its barbs offer less resistance.

c) The mechanism described is repeated by the right and the left galea alternately (with 7–8 cycles per second), the oscillations of the head being synchronized to these motions. When sufficient erectile barbs grip the pulp, the proboscis penetrates on account of the anti-parallel movement alone, without the need of the downward thrust conveyed from the legs to the proboscis by the body of the moth.

d) For the withdrawal of the proboscis the erectile barbs are inclined forwards (as the blood-pressure in the galeae is reduced) and the analogous mechanism as used for the penetration assures now a quick withdrawal.

e) Penetration is followed by incomplete withdrawal and new penetration, this being repeated many times. Thus many shafts are produced, all departing from the same hole and great numbers of pulp cells are torn open. The latter is achieved mainly by the rasping spines which are disposed along the slit-like opening of the food canal.

f) Complete withdrawal of the proboscis occurs when the food supply near the piercing hole is exhausted, the moth is satiated or has been disturbed.

5. Discussion

It is interesting to know why not all Lepidoptera are able to pierce. We have already mentioned the non-piercing fruit-sucking moths which are apparently unable to pierce the fruit. With the morphological data presented in this paper it is possible to give at least a preliminary answer. There are four main, in our opinion decisive differences between the fruit-piercing moths studied in this paper on one hand, and both the non-piercing fruit-sucking and the nectar-sucking moths on the other. First, the ratio of the average thickness to the length of the proboscis is in the three piercing moths *C. thalictri*, *C. eustrigata* and *S. libatrix* at least three times higher than in the nectar-sucking *A. gramma* and the fruit-sucking *L. craccae*. This means that the proboscis of the former is about 10 times stronger than that of the latter. Second, in nectar-suckers and to a lesser extent in the non-piercing fruit-suckers, the proboscis tapers gradually from the base towards the tip (Fig. 16). In the three above-mentioned piercing moths, practically no tapering of the proboscis occurs from the base to about 90% of the length, where a sudden, nearly triangular pointing occurs at the tip. Such tips are also much more sclerotized than those of the non-piercing species. These facts enhance remarkably the already higher stability of the proboscis in the piercing moths. Moreover, we have never observed non-piercing moths stiffening their proboscis by high blood-pressure. Third, the armature of the proboscis of the non-piercing species consists of some rasping spines and/or simple bristles (Fig. 19 d) which are not even firmly fixed, or hairs only (Fig. 19 e). Fourth, the three piercing species dispose over 4 stipital muscles, two of which are adapted to effect the anti-parallel displacement of the galeae. In the non-piercing Lepidoptera maximally 3 stipital muscles occur (SCHMITT, 1938), and anti-parallel displacement actively taking place has, to our knowledge, never been described.

