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**Autor:** Bänziger, Hans

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## Skin-piercing blood-sucking moths III: Feeding act and piercing mechanism of *Calyptra eustrigata* (Hmps.) (Lep., Noctuidae)

HANS BÄNZIGER<sup>1</sup>

Dept. of Entomology, Fac. of Agriculture, Chiangmai University, Chiangmai, Thailand

*Calyptra eustrigata*'s piercing mouth-parts consist of 2 linked stylets which can slide independently in anti-parallel sense and a uniquely functioning armature of erectile barbs and eversible tearing hooks actively moved by blood-pressure. During penetration, an additional peculiarity is torsion of the stylets in a to and fro rotary oscillation.

Piercing sequence: I: The simultaneous anti-parallel movement, oscillatory torsion and directional change of thrust enable the mouth-parts' tip to intrude between or into skin irregularities to establish a hold for the tearing hooks. II: These grip and/or tear the tissue to bore out a hole. III: The proboscis penetrates through the hole by the action of the backwardly erected barbs and the anti-parallel action of the stylets. IV: A succession of partial withdrawals and new penetrations, with the barbs inclined in opposite sense, cause increased blood flow. V: Withdrawal is by the same principle as penetration but with forwardly inclined barbs.

The movements show features characteristic of and otherwise exclusively found in the lepidopterous fruit-piercing feeding; this and morphological-phylogenetic facts indicate that *C. eustrigata*'s feeding is a direct derivative of the fruit-piercing habit. Owing to this, and because the moth is a «novice» among blood-suckers, it is unlikely that biologically transmissible pathogens, with their advanced specialization, have already had time to adapt to the moth as a vector. But mouth-part morphology and way of feeding would be suitable for the mechanical transmission of pathogens.

The present state of knowledge about *Calyptra* [*Calpe*] *eustrigata* (Hmps.), a blood-sucking Noctuid of which adult males were found piercing wounded and healthy skin of large ungulates and elephants (and, in experiments, also of man and of fruit), has been reviewed in a paper on new biological findings about the moth, which includes a.o. details of biotope, distribution, flight period, activity and behaviour, feeding habits, enemies, and resting (BÄNZIGER, 1975). Three additional species, i.e. *C. minuticornis* (GUEN.), *C. orthograpta* (BUTL.) and *C. labilis* (BERIO) [almost certainly = *C. fasciata* (MOORE)] are strongly suspected to be at least occasionally skin-piercing blood-sucking species (BÄNZIGER, 1979).

This unusual feeding habit for a lepidopterous insect, and the possibility that *C. eustrigata* may be a pathogen vector, raise the question of how it pierces. Among Lepidoptera only fruit-piercing moths have been known to pierce. However, despite their importance as pests in fruit orchards, until recently the piercing mechanism adopted was not fully elucidated, previous studies being based mainly on morphology alone (DARWIN, 1875; KÜNCKEL, 1875; BREITENBACH, 1882; NEUBECKER, 1966; SRIVASTAVA & BOGAWAT, 1969). In an attempt to obtain a comprehensive insight both into these moths' mode of piercing and into the likely method adopted by *C. eustrigata*, the closely related, but less rare, fruit-piercing *C. thalictri* (BKH.) was chosen for a first analysis (BÄNZIGER, 1970). A peculiar piercing mechanism and unique adaptations of the mouth-parts, such as an armature of movable barbs activated by blood-pressure were revealed.

<sup>1</sup>Mailing address: c/o Swiss Embassy, P. O. Box 821, Bangkok, Thailand

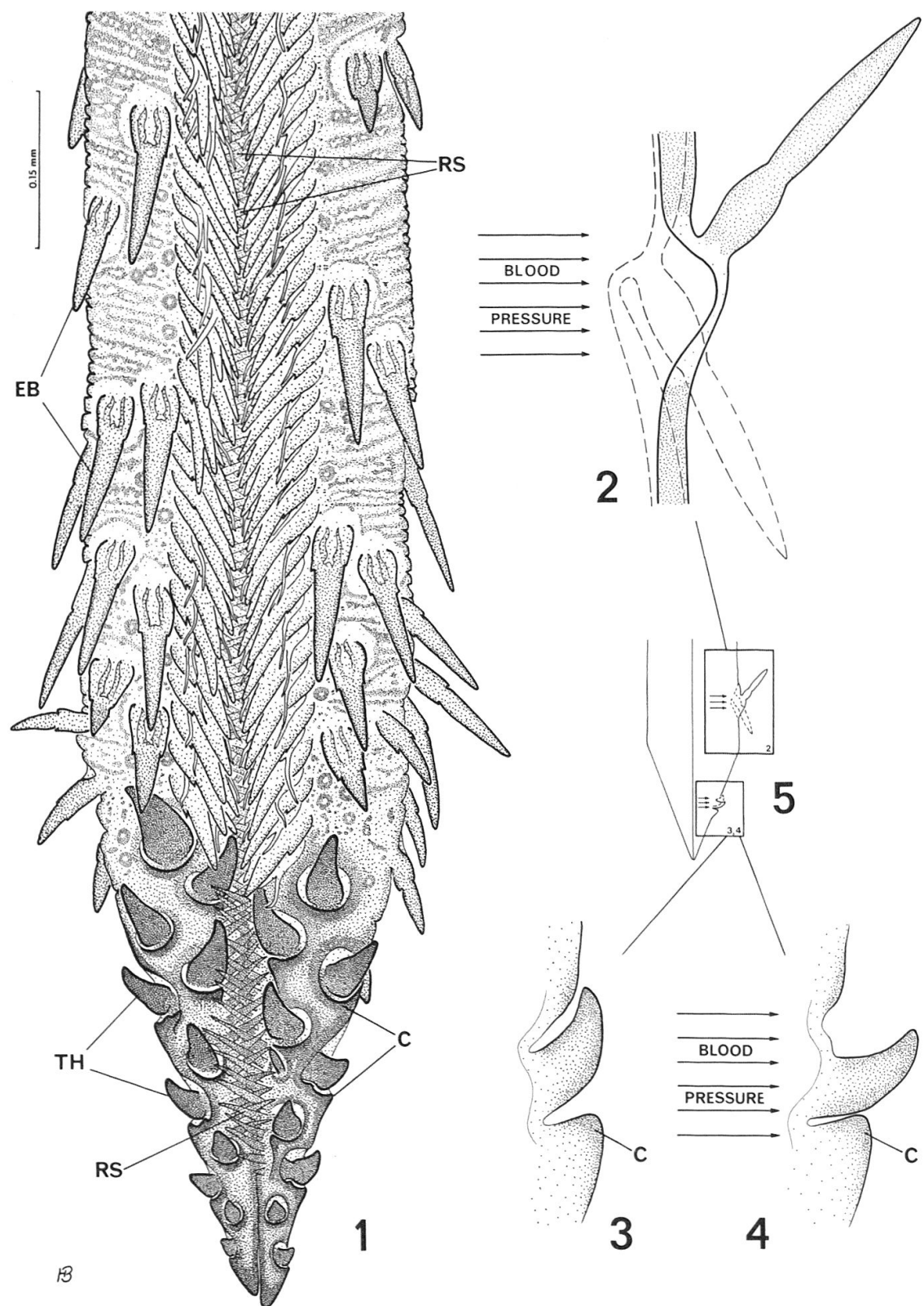


Fig. 1-5: Distal 1/7 of *Calyptra eustrigata*'s proboscis (TH: tearing hooks, EB: erectile barbs, RS: rasping spines, C: collar) (1); Mechanism of erection of the barbs by blood-pressure. Broken lines: at rest; full drawing: erected (high blood-pressure) (2); Mechanism of eversion of the tearing hooks by blood-pressure (3: at rest; 4: everted [high blood-pressure]; C: collar preventing overturning); Location of fig. 2-4 (5).

