Skin-piercing blood-sucking moths IV : biological studies on adults of 4 Calyptra species and 2 subspecies (Lep., Noctuidae)

Autor(en): **Bänziger, Hans**

Objekttyp: **Article**

Zeitschrift: **Mitteilungen der Schweizerischen Entomologischen Gesellschaft = Bulletin de la Société Entomologique Suisse = Journal of the Swiss Entomological Society**

Band (Jahr): **59 (1986)**

Heft 1-2

PDF erstellt am: **13.07.2024**

Persistenter Link: https://doi.org/10.5169/seals-402206

MITTEILUNGEN DER SCHWEIZERISCHEN ENTOMOLOGISCHEN GESELLSCHAFT
BULLETIN DE LA SOCIÉTÉ ENTOMOLOGIQUE SUISSE

59, 111–138, 1986

Skin-piercing blood-sucking moths IV: Biological studies on adults of 4 *Calyptra* species and 2 subspecies (Lep., Noctuidae)

HANS BÄNZIGER
Department of Entomology, Faculty of Agriculture, Chiengmai University, Chiengmai, Thailand

In N. Thailand males of scarce *Calyptra eustrigata* (HMPS.), *C. m. minuticornis* (GUEN.), *C. orthograpta* (BUTL.) and *C.fasciata* (MOORE) sucked blood by piercing deep into various types of skin lesions. But subspecies *C. m. novaepommeraniae* (STRAND) was found not to be haematophagous in Papua New Guinea. Elephant was the principal host; mule and pig were new hosts in addition to 8 already known. Attacks started at nightfall, peaked between 20–21 hours and decreased to virtually nil near midnight. Sucking, lasting for up to over 15 (mean 7) minutes, other behavioural, morphological and further aspects of the feeding habits, are described. The possible role in the transmission of haemorrhagic dermatitis filariae is discussed. Found mostly in or near Mixed Deciduous, Dry Dipterocarp, Semi-evergreen, and Hill Evergreen Forests, *C. eustrigata* is a lowland (less than 1000 m), *C. m. minuticornis* a both lowland and highland, *C. orthograpta* and *C. fasciata* mainly highland (up to at least 1700 m) species. During 109 night inspections at 34 sites in Thailand during 6 ½ years, 44, 44, 31, 21 specimens of these species, respectively, were observed on or near hosts. Only 39 investigations at 9 sites were successful with 1 to 14 *Calyptra* specimens seen per night. There are 4 generations per year in N. Thailand, adult populations peaking early/mid March, late May/early June, mid/late August and mid/late October, with much overlap though none flies between December and February. Morphological, genitalic and behavioural features indicate that *C. fasciata* belongs to a different species group from the other 3 *Calyptra*. Haematophagy is perhaps more likely to have developed monophyletically before the splitting into these species groups than later on as a parallel evolution in both of these; it seems to have been lost secondarily in subspeciating *novaepommeraniae* due to lack of suitable hosts in the Papuan Region.

While the biology of adult skin-piercing blood-sucking *Calyptra eustrigata* (HAMPSON) males has become known to some extent, and a recent study throws new light on the amazing method used by the moth to pierce mammal skin and suck blood (BÄNZIGER, 1980), three further species of the genus so far remained only suspected blood-suckers. *C. minuticornis minuticornis* (GUENÉE), *C. orthograpta* (BUTLER) and *C. fasciata* (MOORE) [=*labilis* (BERIO)] had been observed attacking, settling and attempting to pierce the skin of various mammals; these included the Indian elephant, water buffalo, zebu, sambar deer, and Malayan tapir in Thailand, Malaysia and Laos (BÄNZIGER, 1979). But no actual, successful piercing act by the three species had been witnessed in nature though they pierced the author's skin, and sucked his blood, in experiments.

During the past 6 ½ years, i.e. from mid 1978 to the end of 1984, night research led to direct observation and photographic documentation of the three moth species sucking blood by piercing wounds, scabs, and healing skin lesions of elephant, pig, and mule. These findings, together with other biological aspects, are the main subject of the present paper[1]. The better researched *C. eustrigata,* though, was not overlooked and new data concerning this species are also included.

[1] Part of the results obtained mainly during a Thai-Swiss research and teaching programme.

However, during a recent study trip to Papua New Guinea to study, among other things, especially *C. minuticornis*'s Papuan subspecies *novaepommeraniae* (STRAND), evidence was found that this is not blood-sucking, unlike the Indomalayan subspecies *minuticornis*. This finding sheds some new light on the time when the blood-sucking habit evolved in the genus, as discussed below.

During two journeys to study lachryphagous and other zoophilous Lepidoptera, no trace of adult *Calyptra* species attacking mammals was found in S. W. China (S. Yünnan) and N. W. Indonesia (Sumatra) (BÄNZIGER, 1983, 1986). Because of the geographic proximity and similarity in biotope all four species could have been expected in S. Yünnan, while in Sumatra the latter two are known to occur.

In a taxonomic revision (BÄNZIGER, 1983) of the genus *Calyptra* TREITSCHKE [= *Calpe* BORKHAUSEN], among other findings, two points are of importance in the present context. First, *C. fasciata* (MOORE, 1882) is indeed identical with, and the valid senior synonym of, *C. labilis* (BERIO, 1970), as had earlier been presumed. Secondly, close examination of the taxa *minuticornis* and *novaepommeraniae*, regarded by some authors as different (STRAND, 1917) and by others as identical species (BERIO, 1956), revealed small but consistent differences in the adults' facies and genitalia, and rather greater differences in the larvae. From crossing experiments of two generations it was shown that intermediates are fertile and it was concluded that the taxa differ on a subspecies level.

STUDIES IN THAILAND

Observation sites

Location and description of the places where the night inspections were carried out will be treated in a separate article on lachryphagous Lepidoptera studied in Thailand; however, some sites (e.g. 1c, f, hl, h2) have already been described (BÄNZIGER, 1973, 1975, 1979). The following additional abbreviations of localities are used here: Ban Pang Hai (f6), Mae Nai (f7), forest above Mae Ma (f8), place near Nong Hoi (f9), Mae Nang Kaeo (f10), Chang Khian (f11), Pa Kia (h3), NW Pass of Doi Chiengdao (h4), Pong Düad (h5), Huay Nam Dang (h6), above Ban Khom (il), Piang Luang (i2)(all in Chiengmai Province); Sop Pong (kl) (in Mae Hongson Province).

Biotopes and microclimates

Until recently the biotopes in which the four species, *C. eustrigata, C. m. minuticornis, C. orthograpta and C. fasciata,* had been seen attacking their hosts were known only to a limited extent (loc. cit.). The elevations at which *C. eustrigata, C. m. minuticornis,* and both the other two species had been noted to attack mammals were 0–350 m, 0–600 m, and 300–600 m, respectively. *C. eustrigata* has now been observed on zebu at 890 m (f6), on elephant at 680 m (hl) and at 850 m (f8), and on water buffalo at 820–860 m (i2). *C. m. minuticornis* has been seen attacking elephant at 800 m (f8) and mule at 1470 m (il). *C. orthograpta* was found imbibing dew mixed with organic matter on the author's jeep at 1150 m (h4). *C. fasciata* settled on zebu at 910 m (f6) and at 1150 m (f7), and pierced mule skin at 1470 m (il).

The four species have also been captured at mercury vapour lamps at 1050 m (f9), 1690 m (h6), 1320 m (f1 l) (one specimen caught by Mr. P. SUKUMALANAND),

and 1690 m (h6), respectively (species sequence as above). However, these records from light traps show only that the species may fly, or are blown by winds – commonly experienced at some high altitude sites during light trap collecting – up to these elevations, and not that they feed or breed there, though this is well possible.

In terms of altitudinal distribution it can be concluded that *eustrigata* is present in lowlands, *minuticornis* mainly in lowlands but to some extent also in highlands, *orthograpta* in highlands and in low intramontane plains, and *fasciata* mainly in highlands but occasionally also in low intramontane plains.

Hence, from the much higher elevations recorded in the present study, the biotopes in which the moths are active reach near or well into the lower ranges of the Hill Evergreen Forest (= Moist Lower Montane Forest) Vegetation. This is found at altitudes from 1000 m (on southern slopes) and 800–900 m (northern slopes) to the top of Doi Suthep/Pui (1601/1685 m)(KÜCHLER & SAWYER, 1967); or at altitudes from 1300 to 1800 m on Doi Chiengdao (SMITINAND, 1966), the two main mountain systems where the observation sites are located. An additional biotope of the moths are the lower ranges of what SMITINAND (1966) calls the Open Hill Evergreen Forest Vegetation which ranges from 1100 to over 2000 m in some areas of Doi Chiengdao.

Moreover, *minuticornis* was occasionally found in what KÜCHLER & SAWYER (1967) termed the Thai Village and the Urban/Suburban Vegetation, present in the villages of the Chiengmai plain, as well as around and in the Chiengmai township; at least the larvae – no moth adult as yet – were found in a few instances by the author in such villages as well as in his own garden not very far from the town's centre. However, the biotopes in which the four *Calyptra* are most frequently encountered in N. Thailand belong to the Mixed Deciduous Forest, Dry Dipterocarp Forest, Semi-evergreen Forest and, for *orthograpta* and *fasciata,* also the Hill Evergreen Forest.

The types of vegetation structure (dense forest, shrubland, pasture etc.) where *Calyptra* were observed to attack hosts were as mentioned previously (BÄNZIGER, 1975, 1979).

In the light of these new results based on much more extensive information it seems that, unlike previously assumed (loc. cit.), *eustrigata* is not more common in the zone of the Evergreen Dipterocarp Rain Forest Vegetation than in that of the Deciduous Forest Vegetation. Also, considering all four *Calyptra* species, the bloodsucking habit occurs at least as frequently in these seasonally dry tropical regions of N. Thailand as it does in the more constantly humid S. Thailand and W. Malaysia.

Due to the orography and vegetation cover, the biotopes of the main observation sites (h1, h2) are characterized by marked differences between day and night temperatures and humidity during the cool and dry season but much less so during the rainy season. However, compared to the surrounding more open or cultivated areas, temperature and humidity vary less during the year as a whole. The observation sites, situated at or near the bottom of narrow main and side valleys encompassed by steep slopes, are more than usually shaded. Furthermore, humidity is stabilized at a high level, and temperature at a low one, by a generally continuous forest cover from the bottom, at 380 m where the Ping River flows, to the top of many hills of 500 to over 1000 m. Hence fog formation during the cold season is a normal event; fog disperses only in the late morning. Although it may not rain for months in a stretch and on average only some 80 mm from December to March, dew formation is so abundant from November to February that it "rains" down from the tree canopy. Walking through the grassy shrub vegetation a couple of hours after sunset one will be soaked in a matter of minutes. This is all the more remarkable since in the late afternoon the relative humidity may be less than 40%.

Examples of some representative temperature and humidity data at site (hl) are:

	hot season		rainy season		cold season	
	Temp.	Humid.	Temp.	Humid.	Temp.	Humid.
afternoon	38°C	40–45%	28°C	70–100%	24°C	60–70%
nightfall	30°C	47–50%	25°C	80–100%	18°C	70–80%
midnight	24°C	70–85%	24°C	95–100%	14°C	100%
daybreak	16–22°C	95–97%	23°C	95–100%	11°C	100%

At places near more open or cultivated areas the temperatures are higher and the humidity rather lower, especially during the critical hot season, when in the afternoon the temperatures may rise to and above 40°C and the relative humidity be just 20% and at midnight may still be 33°C and 40–50%, respectively.