As mentioned before, NEUBECKER (1966) observed differences of the piercing movements in *S. chlorea* and *S. partita*. It is therefore
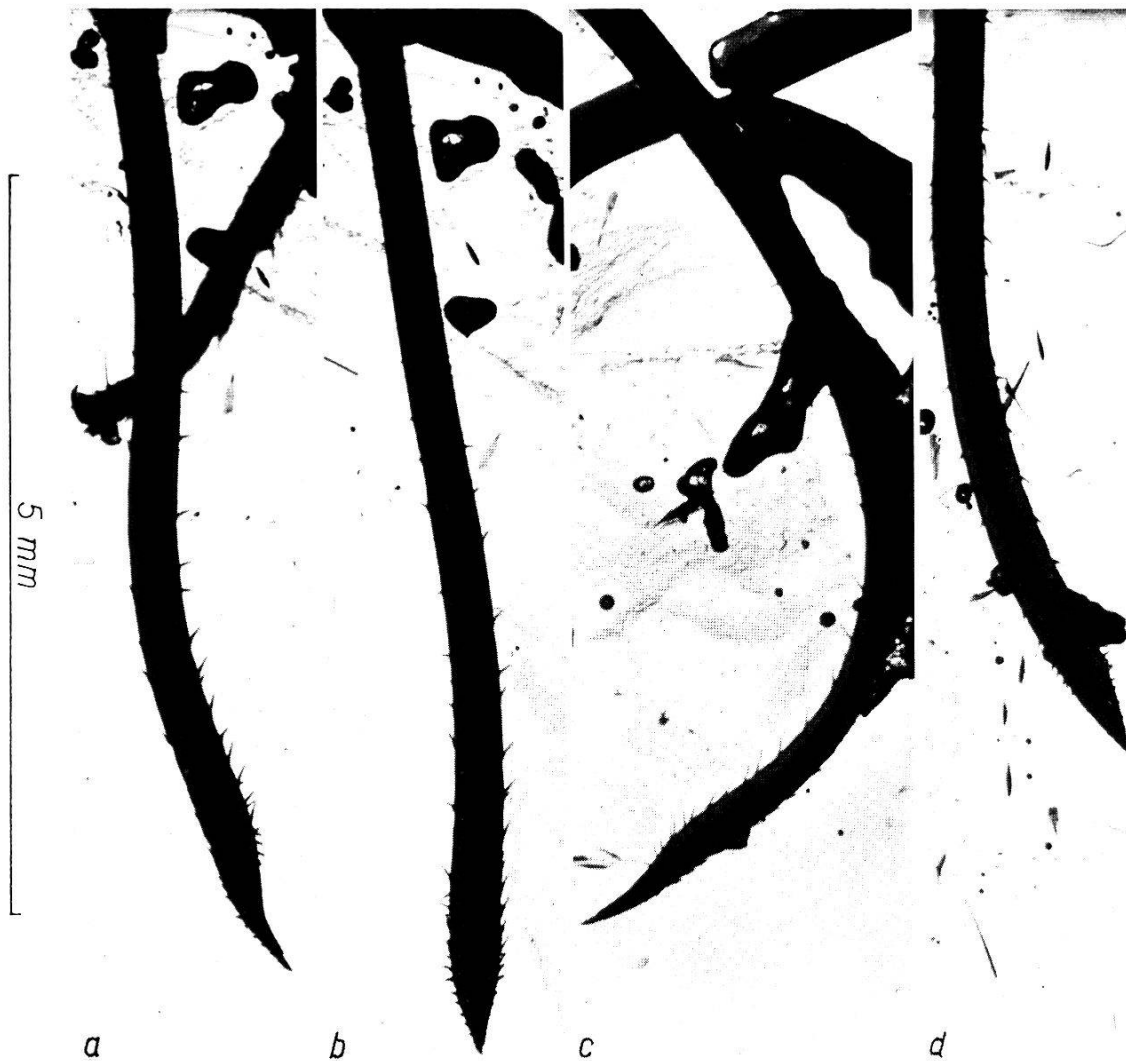
a   b   c   d

Fig. 29. Photographs of the process of penetration and withdrawal of the proboscis of *C. thalictri* piercing agar. a) Left galea has advanced beyond the right which served as anchorage. This is also indicated by the position of the erectile barbs, those of the left galea pointing towards the head, those of the right being pressed forwards to a nearly orthogonal position. b) Intermediary phase between a) and c). c) Reversed phase of a), the position of the galeae and the barbs being inverted. d) Intermediary phase of withdrawal, the barbs being inclined towards the proboscis' tip.

probable that not all piercing moths adopt exactly the same mechanism for piercing. This is further substantiated by the fact that the proboscis of some piercing moths is sharply pointed and has erectile barbs, whereas it is blunt in others and the barbs apparently are not erectile by blood-pressure. To the first group probably belong, besides *Calpe,* the genera *Othreis* and *Serrodes,* to the second *Achaea, Dysgonia* and *Ophiusa.* The study of a specimen of the latter group is planned.

From the point of view of their feeding habits, the fruit-piercing and the skin-piercing blood-sucking moths represent a special case among Lepidoptera. Their piercing apparatus is also unique when compared

with that of members of insect orders having more or less well developed piercing mouth-parts, i.e. Anoplura, Thysanoptera, Hemiptera, Diptera and Aphaniptera. All these orders have in common a piercing apparatus which consists at least of three elements of the mouth-parts, whereas in the piercing Lepidoptera only one member, the maxilla, is involved in piercing.

In all typical piercing insects, including the piercing moths, the saliva plays a rôle during the feeding process. The non-lepidopterous insects have developed an appropriate salivary canal, formed in most cases exclusively by the hypopharynx. In Aphaniptera, Thysanoptera and Hemiptera the hypopharynx is partially replaced by other structures, e.g. in Hemiptera by the maxillae, which have two separate canals, one for the food and one for the saliva (WEBER, 1930). In the piercing moths as in all higher Lepidoptera the hypopharynx is completely reduced and because of the absence of any particular canal for the saliva, the salivary duct, coming from the salivary glands, discharges into the food canal (BORDAS, 1920; DAUBERSCHMIDT, 1933). Secretion of saliva before and during the piercing has often been observed in the blood-sucking *C. eustrigata* (BÄNZIGER, 1968). In this moth the saliva is probably of particular importance since the coagulation of the blood has to be prevented. This may be achieved by the frequent regurgitation and re-ingestion of blood during the feeding, observed in this species, which seems to assure a thorough mixture of blood and saliva. This behaviour could be of great significance for a possible transmission of pathogenic agents.

