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Skin-piercing blood-sucking moths VI: Fruit-piercing habits in *Calyptra* (Noctuidae) and notes on the feeding strategies of zoophilous and frugivorous adult Lepidoptera

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Males and females of 10 species and 2 subspecies of adult *Calyptra* were found to be primary fruit-piercers of 23 species of fruit in nature and/or experiments: *bicolor*, *eustrigata*, *fasciata*, *fletcheri*, *ophideroides*, *orthograptia*, *parva*, *pseudobicolor*, *minuticornis minuticornis* (in S and SE Asia), *minuticornis novaepommeraniae* (in Papua New Guinea), and *thalictri* (in Switzerland). They pierced soft-skinned fruit (e.g. figs, *Rubus* spp.), medium hard-skinned fruit (e.g. apple, mango), and the thick rind of fruit such as mandarin. More wild fruit species were attacked than cultivated ones. Most of these *Calyptra* species are known to be facultatively skin-piercing blood-sucking in the male sex. In experiments, fruit sap was required for male and female survival for up to 3–4 weeks, while with blood or water alone males lived only 5–6 days. They lacked proteases but NaCl was one of the substances they sequestered from blood (by 85–95 %). On the other hand, proteases were present in both sexes of tear drinking noctuids *Lobocraspis griseifusa* and *Arcyophora* (3 spp.), where males and females suck lachrymation, an important source of protein and salt. But the great majority of lachryphagous species are Geometridae, Pyralidae, Notodontidae, Thyatiridae and Sphingidae, where only males take tears, besides other body fluids. There is indication that proteases are present in some of these species but absent in others. It is proposed that in the species capable of protein digestion, the resulting amino acids represent a «male dowry» which may be transferred to females via spermatophores during mating, whereas in the other species only salt is transferred. In *Calyptra*, as yet unknown substances from blood may play an additional role.

The data further corroborate the view that hematophagy in *Calyptra* is evidently derived from fruit-piercing, while lachryphagy on mammals developed on separate lines. Serious misquotations in related publications are rectified and a hypothesis about the evolution of lachryphagy with birds as hosts in Madagascar is reinterpreted.

Keywords: *Calyptra*, *Arcyophora*, *Lobocraspis*, digestion, fruit-piercing, hematophagy, lachryphagy, proboscis morphology, proteases, tear drinking.

INTRODUCTION

Several species of *Calyptra* have been reported to pierce various kinds of fruits in temperate and subtropical regions of Asia. Some, such as *C. gruesa* (Draudt), *C. hokkaida* (Wileman), *C. lata* (Butler), *C. ophideroides* (Guenée) at times can be fairly common to become occasional pests in fruit orchards in Japan and India (Ramakrishna Ayyar 1944; Matsuzawa 1961; Hattori 1962; Miyashita & Tchiku 1962; Nomura & Hattori 1967). Other species, like *C. bicolor* (Moore), *C. fasciata* (Moore), *C. minuticornis* (Guenée) in India (Ramakrishna Ayyar 1944), *C. thalictri* (Borkhausen) in Japan (Nomura & Hattori 1967; Hattori 1962) are too scarce to cause appreciable damage. The palaeartic *C. thalictri* is of special interest because it is the only species of the genus present in Europe and, although being the earliest known species – since the time of Borkhausen (1790) – so far there seem to be no published details of its piercing fruit in nature in the continent.

However, in this genus of 17 species (Bänziger 1983) there are uncommon to rare taxa which are unique among Lepidoptera in taking blood by a piercing act. Seven S and SE Asian species are confirmed to be hematophagous: *C. bicolor* (Moore), *C. eustrigata* (Hampson), *C. fasciata* (Moore), *C. minuticornis minuticornis* (Guenée), *C. orthograptata* (Butler), *C. parva* Bänziger, *C. pseudobicolor* Bänziger. Hematophagy is less developed in *C. ophideroides* (Guenée), while in *C. fletcheri* (Berio), closely related to the *bicolor* group, so far it is confirmed only in experiments. With a special drilling mechanism and proboscis armature *Calyptra* mainly pierce tissues underlying scars, excoriations, blood-crusts, fissures, fresh and old sores of large ungulates and elephants; in the rare natural attacks on man they drill mainly intact skin. The habit is facultative and only males but not females are involved. Taxonomy, ecology, ethology, piercing mechanism, evolution and other aspects have been treated in a series of papers (see Bänziger 1989).

Calyptra are different from other zoophilous moths which occasionally «lick», without a piercing act, blood and exudates from open wounds and the tiny blood-droplets excreted by mosquitoes. These moths, mostly Geometridae, Pyralidae and Notodontidae, more normally are lachryphagous (eye-frequenting, ophthalmotropic), a feeding habit exhibited by many dozens of species belonging to the Geometridae, Pyralidae, Notodontidae, Noctuidae, Thyatiridae and Sphingidae (most papers by Büttiker, e.g. 1962, 1967, 1969a, 1969b, 1997, and Bänziger, e.g. 1973, 1988a, 1988b, 1992, 1995). They all lack piercing mouth parts.

Recently two exciting new findings have been reported. Zaspel *et al.* (2007) found that E Russian populations of *C. thalictri* drew blood by piercing human skin under special circumstances. This finding is important because *C. thalictri* is not closely related to the hematophagous taxa of the genus, and is from a temperate region. However, the data are from experiments under enclosed conditions, hence there is need of verification with natural field observation since it is well-known that insects can behave very differently when not free in nature.

Secondly, the noctuid *Hemiceratoides hieroglyphica* (Saalmüller) was photographed with its proboscis inserted between the eye lids of sleeping birds in Madagascar (Hilgartner *et al.* 2007). This fine discovery of birds as hosts is treated in some detail below because of unfortunate discrepancies in the authors' discussion.

In my *Calyptra* studies I have mentioned the less interesting fruit-piercing aspect only on the sidelines and relegated it for detailed treatment to a later date. This is now made up for with the present compilation of data. The second purpose was to examine their feeding physiology and proboscis morphology to try understanding *Calyptra*'s unusual habits and compare them with those of lachryphagous species.

METHODS

Terminology. Eulachryphagy: exclusive sucking of tears when settled on animals. Hemilachryphagy: besides tears, various other body fluids (sweat, nasal and salival fluids, urine, dung, wound exudates including blood, and the anally extruded blood droplets of mosquitoes) are imbibed, whether directly from the host or where they have been smeared off onto the vegetation, or dropped to the ground. For simplicity reasons, oligolachryphagy is not used here (denotes a much rarer tear drinking in favour of other body fluids). Lachryphagy does not exclude nectar feeding.

The field data presented here were obtained mainly during surveys on the overall situation of fruit-piercing moths in Thailand, Nepal, India, Indonesia, Papua New Guinea, and brief investigations in Switzerland, especially in fruit cultivations (Bänziger 1982, 1987, and unpubl. since 1969). For the more forest-bound *Calyptra*, promising, mainly non-cultivated trees and shrubs were sought and mapped in or near forests, as well as in fruit gardens of small villages inside or in proximity of forests. Fruits were inspected with a head light with adjustable light intensity and, where the distance required it, by binoculars. Selected sites were inspected nearly every night during fruiting, some sites for more than five years. Collection at mercury vapour lamps yielded additional material, including much needed females. Lachryphagous moths were studied along with *Calyptra*. Identification of difficult taxa was by genitalia examination.