Sites at higher elevations have less predictable temperature and humidity. Wind and solar irradiation can be stronger than in the narrow valley bottoms; and, while generally being obviously cooler, sometimes these sites are in fact warmer (especially at night in the cold season) due to frequent temperature inversion. But at (il), one of the highest (1470 m) and most northerly study sites, freezing occurs occasionally even during an average year.

The lowest temperature at which adult *eustrigata* have been seen feeding upon blood was 17°C while the highest was well above 30°C.

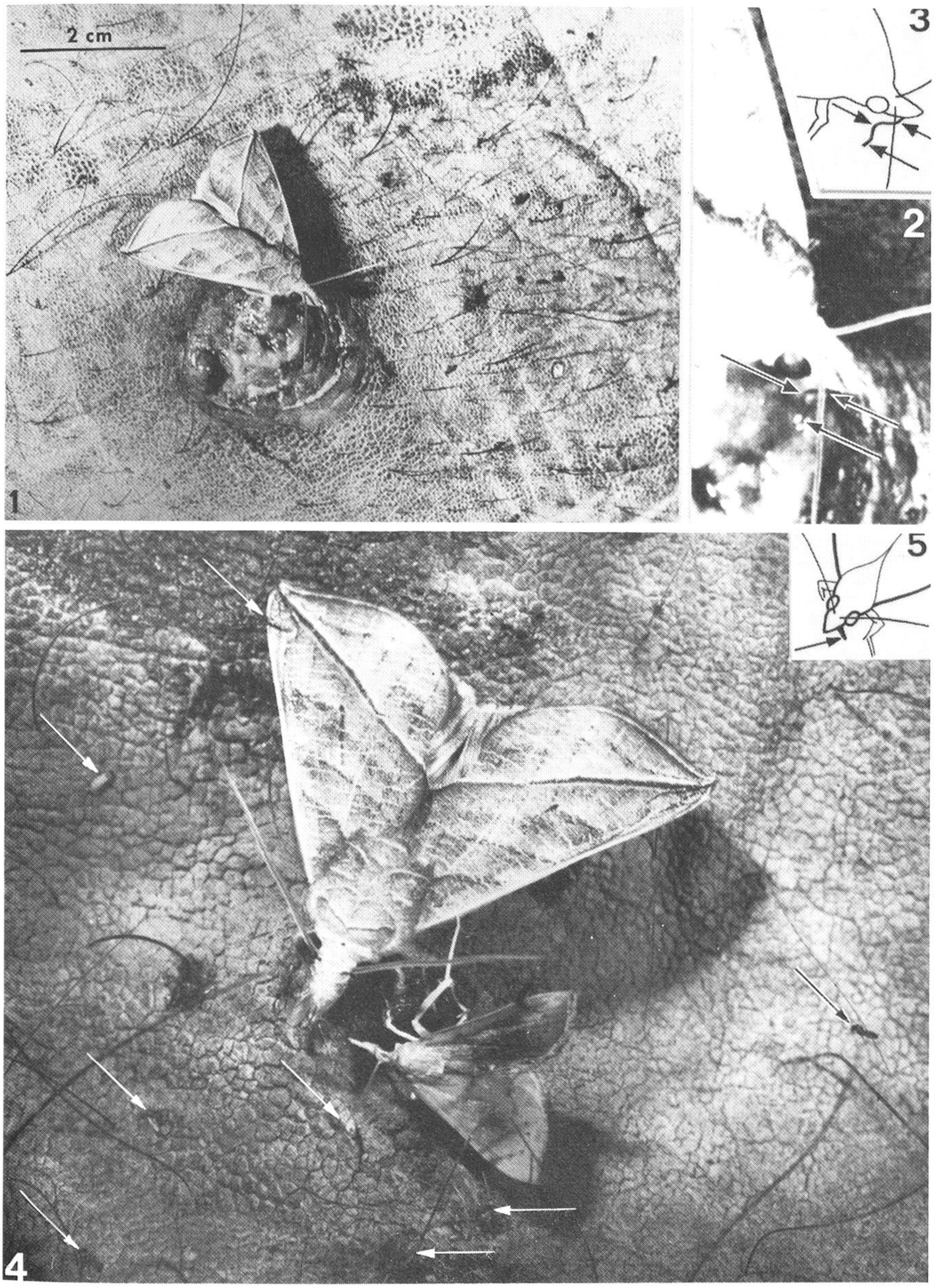
Another factor of importance is fire since vast areas, wastelands as well as forests, reserved or not, are burnt during the dry season. The direct effect of fire on adult *Calyptra*, all good fliers, is probably small as the moths should be able to fly off from the danger. But smoke keeps them from attacking hosts and feeding; at least the author has never seen a *Calyptra* flying around, let alone feeding from, a water buffalo or zebu when a profuse smoke producing fire was lit by farmers near their animals to keep mosquitoes away. The impact of fire on immatures, however, could be decisive.

Animals attacked

The present study proves for the first time that adult *C. m. minuticornis, C. orthograpta* and *C. fasciata* do indeed suck blood by piercing mammalian skin under natural conditions (Figs. 6–20, Tables 1–5), an activity already known in *C. eustrigata* (Figs. 1–5, Tab. 1) but only suspected in the other 3 species (l. c.).

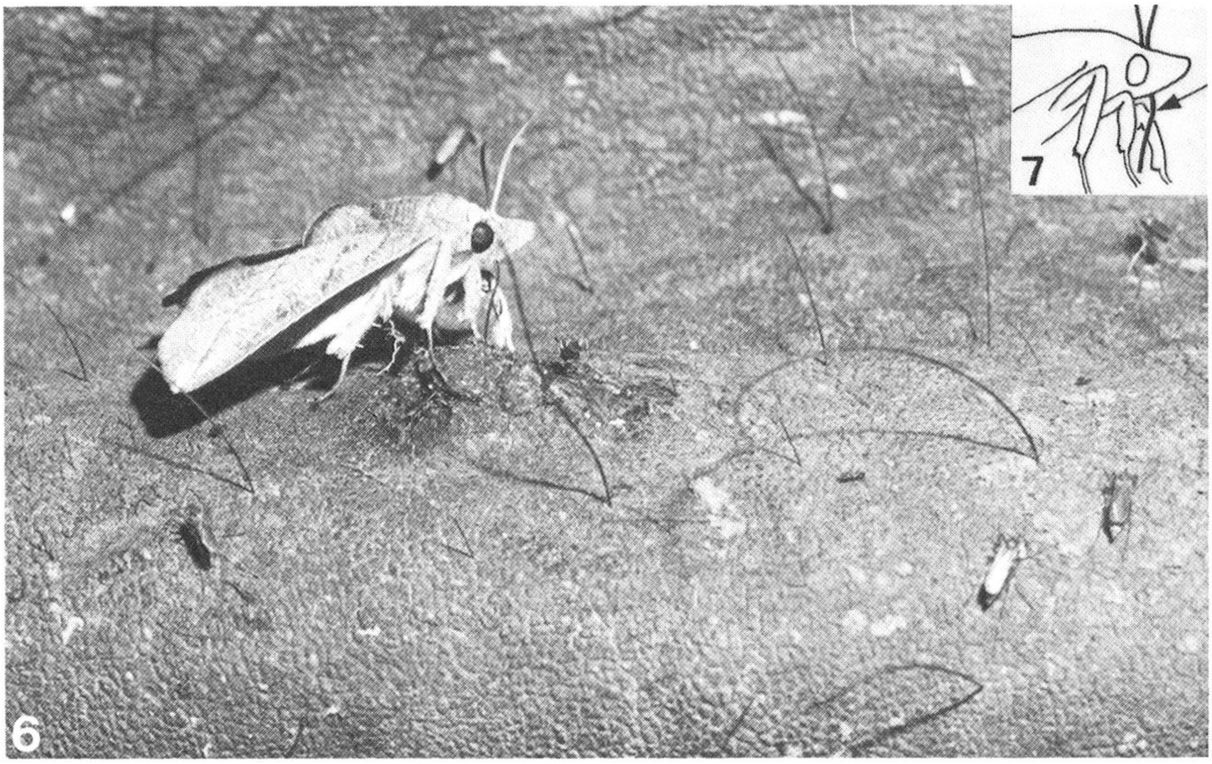
Since one of the main topics of this study was to establish whether *Calyptra* species other than *eustrigata* feed upon blood by a piercing act, little effort was made to investigate a broad range of mammals to assess the host spectrum, observations being focussed mainly on the elephant which promised best results for the study on the feeding habits of the moths. Nevertheless, two new hosts were found: the mule (*Equus caballus* L. x *E. asinus* L.) (Fig. 19, 20) and the pig (*Sus scrofa* L.).

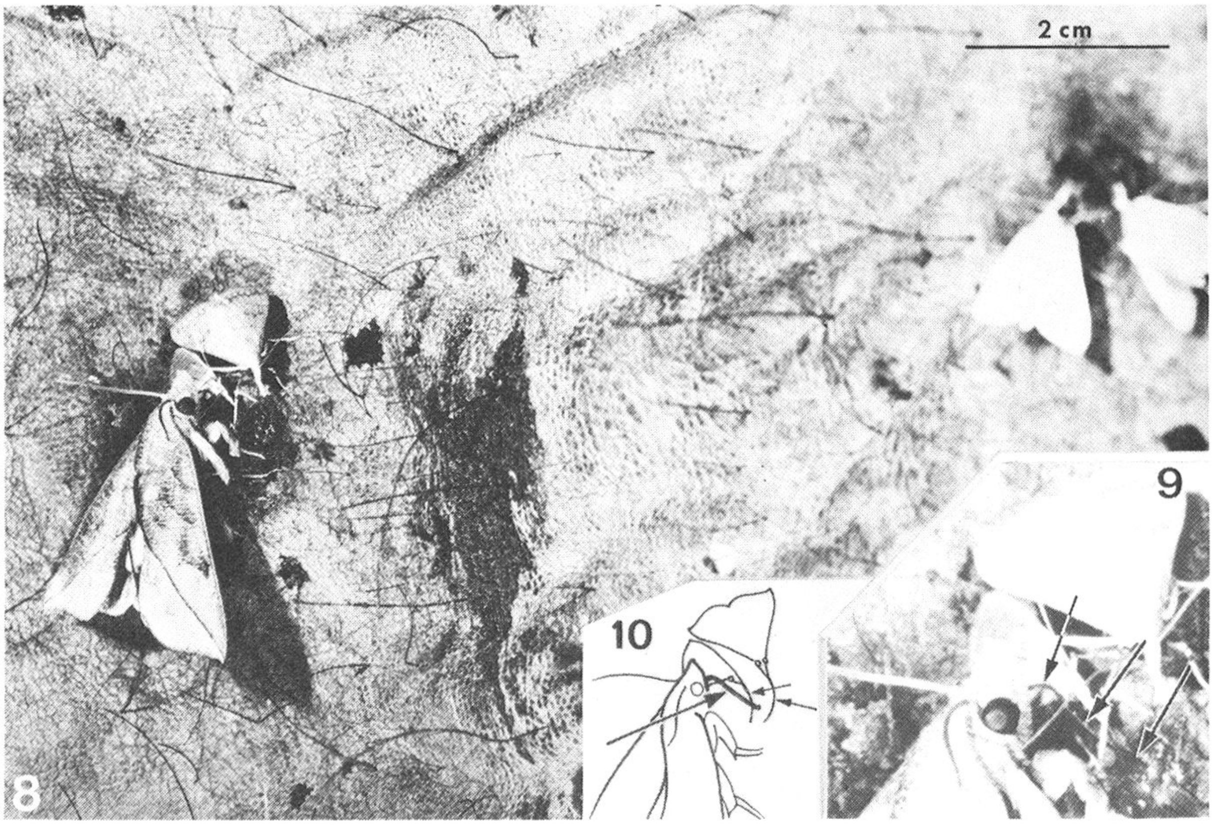
Other mammals observed to be attacked by the 3 moths during the present investigation include Indian elephant (*Elephas maximus* L.) (Figs. 1–18), water buffalo (*Bubalus bubalis* (L.)) and zebu (*Bos indicus* L.) (Tables 1–5). A further 6 mammal species, all previously confirmed to be sought after by *eustrigata* (l. c.) were not available for inspection at the present study sites. They include Malayan tapir



Figs. 1–3. *C. eustrigata* sucking blood by piercing a typical open sore in the skin of an elephant (1). – Same but magnified, showing details of piercing proboscis (arrows) (2). – Drawing of same, clarifying the position of the proboscis (arrows) (3).