On account of its great length, Lepidoptera coil their proboscis under the head. This is possible only because of the great elasticity of the organ. It is therefore comprehensible that the piercing ability of Lepidoptera has so long been doubted. In fact the piercing elements of the mouth-parts in the typical piercing insects are straight, with only the Hemiptera as a partial exception. In the fungus sucking Aradidae, for instance, the extremely long maxillary and mandibular stylets are coiled up inside the head. The inner walls of the head and the labium serve as conveyors and, as the muscles attached to the base of the stylets come into action, the stylets are guided in a longitudinal direction (SPOONER, 1920; WEBER, 1930). However, although the proboscis of piercing Lepidoptera does not benefit from such a conveying arrangement, it is nonetheless adapted for piercing because its turgescence and its consequent rigidity can be highly increased by blood-pressure. This is a further peculiarity which does not occur in any of the other piercing insects. A kind of self-conveying system, adopted by most of the typical piercing insects, occurs also in the proboscis of Lepidoptera. During the piercing, one galea moves and one remains on the spot, serving to guide the moving galea thanks to the link between them.

The spindle formation and the oscillations of the head are very striking, but some peculiar behaviour or movement occurs also in other piercing insects: some Thysanoptera pierce the plant cells by a rapid tapping with the head (PETERSON, 1915) and the sucking black fly *Simulium venustum* Say jerks the thorax and abdomen back and forth in a pumping movement (DAVIES & PETERSON, 1956).

The erectile barbs on the proboscis are a unique speciality of the piercing moths. Most of the typical piercing insects have tooth-like armatures on their piercing stylets, but the teeth themselves are never movable on their support. Although a number of piercing insects have developed an armature on their piercing mouth-parts which has an effect comparable to that of the erectile barbs, the underlying mechanisms are completely different. Thus the proboscis of the elephant louse *Haematomyzus elephantis* Piaget, a mandibulate sucking louse, has, besides a number of hooks, two tooth-like structures which can be moved by muscles. These teeth are in reality the mandibles (FERRIS, 1931), whereas the erectile barbs seem to be modified bristles of the maxillae and are moved by blood-pressure.

The Anoplura (VOGEL, 1921; LAVOIPIERRE, 1967) and some Diptera, such as Glossinae and Pupipara (JOBLING, 1926; 1928; 1929; 1933), have developed eversible teeth. These, however, are *firmly fixed* to the inner wall of the labrum in the Anoplura or the modified labium in the Diptera. Moreover, the eversion is the result of a muscle action which retracts the outer wall and protracts the inner one, thus bringing the teeth to the outside in an inverted position.

These facts show that the piercing apparatus of moths represents a specific development which differs considerably from that of other insect groups. This can be understood if it is kept in mind that the mouth-parts of the higher Lepidoptera are already highly specialized, and provided the mouth-parts of the piercing moths represent the most evolved stage of these organs. Nectar-sucking would thus represent the more primitive feeding habit. This view is supported by the fact that in the primitive pollen-eating Micropterygidae, which have mandibulate mouth-parts, the hypopharynx is well developed and functional. Since, however, the hypopharynx was evidently not necessary for nectar-suckers it was lost in the course of the evolution. If the piercing moths were more primitive than the nectar-sucking Lepidoptera, one would expect to find a fairly well developed hypopharynx forming the entire salivary canal, or at least a part of it, as in all other piercing insects.

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8. Zusammenfassung

Die Morphologie des Stechapparates und der Stechmechanismus der Noctuide *Calpe thalictri* Bkh. wurden untersucht. Der besonders starke Rüssel ist mit Aufreißhaken, mit durch Blutdruck aktiv aufrichtbaren Zähnchen und mit einer speziellen Muskulatur des Stipes ausgestattet. Im Fehlen dieser Eigenschaften liegt wohl bei den meisten Lepidopteren die Ursache ihrer Unfähigkeit zu stechen.

Der Stechakt zerfällt in zwei Phasen: 1. Durchstechen der Fruchtschale und 2. Eindringen in das Fruchtfleisch.