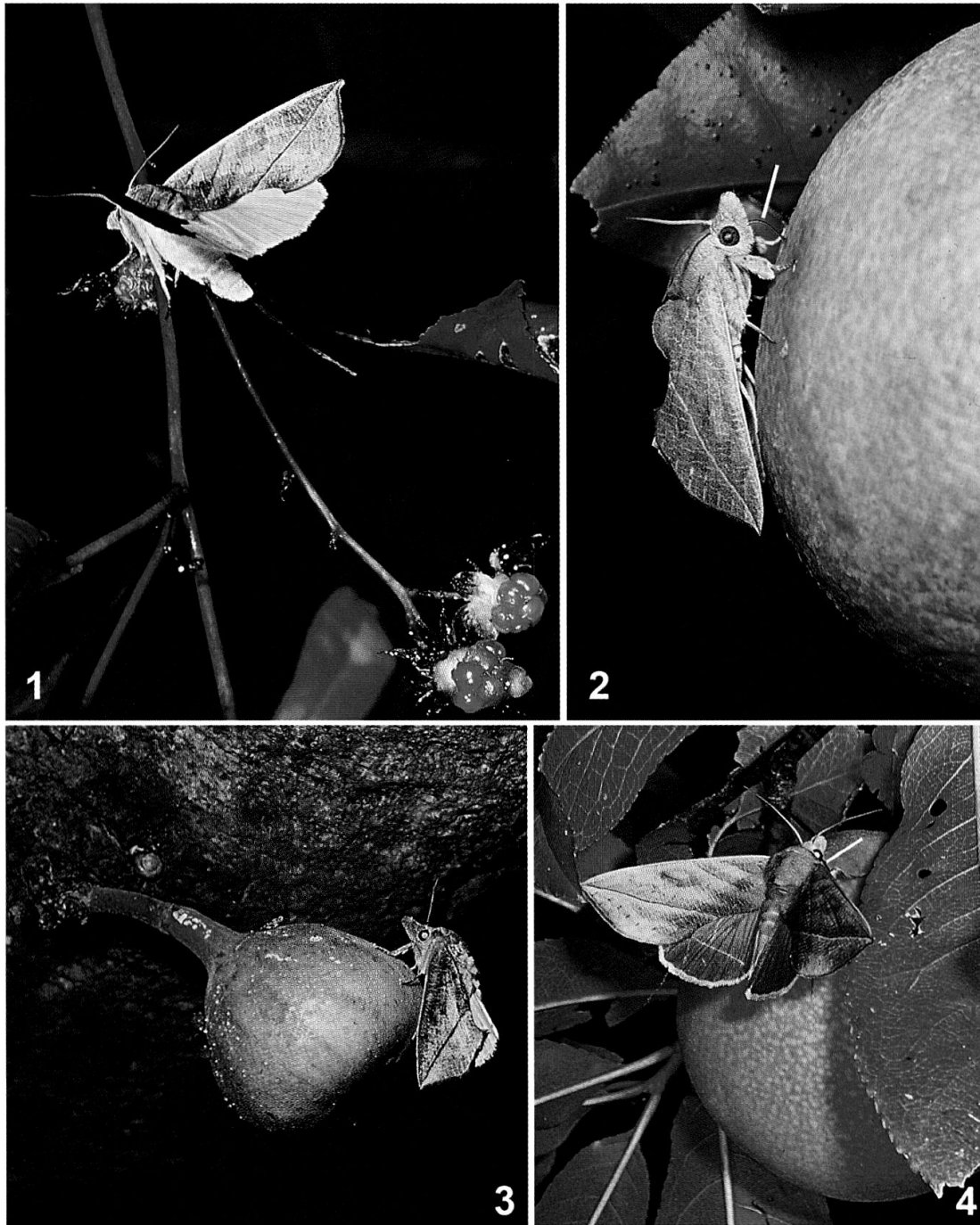
Proboscides were studied both in the fresh state (cut from euthanized moths), mounted on microscope slides in water, ethanol (65 %) or Hoyer's (Faure's) aqueous medium. Where fresh material was not available, ethanol preserved specimens were used. Drying (such as in collection specimens or as required for SEM preparation) tends to deform the walls in species with delicate (non-sclerotized) proboscis endings, such as found in lachryphagous moths. The danger caused by indiscriminate application of SEM methodology is exemplified in Fig. 6b of Gouws *et al.* (1995), where in the eye-frequenting *Arcyophora longivalvis* Guenée the outer lower wall of the proboscis had collapsed from convex to concave to such an extent to become gutter-shaped: the authors misinterpreted it as the food canal! (In their Fig. 6a the food canal is correctly designated.) SEM imagery can show much finer details than conventional techniques, but the required metallic coating hides underlying tissues, e.g. whether it is membraneous or sclerotized, a crucial issue in proboscis morphology and function. In SEM micrographs membraneous walls appear as solid as in sclerotized ones, whereas they are readily distinguishable by light microscopy.

Moth longevity was determined by withholding food (fruit, blood from the author) from caged moths given only water, compared to those given access to food. Assessed were *C. eustrigata* (5 males, 2 females), *C. minuticornis* (5 males, 5 females), *C. fasciata* (2 males, 1 female), *C. pseudobicolor* (2 males, 2 females), *C. fletcheri* (1 male), *C. ophideroides* (1 male, 1 female).

The method for assessing the presence of proteases in moth midgut has been described in Bänziger (1973, p 1386), but here the enema was omitted. Examined were males of 5 *C. eustrigata*, 2 *C. minuticornis*, 1 *C. orthograptus*, 1 *C. fasciata*, 1 *C. bicolor*. Eulachryphagous *Lobocraspis griseifusa* Hampson, previously shown to have proteases, was reassessed in 5 females and 3 males. Newly examined eulachryphagous noctuids were 1 *Arcyophora bothrophora* Hampson, 1 *A. icterica* (Swinhoe), 1 *A. dentula* (Lederer), all females.

The presence and condition of blood cells in anal excreta (dark red blobs) of blood-engorged *Calyptra* was examined by light microscope in Giemsa-stained smears. These were prepared from anal drops naturally expelled by each *Calyptra* male $\frac{1}{2}$ –1 h and again 2–6 h after piercing commenced on the author's finger in experiments. Examined were 3 *C. eustrigata*, 2 *C. minuticornis*, 1 *C. fasciata*, 1 *C. parva*, all males.