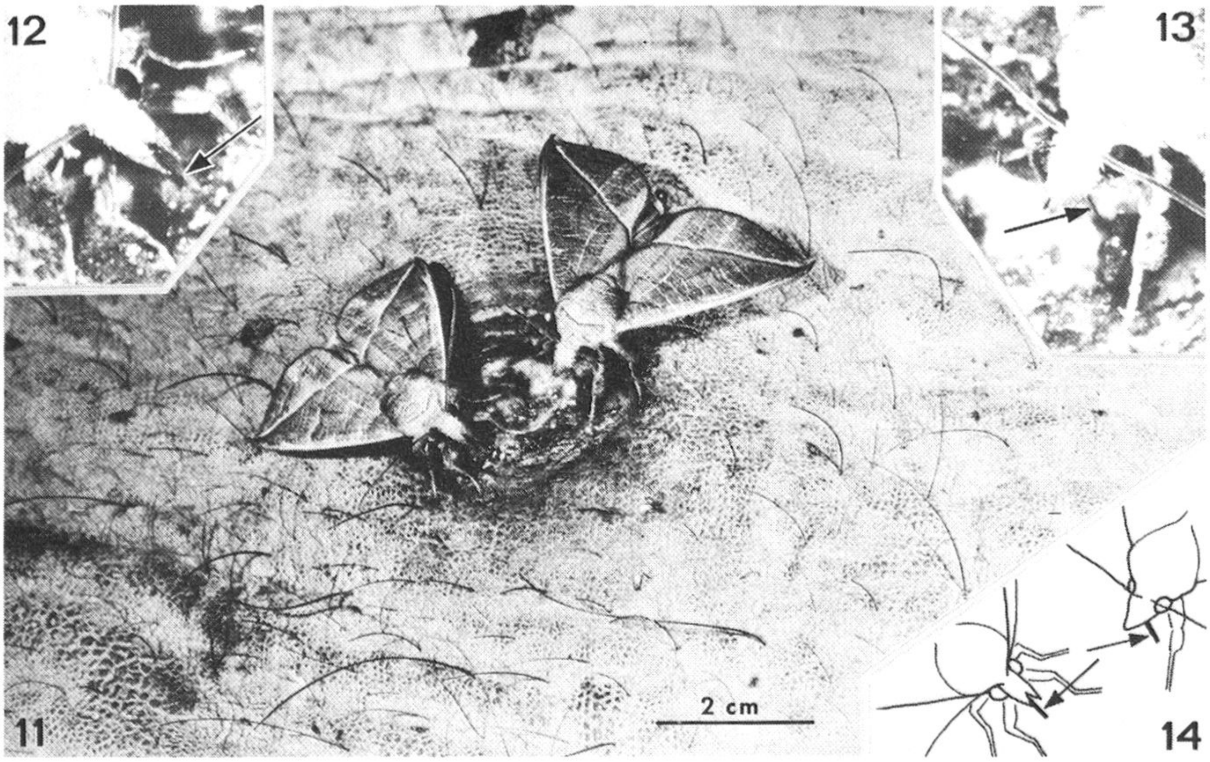
Figs. 4–5. *C. eustrigata* sucking blood by piercing a nearly healed sore in the skin of an elephant. Below it, pyralid *Placosaris ustulalis* Hmps., incapable of piercing, is licking wound exudates at the same spot. Horizontal arrows show some of the engorging mosquitoes, diagonal arrows show ceratopogonids – one flying on the far right and one on the costal vein of *C. eustrigata*'s wing where it is not clear if resting or sucking blood from the moth (4). – Drawing clarifying the position of *C. eustrigata*'s piercing proboscis (arrow) (5).

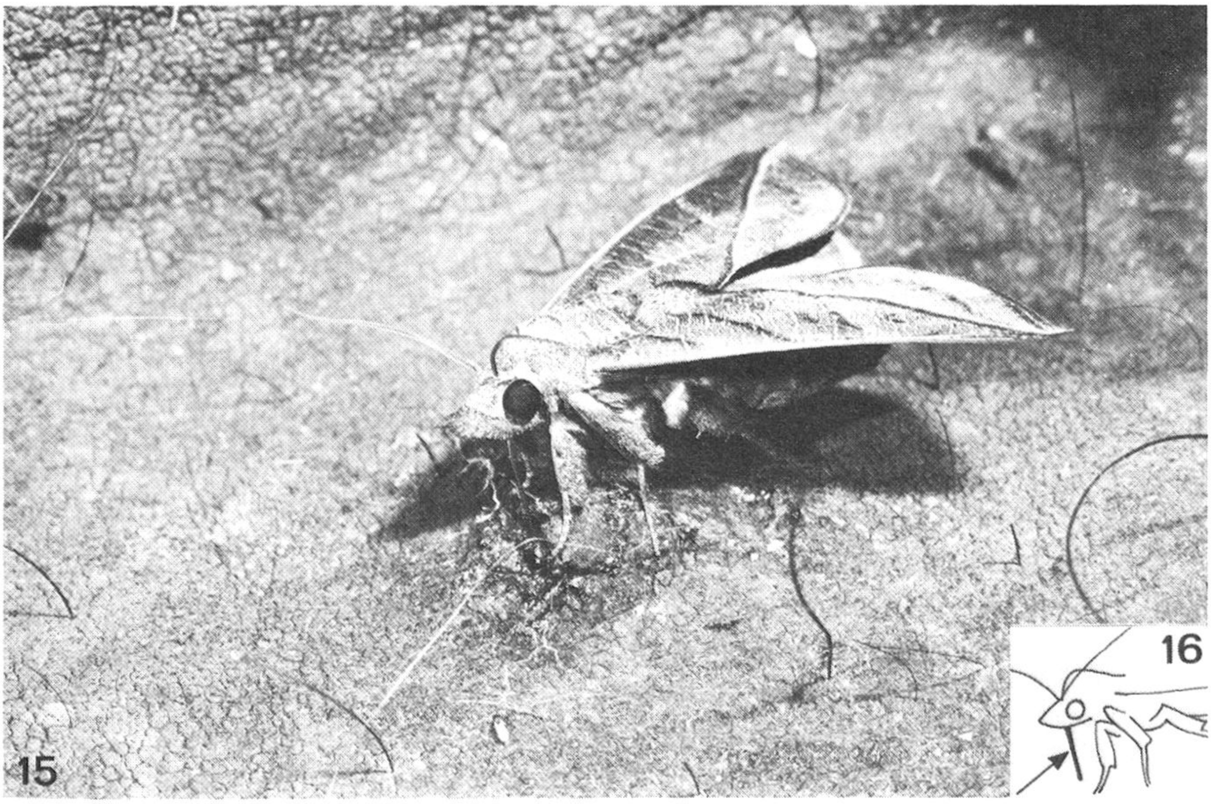




Figs. 6–7. *C. m. minuticornis* sucking blood by piercing through a scab of a sore on top of a nodule in the skin on the belly of an elephant. Mosquitoes and ceratopogonids are also sucking blood (6). – Drawing clarifying the position of the proboscis (arrow) (7).

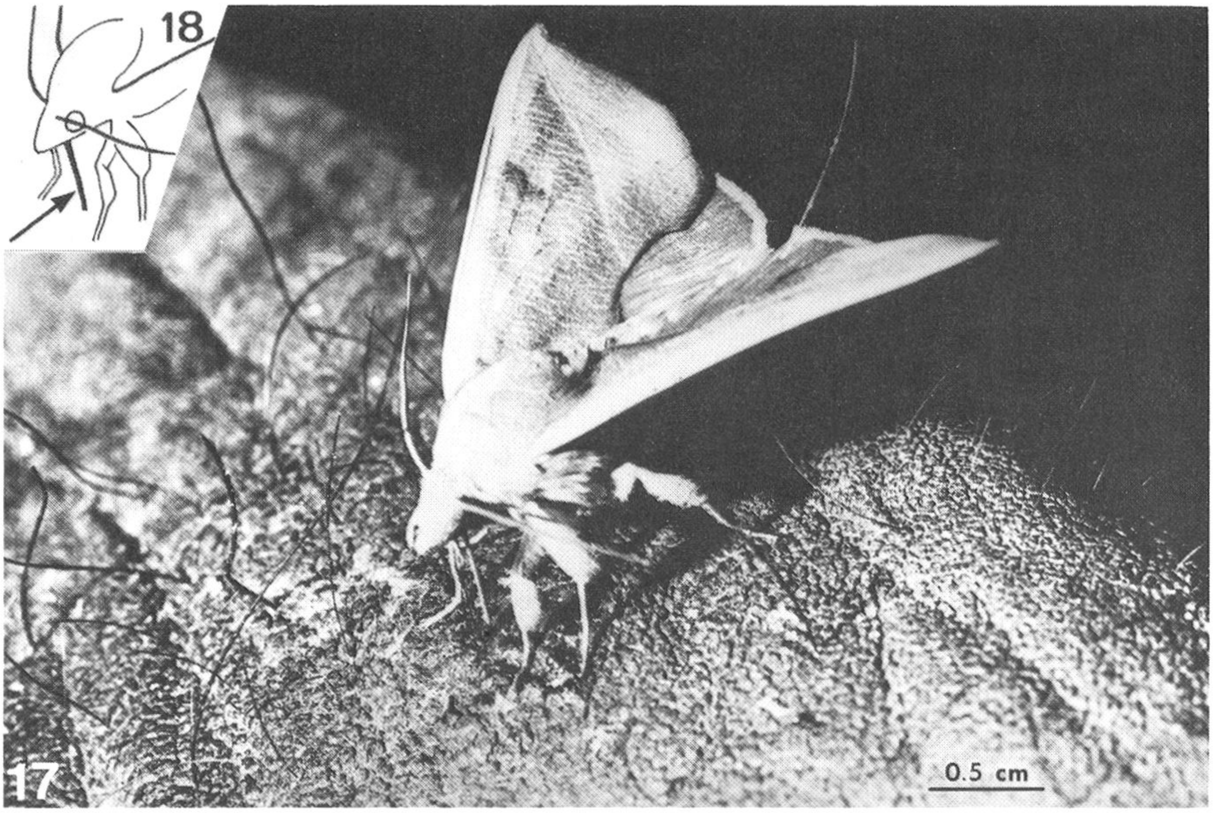
Figs. 8–10. *C. m. minuticornis* sucking blood by piercing a partially open sore in the skin of an elephant. Above the moth is *Pagyda lustralis* Snellen and partly covered by *minuticornis*'s head is *Mabra* probably *lacriphaga* Bänziger (and on the far right 2 more specimens of this species at another sore), all pyralids imbibing wound exudates without piercing (8). – Same but magnified, showing details of *minuticornis*'s piercing proboscis (arrows) (9). – Drawing of same clarifying the position of the proboscides: strong one piercing (*minuticornis*, long arrow), weak ones licking (pyralids, short arrows) (10).