More recent publications on fruit-piercing moths are scanty, especially when compared, for example, with some 500 articles connected in some way with plant penetration and feeding by aphids, listed in a review by POLLARD (1973).

The present series of studies on blood-sucking moths will be continued with investigations into life cycle, physiology, and other biological aspects.

#### NOTES ON MORPHOLOGY AND DYNAMICS OF PROBOSCIS AND ARMATURE

The study presented here is based on the author's 1970 paper which contains many morphological and dynamical details not repeated here. *C. eustrigata* differs from *C. thalictri* in the following respects. The proboscis's walls and its conoid-shaped, stiff point are stronger owing to heavier sclerotization. The tearing hooks (TH, fig. 1), all 22–24 situated dorso-laterally on the point, are stronger and about double in size. The erectile barbs (EB) are fewer (70–80, not counting those with processi along the entrance to the food canal), but double in length. The rasping spines (RS) are likely to have more a filtering and galeal-linking than a tissue-rasping function.

A brief explanation of the essential mouth-part dynamics follows. The anti-parallel movement of the proboscis is the protraction ( $\sim 0.2$  mm) of one galea (one of the gutter shaped halves forming the proboscis and also one of the only two stylets) and simultaneous retraction of the other, and *vice versa*. It is achieved by the respective pro- and retractor muscles and not by the head oscillations, though the latter may increase it to some extent.

The turning aside of the proboscis, a lateral deflection of some  $15^\circ$ , is linked to the anti-parallel movement and is due to the pivoting of the stipita to which the galeae are attached at an angle.

The spindle movement (fig. 13 and 14) arises when the central part of the proboscis is bent to the right and the left so rapidly (15–20 Hz) as to simulate a spindle (actually the proboscis describes only a section of the surface of a spindle-like body). It is caused by the inability of the proboscis's point, which is fixed onto the skin, to follow the turning aside of the proboscis, which therefore bends.

The barbs are erected (fig. 2 and 5) when the depressions in which they are attached in a forwardly inclined position are bulged out by an increase in blood-pressure within the galea, causing them to turn so as to be backwardly inclined on a protrusion. The more basally located barbs are generally less erected (cf. fig. 16 and 17); this is probably due to a harder or shorter endocuticular base on which they are attached.

The eversion of the tearing hooks, also by blood-pressure, is illustrated in fig. 3–5. The sclerotized collar (C), protruding mainly distally from the cavity in which the hooks are attached, gives firm support and thus prevents overturning. The turning angle may reach  $\sim 45^\circ$ . This feature was not mentioned in the account of *C. thalictri* but it is likely to occur to some extent also in that species. A similar splaying mechanism has been assumed to take place also with the «Widerhakenborsten» of the mouth-parts of the elephant louse, *Haematomyzus elephantis* PIAGET (WEBER, 1970).

The proboscis's mechanism of extension (by blood-pressure) and coiling (mainly by muscle contraction, partially by elasticity) has been analysed experimentally and explained in detail (BÄNZIGER, 1971b).

Torsion is the twisting of the distal 3/4 of the proboscis in a to and fro rotary oscillation around the mouth-part's axis (fig. 13 and 14). The total angular rotation



is estimated at  $40\text{--}60^\circ$  during phase I, but may reach  $180^\circ$  during phase III and IV when the proboscis does not oscillate. The oscillation's frequency is the same as that of the spindle movement. Two mechanisms accomplish torsion: (1) during the spindle movement, the ventral walls – the most extensible part – of the distal  $3/4$  of the proboscis, tend to be on the most stretched side of the curved proboscis, i.e. on the outer side of the spindle. Thus, as the proboscis is bent to the right and the left, it is induced to turn accordingly around its axis; but as the base cannot turn, twisting ensues. The somewhat flattened shape of the proboscis increases this effect. The principle is shown in modified form in fig. 6 and 7. (According to R.KÖCHLE [pers. comm.] torsion would arise also in an elastically homogeneous, *already curved*, proboscis when bent laterally, though not when not curved (fig. 6). The author feels that the previous mechanism is dominant, though further research is needed to assess this). (2) in analogy to the elastic rods model (fig. 8–11), twisting of the proboscis arises when the galeae tend to diverge dorso-ventrally. This is accomplished when muscle contraction in one galea tends to coil it while the persisting or increased blood-pressure in the other keeps this uncoiled. (1) and (2) probably take place mainly during phases I and IV, respectively, though (2) may be active also in I. Torsion was not mentioned in the previous analysis of *C. thalictri* as it does not seem to play a significant, if any role in that species; at least it was not apparent on photographs. Oscillatory torsion generates special rotational effects with the proboscis's tip: it enables intrusion between narrow interstices and has some boring action somewhat comparable to that of a rotary boring machine.