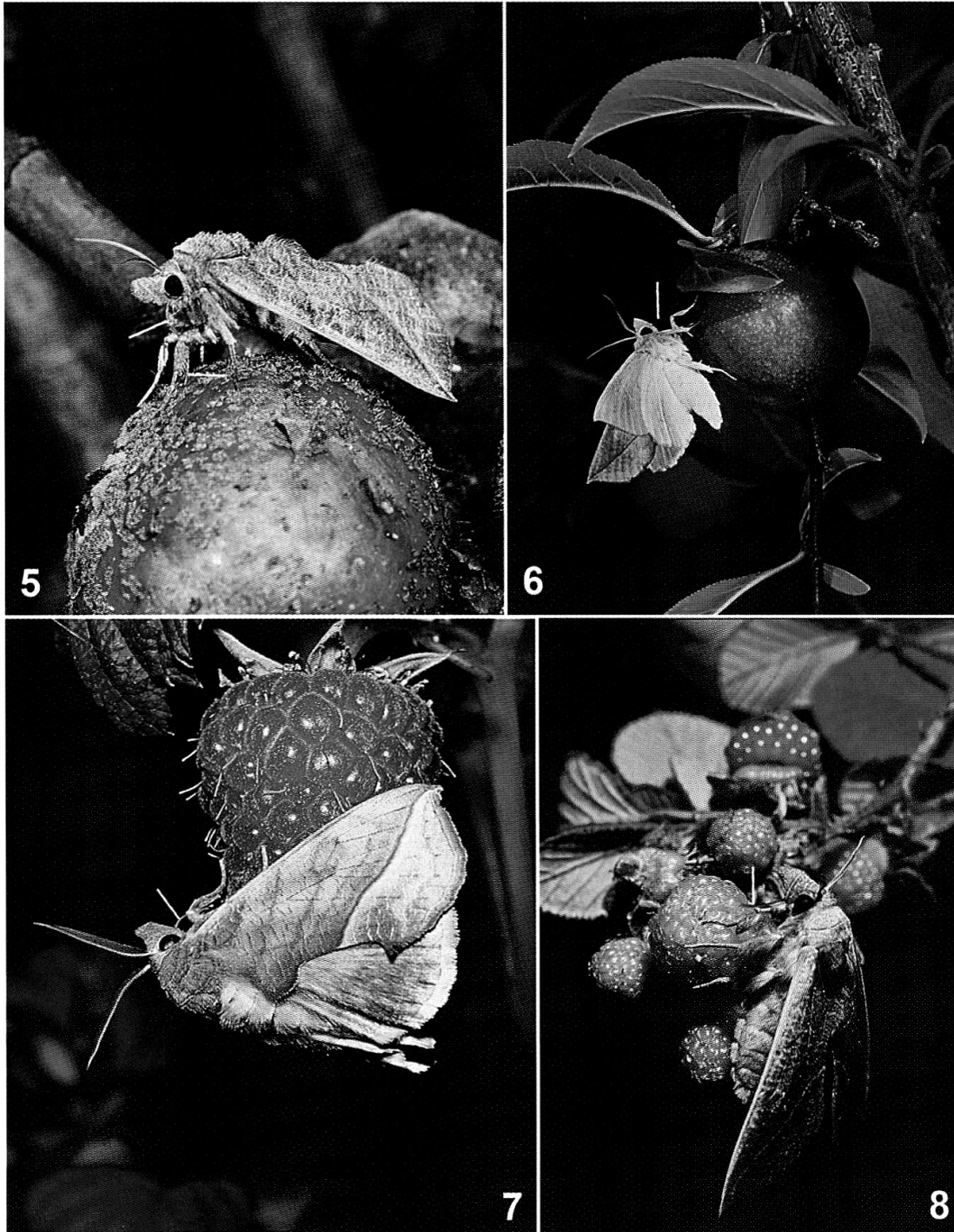
The sequestration of NaCl from ingested blood was evidenced by atomic absorption spectrophotometry of anal excreta of 2 *C. fasciata* and 2 *C. parva* males,



Figs 1–4. *Calyptra* piercing fruits. All natural events. White lines indicate the proboscis; in Figs 1 and 3 the proboscis is hidden between the fore legs. – 1. Female *C. bicolor* piercing *Rubus acuminatus*, Nepal. – 2. Male *C. minuticornis* piercing mandarin, N Thailand. – 3. Female *C. ophideroides* piercing *Ficus auriculata*, NW India. – 4. Female *C. fasciata* piercing peach, NW India.

and compared to blood of their donor hosts, a mule and the author, as controls. In *C. fasciata* the blood analyzed was excreted 20 and 35 min, respectively, after piercing mule skin in natural events. In *C. parva* blood was naturally excreted 45 and 90 min, respectively, after piercing the author's finger in experiments. The spectrophotometer analyses were carried out by Dr. T. Prapamontol, Chiang Mai University.

All illustrations are by Bänziger except the SEM micrograph of Fig. 11 which is by J. Zaspel.



Figs 5–8. *Calyptra* piercing fruits. All natural events except Fig. 8 which is an experiment. White lines indicate proboscis. – 5. Female *C. parva* piercing *Ficus semicordata*, N Thailand. – 6. Male *C. pseudobicolor* piercing plum, Nepal. – 7. Male *C. thalictri* piercing raspberry, S Switzerland. – 8. Male *C. fletcheri* piercing *Rubus ellipticus*, Nepal.

RESULTS

Below is a list of ten species of *Calyptra* found to pierce 23 species of fruit. *Calyptra* pierced them as primary fruit piercers, i.e. they bored by themselves a hole into the intact skin of the fruit, unlike secondary fruit piercers which use pre-exis-

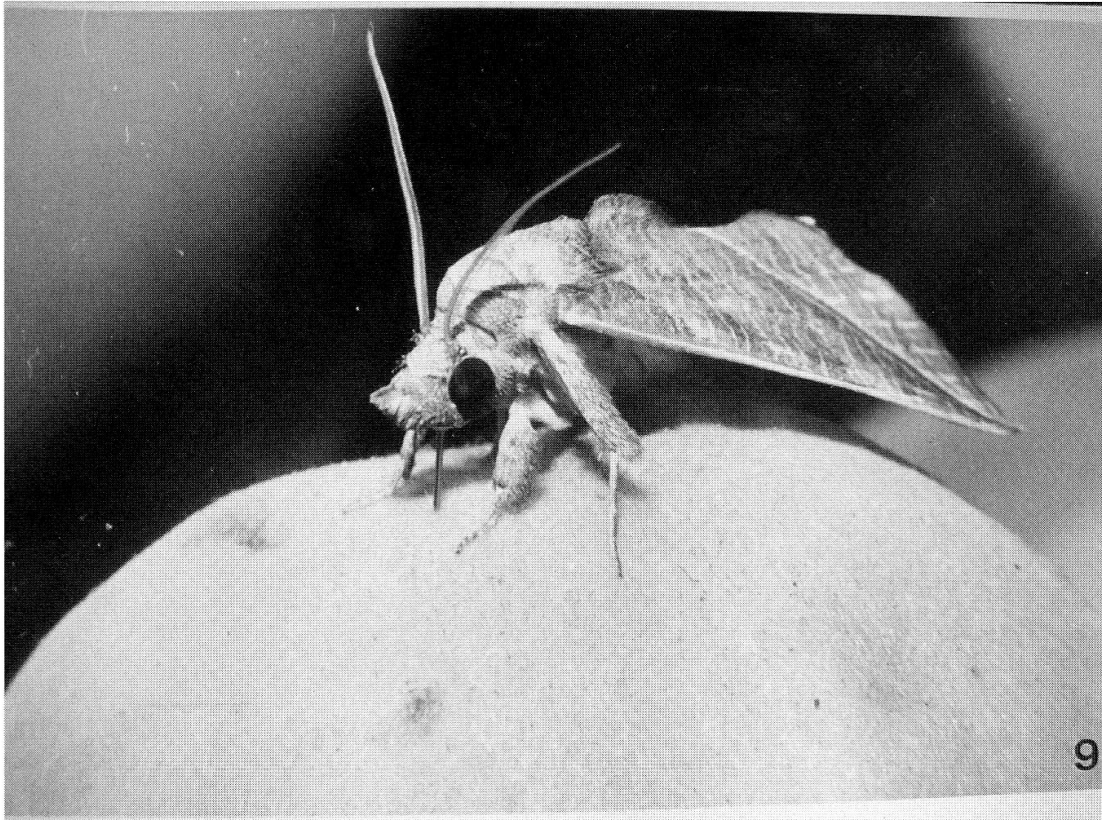


Fig. 9. Male *Calyptra eustrigata* piercing peach. W Malaysia, experiment.

ting holes drived by primary species, or through other entrances already present (e.g. cracks in the wall). Where the sex is not clear it is mentioned as «specimen».

C. bicolor (Fig. 1)

Natural conditions: *Rubus acuminatus* Sm., 1 female, 16.9.84. Another specimen, presumably this species, flew by *R. acuminatus*, 13.9.88, Phulchoki, around 1600 m, C Nepal.