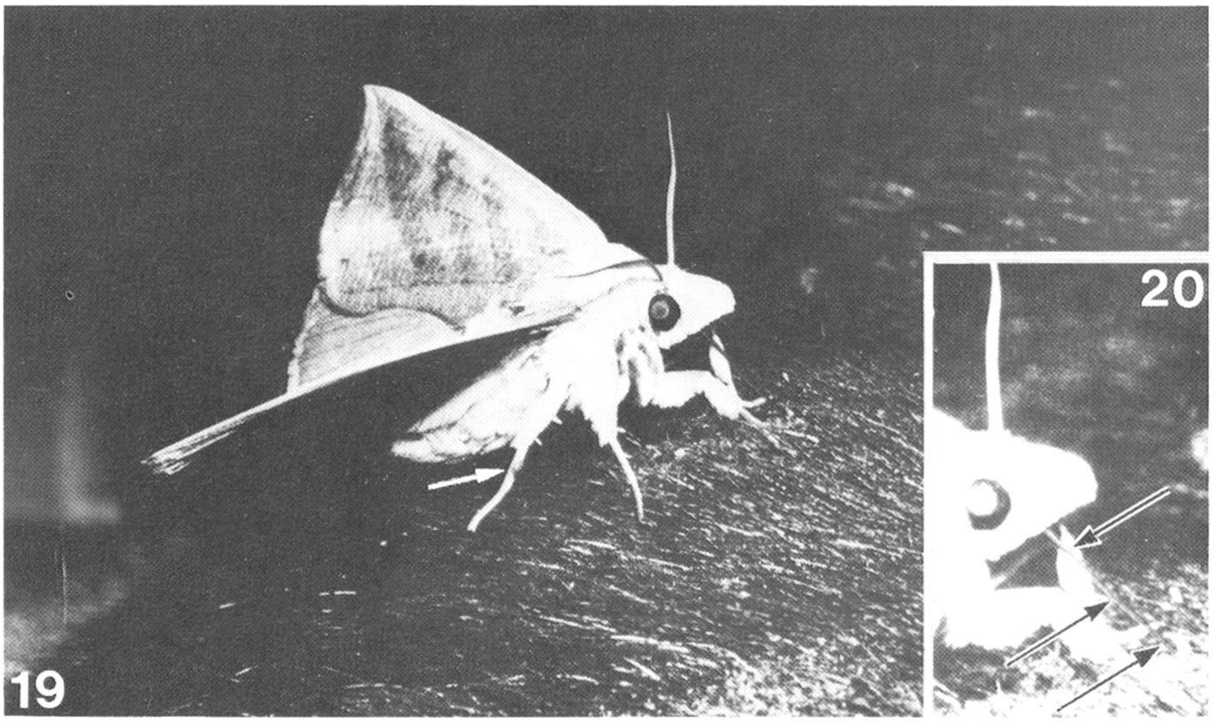




Figs. 11–14. Two *C. orthograpta* sucking blood by piercing a typical open sore in the skin of an elephant (11). – Same but magnified, showing detail of piercing proboscis (arrow) (12–13). – Drawing of same, clarifying the position of the piercing proboscides (arrows) (14).

Figs. 15–16. *C. orthograpta* sucking blood by piercing through a crack in the scab of a sore in the skin of an elephant. Engorging ceratopogonids and mosquitoes are also present (15). – Drawing clarifying the position of the moth's piercing proboscis (16).





Figs. 17–18. *C. fasciata* sucking blood by piercing a nearly healed sore in the skin of an elephant (17). – Drawing of the same clarifying the position of the piercing proboscis (18).

Figs. 19–20. *C. fasciata* sucking blood by piercing a nearly healed sore in the skin of a mule. A red mite is sucking blood from the moth's right hind tarsus (arrow) (19). – Magnification of the moth's front portion, showing the position of the piercing proboscis (arrows) (20).

Tab. 1. Observed frequencies of behavioural elements of *C. eustrigata* near or on mammals

	flying nearby	circling around	landing attempts	successful landing		piercing attempts	successful piercing
				short	long		
Indian elephant	39	32	25	7	8	7	7
water buffalo	1	(1)	(1)		(1)	(1)	(1)*
zebu	2	1	1	1			

*Caught while flying off the host; regurgitation and excretion of blood prove that it sucked blood, but mode of uptake is not certain. Another specimen flew at some 50 m from an enclosure with zebu.

Tab. 2. Observed frequencies of behavioural elements of *C. m. minuticornis* near or on mammals

	flying nearby	circling around	landing attempts	successful landing		piercing attempts	successful piercing
				short	long		
Indian elephant	40	33	19	6	16	16	13
mule	1	1	1	1	1	1	1
man	2	2	2	2			

In addition, 1 specimen caught flying near elephant excreted blood in captivity (mode of blood uptake not known).

Tab. 3. Observed frequencies of behavioural elements of *C. orthograpta* near or on mammals

	flying nearby	circling around	landing attempts	successful landing		piercing attempts	successful piercing
				short	long		
Indian elephant	32	30	22	7	10	8	7

In addition, 1 specimen was found on the ground near the elephant which must have struck it (by trunk or tail) while sucking blood as such was excreted later on in captivity; another flew at some 50 m from a shed with zebu.

Tab. 4. Observed frequencies of behavioural elements of *C. fasciata* near or on mammals

	flying nearby	circling around	landing attempts	successful landing		piercing attempts	successful piercing
				short	long		
Indian elephant	7	5	3	3	3	3	3
zebu	4	4	4	2			
mule	15	15	15		14	14	11
pig	1	1	1		1	3*	3*
man	4	4	4	3			

*1 Specimen pierced 3 holes.

Tab. 5. Observed frequencies of behavioural elements of unidentified *Calyptra* spp.* near or on mammals

	flying nearby	circling around	landing attempts	successful landing short	successful landing long	piercing attempts	successful piercing
Indian elephant	11	11	2	2			

*Any of the 4 species treated above; they escaped capture or sufficiently close inspection to allow exact identification.

N. B. Numbers in tables 1–5 may not correspond to total number of *Calyptra* specimens observed as some individuals attacked more than once.

(*Tapirus indicus* DESMAREST), black rhinoceros (*Diceros bicornis* L.), sambar deer (*Cervus unicolor* KERR), red deer (*C. elaphus* L.), fallow deer (*C. dama* L.), and nilgai antelope (*Boselaphus tragocamelus* (PALLAS)). There is little doubt that these mammals are also hosts of the other 3 *Calyptra* species.

The elephant would now seem to be the most attractive host, at least in N. Thailand. This is probably due to its large size and hence release of profuse body scent, relatively delicate skin with sparse hair cover, and habitat in forests. If present and previous results are combined, and successful attacks given particular emphasis, the moths' host preference sequence would then continue with the tapir, rhinoceros, mule, sambar, water buffalo, pig, and the remaining mammals. This sequence, though, is almost certainly influenced by the coincidental presence, or absence, of easy to pierce spots such as excoriations, scabs, etc., as discussed below, besides of course being dependent on whether or not a host is at a suitable site at the right time.

It is interesting to note that, although belonging to a different subfamily, the most closely related zoophilous moth, *Lobocraspis griseifusa* HAMPSON, a species which apparently feeds exclusively from lachrymation (BÄNZIGER, 1973), distinctly prefers large Artiodactyla; only very exceptionally has the author seen it at the eye of elephant. On the other hand, the less close lachryphagous and/or zoophilous Notodontidae, Geometridae, Pyralidae are mostly attracted more by elephants than by any other mammal.

The reactions of the hosts to attacking or piercing *Calyptra* were the same as those already described for *eustrigata* (l. c.). More is mentioned on pp. 122 and 128. In addition, one elephant dislodged and somewhat damaged one *minuticornis* by a stroke of the foot and killed one *eustrigata* with the tail. Generally, however, as with mules which vibrated the skin without being able to dislodge biting *fasciata*, the reactions were less strong and surprisingly ineffective. One pig slept whilst *fasciata* pierced three holes in the ear and sucked blood for some 6 minutes.

Attacks on man

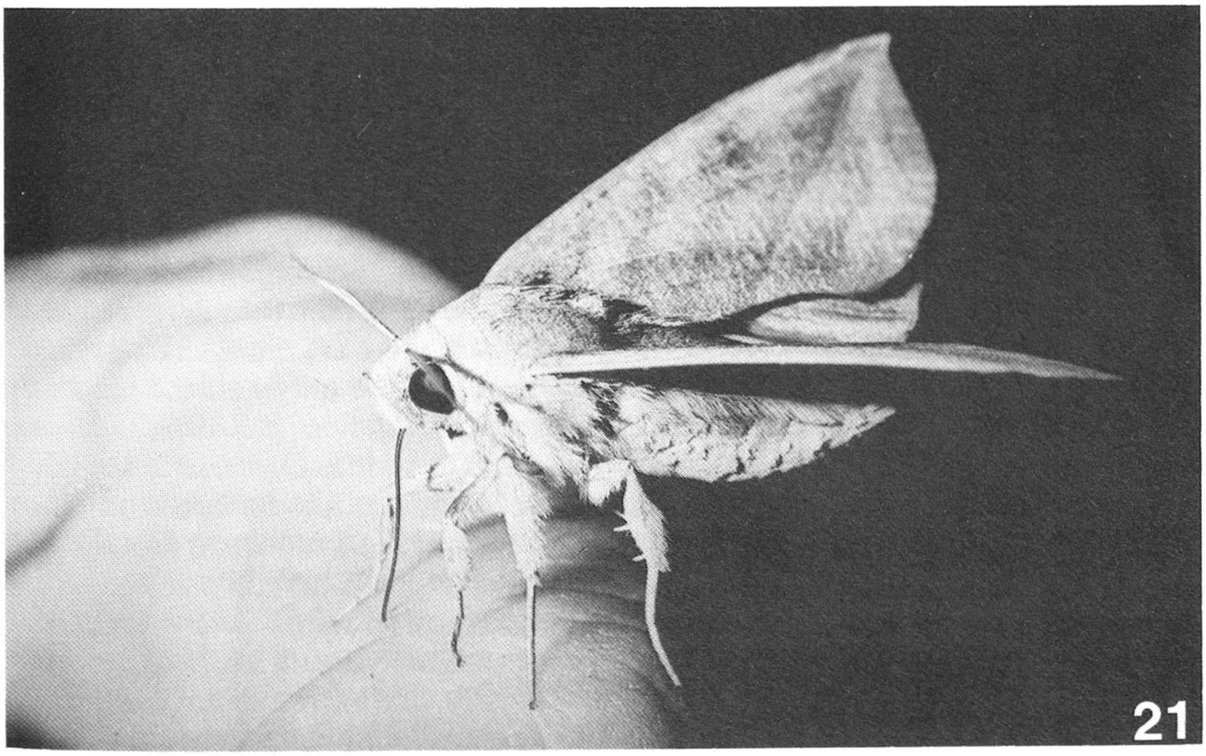
One *minuticornis* settled twice near the tip of the trousers of a Karen highlander assisting the author during observations on zoophilous moths of elephant (site h). The trousers were wet and the assistant's foot had a small wound, some blood probably having been smeared onto the trousers. However, the assistant was very fearful of the moth and was flipping it away whenever it flew near his leg. Only after insistent imploration by the author did he allow the moth to settle for an instant before kicking it off again.