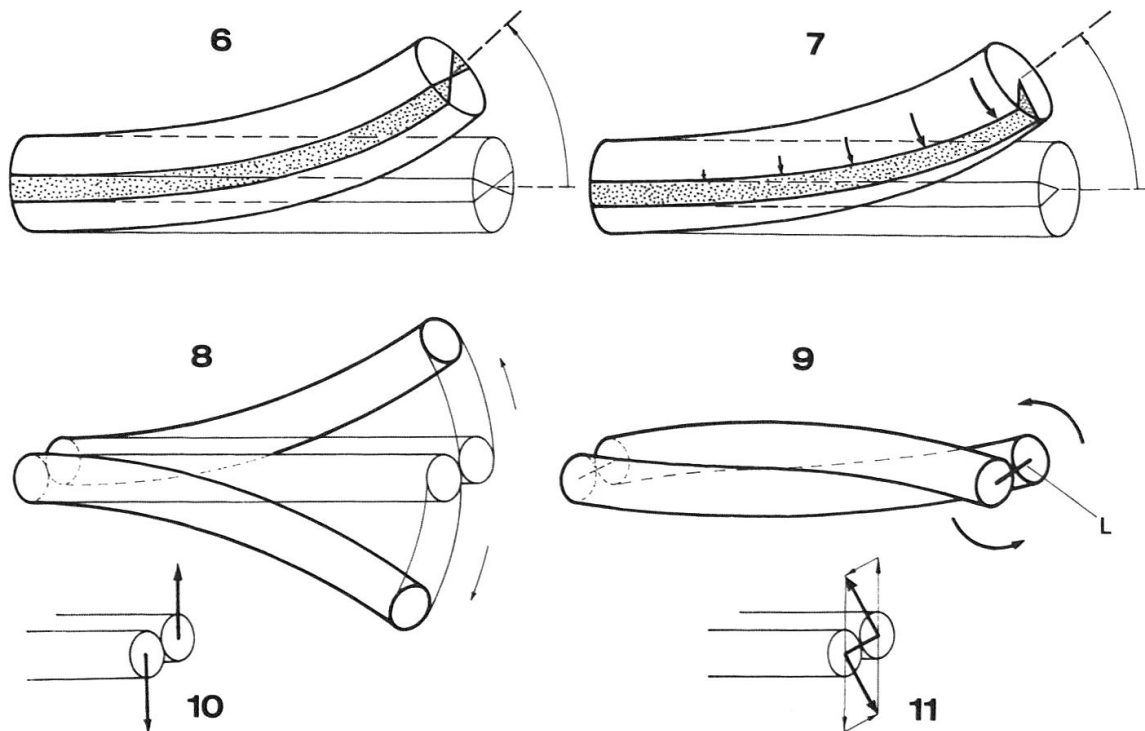


Fig. 6–11: Model of formation of torsion as a compensatory reaction to the bending of a rod with asymmetrical elasticity (6 and 7) (6: no torsion due to symmetrical position of a hard core [dark] in a softer rod; 7: torsion arises due to the asymmetrical position of the core); Model of formation of torsion by inverse curving (8–11) (8: diverging when not linked; 9: twisting around each other when linked; 10, 11: the relative acting forces; L: link).

## PRE-PIERCING BEHAVIOUR: PALPATING, LICKING AND RASPING

Evidently in an exploratory action to find a suitable piercing spot, the moth, settled on a host, palpates the skin's surface with the proboscis in the «flamingo» position, i.e. the dorsal distal end is in contact with the surface (fig. 12). Uneven skin structures, fissures, hairless scars, abrasions and wounds are preferred. The proboscis is tipped up and down continuously while palpating the area within a circle of about 1 cm radius while the head is lifted up and down, turned to the right and the left. Generally the moth does not walk, but if it does so, it takes only a few steps. The antennae are lowered intermittently to touch the surface; the wings are kept in a flat delta shape.

Fluids such as rain or condensation droplets, skin exudates, serum, blood, pus and decaying tissue of sores are probably licked up, though, according to field observations, only in small amounts even if profusely present.

The moth may also rasp superficially the host's skin, in particular tissues damaged by intensive scratching, fighting, etc., for short periods. For this action, the distal quarter to half of the proboscis is pressed onto the tissue. By virtue of the anti-parallel movement, the armature of the proboscis – mainly the erectile barbs – rasp the tissue while the proboscis advances or recedes. Occasionally, a recurved hair is used as a leverage to increase adherence and so, also, the rasping effect. It is possible that superficial cells and some capillary vessels of exposed skin may thus be torn by the armature, but the rasping as a means to tap blood does not seem to be relevant, especially when compared to the actual piercing.

In captivity, possibly because man was used as a «surrogate» host, the above mentioned pre-piercing behavioural elements often lasted for minutes, only sometimes interrupted by short piercing attempts. When on a «natural» host in the field, the moth generally palpated for a considerably shorter time.

## PIERCING BEHAVIOUR

Although most of the behaviour described below has been observed in *C. eustrigata* whilst feeding both on human and animal hosts, the following is mainly based on experiments with myself as host. The advantages of *feeling* what is going on, and of using laboratory instruments over making field observations on hosts such as rhinoceros or deer, are obvious.

To pierce the moth raises the anterior part of the body away from the surface to be pierced and thrusts the proboscis vertically, or in a slight acute angle away from its body, onto the skin, at a position between the anterior tarsi or a little in front of them. The raised tarsi evidence the force used (fig. 13 and 14). The proboscis is stiffened by blood turgidity, the tearing hooks are everted and the barbs erected backwardly (fig. 13 and 14). When seen from the side, the proboscis assumes a slight «S» shape. (According to R.KÖCHLE [pers. comm.], when bent in an «S» shape a rod can transfer a roughly 4-fold longitudinal thrust as compared to a rod bent in a simple arc.) The wings are turned down to a more steep roof-like position. Now the spindle movement and, evidenced by photographs, oscillatory torsion are performed (fig. 13 and 14). A peculiar sensation somewhat like minute, rapidly vibrating scratching is experienced at the piercing spot. Saliva may appear there or, sometimes, is seen to run down the outer side of the proboscis. The spindle movement and torsion may last a few seconds up to more than a minute,

but generally only some 10 seconds, after which they are repeated at the same or at a spot adjacent, until the skin gives way (fig. 15). If successful in penetrating, strong pain is felt. As the proboscis penetrates the spindle becomes irregular as it