Enclosed conditions: *Rubus rugosus* Sm., peach, plum, guava.

C. eustrigata (Fig. 9)

Natural conditions: not yet seen on fruit.

Enclosed conditions: guava (*Psidium guajava* L.), mango (*Mangifera indica* L.), peach (*Prunus persica* (L.) Batsch), mandarin (*Citrus reticulata* Blanco), langsat (*Lansium domesticum* Correa), grape (*Vitis vinifera* L.), apple (*Pyrus malus* L.), plum (*Prunus domestica* L.), rose-apple (*Syzygium jambos* (L.) Alston), plum mango (*Bouea oppositifolia* (Roxb.) Meisn.).

C. fasciata (Fig. 4)

Natural conditions: peach, 6 females, 2 males, 1 specimen, 8, 9, 11, 13, 16, 23.7.87; *Ficus auriculata* Lour., 1 male, 1 specimen, 8, 9.7.87; *Ficus* sp., 1 spec-

imen, 10.7.87, all Kumaon Hills, 1450 m, Nainital, Uttar Pradesh, India. *R. acuminatus*, 2 specimens, Phulchoki, Nepal, 30.9.88.

Enclosed condition: mandarin, grape.

C. fletcheri (Fig. 8)

Natural conditions: not yet seen on fruit.

Enclosed conditions: *Rubus niveus* Thunb., 1 male, 19.6.85, Phulchoki, Nepal.

C. minuticornis minuticornis (Fig. 2)

Natural conditions: mandarin, 1 male, 2 females, 2 specimens, 20.7.72; 2 males 2.8.72; 1 female 9.8.72; 2 males, 11.8.72; 1 male 19.8.72; peach, 1 male, 7.6.75; *Ficus hispida* L., 1 female, 20.6.75, all foot of Doi Suthep; *Ficus racemosa* L., 3 specimens, 26.8.79, 28.11.80; *Ficus semicordata* Buch.-Ham. ex Sm., 1 female, 1 specimen, 23.10.83, 28.10.85, all Doi Chiang Dao; peach, 1 specimen, 15.6.84, Doi Ang Khang, all Chiang Mai Province. Panama berry (*Muntinja calabura* L.), 1 male, 1 female, 24.7.83, Soppong, Mae Hongson Province. *Ficus* sp., 3 specimens, 28.5.80, Khao Chong, Trang Province, all Thailand. Peach, plum, 2 specimens, 2.7.85; 3 specimens, *R. acuminatus*, 17.9.88, 3.10.88, Phulchoki, Nepal.

Enclosed conditions: mandarin, grape.

C. minuticornis novaepommeraniae

Natural conditions: not yet seen on fruits (Lae, Papua New Guinea).

Enclosed conditions: *Ficus calopilina*, mandarin, grape.

C. ophideroides (Fig. 3)

Natural conditions: plum, 2 specimens; peach, males and a females (about a dozen), 2, 3 and 5.7.78; 6, 11, 12, 14, 18, 21, 22.7.87. *F. auriculata*, 2 specimens, 11, 13.7.87, Kumaon Hills, India.

Enclosed conditions: peach, plum, guava, grapes.

C. orthograptia (Fig. 14)

Natural conditions: not yet seen on fruits.

Enclosed conditions: plum mango (*Bouea macrophylla* Griff.), mango, rose-apple.

C. parva (Fig. 5)

Natural conditions: *F. semicordata*, 1 female, 3 specimens, 23.10.83; 1 female 30.10.83; 9 specimens, 31.10.83; 1 female, 1 specimen 6.11.83; 1 female, 13.11.83; 1 female, 2 specimens, 9.10.84; 1 specimen 18.10.84; 5 females, 28.10.85; 1 female, 2 specimens, 15.10.86; 1 specimen, 24.5.88, all Doi Chiang Dao, Thailand.

Enclosed conditions: mandarin, grape.

C. pseudobicolor (Fig. 6)

Natural conditions: *R. acuminatus*, 1 male 14.9.84; 1 female 15.9.84; 2 females, 16.9.84; 1 specimen 13.9.88; 2 specimens 22.9.88; 1 specimen 23.9.88; 4

specimens 30.9.88; plum, 1 female, 11.6.85; 1 male, 12.6.85; peach, 1 specimen, 24.6.85, all Phulchoki, Nepal.

Enclosed conditions: peach, plum, guava.

C. thalictri (Fig. 7)

Natural conditions: raspberry (*Rubus idaeus* L.), 16 specimens of both sexes, 28, 29.6. 69; 3–5.7.70, Magadino Valley, Switzerland.

Enclosed condition: cherry, redcurrant (*Ribes rubrum* L.), grape.

General notes on feeding

No significant difference in the piercing and sucking behaviour was observed among the 10 *Calyptra* species when feeding from fruit. Occasionally, *C. bicolor*, *C. fasciata* and *C. pseudobicolor* held the wings in «V» position (Figs 1, 4, 6) instead of the normal «roof-like» fashion, or even beat the wings while feeding. In some cases this may have been due to disturbance by my presence (or other intruders, such as competitor or predator, insect or other animal). In other cases it may have been in order to produce heat in response to cool nights at high altitude.

Of the 23 species of fruit pierced by *Calyptra*, 11 were attacked under natural conditions, nine of which were wild or semi-wild (peach, raspberry and the naturalized Panama berry). But cultivated peach was also attacked. As a general rule, sweet, soft-skinned fruit (*Ficus*, *Rubus*) were preferred, but plum and the thick rind of citrus were also drilled. It is not yet clear whether the thin but relatively hard skin of longan (*Dimocarpus longan* Lour.), a major crop in N Thailand, can be pierced by *Calyptra*, but soft varieties possibly are. In two experiments, *C. minuticornis* was unable to penetrate their skin, but in picked fruit the skins hardens. The much bigger, non-zoophilous fruit-piercers *Adris*, *Eudocima*, *Othreis*, *Rhytia* (now unfortunately regarded by many workers as one genus, viz. *Eudocima*) have a larger, stronger proboscis equipped with an additional ventral serration with which they bore into longan, causing significant damage in years of mass outbreaks.

One of the feeding phases, viz. the repeated penetration and partial withdrawals of the proboscis, occurs in all 10 *Calyptra* species. This phase is typical also for moths which are exclusively fruit-piercing, e.g. *Adris tyrannus* (Guenée), *Othreis fullonia* (Clerck), *Rhytia hypermnestra* (Stoll), *Eudocima salaminia* (Cram.), *Oraesia emarginata* (F.), etc. With these movements new shafts are bored into the pulp of the fruit from the same entrance hole. This is evidently in order to release sap contained in the tissue. This peculiar feeding phase is exhibited also when male *Calyptra* suck blood from mammals, although it seems unnecessary since blood flows into the pool pierced, as is observed in «classical pool feeders» (e.g. tabanids). The behaviour has been interpreted as a vestige of the fruit-piercing habit in *Calyptra* which is a «clumsy newcomer» among blood suckers.

Examination by stereo and light microscope of the proboscis of *Calyptra* showed that it is essentially the same in the species examined, with only slight variation in number or size of the erectile barbs and tearing hooks, and the extent of sclerotization and size of the proboscis.