On another occasion, while the author was investigating mules attacked by *fasciata* (site i1), one specimen circled persistently around him upon which he rolled up trousers and sleeves to give the moth a better chance to pierce. However, although the author did not move in order not to discourage the moth, it settled only for very short periods, though several times. It then flew to the mule near-by and pierced two healing wounds.

So there is still no direct evidence that any of the four *Calyptra* species actually pierce human skin to suck blood in nature, although they all did so under experimental conditions (Fig. 21; also Bänziger, 1979: Figs. 6, 7, and 1980: Figs. 13–21). However, the fact that attacks in nature occurred repeatedly on humans without any wounds (except the above cases with *minuticornis* which was given no chance to pierce), points out that, after all, it can be expected that the four *Calyptra* species occasionally do pierce human skin.

Flight, pre-feeding, and feeding behaviour

Except for the three features mentioned below, flying, search for and circling around the host, alighting, crawling, licking, piercing, imbibing of blood and position during this behaviour, are essentially the same as in *eustrigata* (l.c.). The fol-



Figs. 21. *C. fasciata* sucking blood from the author's finger. Early piercing act, the proboscis just having succeeded to pierce the skin at an undamaged spot (experiment in the laboratory; all other photographs were taken under natural conditions at night in the forest).

lowing differences were observed: (i) in *orthograpta* and *fasciata* the flight is more vigorous than in the other two species; (ii) in *fasciata* the position of the wings during piercing, especially during the initial period, is in a raised, "V"-like shape (Figs. 17–19) while in the other species it is in a flat or lowered, roof-like configuration (Figs. 1–15). This is an important feature which allows quick identification of *fasciata* against the other 3 species and also has phylogenetic implications as discussed later on; (iii) when at higher altitudes, e.g. at 1470 m (site i1), *fasciata* may, whilst sucking blood, start to beat the wings as if wanting to fly off. Without interrupting the feeding it may continue to do so for ½ to 1 minute and then stop for a long while before starting again. This activity may prevent the moth from cooling down too much in the fresh mountain air at night and ensure its readiness to fly off in case of danger.

Sucking of blood lasted from 3 to over 15 minutes in 14 specimens of the four species recorded, with a mean of 7 minutes. When sucking for a long period, the moth may "rest" for short periods with the proboscis inserted in the skin. Thus the actual imbibing of blood is accordingly shorter. On the other hand, in many cases the moths were either dislodged by the host or disturbed by the flashlight photographing, or captured, by the author while it was still feeding. This probably accounts for the shorter feeding time recorded during the present study compared to that in the previous one (1.c.), when the mean time was 12 minutes.

In some cases the proboscis was seen to penetrate as deep as ¾ up to its near total length into the skin, which is somewhat more than when piercing human skin (the author's), but less than when piercing fruit, both as witnessed in experiments.

Whilst engorging the moth can be quite persistent. In one case, a strong blow of air from an elephant's proboscis failed to dislodge an *orthograpta* although the air flow was strong enough to cause the moth's wings to quiver; to capture it the author had then to push it off the wound into the collecting tube.

Proboscis morphology and piercing mechanism

Proboscis morphology and piercing mechanism have been explained in great detail for *eustrigata* (l. c.). Except for that of *fasciata,* and this only to some extent, the proboscides of the three *Calyptra* differ only in some minor details from that of *eustrigata,* as can be seen in Tab. 6. In *minuticornis* there are a few more but slightly shorter erectile barbs. In *orthograpta* the proboscis is somewhat longer and thicker, has slightly longer tearing hooks and erectile barbs, the former less and the latter more numerous. In *fasciata,* on the other hand, there are more tearing hooks, fewer erectile barbs and, remarkably, the longest ones are only half the length of those in *eustrigata.* Hence, *orthograpta*, the biggest of the four, has also the largest and strongest stylets with the fiercest armature of the group. *C. fasciata,* the body size and wingspan of which are nearly the same as those of *orthograpta* and much greater than those of the other two, has the least impressive proboscis armature of the four though this does not seem to impare its piercing capability.

The piercing mechanism has not been specifically studied for the three species. But the characteristic movements of *eustrigata*'s body, head, legs, and especially of the proboscis (i.e. the anti-parallel and spindle motions, torsion, erection of barbs, eversion of hooks) have been confirmed to take place *in toto* or in the essential parts also in these species. These observations were carried out during experiments with the author as host (Fig. 21, and 1.c.) and, whenever feasible, also with animals in nature.

Tab. 6. Some morphological data on the proboscis of *Calyptra* spp.

	Calyptra eustrigata	*Calyptra m. minuticornis*	*Calyptra orthograpta*	*Calyptra fasciata*
length of proboscis (mm)	10.5-11	10-10.5	11.5-12	10.5-11
width of proboscis (mm)	0.37-046	0.34-0.46	0.46-0.51	0.37-0.40
number of tearing hooks	22-24	22-23	20-22	23-28
length of longest tearing hook (mm)	0.079-0.086	0.063-0.085	0.091-0.10	0.085
number of erectile barbs	70-84	85-98	79-98	64-77
length of longest erectile barb (mm)	0.23	0.21	0.23	0.11
number of specimens analyzed	6	6	5	5

Since both the proboscis morphology and the piercing behaviour are essentially the same as in *eustrigata,* it is concluded that in the three species the piercing mechanism operates in the same way as it does in *eustrigata.*

Feeding spots and possible vector role

As can be seen from Tab. 7, *Calyptra* prefer skin with various types of lesions to undamaged skin. But, as had been stressed also previously (l.c.), no matter whether blood was freely available at a wound, *Calyptra* were always seen to pierce the wound to obtain their blood meal. It is also clear from the table that attacks on elephant, mule and pig were followed by successful piercing and sucking of blood only at points where the hosts' skin was in some way – mechanically or pathologically – damaged or at least not in a fully normal condition. Attempts to pierce healthy skin of elephant, though, were observed repeatedly; *eustrigata* and *fasciata* also tried, at least briefly, and without success, to pierce the skin of zebu without apparent wound. In another case, one *eustrigata,* caught as if flew off the back of a water buffalo, excreted blood upon introduction into the portable cage. Excretion of blood is a normal feature with blood-engorged or still feeding *Calyptra,* but shock due to capture can hasten this porcess. A check of the host's skin revealed no readily visible wound. Unfortunately, not knowing the spot where the moth fed, it was not possible to make absolutely sure that there was not any tiny wound present there. However, there is some likelihood that the moth pierced intact skin, as discussed below.

Tab. 7. Number of specimens of 4 *Calyptra* spp. and condition of skin at feeding or attempted feeding spot on various hosts

	normal healthy spot	scab of wound (nearly fully healed in pig, mule)	open wound, exudates and/or blood dry	fresh wound, exudates and/or blood still liquid	wound festering or chronically open, no blood superficially, only liquid exudates
ELEPHANT					
C. eustrigata	7 (0)			4 (4)*	3 (2)
C. m. minuticornis	1 (0)	3 (3)	3 (2)	4 (4)	6 (6)
C. orthograpta	3 (0)	2 (2)		1 (1)	4 (4)
C. fasciata			3 (3)		
MULE					
C. m. minuticornis		1 (1)			
C. fasciata	1 (0)**	13 (11)			
PIG					
C. fasciata		1 (3)***			
ZEBU					
C. fasciata	2 (0)				
WATER BUFFALO					
C. eustrigata	1 (1)****				

In brackets: ascertained piercing; *one more specimen pierced a wound the condition of which was not noted; **piercing possibly successful as host reacted strongly by skin vibration; ***one specimen pierced three holes; ****moth caught as flying off, location of piercing spot not certain but host had no apparent wound.

The skin of the elephants investigated had no fissures or excoriations of the types as observed on rhinoceros or tapir (l. c.) though mechanically caused cuts and scratches were at times present. Of a very different nature, the wounds which *Calyptra* mostly pierced were present especially on an old elephant. They mostly appeared on nodules on the belly, lower region of the flanks and upper parts of the legs. Such nodules, measuring up to 5 cm in diameter, persisted for years but the centre erupted at intervals of several days to weeks, remaining open for many days before healing over superficially. At the eruption the underlying epidermal tissue was exposed and fluids, in part blood, but mainly serum, with or without pus depending upon whether or not the wound was infected, were present. In dry air these hardened to a scab; but by moving through the vegetation or actively scratching, the scab could be partly torn and/or mollified by dew or rain. During the rainy season the sores were generally more persistent. It was remarkable how quickly such wounds sometimes were located and alighted upon by the moths. Also, it was repeatedly observed that when more than one such open nodule were present the moths preferred one of them, often the less conspicuous and already healing one. Occasionally two *Calyptra* were piercing one wound at the same time (Fig. 11). Or, more frequently, one to several non-piercing geometrids and/or pyralids were licking exudates simultaneously at such a spot (Figs. 4, 8). The inability of the latter two moth groups to pierce has been explained elsewhere (e.g., BÄNZIGER, 1973, 1975) and is evident in Fig. 9 and 10 from the thinness and the forwardly/laterally extended position of the proboscis unlike the much stronger proboscis of *Calyptra* which is held rather straight and vertically.

The lesions on mules were of three types. (i) nearly completely healed wounds looking like a hairless scar, with barely any traces of a scab left. Difficult to see, one was located near the base of the throat and another at the knee of one mule inspected. They were sometimes visited by flies during the day. These were the lesions most frequently sought after by *fasciata* and *minuticornis.* (ii) open wounds, slightly bleeding, though mainly serous, of up to 10 cm length and 1–3 cm width. They were located obliquely downwards from the inner angle of one or both eyes of three mules. This is the obvious flow path of the lachrymation. During the rainy season this flow path was densely covered by flies among which were *Musca conducens* WALKER and *Musca* probably *bezzii* PATTON. The former has prestomal teeth on the labellum which enable it to "scratch" up scabs (PATTON, 1933) and possibly softened tissue. The author assumes that lachrymation to some extent mollified the skin when this was still normal and that continuous scratching by the flies finally resulted in the sores mentioned. (iii) excoriations in which the skin was rubbed to such an extent as to expose a whitish-pink layer, without blood flow. They were present on the cheeks not far from the nose where too tight a rope caused this condition on all three mules. Flies frequented also these. *Calyptra* repeatedly attempted to settle on both type (ii) and type (iii) lesions but were not successful as the mules reacted violently to the approaching moths by shaking the head. But non-piercing bloodsucking, and lachryphagous geometrids, like the smaller *Hypochrosis abstractaria* WALKER, *Hypochrosis* sp.1 and *Problepsis* sp., occasionally were able to alight gently on the head at spots out of sight of the host and then crawl to the lesion and imbibe its fluids, probably mixed with some lachrymation.