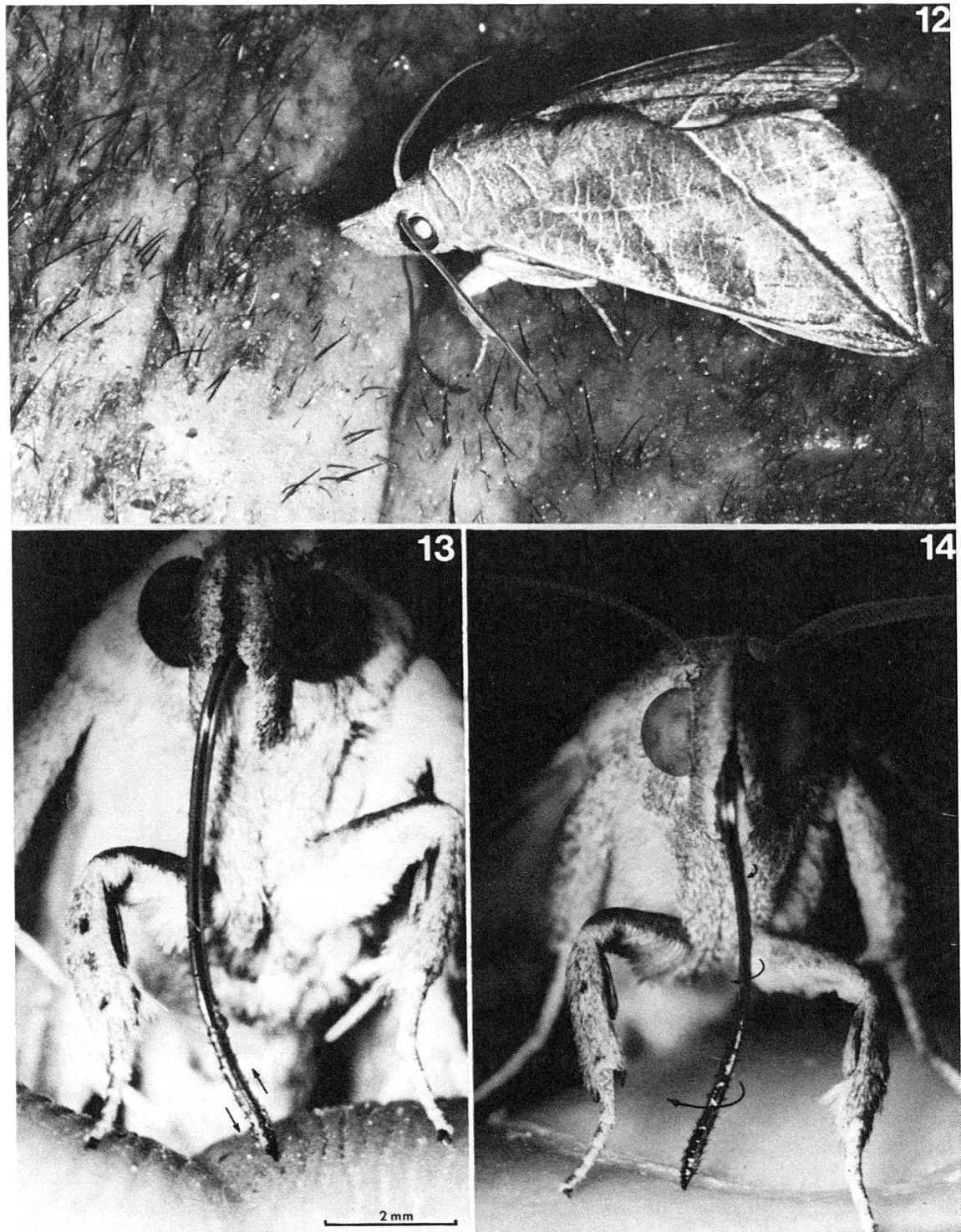


Fig. 12-14: *Calyptra eustrigata* palpating a sore on a Malayan tapir (*Tapirus indicus*) shortly before the piercing act (12); Piercing *C. eustrigata*, phase I (13 and 14) (13: spindle movement and anti-parallel movement [outer galea protracted, inner retracted, as can be seen at the proboscis's tip]. Torsion less conspicuous. Note raised tarsi - 14: oscillatory torsion [clockwise, well visible in the middle and distal portion of the proboscis, as shown by arrows]. Spindle movement to the opposite side. Anti-parallel movement less conspicuous).

is gradually suppressed, together with the oscillatory torsion. Instead, the head begins to oscillate remarkably (fig. 20). Over half of the proboscis may penetrate the tissue (fig. 21). Blood is imbibed continuously. A striking, irregular but frequent sequence of partial withdrawals (fig. 19) and re-insertions of the proboscis follows, the head oscillating accordingly. The inclination of the proboscis indicates that new channels are bored. Torsion, without oscillation, may occur (fig. 18). The pain is continuous but at irregular times particularly intensive peaks are experienced. These are evidently due to the lacerating action of the inversely inclined barbs (fig. 17). Often a ball of rasped-out material (probably tissue fragments too large to pass into the proboscis) of a size of up to the diameter of the proboscis forms dorsally on it and, due to the anti-parallel movement, may move up and down the middle portion of the proboscis.

Blood may be regurgitated into the canal or onto the skin above it (fig. 21); it is always re-imbibed. The moth may pause with inserted proboscis. Occasionally new holes are pierced near by. When feeding for long periods, a few droplets of

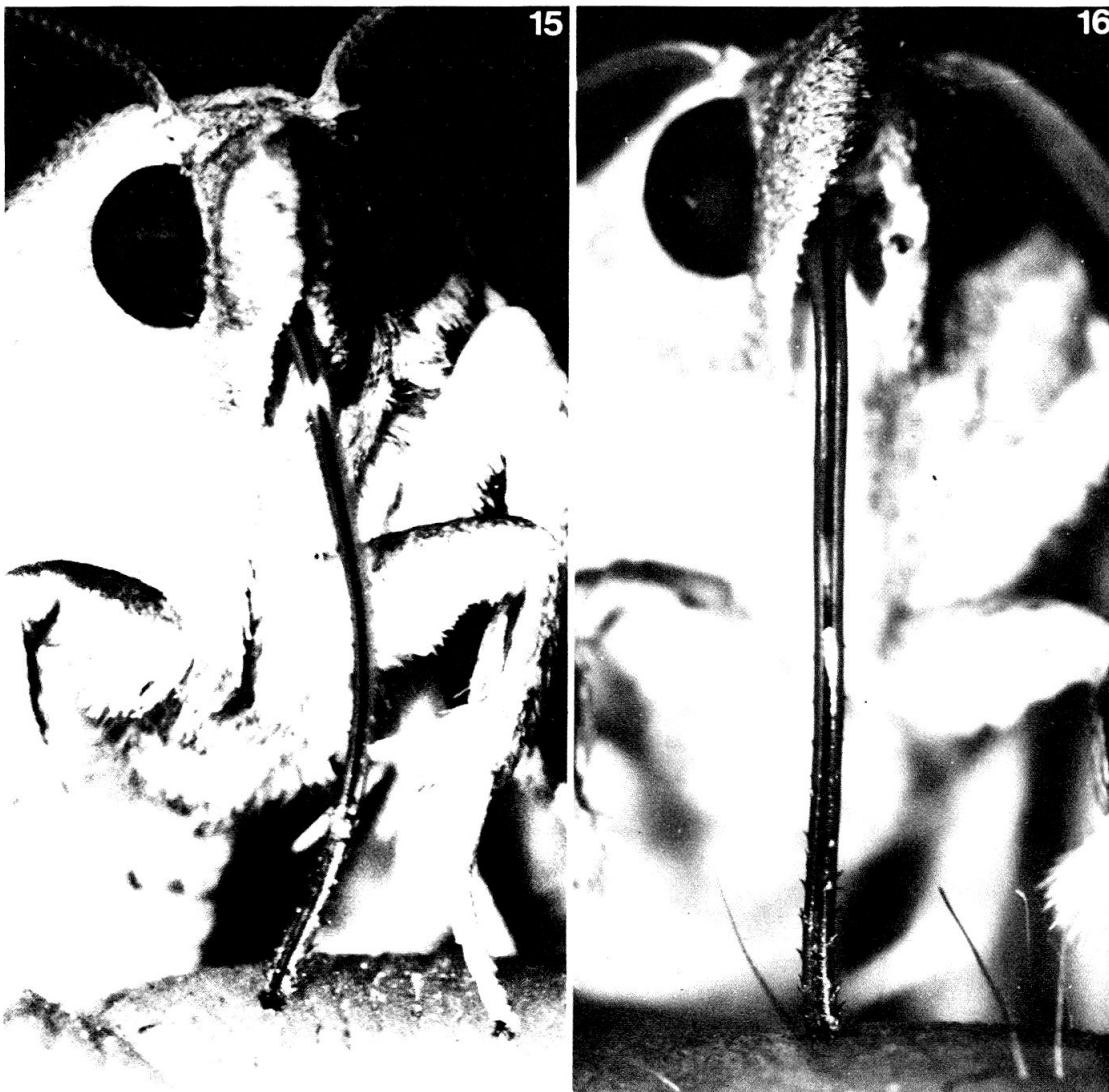


Fig. 15-16: Piercing *Calyptra eustrigata*. Phase II (15): tearing hooks grip and bore a hole as the proboscis's tip penetrates the skin. Oscillatory torsion and spindle movement still visible – Phase III (16): distal part of proboscis with erected barbs penetrates the tissue.