Erste Phase:

a) Der Falter klammert sich an die Frucht fest. Der durch hohen Blutdruck steif gemachte Rüssel wird gegen die Frucht gestemmt.

b) Die Galeae werden antiparallel (d. h. in der Längsrichtung entgegengesetzt) durch die entsprechenden Protraktor- und Retraktormuskeln verschoben, z. B. die rechte Galea vorwärts und die linke rückwärts.

c) Diese Bewegung verursacht aus morphologischen Gegebenheiten eine Biegung des Rüssels nach rechts, welche möglicherweise noch durch einen besonderen Krümmungsmechanismus (hoher Blutdruck in der rechten Galea und/oder Kontraktion der schiefen Muskeln in der linken) verstärkt wird. Die Rückwärtsbewegung zur ungebogenen Lage wird nur durch diesen Krümmungsmechanismus (aber in entgegengesetzter Phase) vollbracht.

d) Etwa bis zum Moment, wo der Rüssel wieder mehr oder weniger gerade ist, werden die Galeae im verschobenen Zustande beibehalten. Hierdurch wird ein Druckeffekt erzeugt (hervorgerufen durch die relative Verlängerung des Rüssels infolge seiner Streckung aus der gekrümmten Lage), der noch verstärkt wird, da nur eine Galea den ganzen Druck ausübt.

e) Die Galeae werden nun in die normale Lage zurückverschoben, wonach der Rüssel gleich zur gegenüberliegenden Seite gebogen wird, entsprechend dem erwähnten Mechanismus. Wegen der Geschwindigkeit dieser Bewegungen (16 bis 19 Hz) wird eine Spindel vorgetäuscht. Sobald ein Loch gebohrt ist, verschwindet die Spindel, und die Aufreißhaken an der Rüsselspitze reißen die Schale auf den benötigten Durchmesser auf.

Zweite Phase:

a) Durch die antiparallele Verschiebung der Galeae wird eine von ihnen durch die Öffnung in die Frucht hineingestoßen; gleichzeitig drehen die Muskeln im Nacken den Kopf so, daß die Bildung der jetzt hinderlichen Spindel abgefangen wird.

b) Die antiparallele Galeaverschiebung und die Drehung des Kopfes werden in umgekehrter Richtung durchgeführt. Die durch Blutdruck aufgerichtet gehaltenen Zähnchen der zurückweichenden Galea verfangen sich im Fruchtfleisch und verankern die Galea. Die andere, weniger Widerstand leistende Galea wird durch die antiparallele Verschiebung über die verankerte Galea hinaus vorgeschoben.

c) Diese Galeabewegungen und die dazu synchronisierten Kopfoszillationen werden alternierend wiederholt (Frequenz: 7–8 Hz). Sobald genügend viele Zähnchen in der Frucht sind, dringt der Rüssel allein durch die Wirkung der antiparallelen Verschiebung ein, ohne die zusätzliche Schubkraft des Kopfes.

d) Für das Herausziehen des Rüssels ist wieder derselbe Mechanismus wirksam, nur sind die Zähnchen wegen Blutdruckverminderung nach vorne geneigt.

e) Dem Eindringen folgt partielles Herausziehen und abermaliges Eindringen, welche häufig und in schneller Folge wiederholt werden. Mehrere, alle von demselben Einstichloch ausgehende Gänge entstehen, wobei eine große Anzahl von Zellen aufgerissen werden; dabei spielen die der schlitzförmigen Öffnung des Nahrungskanals entlang sitzenden Dornen wahrscheinlich eine wichtige mechanische Rolle. Wegen ihrer verflochtenen Anordnung wirken sie wohl auch als Filter. Vollständiges Herausziehen des Rüssels erfolgt, wenn der Saft der betreffenden Einstichstelle versiegt, der Falter satt ist oder gestört wurde.

Morphologie des Rüssels und Stechverhalten sind bei der nahverwandten blutsaugenden *C. eustrigata* Hmps. ziemlich übereinstimmend, und es ist wahrscheinlich, daß auch der Stechmechanismus auf ähnlichen Prinzipien beruht.

Die Morphologie und das Funktionieren des Stechapparates unterscheiden sich deutlich von denen aller anderen stechenden Insekten: nur die Maxillen sind beim Stechen beteiligt; die Leitung der Nahrung und des Speichels geschieht durch einen einzigen gemeinsamen Kanal; aktiv aufrichtbare Zähnchen sind entwickelt worden. Diese Besonderheiten lassen es als sehr wahrscheinlich erscheinen, daß die stechenden Lepidopteren eine Weiterentwicklung der (somit ursprünglicheren) nektarsaugenden Lepidopteren darstellen.

9. Résumé

Le présent travail traite du mécanisme de la perforation des fruits par la Noctuelle *Calpe thalictri* Bkh., ainsi que de la morphologie de son appareil piqueur. Celui-ci présente un certain nombre de particularités adaptatives : développement d'une forte trompe munie de dents érectiles par pression sanguine, pré-

sence de crochets tranchants, présence d'une musculature spéciale du stipe. L'absence de telles particularités chez l'appareil buccal de la plupart des papillons explique peut-être pourquoi ceux-ci ne peuvent perforer les tissus des plantes et des animaux.