The three holes pierced by one *fasciata* on a pig were located near the base on the exterior of the ear. The skin at that spot looked normal, only part of what probably had been scabs remained, similar to the lesions of type (i) found on mule. Some other pigs lying near-by in the same stable (without walls on two sides), had much more obvious, partly bleeding wounds; but these were not visited by *Calyptra.*

The lesions of the elephant skin seem to be the external symptoms of what SCHMIDT (1978) calls haemorrhagic dermatitis, a filariasis of elephants already noted by FERRIER (1947). MADSEN *et al.* (1956) mention the finding of microfilariae in elephants by them and several other authors. *Stephanofilaria dedoesi* IHLE & IHLE-LANDENBERG cause a related disease, "cascado", in cattle in Indonesia (BUBBERMAN& KRANEVELD, 1933; IHLE & IHLE-LANDENBERG, 1933), and *S. zaheeri* SINGH the "ear-sore" in water buffalo in India (GOPALAKRISHNAN, 1948; SINGH, 1958). RAHMAN (1957), SRIVASTAVA & DUTT (1963), IVASHKIN *et al.* (1963), and PATNAIK & ROY

(1966) showed that flies (*Musca* and *Lyperosia* spp.) are the intermediate hosts and vectors of the filariae.

The mode of transmission seems, therefore, to be biological and, since *Calyptra* belong to a completely different insect order, it is unlikely that they play a role as vector hosts of such nematodes. Nevertheless, in another genus of filarioid nematodes, *Dipetalonema,* the different species develop in such distantly related arthropods as mosquitoes, ceratopogonids, fleas, and ticks (HAWKING & WORMS, 1961). Moreover, LOKE & RAMACHANDRAN (1967) in a study of the histopathology of the "krian sore", yet another related type of dermatitis caused by *S. kaeli* BUCKLEY in cattle in Malaysia (BUCKLEY, 1937), as well as RAHMAN (1957), are of the opinion that in certain cases flies may just play a mechanical and contaminative role in the transmission. In *Calyptra* some features, such as the proboscis morphology and method of piercing, had been mentioned in a discussion as being exceptionally well suited for the mechanical transmission of pathogens (BÄNZIGER, 1980). Hence it cannot be excluded that *Calyptra* may after all be involved in some way in the transmission. Investigation into the potential vector role of the moths is being continued.

Liquid intake other than blood

One *C. orthograpta* alighted on the cheek below the eye of an elephant where lachrymation had flowed down. From the moth's behaviour it can be concluded that it imbibed lachrymal fluid. However, it was unusually restless and climbed up and down along the flow path of the lachrymation and occasionally performed piercing attempts. The elephant was very nervous and would have long flipped the moth off with the proboscis had the *mahout* not prevented it from doing so. On a subsequent investigation something similar happened again with another *orthograpta* settling twice at the flow of lachrymation of the same eye of the same elephant. This time, though, it could not be ascertained whether the moth actually imbibed any lachrymation. Four months later the same happened again with one *eustrigata*, also near the same eye of the same elephant.

The eye region was carefully checked for the presence of any small wound which might have attracted the moths but nothing could be detected though one of the spots visited was paler than the surrounding skin, possibly rubbed by the proboscis and somewhat mollified, with slimy whitish fluid.

These 3 observations of *Calyptra* moths taking fluids below or settling near elephant eyes came as a big surprise. This was despite BÜTTIKER's (1962a, 1969, and pers. comm.) observation of one *minuticornis*[2] and one *eustrigata* at or flying off the eyes of a water buffalo/cattle and cattle, respectively. During some 16 years of night observations of over 370 specimens of the 4 *Calyptra* species on or near mammal hosts, in different biotopes, climatic regions, elevations and across all months of the year, I had never previously seen a specimen being attracted to, much less sucking from, eye discharges.

However, although the imbibing of lachrymal fluids evidently can occur, albeit extremely sporadically (2 proved cases, 3 possible cases – being at an eye does not

[2] BÜTTIKER (1962a) mentions it as a female but dissection and analysis of the specimen's genitalia proves it a male. Moreover, he states that the host was buffalo in 1962b but cattle in 1969.

prove sucking of tears), this should not lead to the conclusion that these *Calyptra* species are lachryphagous: the behaviour is obviously accidental, as the following considerations indicate. (i) eyes and the frequent lachrymation flows down the elephant's cheek are a most readily and always available source of food or moisture. Wounds on the other hand, if present at all, tend to be much smaller in area and hence more difficult to find. More importantly, they must be pierced. In spite of this, except for the above cases, the moths fed or tried to do so only from sores, healing lesions or unscathed skin. Most remarkably of all, when not successful, *Calyptra* flew off without feeding rather than take lachrymation. (ii) unlike when feeding upon blood, during which they may remain on the very spot for an average of 7 minutes, *Calyptra* were restless when in the eye region, evidently not satisfied with lachrymation. Typical lachryphagous moths do not move from the spot for up to two hours when sucking lachrymation. (iii) the three cases of *Calyptra* settling near the eye occurred at the same locality, on two consecutive investigations, and on another a few months later, below the same eye of the same host instead of more randomly during the 16 years long research on these moths. They might have been misled by some clue (e.g. latently diseased skin) present in that particular host's eye region. Since lachryphagy would be such an easier way of feeding but has only very sporadically been observed in *Calyptra,* and since also the feeding behaviour and the exceptional time-limited occurrence near one particular eye of one host, were all unusual, the evidence is overwhelmingly in favour of regarding the four *Calyptra* species as plain non-lachryphagous. Moreover, it has been pointed out elsewhere (BÄNZIGER, 1975, 1979, 1980) that the morphology of *Calyptra*'s proboscis is not of the lachryphagous type.

The mentioned cases of accidental lachryphagy should not be confused with occasional lachryphagy, termed as oligolachryphagy. This latter denotes the habit of many Geometridae and Pyralidae which only occasionally suck lachrymation. Lachryphagy in these moths is uncommonly seen but perfectly normal, while by "accidental" the author denotes an abnormal, mistaken behaviour, a feature which has been observed now and again in many insects and other animals.

It has been mentioned several times that for a number of reasons fruit must be an important source of food for the four *Calyptra.* In captivity they will readily pierce fruit of many kinds and live on a diet of sap alone. And yet, except for *minuticornis,* the remaining three species so far have not been seen to pierce fruit in nature in the study area despite the intensive search for this by the author during his decade long involvement with fruit-piercing moth studies (e.g. BÄNZIGER, 1982).

This lack of evidence together with the fact that the four *Calyptra* species' females have never been seen attacking mammals, are still some of the most intriguing features. It is to be expected that the females live mainly if not exclusively upon fruit. Such may possibly belong to a particular group of plants which the author has not yet had the chance to come across at the right moment. Moreover, from feeding experiments and other observations it would now seem that the males' taking of blood does not cover their energy needs. There is indication that, like females, males also are largely dependent on fruit sap for their energy requirements. Investigations of this nutritional aspect are under way and they will be reported in due course.

Abundancy and population fluctuation (Figs. 22–26)

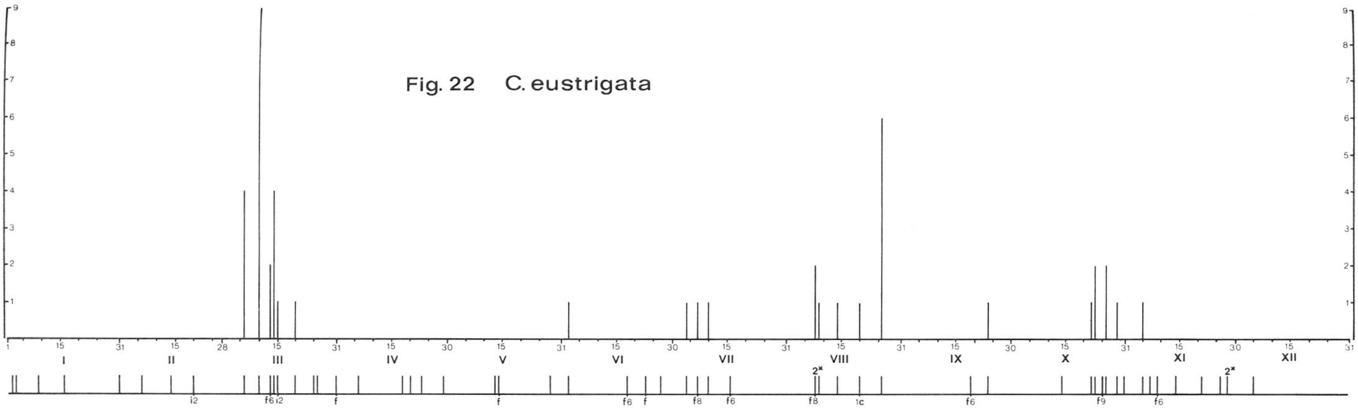
A total of 151 *Calyptra* adults were observed on or near mammal hosts during 82 night inspections in the course of 6½ years at 9 study sites in N. Thailand: 44 *eustrigata,* 44 *minuticornis,* 31 *orthograpta,* 21 *fasciata,* and 11 unidentified specimens (not certain which of the 4 species). None was found on an additional 8 inspections at four other sites (h3, h5, f9, kl)(Figs. 22–25). Further 8 inspections in S. Thailand (Khao Chong, Trang Prov., 18–24.3.79 and 20–28.5.80) were also negative. The above records pertain only to localities where adult *Calyptra* are proved to occur. Altogether 1 to a maximum of 14 *Calyptra* specimens were seen on a single night during 39 inspections, while no moth was found on 59 investigations (including the above 16 investigations at places where no attacks were witnessed).

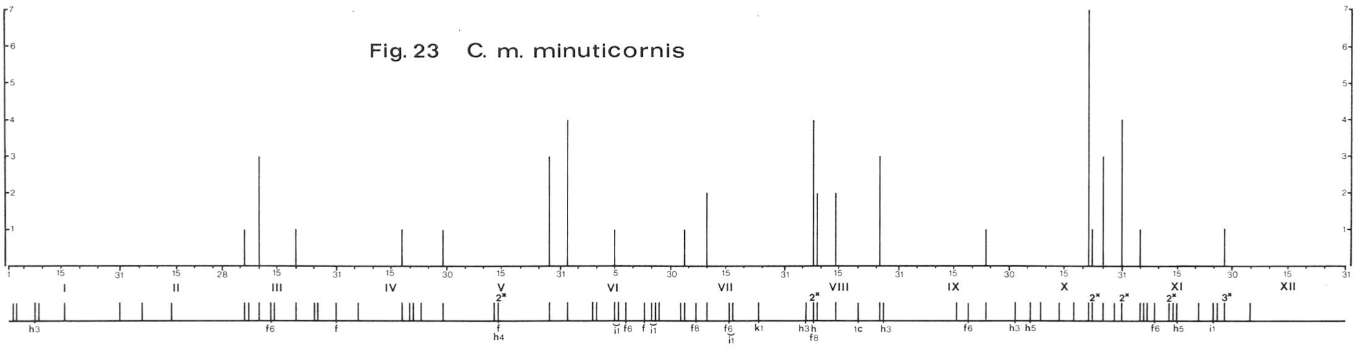
No *Calyptra* was observed during an additional 11 night inspections at 9 different locations in N. Thailand which looked promising for the presence of *Calyptra* but, as yet, had not yielded any positive finding: Ban Meo Bon Doi Suthep, Samoeng, Ban Mae Tho, Ban Doi Khun Jä (Phrao Distr.)(all Chiengmai Prov.); Mae Ping Luang (Pai Distr.), Ban Hua Pon (Khun Yuom Distr.)(both Mae Hongson Prov.); Ban Pha Lü (Mae Jan Distr.)(Chiengmai Prov.); Ban Pang (Li Distr.) (Lamphun Prov.).