blood may be excreted anally. Towards the end of the feeding the moth mostly lays the antennae against the abdomen. Complete withdrawal, like partial withdrawal, is generally rapid, but occasionally the moth has difficulty to extract the proboscis out of the wound, especially when a host undertakes sudden defensive reactions. The moth then draws the proboscis with rapid jerks of the head, propping movements of the legs and irregular beats of the wings. To coil up the proboscis tightly the coils are repeatedly loosened and redrawn asymmetrically.

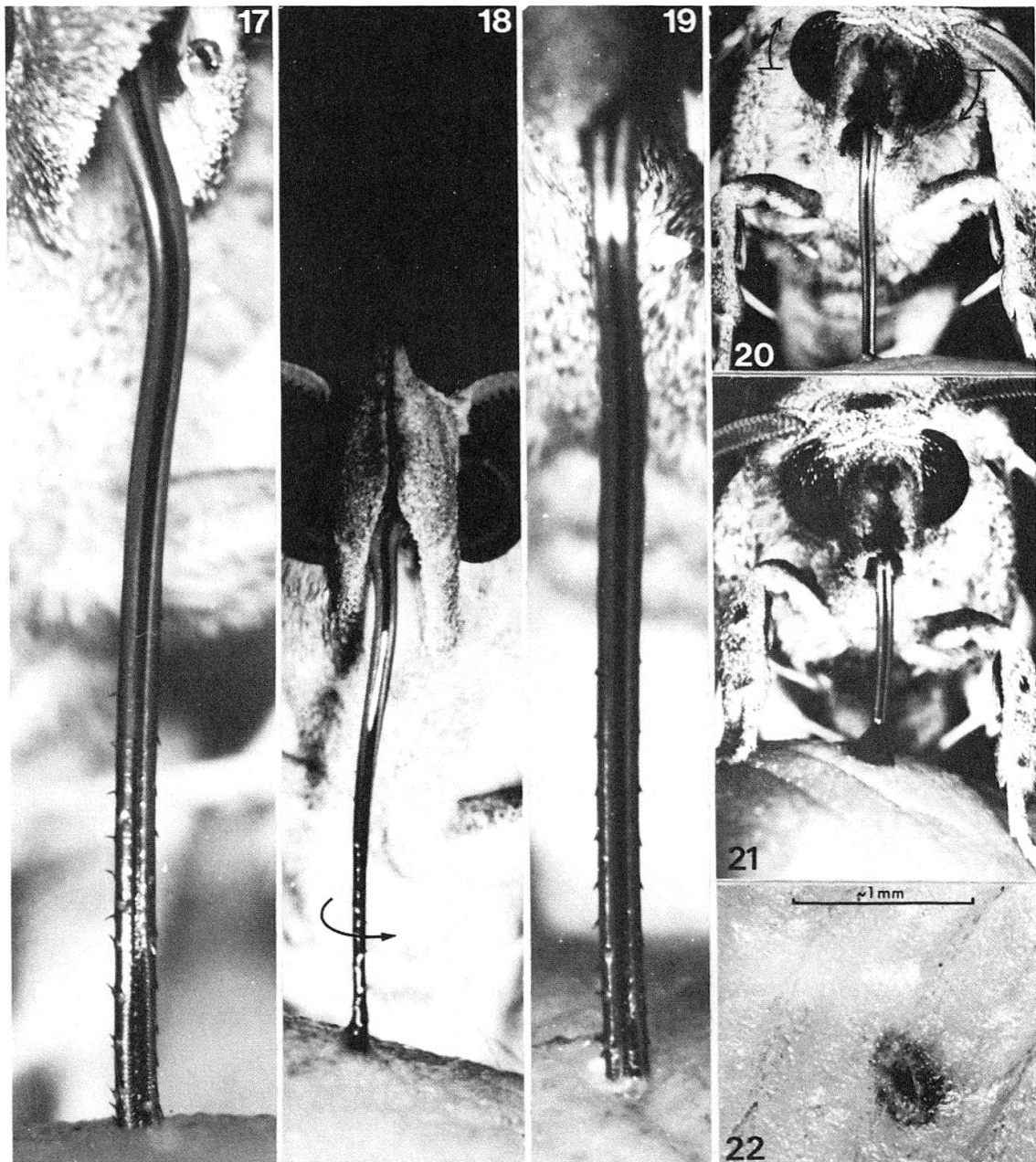


Fig. 17-22: Piercing *Calyptra eustrigata*. Phase IV (17): laceration of the tissue by inversely inclined erectile barbs - Phase IV (18): torsion of proboscis (counter-clockwise) to sever the tissue on all sides of the bored shaft - Phase IV and V (19): withdrawing proboscis, with forwardly inclined barbs - Phase IV (20): proboscis penetrates again; head oscillation (which neutralizes the spindle) is well visible - Phase IV (21): very deep penetration and regurgitation of some blood (probably to mix it with saliva) which will be quickly re-imbibed - Piercing hole bored out by *C. eustrigata*, 24 h after feeding (22). Photographs 13-22 are of experiments on the author's finger.

The perforation of a smooth skinned fruit, e.g. a grape, by *C. thalictri*'s proboscis is assumed to be realized chiefly by the «pneumatic hammer» effect (caused by the spindle movement) which eventually breaks the poorly ductile skin by countlessly repeated blows. As the very elastic mammal skin will not give in so easily to this procedure, *C. eustrigata* adopts first an «intruding» technique: special to and fro movements (15–20 Hz) of the proboscis force its tip to intrude between or into uneven structures of the skin (folds, pores, etc.) so that the tearing hooks can grip firmly. Then an opening is bored to allow penetration into the tissue. Penetration is based on the same principle as in *C. thalictri*, namely, the anti-parallel movement of the galeae causes pro- or regression of the proboscis through the tissue, the direction depending on the inclination of the erectile barbs; when erected backward the proboscis more easily advances, when inclined forward it more easily withdraws. This movement's frequency is 7–10 Hz. The action of the erectile barbs *inside* the medium being pierced has been evidenced also by transillumination photography (BÄNZIGER, 1970: fig. 29 a–d). The hole at the piercing site (fig. 22) shows that hooks and barbs actually bore out an opening into the skin.