Male *Calyptra* survived for only five to six days when given only blood and/or water. But with fruits, males and females, lived for up to 3–4 weeks. Male anal excretions from blood meals essentially were densely packed masses of undigested

Tab. 1. Salt (NaCl) sequestration by blood-engorged male *Calyptra*. Na⁺ content (meq/l = milli-equivalent per liter) in blood after gut passage (anal excretion), compared to host blood (author in experiments, mule in natural events).

| Moth species | Time after feeding | Na ⁺ content in anal secretion | Na ⁺ content donor blood | Amount sequestered |
|--------------------------|--------------------|---|-------------------------------------|--------------------|
| <i>C. parva</i> No. 1 | 90 min | 15.65 meq/l | 94.65 meq/l (man) | 84.5 % |
| | 4 h | 10.47 meq/l | 94.65 meq/l (man) | 88.9 % |
| <i>C. parva</i> No. 2 | 45 min | 14.30 meq/l | 94.65 meq/l (man) | 84.9 % |
| | 6 h | 5.60 meq/l | 94.65 meq/l (man) | 94.1 % |
| <i>C. fasciata</i> No. 1 | 35 min | 6.79 meq/l | 105.61 meq/l (mule) | 93.6 % |
| <i>C. fasciata</i> No. 2 | 20 min | 5.39 meq/l | 105.61 meq/l (mule) | 94.9 % |

erythrocytes. Results of the protease analyses were negative in the five hematophagous species tested, *C. bicolor*, *C. eustrigata*, *C. fasciata*, *C. minuticornis*, *C. orthograpta*, but positive in eulachryphagous *L. griseifusa*, *A. bothrophora*, *A. dentula* and *A. icterica*. The anal excretion of blood-fed *Calyptra* had far lower salt (NaCl) content than the blood ingested from hosts attacked: in two *C. parva* salt sequestration was 85–94 %, 45 min–6 h after feeding, and in two *C. fasciata* it was 94–95 % after 20–35 min (Tab. 1).

DISCUSSION

Unexpectedly, *C. eustrigata*, *C. fletcheri* and *C. orthograpta* so far have not yet been seen to pierce fruit in the wild. This must be incidental rather than reflect different feeding habits. In the study areas these moths were among the rarest of the genus. Moreover, since *Calyptra* are much more forest-bound than the better known fruit-piercing pest species, they are more likely to be overlooked because, unlike in fruit orchards, any particular fruit-bearing species tends to be thinly distributed in the highly diverse tropical forests, the fruits often high above the ground, and in more or less impenetrable thickets. As found in experiments, *C. eustrigata*, *C. fletcheri* and *C. orthograpta* eagerly pierced fruit like the other *Calyptra*.

The finding that both male and female *Calyptra* feed from fruit is in clear contrast with *Calyptra*'s hematophagous habits which are an exclusive male prerogative. In fact, fruit-piercing is shown to be obligatory for both sexes, evidently to cover their energy requirements, without which they do not survive for more than five to six days. Sucking of blood, on the other hand, is not required for survival, since it extends the male's life expectancy only minimally (at most a day or so in case of very abundant and frequent blood meals, probably thanks to blood sugars). Also, erythrocytes are passed through the digestive tract undigested, and tests for the presence of proteases are negative. Significantly, on the other hand, the anal excretion of blood-fed *C. parva* and *C. fasciata* has very much less salt (NaCl) than the donor blood, 85–95 % having been sequestered by the moths. Thus, surprisingly for a blood-sucker, not protein but salt is one, possibly a main, substance sought.

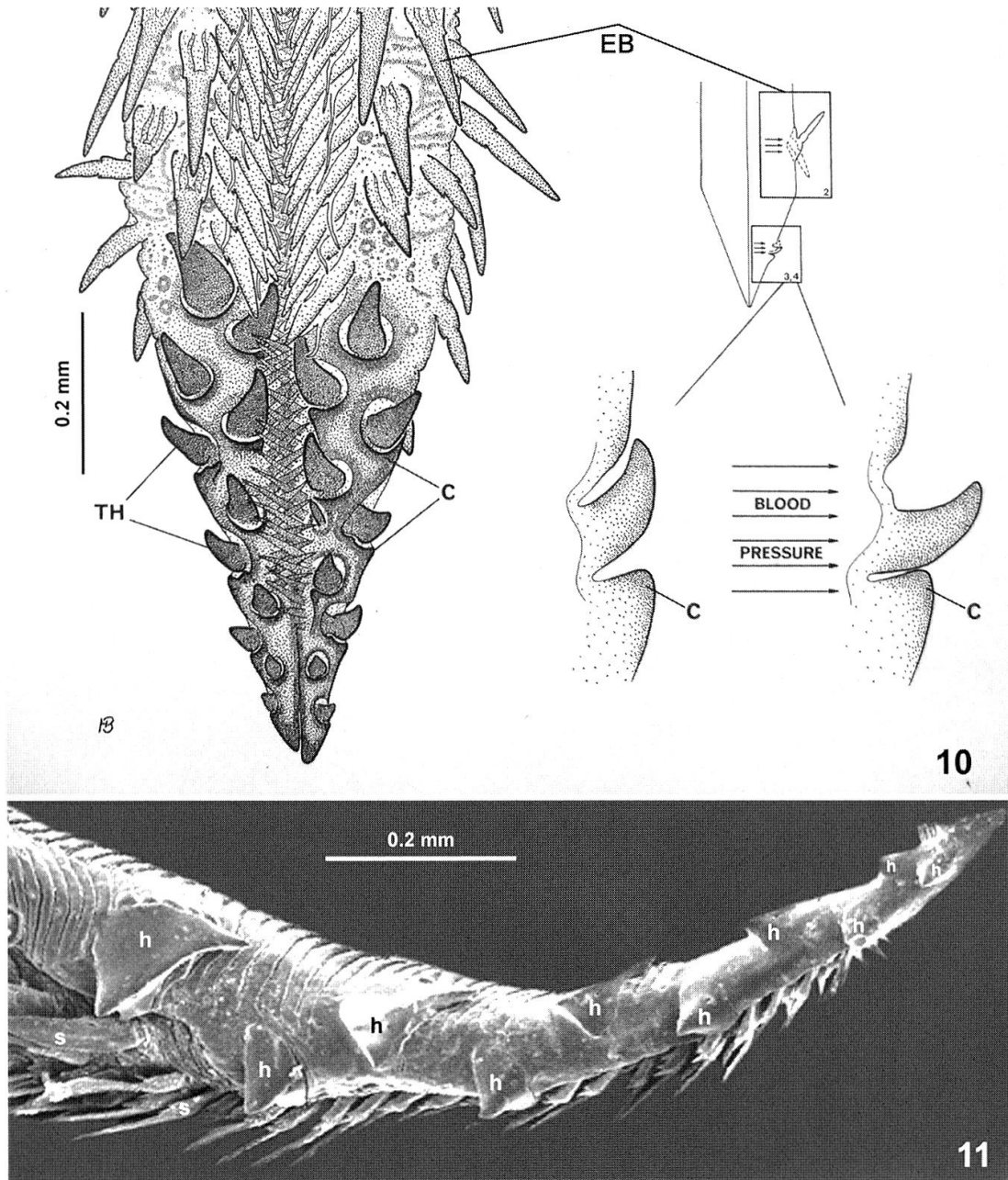
It is interesting to note that although male *Calyptra* evidently seek salt from blood, they do not take tears from their victims (rare freaks excepted). Despite the

fact that lachrymation is always and easily available, *Calyptra* do not specifically seek eyes when circling around a host to find a suitable feeding spot, but preferentially legs, flanks, bellies, back, neck and throat, in that sequence. When not successful, they give up searching and fly off, rather than alight at eyes. Eye-frequenting moths, especially the eulachryphagous species, mainly fly around the head to settle at eyes. *Calyptra* are inveterate piercers and, were they supposedly had an urge to attempt obtaining tears, evolution evidently denied them success in developing lachryphagy, presumably because their formidable proboscis armature and aggressive behaviour was not welcome at the sensitive eye. Their compulsion to pierce for feeding is also evident from the fact that in nature they do not «lick» freely available blood from open wounds but, at most after a brief probing, they always drill into the tissue at or near such spots. Also when on damaged fruit, they do not simply suck the oozing sap, but pierce the tissue, often by boring a new hole into the fruit's skin.