La perforation d'un grain de raisin par la Noctuelle se déroule en deux phases distinctes : 1⁰ perforation de la peau du fruit, 2⁰ pénétration de la trompe dans la pulpe du fruit.

Première phase :

a) Le papillon s'agrippe au fruit et presse contre sa surface l'extrémité de sa trompe rendue rigide par la pression sanguine exercée à l'intérieur des galéas.

b) Sous l'action de muscles antagonistes, les galéas glissent l'une contre l'autre et en sens contraire, la galéa droite, par exemple, étant légèrement projetée en avant et celle de gauche retirée en arrière.

c) Par un effet secondaire du mouvement des galéas, la trompe est alors arquée vers la droite. D'autres mécanismes (haute pression dans la galéa gauche, ou contraction des muscles obliques dans la galéa droite, ou action simultanée de ces deux phénomènes) aident éventuellement à courber la trompe latéralement. Le redressement de la trompe est très probablement réalisé par un mécanisme de ce genre s'exerçant en direction opposée.

d) Jusqu'à ce que la trompe ait repris sa position rectiligne, les galéas sont tenues décalées l'une par rapport à l'autre, assurant ainsi une forte pression sur le fruit, du fait que la trompe, lors de son redressement, devient plus longue que la distance tête-fruit. En outre, toute la force ne porte que sur la pointe d'une seule galéa.

e) Les galéas sont alors ramenées dans une position parallèle et rectiligne, puis la trompe est arquée dans l'autre direction, selon le mécanisme décrit. La rapidité de ces mouvements (16–19 cycles par seconde) fait apparaître à l'œil l'image d'un fuseau orienté dans un seul plan, qui dure jusqu'à ce que la trompe ait pratiqué un trou dans la peau du fruit. Les crochets tranchants de l'extrémité des galéas déchirent la peau du fruit, agrandissant le trou au diamètre de la trompe.

Deuxième phase :

a) Sous l'effet de la pression de la tête et du glissement antiparallèle des galéas, l'une d'elle pénètre dans la pulpe, en même temps que les muscles de la nuque font tourner la tête, ceci afin d'éviter que la trompe ne s'arque.

b) Les mouvements antiparallèles des deux galéas et la rotation de la tête sont ensuite inversés. La galéa la plus avancée est légèrement retirée tout en restant plantée dans le fruit ; les dents érectiles qui la garnissent, érigées par la pression sanguine, s'agrippent dans la pulpe.

c) L'autre galéa est alors projetée au-delà de la galéa ancrée ; ses dents érectiles, dirigées vers l'arrière, présentent moins de résistance.

d) Les mouvements antiparallèles de deux galéas se répètent à une fréquence de 7–8 cycles par seconde, la trompe pénétrant ainsi dans le fruit. Dès qu'un certain nombre de dents érectiles sont en contact avec la pulpe, la trompe ne pénètre plus que grâce au mouvement antiparallèle des galéas, sans qu'intervienne la pression de la tête.

e) La trompe peut pénétrer entièrement dans le fruit. Elle est ensuite quelque peu retirée, puis renfoncée, ce qui a pour effet de déchirer la pulpe et de donner naissance à de nouveaux canaux. Les épines, disposées le long de la fente du canal nutritif, semblent prendre une part importante dans la lacération de la pulpe. De plus, grâce à leur entrelacement, elles jouent probablement un rôle de filtre.

f) Pour retirer la trompe, l'insecte diminue la pression sanguine dans les galéas, ce qui a pour effet d'incliner en avant les dents érectiles. La trompe est alors retirée par le même mécanisme que pour la pénétration.

La morphologie de la trompe, ainsi que l'éthologie de la piqûre, sont très semblables chez *C. eustrigata* Hmps., un proche parent hématophage qui pique les animaux. La perforation s'explique vraisemblablement par des mécanismes semblables à ceux décrits ci-dessus.

L'appareil perforateur de ces lépidoptères, ainsi que son fonctionnement, se distingue de celui des autres insectes piqueurs. Chez ceux-ci, une seule paire de pièces buccales, les maxilles, forme l'appareil piqueur. De plus, il n'y a qu'un seul canal pour la salive et pour la nourriture. La présence de dents érectiles constitue un cas unique chez les insectes. Il est très probable que ces particularités sont dues à une évolution secondaire des papillons suceurs de nectar. Ces derniers seraient donc moins évolués que les perceurs de fruits.