In the beginning the head obviously thrusts the proboscis into the tissue, as evidenced by the raised position of the tarsi. But as soon as sufficient number of erectile barbs can grip, thrust conveyed from the legs to the proboscis by the body of the moth is no longer necessary. This startling piercing efficiency had been tested experimentally for *C. thalictri* (*loc. cit.*, p. 78) and is also present in *C. eustrigata*. In a different experiment a guava fruit with a feeding specimen was turned so that the moth came to be in a supine position on the lower side of the fruit. A small paper strip was gently introduced between the fruit and the first and second tarsi on each side. The fore legs being prevented from clinging to the fruit, any insect would be expected to lose grip and fall as, indeed, did *C. eustrigata* when not piercing. However, when piercing, the moth not only did not fall, but also advanced the proboscis further into the fruit, raising the moth despite the increased weight due to the papers.

In the fruit-piercing *C. thalictri* 2 phases, viz perforation of the skin and penetration into the pulp, were recognized. For the sake of clarity, the analogous but more complex piercing mechanism of *C. eustrigata* is divided into 5 phases with the following sequences:

#### I *Intrusion and establishment of a hold for the tearing hooks (fig. 23 and 24, a–e).*

- 1 The tip of the proboscis is thrust between or into uneven structures of the skin (fold, ditch, hair pore, fissure; excoriation; the soft tissue of a sore or a crack in its crust), while the moth firmly clings to the host. The proboscis is stiffened by blood turgidity and slight «S»-like curving. The tearing hooks are everted and the barbs erected, both by blood-pressure, and are ready for action.
- 2 The proboscis's fast bending to the right and the left (spindle movement) and the ensuing continuous directional change of thrust allow the tip to proceed more deeply between or into uneven skin structures. Because of the anti-parallel movement the whole thrust is conveyed only through the galea (stylet) which is protracted at the time, the protraction of each galea occurring in rapidly alternating sequence.



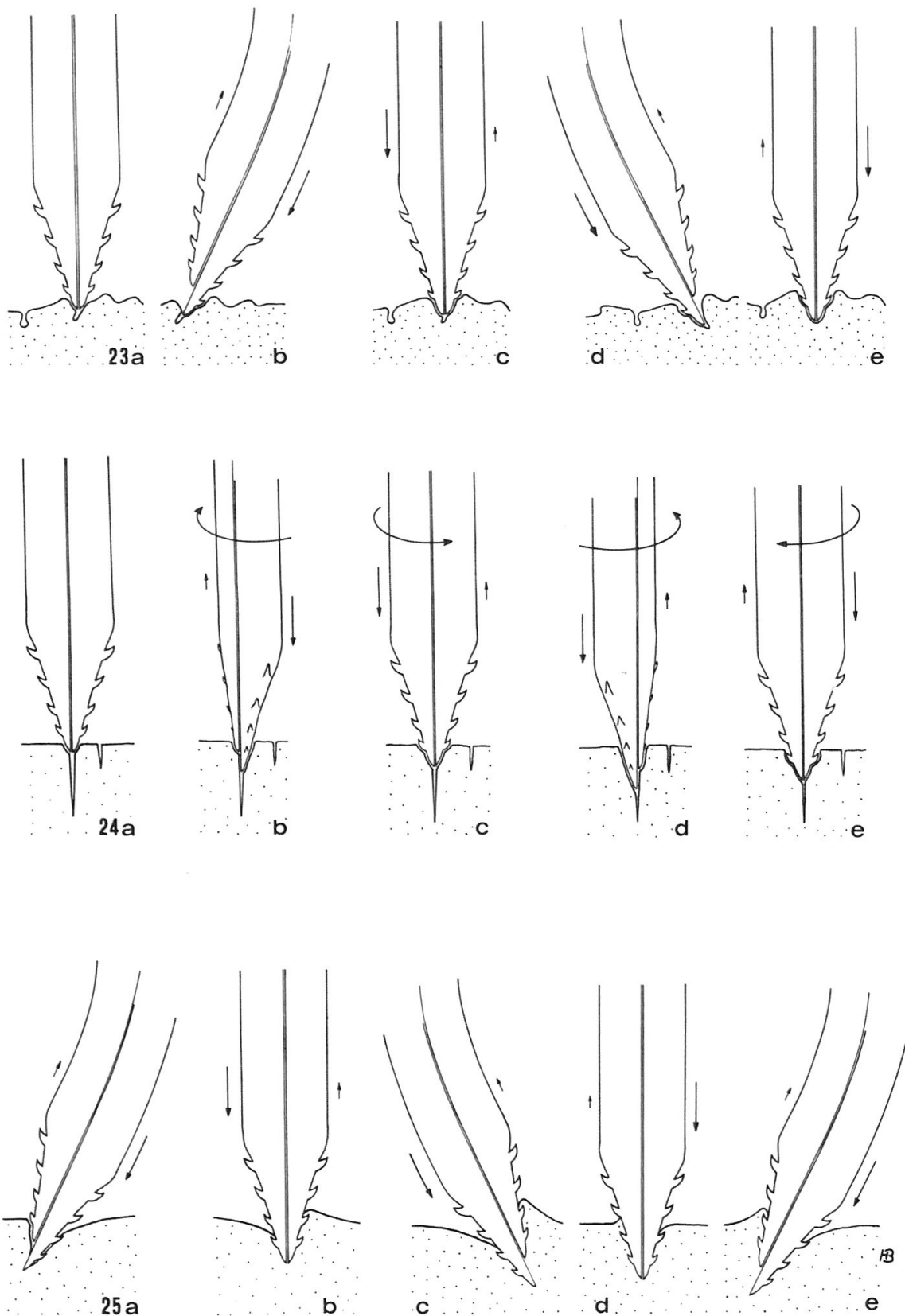


Fig. 23-25: Piercing mechanism of *Calyptra eustrigata*. Phase I: intruding into a fold or fissure to establish a hold for the tearing hooks, by simultaneous directional change of thrust (spindle movement) (23 a-e), oscillatory torsion (24 a-e), and anti-parallel movement (23, 24). Phase II: gripping of the tissue and boring of a hole (torsion omitted for reason of clarity) (25 a-e). Explanations on pp 135, 137.

- 3 Simultaneously, the proboscis's oscillatory torsion even more efficaciously intrudes the tip into the uneven skin structures. In addition, torsion also has some boring action.
- 4 These actions continue until the tip is deep enough to bring sufficient tearing hooks into action, i.e. in contact with the aforementioned unevenness. Generally, if not successful within some 10 sec, the process is repeated at a new spot, an event which happens frequently.