Until the early '70ies all research pointed out that adult Lepidoptera were unable to digest proteins (Stober 1929; Davey 1965; Engelmann 1970; Wigglesworth 1973 and other references in it) but eulachryphagous *L. griseifusa*, both males and females, was the first exception (Bänziger 1973). The present study confirms this and adds three additional species with proteases, viz. *A. bothrophora*, *A. dentula* and *A. icterica*. They are closely related to *L. griseifusa* (formerly Westermanninae, then Chloephorinae, now Chloephorini in Nolinae of the Noctuidae (Kitching, pers. comm. 2007)), taxonomically as well as behaviourally. Male and female *A. bothrophora* are eye-frequenting in Bangladesh and Thailand (Büttiker 1969b; Bänziger 1973), *A. icterica* in Nepal, S and NW India (Büttiker, 1967, 1969a; Bänziger unpubl.), and *A. dentula* in NW India (Bänziger unpubl.).

There are compelling experimental indications (Bänziger unpubl.) that in hemilachryphagous moths both types of digestion occur: proteases are present in geometrids *Hypochrosis abstractaria* Walker, *H. baenzigeri* Inoue, *H. flavifusata* Moore, *H. hyadaria* Guenée, *H. iris* Butler, in pyralids *Paliga* (previously *Pionea*) *damastesalis* (Lederer), *Thliptoceras* (2 species), and in thyatirids *Chaeopsestis ludovicæ* Le Cerf and *Neotogaria hoenei* (Sick), all males. They are lacking in geometrids *Chiasmia* (previously *Godonela*, *Semiothisa*) *clivicola* (Prout), *C. eleonora* (Stoll), *C. lannaensis* (Bänziger & Fletcher), *C. trilinearia* (Moore), *C. xanthonora* (Walker), and in pyralids *Microstega homocolorum* Bänziger and *Filodes mirificalis* Lederer, all males. Among the very numerous species of moths which do not settle on animals but suck fluids from the decomposing mixture of sodden earth, urine and dung, only a few were tested. Results were negative in males of geometrids *Ascotis selenaria imparata* (Walker), *Ctenognophos fuscobrunnea* Sato, *Hyperythra lutea ennomaria* (Guenée), *Metapercniæ ductaria* (Walker) (all four H. Inoue det.). Larger species samples may well register positive tests in some taxa, especially in non-lachryphagous species which occasionally settle on animals.

The presence of proteases has not yet been tested in any of the many species of butterflies visiting mud puddles. This behaviour of butterflies and moths is evidently related, though moths seem to visit more dryer substrates (damp soil) in N Thailand (pers. observ.), while butterflies gather more at puddles, possibly because during the day the water stress is higher. In puddling butterflies the sex involved is, like in the moths (except the few eulachryphagous species), again male (Arms *et al.* 1974; Adler 1982; Adler & Pearson 1982; Beck *et al.* 1999). However, the detailed



Figs 10–11. Distal part of proboscis of *Calyptra eustrigata* and *Hemiceratoides hieroglyphica* compared to show the differences. – 10. *Calyptra eustrigata*, dorsal view. Note the curved tearing hooks (TH) which can be everted by blood pressure and the collar (C) preventing their overturning. EB = erectile barb. (Detail from Bänziger 1980). – 11. *Hemiceratoides hieroglyphica*, lateral view. Note the cuticular hooks (h), deltoid-pyramidal to wedge-like in shape. They are fused to the proboscis wall and lack the collar. S = modified sensilla. SEM micrograph by J. Zaspel.

study by Beck *et al.* (1999) found some differentiations in the feeding habits of such butterflies. Lycaenidae, Nymphalidae and Hesperidae to a certain extent preferred protein-containing baits to those with NaCl, while the opposite was found in Papilionidae and Pieridae. However, while all accepted proteins, amino acids baits were not or very little attractive, as also found by Arms *et al.* (1974). This is surprising, because amino acids boost longevity and reproduction in *Heliconius* butterflies (Gil-

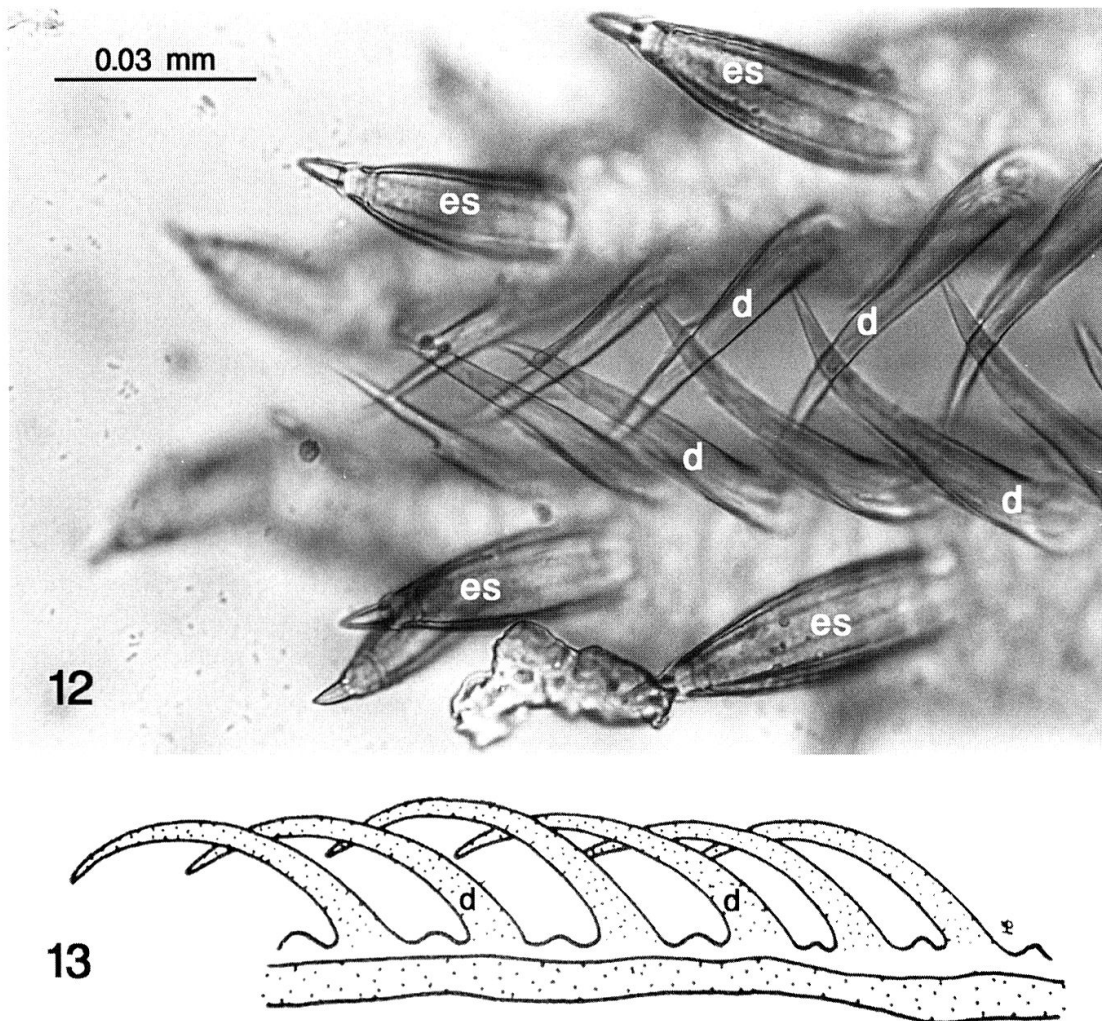
bert 1972), and can be assimilated without the need of further digestion. Evidently *Calyptra* do not stand alone in exhibiting unexpected feeding strategies.