Moreover, mercury vapour light collecting at 20 different sites on 41 occasions yielded 3 *eustrigata* (f9, f10), 11 *minuticornis* and 6 *fasciata* (both from f10, h3, h6, f11). Thirteen of these outings were made with the author's Department colleagues when Mr. P. Sukumalanan, Dr. S. Ratanabhumma, and Dr. V. Hengsawad caught additionally 1 *orthograpta* and 3 *fasciata* (at h3, h6, f11).

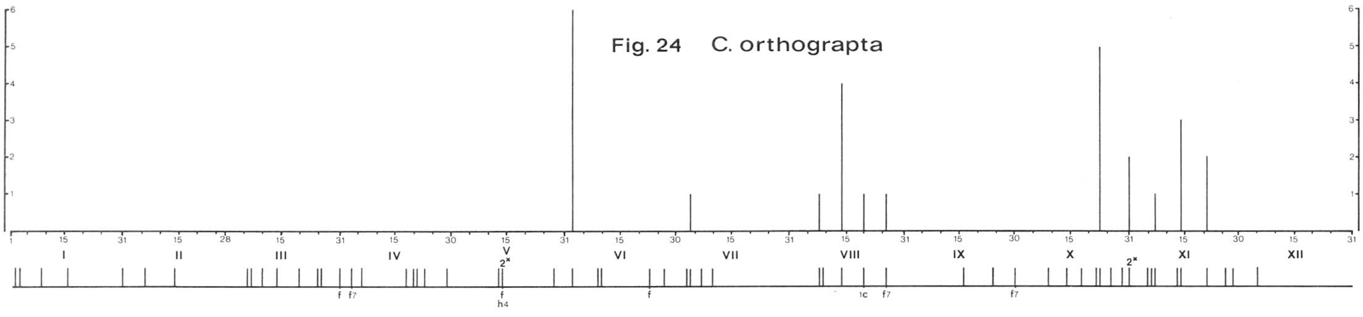
Results shown in Figs. 22–25 have been combined with those of previous studies (l. c.) in Fig. 26 to obtain, with data over a period of 13 years, the best information so far on the adult *Calyptra* population throughout the year in N. Thailand. The idealized curve (thick line) is a theoretical synthesis obtained by: (i) plotting, on a weekly basis throughout the year, the number of all *Calyptra* moths observed on or near mammals against the number of inspections carried out during the present and previous studies in N. Thailand (1972–1984). (ii) giving site (hl) preeminent importance as it is where observations were carried out most regularly and frequently, and where all 4 *Calyptra* species occur. (iii) pre- and postdating, compared to site (hl), the data from the higher or lower altitudes, respectively, in order to take into account the somewhat later or earlier emergence of the moths in such places.

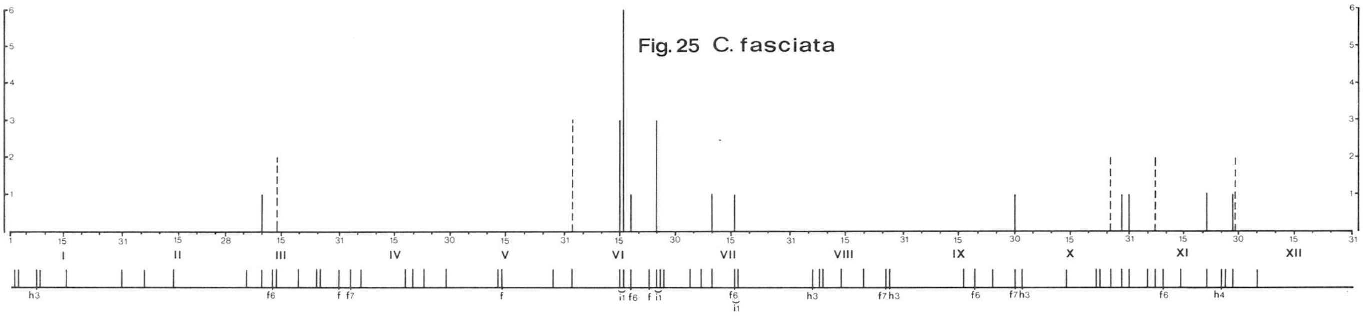
From Fig. 26 it is obvious that the four species, which fly at about the same periods of the year in N. Thailand, occur in four abundancy peaks from March through to November. No adults were found from December to February (exception: 1 *minuticornis* on 27. ii.1977). It is concluded that there are 4 generations per year, with adult populations peaking in about early/mid March, end May/beginning June, mid/late August, and mid/late October. The generations overlap to quite an extent so that *Calyptra* can be found throughout March to November. Hence a generation (egg to egg) requires about 8–11 weeks to complete, which is corroborated by experimental breeding. The period from December to February, when there is a development slowdown, is probably passed as immatures. It seems very unlikely that there is a low abundancy peak of a potential fifth generation during this period which may have escaped detection.





Figs. 22, 23. Records of *C. eustrigata* (22) and *C. m. minuticornis* (23) on or near hosts in N. Thailand, 1978–1984. Abscissa: days and months of the year; below: the dates of the relative inspections and code of localities (inspections without code pertain to site h1, h2; 2×, 3× means that the date coincides with 2, 3 inspections). Ordinate: number of specimens observed.





Figs. 24, 25. Records of *C. orthograpta* (24), *C. fasciata* (25) and unidentified *Calyptra* species (one of the four species) (25) on or near hosts in N. Thailand, 1978–1984. Abscissa: days and months of the year; below: the dates of the relative inspections and code of localities (inspections without code pertain to site h1, h2; 2×, 3× means that the date coincides with 2,3 inspections). Ordinate: number of specimens observed (dotted line: unidentified *Calyptra* species).

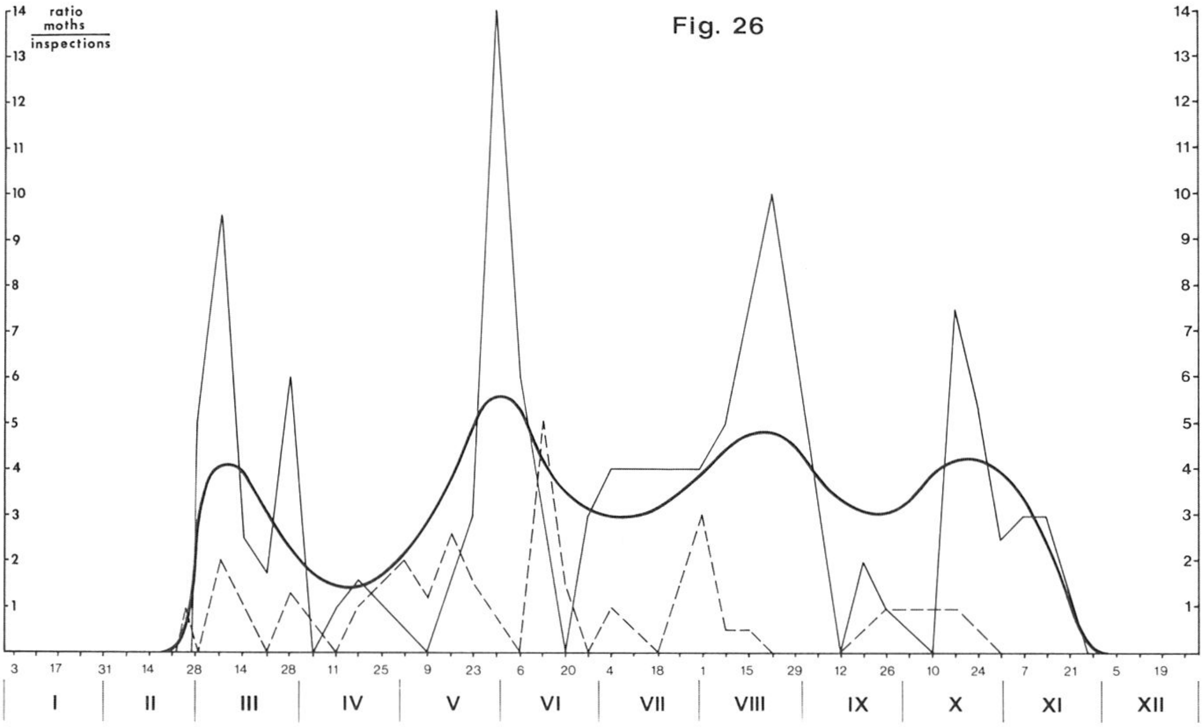


Fig. 26. Population fluctuation of adult *C. eustrigata, C. m. minuticornis, C. orthograpta* and *C. fasciata* (considered as if one entity) during the year in N. Thailand (data from a 13 years' long study period). Thin line: results of present study (1978–1984); dotted line: results of 1972–1977; thick line: idealized curve, combined results 1972–1984 (cf. text p 128). Abscissa: days and months of the year. Ordinate: number of moths per night inspection.

In Peninsular Malaysia and the very south of Thailand, where *orthograpta* and *fasciata* do not seem to occur, *eustrigata* and *minuticornis* are more evenly distributed throughout the year, including December to February (l. c.). There is little doubt that there are 5 generations of *Calyptra* per year there. This must be due to the lack of, or much milder, cold and dry seasons, characteristic of the tropical everwet climate of that area. There is no slowdown in the development of the immatures and the night activity of the adults is not impared by low temperatures; moreover, continuous thriving of various types of evergreen vegetation is possible and hence also of the insects dependent on them.

Considering that studies in the northern Thai highlands (1000–2000 m) were given increased attention only recently, it is likely that the essentially highland species *fasciata* is actually more common than *orthograpta,* and *minuticornis* more than *eustrigata.*

However, there may be quite some variation in the abundance of individuals of *Calyptra* species between years, though this may be due, at least in part, to the statistically low number of records: *eustrigata* was exceedingly scarce in 1974, 1976, 1977 (a total of only 2 specimens seen) and "common" in 1979 (16 specimens); *minuticornis* was scarce in 1973, 1979 (4 specimens) and "common" in 1980, 1983 (22 specimens); *orthograpta* was rare in 1977, 1983, 1984 (3 specimens) and "common" in 1973, 1980, 1982 (34 specimens); *fasciata* consistently scarce except in 1984 (13 specimens).

As knowledge about the four *Calyptra* species has now increased significantly, it is evident that, if not actually less scarce, they are at least more widely distributed than previously assumed, though research on them remains frustratingly arduous.

Time of activity

At site (hl) *eustrigata, minuticornis* and *orthograpta* attacked their hosts as early as 1915 hours, that is quite soon after dark, rapidly attaining the nightly peak at about 20.00–20.15 hours, and decreasing thereafter to virtually nil near midnight (Figs. 27–29, 31). At the same site *fasciata* arrived and peaked about an hour later (Fig. 30). At other less regularly researched sites, the 4 species appeared later at night. This was also found in the previous studies (l.c.), especially for *eustrigata* at site (a) in W. Malaysia where the main night flight period was between 22 and 24 hours.