## II *Gripping and boring of a hole (fig. 25 a-e)*

- 5 Owing to the lateral bending (spindle movement) of the proboscis (e.g. to the right), the tearing hooks of the protracted galea (right) are brought into contact with the tissue unevenness.
- 6 The hooks grip and/or tear the unevenness as the anti-parallel movement is about to be reversed (the right galea retracted and the left protracted, while the proboscis is being bent to the left).
- 7 Owing to the hooks' gripping, further bending to the left causes the proboscis's tip and armature to be thrust with increased force against the skin by leverage, enhanced by the left galea's protraction. The strong collar behind the hooks prevents their collapse.
- 8 Maximal bending to the left is now reached, the left galea has been protracted beyond the right and deeper into the skin. As only one galea advances at a time and because of torsion, the piercing effect is much improved. More hooks are now available for exerting firm grip and/or tearing.
- 9 The anti-parallel movement is again reversed and sequence 6-8 begins anew. As the whole process proceeds the proboscis's tip rapidly penetrates, produces an entrance and begins to bore a hole. Torsion and spindle movement are then steadily reduced. Phase II generally lasts only a few seconds.

## III *Penetration into the tissue (fig. 26 a-e)*

- 10 Through the hole in the skin one galea is pushed into the underlying tissue by the anti-parallel movement assisted by the thrusting force of the head. At the same time muscles turn the head neutralizing thereby the spindle movement which otherwise would hinder penetration.
- 11 All movements are reversed and, as the galea is induced to recede, the erectile barbs grip the tissue – high blood-pressure keeps them inclined backward – preventing full retraction. Thus the other galea is forced to advance beyond the anchored galea by the anti-parallel movement.
- 12 The sequence 10-11 is repeated by the right and the left galea alternately, the oscillations of the head being synchronized with these movements. When sufficient erectile barbs grip the tissue, 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.
- 13 Penetration produces discharge of blood; this is rapidly imbibed. The proboscis's tip and tearing hooks and, especially, the elongated barbs lacerate the tissue and enlarge the entrance. This phase lasts much longer than the preceding one.

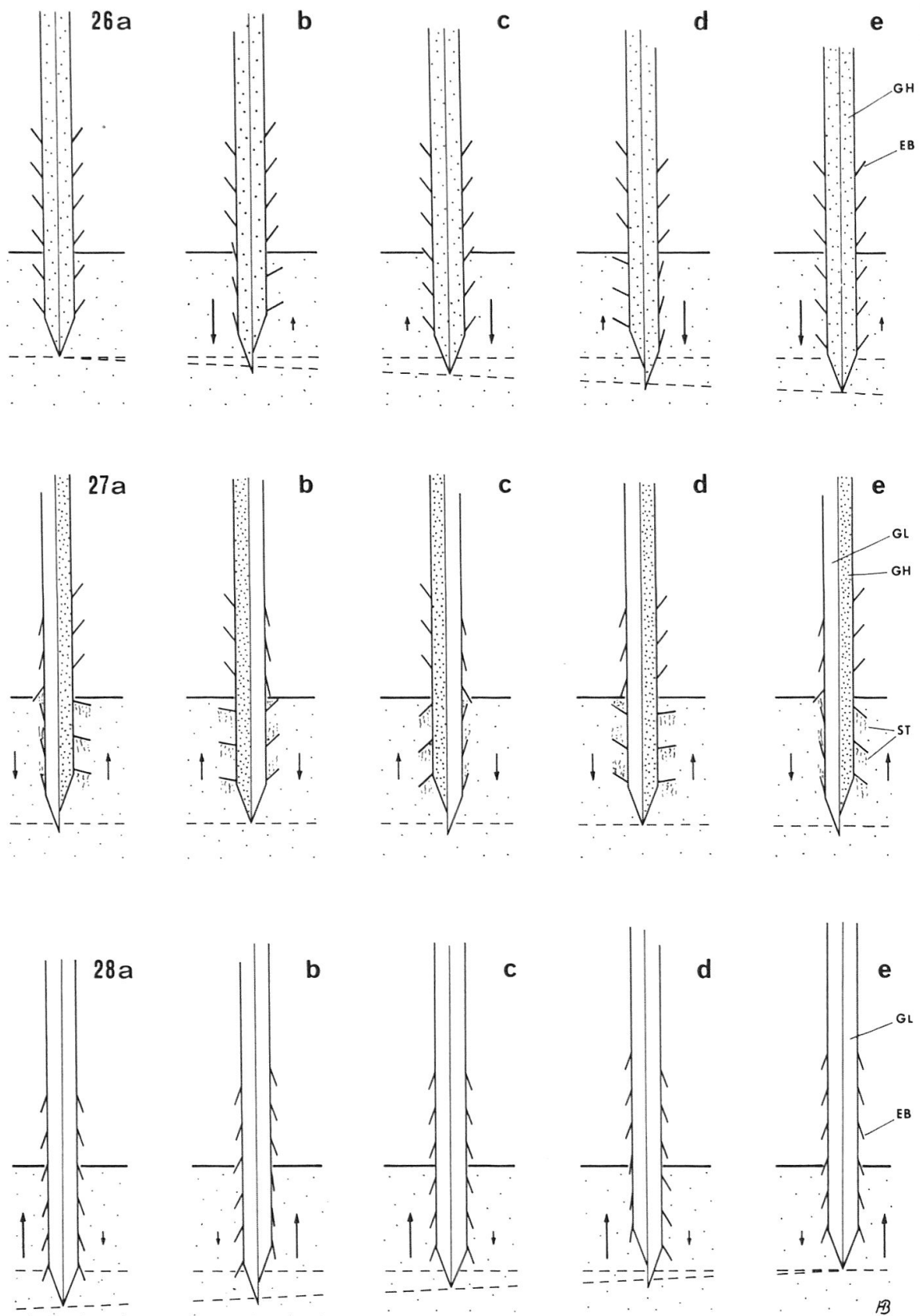


Fig. 26-28: Piercing mechanism of *Calyptra eustrigata*. Phase III: penetration into the tissue (26a-e). Phase IV: laceration of the tissue, sequence 15 (27 a-e). Phase V: withdrawal (28 a-e). EB: erectile barb; GH: galea with high blood-pressure, GL: with low pressure; ST: slashed tissue. Explanations on pp 137, 139.

#### IV Laceration of the tissue (fig. 27a-e, showing sequence 15 only)

- 14 Penetration is followed by incomplete withdrawal and new penetration, this being repeated frequently. More tissue is thus torn and deeper and new shafts may be produced.
- 15 Tissue laceration is enhanced when the galea to be protracted has forwardly inclined barbs and the one to be retracted backwardly inclined ones: the mutually counteracting movements cause intense slashing as the barbs reach an orthogonal position when forced to swivel by the tissue, or when they rip through it without turning.
- 16 Irregularly, slow-moving torsion of the proboscis helps to tear tissue on different sides of the canal – there is less armature ventrally on the proboscis – and facilitates the boring of new shafts. This is, by far, the longest phase, and may last many minutes.