One reason for the uptake of salts by male lepidopterans is that it plays a role, at least in some species, during mating, when Na is transferred by the spermatophore from males to females to replenish losses incurred by oviposition (Adler & Pearson 1982). This is likely to be the case also with *Calyptra* and the lachryphagous moths, but remains to be confirmed. Moreover, in those tear drinkers which are capable of protein digestion, the resulting amino acids may well be an additional «male dowry» for improved egg production, if they are indeed transferred via spermatophore. Whereas proteins may potentially be used for energy production, normally carbohydrates are the source for energy in insects, and amino acids the main raw materials for growth (Wigglesworth 1973). In *Calyptra*, salt sequestration may just be one side process. Blood offers a far more diverse palette of substances than tears. It may contain more seductive nuptial gifts than salt, or have other adjunct substances for improving fitness in the complex life of *Calyptra*.

Recently an unexpected feeding has been reported from Madagascar: three specimens of the noctuid *Hemiceratoides hieroglyphica* (Saalmüller) were observed with the proboscis inserted between the eye-lids of small, sleeping birds, two *Newtonia brunneicauda* (Newton) and one *Copsychus albospecularis* (Eydoux & Gervais), presumably sucking tears (Hilgartner *et al.* 2007). Unfortunately, this exciting observation documented with excellent photographs is marred by very serious misquotations and misrepresentations in the discussion which require rectification to avoid future work being misled.

— 1. They state that «The proboscis morphology of *H. hieroglyphica* is consistent with an evolution of ophthalmotropy from fruit-piercing in the Calpini lineage (Kitching & Rawlins 1998)». However, these authors did not write the pages quoted (pp. 41–49, which actually are by Kristensen 1988) in the references of Hilgartner *et al.* (2007) but pp. 355–401. However, in neither is such an evolution mentioned. In a way, this is the opposite of what Downes (1973) proposed, namely that the skin-piercing habit in hematophagous *Calyptra* (which are also fruit-piercing), evolved from lachryphagy. I had found this unconvincing for several reasons (Bänziger 1980), and the new hypothesis is also problematic (see below).

— 2. «Exactly the same features [i.e. proboscis structures of *Calyptra*] occur on the proboscis of *H. hieroglyphica*.» In reality the proboscis armature of the two species is morphologically and functionally clearly different (cf. Figs 10, 11). In *H. hieroglyphica* the cuticular hooks are deltoid-pyramidal to wedge-like in shape, have both cutting edges and cutting points, which are oriented in several directions; the cuticular hooks are fused with the proboscis wall, hence not movable by blood-pressure; and no collar is present. In *Calyptra* there are curved tearing hooks which are not fused to the wall but can be everted by blood pressure (to better tear the skin), and they are surrounded by a collar which ensures that the hooks are not overturned during boring (Bänziger 1980). The erectile barbs in *Calyptra* and the corresponding modified sensilla in *H. hieroglyphica* are not the same either and possibly cannot be erected by blood pressure in the latter. The armature therefore is basically different and evidently the result of a different evolutionary line. Indeed, preliminary molecular genetic analysis indicates that *H. hieroglyphica* does not belong to the Calpini (Zaspel, pers. com.).



Figs 12–13. Proboscis of eulachryphagous *Lobocraspis griseifusa*. – 12. Dorsal view of the tip region; galeae joined in the natural state. Note the tip of the spines (d) being below the curved spine of the opposite side; tips are out of focus because on a lower level. The spines' effect on the eye ball or conjunctiva is neither saw-like nor rasp-like, but more akin to that of a slightly undulating series of shallow ribs. The elongate sensillae (es) overtop them by half their length. – 13. Lateral view for improved visualization of the position of the spines (only the left galea drawn for clarity).

The Calpini (which comprise *Calyptra* and several genera of wide-spread fruit-piercing moths such as *Eudocima*) have developed the most advanced piercing armoury among Lepidoptera (Künckel 1875; Darwin 1875; Breitenbach 1877; Hattori 1962; Neubecker 1966; Srivastava & Bogawat 1969; Cochereau 1977; Bänzinger 1980). Of all Lepidoptera the Calpini seem the least likely to evolve lachryphagy and in fact none of the over 100 species of fruit-piercing moths (Calpini and other tribes) studied in Thailand is confirmed to be lachryphagous. They are conspicuous for their absence among the many moths seeking mammalian hosts (except *Calyptra*). No author of more than 70 papers on fruit-piercing moths I consulted (the bulk of the literature on the subject) mentions any link between these two feeding habits, except Büttiker (1962 and subsequent papers pertaining to the same case) who noted a similarity in proboscis armature. But his misinterpretation of the galeal linking mechanism as a saw-like armature in eye-frequenting moths had

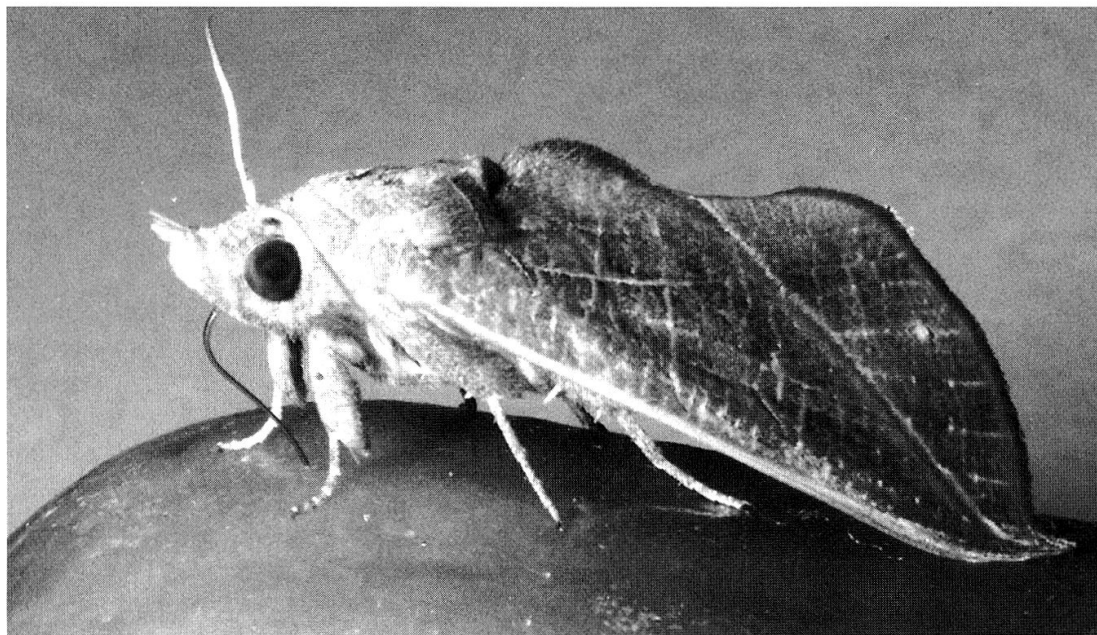


Fig. 14. Male *Calyptra orthograpta* piercing rose-apple. N Thailand, experiment.