#### V Withdrawal (fig. 28a-e)

- 17 Reduced blood-pressure allows the erectile barbs to return by elasticity to a forward inclination; a mechanism analogous to that used for penetration, together with the pulling force of the head, ensure quick withdrawal, often in less than a second.

#### DISCUSSION

The unique functioning of the erectile barbs has already been pointed out. Another speciality not known to occur in other insects is the fast, oscillatory torsion – equivalent to a back and forth rotation – of *C. eustrigata*'s galeae or stylets which enables them to intrude between folds, fissures, pores, etc. and which, to some extent, assists in boring a hole. Although rotation of the stylets was found to occur in some Hemiptera, i.e. *Oncopeltus fasciatus* DALLAS (Lygaeidae) (BUTT, 1943), *Aphis gossypii* GLOVER (Aphididae) and *Eupteryx melissae* CURTIS (Cicadellidae) (POLLARD, 1958, 1968), the movement is not oscillatory. It is mainly static, temporary, and evidently allows the stylets to advance in a new plane of penetration in order to tap new tissue; and it is assumed to be induced by a twisting of the labium (POLLARD, 1968, 1971). No stylet rotation is mentioned in the classical works on piercing mosquitoes (ROBINSON, 1939; GORDON & LUMSDEN, 1939), horse flies (DICKERSON & LAVOPIERRE, 1959), tsetse flies (JOBLING, 1933), simuliids (WENK, 1962), lice (LAVOPIERRE, 1967), and flea (WENK, 1953).

A study of the evolution of feeding habits is not only of scientific interest but can also help assess the medical and veterinary importance of a species. It has been shown that in *Calyptra* the skin-piercing blood-sucking feeding probably evolved from the fruit-piercing feeding (BÄNZIGER, 1971a, 1975, 1976). *C. eustrigata* displays both. But DOWNES (1973) commented that since fruit and animal fluids provide insects with «entirely» different nutrients, it is very improbable that blood-sucking is a derivative of fruit-piercing in the moth. He proposed that it represent a further specialization of lachryphagy (feeding upon lachrymal secretion from mammal eyes) or at least of a related feeding upon animal fluids.

In reality, however, there are fluids containing appreciable amounts of proteins, e.g. durian (*Durio zibethinus*) and tamarind (*Tamarindus indica*) with 3.2 and 2.9%, respectively (FAO & USDH, 1972), while blood also contains sugar. Not only do certain fruits smell like decomposing animal matter when overripe but the

chemicals involved are much the same, e.g. decaying amino acids. Thus the transition from fruit juices to animal fluids is acceptably gradual and could certainly be tempting enough to represent a likely evolutionary pathway. But the main reasons why DOWNES' proposal is not tenable stems from ethological, morphological and phylogenetic facts:

(1) the repeated incomplete withdrawals and re-insertions of the proboscis when piercing animal tissue is an unmistakeable vestige of the fruit-piercing feeding. In this the sap contained in cells must continually be freshly tapped. The continuous lacerating of tissue to obtain blood when this is already flowing into the pool from torn vessels, would be difficult to explain if *C. eustrigata* did not have a feeding strategy directly derived from fruit-piercing.

(2) between the lachryphagous and the skin-piercing feeding there is a virtually unbridgeable evolutionary gap as far as morphological mouth-part adaptations are concerned. All odds of selective pressure are against the development of a piercing armature in a lachryphagous moth. Such a sensitive spot as the eye region will never allow the development of such a fierce armature as that found in *Calyptra*. The proboscis of lachryphagous moths is soft and without piercing armature (BÄNZIGER, 1972).

(3) if lachryphagy were an evolutionary stage preceeding skin-piercing one would expect transitional stages to occur as they do between the fruit-piercing and skin-piercing habits, a far less common complex. Of the some 100 zoophilous Pyralids, Geometrids, Notodontids observed, none is confirmed to be fruit-piercing and/or skin-piercing blood-sucking, though there are all transitional stages from the suckers of sweat and excreta to those imbibing eye-secretions. On the other hand, as previously shown (BÄNZIGER, 1975, 1979), no *Calyptra* and none of its close relatives *Oraesia*, or less close *Othreis*, *Eudocima*, *Rhytia* (all typical fruit-piercers) is lachryphagous; in fact, in these 5 genera's vast subfamily Ophiderinae there appears to be no confirmed lachryphagous species. In Noctuidae lachryphagy has been confirmed only in a number of species of Chloephorinae (= Westermanninae) and possibly 2 Acontiinae none of which displays fruit-piercing and/or skin-piercing habits.

Based on the present and earlier studies it is concluded that, owing to a tendency, as yet not fully understood, mainly in males of several lepidopterous families to search for food of animal origin, two main evolutionary pathways to satisfy this need resulted, without necessarily giving up the original nectar feeding habits: (a) from nectar-sucking to the imbibing of animal excreta and secretions, to oligo-, hemi- and finally eulachryphagy. The last stage features important physiological adaptations of the digestive system. (b) from nectar-sucking to fruit-piercing to skin-piercing blood-sucking. The latter appears to be a recent development as this study and earlier conclusions show (*loc. cit.*).

From the present analysis disease transmission by *C. eustrigata* might occur through (1) salivary injection, (2) regurgitation of ingested blood, (3) anally excreted blood, (4) contamination by piercing proboscis and (5) superficial contact of infected legs, abdomen, wings, antennae or licking proboscis. Pathogens of biologically transmitted diseases may potentially be vectored by (1) and, to a lesser extent, by (2) and (3). However, as *C. eustrigata*'s feeding habit appears to be a rather recent development and a derivative of plant feeding it is unlikely that pathogens with such sophisticated life-cycles and physiology have already had

time to adapt. However, pathogens of mechanically transmitted diseases, needing much less adaptation to a potential new carrier such as *C. eustrigata*, could well be transmitted, especially by (4). Successful transmission depends mainly on the size of the mouth-parts ( $10\text{mm}^2$ ), depth of their penetration (up to at least 7 mm), extent of lesions inflicted (vast, cf. phase IV), quantity of blood residues caught externally on the proboscis (potentially very large in interstices of armature and galeal linkage), feeding time (average 12 min), and frequency and rapidity with which the moth changes a feeding spot from one host to another. *C. eustrigata* is thus exceptionally well equipped as a potential vector, comparable to the horse flies, a very important group of vectors of livestock disease pathogens. However, blood-sucking *C. eustrigata* is rare, present only in some, mainly humid, tropical areas of the Oriental Region, and restricted to forests and their neighbourhoods. Hosts are mainly large wild ungulates, though domestic elephant, water buffalo and cattle are not spared. No confirmed piercing of man in nature has been published. Thus its medical-veterinary importance is likely to be minimal.

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