already been pointed out by Bourgoigne (1970). Büttiker *et al.* (1996) misquote Reid (1954) that these structures have «... the appearance of a saw-like armature ...» because he did not study the mouth parts and made no such statement. Krenn & Penz (1998) misquote Bänziger (1973) as saying that «... the [galeal] linking structures of the tip form a rasp-like organ ...», and Büttiker *et al.* (1996) misquote him that «... these dentate structures result in a rough surface which is able to painfully irritate ... in addition, rasping over the surface of the eye scrapes off cells ...». In reality Bänziger (1973) attributed the pain he felt at his own lids of closed eyes to the elongated sensillae and the triangular, sharp, firmly fixed, very numerous but minute blades («Sperrdornen», Bänziger (1971, 1973, Figs 54, 60, 65, 66)). He pointed out that in eulachryphagous *L. griseifusa* the spines («Dornfortsätze») of the galeal linkage are recurved diagonally inwards so that the pointed endings are below the curvature of the spines of the opposite side, as shown in Figs 12, 13, this study, and Fig. 2 in Büttiker (1997). The elongated sensillae overtop them by half their length. In this configuration it is evident that the spines do not work in a saw-like or rasp-like manner, but more like a slightly undulating, inoffensive series of shallow ribs. Although near the tip the spines may be less incurved, the proboscis wall there is membranous, hence unable to bear pressure onto the conjunctiva. Figs 6a, b in Gouws *et al.* (1995) and Figs 1–3, 10–14 in Büttiker *et al.* (1996) are problematic due to SEM preparatory techniques (cf. Methods). These figures can lead to misunderstandings because in some cases, parts of the proboscis walls are deformed and/or shown with disjointed galeae, i.e. in an unnatural separated state of the proboscis. Due to this, some structures become seen from an angle which gives the wrong impression that the spines' tip protrude outwardly. Bänziger (1973, p. 1447) suggested that a function of the peculiar and broad-meshed arrangement of the spines probably is to facilitate the rapid uptake of tears including small clumps of leucocytes through the wide gaps, a theme taken up by Büttiker *et al.* (1996). Since the elongated sensillae are not firmly fixed, the minute blades exceeding small, and

the spines incurved, it is doubtful that they can scrape off cells by rasping the surface. Indeed, there is no incentive for this since tears already contain substantial amounts of dissolved proteins.

— 3. «... analysis of moth gut [*Arcyophora* spp., *L. griseifusa*] contents has shown the midgut digestion of leucocytes (Büttiker 1997).» However, no analysis of whether digestion actually occurs has been carried out in that paper. It is mere conjecture.

— 4. «Bänziger (1988) suggested that tear drinking moths seek salt and/or moisture during hot dry weather» then they go on saying that «We [Hilgartner *et al.* 2007] observed tear drinking during the rainy season ... and the need for salt and/or proteins would better explain ...». Besides the fact that my article has D. S. Fletcher as co-author, it is about taxonomy and nowhere does it state the above misquotation. Also, contrary to what the Malagasy paper suggests, Bänziger (1973) stressed the significance of protein/proteases, that lachrymation is filtered and proteins concentrated in the midgut, while superfluous water is expelled; that eulachryphagous *L. griseifusa* is present in all seasons and that hemilachryphagous moths are common during the rainy season.

— 5. The Malagasy «*Calyptra*» *triobliqua* (Saalmüller) does not belong to this genus but to *Oraesia* or a relative.

On the other hand, Hilgartner *et al.* (2007) are probably correct in suggesting that ophthalmotropy with birds as hosts is possibly due to the peculiar fauna of Madagascar, where the typical hosts of these moths (ungulates, elephants) are missing. I would propose that *H. hieroglyphica* is similarly unusual. Not being directly related to the Calpini, it has undergone a different evolution. Three examples are worth considering: The size of *H. hieroglyphica* compared to its small avian host is exceptional. The moth's body length is about half of that of the host. Thus the moth literally has to ride on the bird's back, but avoid being dismounted. In Asia some of the largest tear drinkers are *Rhagastis olivacea* Moore (Sphingidae) and *Tarsolepis elephantorum* Bänziger (Notodontidae), with a body length of 3.5–4 and 3–3.5 cm, respectively, while their smallest host, man (Bänziger 1988a, 1992), is 170 cm tall, a ratio of 1: 40–60. The majority of moths are much smaller and *Paliga* (*Pionea*) *damastesalis* (not the smallest) is only 1 cm long, a ratio of some 1:300 compared to its largest host, the elephant (Büttiker 1967; Bänziger unpubl.). Secondly, it is surprising that while the feeding act of *L. griseifusa* is more painful when sucking at closed eyes than at open ones (personal experience), *H. hieroglyphica* seems to be well-tolerated by what one would assume to be a very sensitive host, with closed eyes, and despite *H. hieroglyphica*'s offensive proboscis armature (lacking in *L. griseifusa*). In Fig. 1b, d, the bird seems to have turned its head slightly to the right, toward the proboscis, as if pleased by its action. Given the peculiar fauna of Madagascar, could it be that the proboscis gently cleans the eye by removing (mechanically and/or chemically by saliva) incrustations, dirt and small parasites (e.g. mites, nematodes) potentially afflicting the host's lids and conjunctiva, and imbibe them as food? At any rate, the soft manners of *Hemiceratoides* and the aggressive tactics of *Calyptra* set the two genera strikingly apart. Third, the ability of *H. hieroglyphica* to find such a small host, and locate its eye hidden behind a tiny slit, is unmatched in classical tear drinkers. These choose to settle at open eyes, generally much larger than themselves. In birds, moreover, superfluous tears are not drained into the nasal cavity by the nasal duct as in mammals, but into an opening

in the palate, and swallowed. Thus the nares do not serve as an alternative or additional attractive source of tears (mammal nostrils are occasionally visited by hemilachryphagous moths). But perhaps another peculiarity in birds may hold the clue. They have salt glands which expel excessive salt into the nasal cavity. This opening is easy to locate, both visually and by its breath odour, and salt is readily accessible there. However, in most bird species these glands are atrophied, only marine birds and some other birds such as ostriches, raptors, Cuculidae and Phasianidae have functional salt glands (various authors in Shoemaker 1972). Thus, for some species of salt seeking moths, not eyes but avian noses may have been the original source of salt. «Nose-frequenting» moths may still be around but have remained undetected so far. In the course of evolution, moths like *H. hieroglyphica* may have adapted to exploit tears from the eyes of birds lacking salt glands.

It would be desirable to find out whether *H. hieroglyphica* actually suck tears, whether mammals are visited, or other food is taken, including carrion and dung. Above all, whether they are fruit-piercing, or might have adapted to obtain nectar concealed in extremely narrow corollas, impenetrable by ordinary proboscides, but accessible when aided by a special armature and gentle movements of the proboscis. An ability to intrude without causing discomfort seems a prerequisite for taking tears from small birds. Finally, whether the birds attacked were «normal» (not sick or emaciated to allow unchallenged access to their eyes), and whether the cases were freaks or normal occurrences.

The present study further corroborates the view that hematophagy in *Calyptra* is derived from fruit-piercing, while lepidopterous lachryphagy (at least on mammals – the special case of *H. hieroglyphica* remains to be cleared) is a separate development, initially probably evolved from taking fluids from contaminated soil, via licking of various body fluids directly on animals, to the increasingly specialized tear-drinking. This is most evolved in eulachryphagous noctuids. Also, if hematophagy were linked to lachryphagy in *Calyptra*, one would expect that as a noctuid it would have proteases and that both sexes were involved in the habit.

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