If all the data since 1972, and including those from Malaysia (1971) are considered (Fig. 32), it is clear that the time when the 4 *Calyptra* attack their hosts is restricted mainly to the first half of the night. The early appearance and peaking of *Calyptra* (except *fasciata*) at site (hl) compared to the later times elsewhere, is interpreted as being due to the location of the moths' breeding places. These are assumed to be near or far from these sites, requiring a shorter or a longer time, respectively, to fly to the hosts.

During the rainy season the four species arrived as early as during the dry season although in June-August darkness falls about ½ hour later than in March. They also were active up to much later at night during the rainy season, possibly because of the less marked decrease in temperature.

STUDIES IN PAPUA NEW GUINEA

The subspecies *C. minuticornis novaepommeraniae,* biologically completely unknown and systematically problematic until recently clarified, was, together with other zoophilous and fruit-piercing Lepidoptera, the principal object of study of a research trip to its main distributional area, Papua New Guinea. The moth's immatures and their host plant were discovered there, before crossing experiments were carried out (in Thailand) with the closely related *C. m. minuticornis* to assess the degree of relationship, results of which have been reported (BÄNZIGER, 1983).

Apart from having only very slightly longer erectile barbs (length of longest 0.22–0.24 mm, Tab. 6), *novaepommeraniae*'s proboscis morphology agrees with that of *minuticornis.* The biotope of the site where *novaepommeraniae* immatures were observed consists of evergreen vegetation as in *minuticornis*'s area of distribution in W. Malaysia. The population dynamics are assumed to follow the pattern of the Malaysian subspecies.

The main interest for the present study was the question of whether adult *novaepommeraniae* males are blood suckers or not – a matter of some interest as the area did not originally harbour any mammals attacked by *Calyptra.*

Several herds of cattle, water buffalo and pig were checked during 15 night inspections at several places in the Lae area, Morobe Province, and during 2 inspections at Laloki, near Port Moresby, from 15.iv. to 11.v.1982. No evidence of adult *novaepommeraniae* attacking these mammals was found. In at least one place the occurrence of the moth in the area of one herd of cattle inspected was proved, as immatures of *novaepommeraniae* were found within the adult's assumed flying distance capability from the cattle pasture.

Experiments to induce the moth to pierce the author's skin failed. Such experiments had been successful with the subspecies *minuticornis* as well as with the other 3 *Calyptra* species treated.

Fig. 27 C. eustrigata

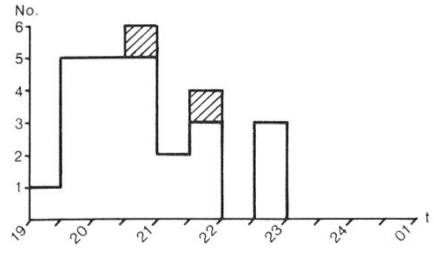


Fig. 28 C. m. minuticornis

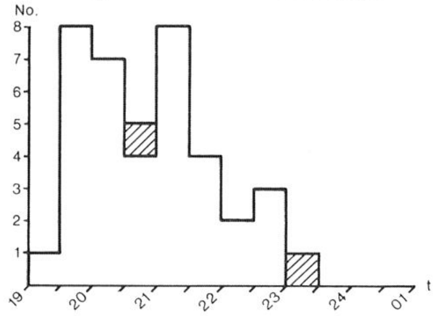


Fig. 29 C. orthograpta

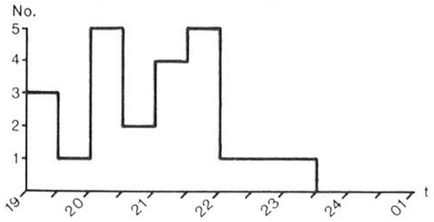
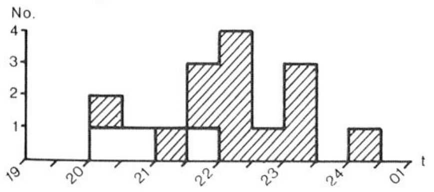
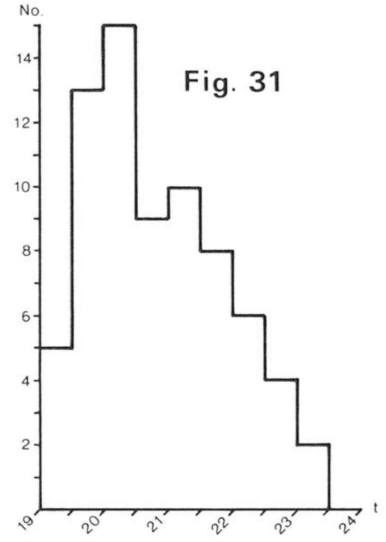
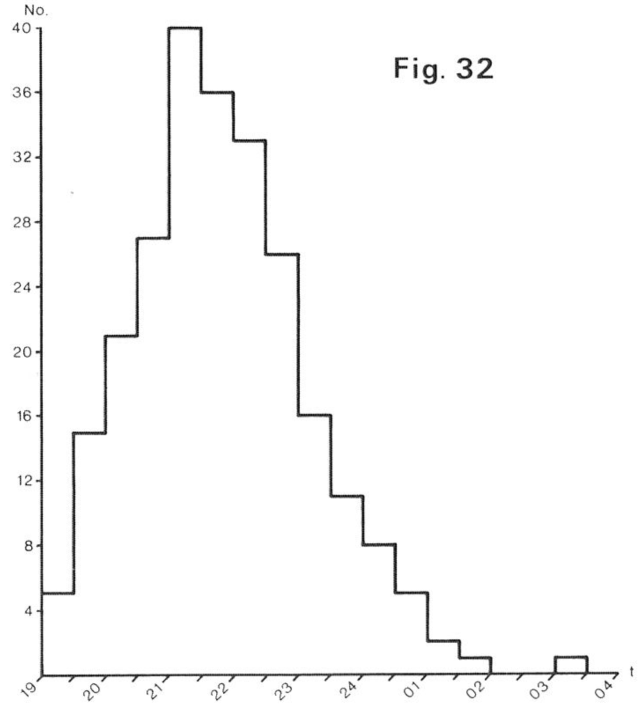


Fig. 30 C. fasciata







Figs. 27–30. Time of appearance of *C. eustrigata* (27), *C. m. minuticornis* (28), *C. orthograpta* (29), and *C. fasciata* (30) on or near hosts at site h1 (blank) and at sites other than h1 (hatched), 1978–1984. No.=number of moths observed (not all moths recorded), t=time of the night.

Fig. 31. Time of appearance of *C. eustrigata, C. m. minuticornis* and *C. orthograpta* together (but without *C. fasciata)*, on or near hosts at site h1, 1972–1984.

Fig. 32. Time of appearance of *C. eustrigata, C. m. minuticornis, C. orthograpta* and *C. fasciata* together, on or near hosts at all sites (including those in Malaysia), 1971–1984.

It is concluded, therefore, that the subspecies *novaepommeraniae* apparently is not a blood sucker but a fruit piercer only. In captivity the subspecies eagerly pierced, lived and reproduced upon a variety of fruits.

Many of the findings of the present study have already been discussed in the relative chapters. The issue whether *Calyptra* can feed primarily from intact healthy skin or is dependent on pre-existing injuries is of some interest. From recent results (BÄNZIGER, 1979, and present study) none of the 4 *Calyptra* species was observed, or is assumed to be able, to pierce fully normal skin of elephant. Of the over 180 attacks witnessed – about 3 times as many as with the next most frequently visited host, the tapir – there is not a single case of a *Calyptra* having successfully pierced intact elephant skin. This is probably too tough for the moths to pierce. Neither are there any indications yet that they pierced undamaged skin of such hosts as zebu, mule, pig though this is more likely to occur, especially with the latter two, than with elephant. A possibly successful piercing of normal skin of water buffalo has been mentioned. Earlier conclusions (BÄNZIGER, 1975) maintained that *C. eustrigata* is capable of piercing intact skin of tapir, rhinoceros (which has a relatively delicate outer skin layer), and nilgai. If sharp criticism is exercised, however, in these cases it is of course impossible to dismiss with complete certainty the existence of a minuscule cut or nearly completely healed spot at the piercing point. Absolute certainty, though, remains that the 4 species are able to pierce fully normal, intact human skin (the author's) in experiments.

In retrospect, in the light of these new results, it might have been more to the point to call these moths "wound-piercing blood-sucking". But at the time when this behaviour was discovered in 1967, still little was known about the feeding habits of these scarce moths. Best would have been to adopt the term from the German "piercing blood-sucking" (*stechend blutsaugend*) if only the English grammar would allow it. Nevertheless, what the moths pierce after all is skin, albeit in a more or less "abnormal" condition.

From the parasitological point of view at any rate, whether or not *Calyptra* can pierce intact skin of some of their hosts is not likely to reduce much the moth's potential role – almost certainly a marginal one – as a vector of pathogens. In fact, hosts with wholly intact skin probably are not much more common than ones with at least some small cuts. More importantly, where a host's skin is injured there is more likelyhood of pathogens being present, and as a consequence being acquired and then transmitted to another host by a vector feeding on it, than where the skin is intact.

Man's hunting for food and his destruction of natural habitats have depleted the wild fauna of the region to such an extent that large wild mammals are rarely encountered in nature. It had become questionable, indeed, whether *Calyptra* adults' host species – until this study considered to be a few mostly rare or little attractive mammals – would be numerically sufficient as a blood source for the moths, the more so, perhaps, since it has now become clear that, at least with some host species, the presence of damaged skin of some sort seems to be essential for the moths to pierce. However, the finding of two new important hosts, mule and pig, and the confirmation of the elephant as the most attractive host, now seems to have solved this question.

A cross between horse and donkey, the mule makes both parent species also virtually certain hosts of *Calyptra* since less closely related members of the two other families of Perissodactyla, the tapir and the rhinoceros, are already proven hosts of *Calyptra*. Far more importantly, the mule, and with it the horse and the donkey, have a very much wider and denser distribution than the two wild perissodactyls.

Despite the mechanisation of transportation, mule and horse, and to a lesser extent also the elephant, still play a pre-eminent role as beasts of burden in difficult mountain and jungle terrain in remote areas of Thailand and other S.E. Asian countries. Single or in caravans of up to many dozens of animals, they regularly transport local produce or move across the borders of the "Golden Triangle" carrying the infamous opium, jade and other produce, licit or illicit. Domesticated elephants are still widely employed to extract timber from the forest.

The pig belongs to a separate, non-ruminating group of the Artiodactyla. It is bred over most of non-muslim S.E. Asia and even more than mule by the highlanders of N. Thailand, where it roams around in a semi-wild state. The Southeast Asian wild boar (*Sus scrofa jubatus* MILLER), which differs only on a subspecies level from the pig, is one of the few large mammals which has survived to some extent successfully the onslaught of man. This is particularly true for countries with large muslim populations like Peninsular Malaysia where it is not hunted for food. In addition, in Malaysia there is also another, though rare, wild species: the bearded pig (*Sus barbatus* MÜLLER) (MEDWAY, 1969). It can be assumed with fair certainty that these wild pigs are also attacked by *Calyptra.*

At night mules and pigs – like zebus and water buffaloes – are generally kept in a small enclosure under a roof, or under the owner's house on stilts, sometimes with the side exposed to rain and wind protected by a wall of wooden boards. But during the dry season, they are often loose to roam around in search of food. Elephants are let to themselves in the forest where they feed all night, bound on a very long chain or with the fore-feet closely chained to slow down movement. Hence blood-sucking *Calyptra* moths do not need to overcome any protective device erected by man and find domesticated hosts fully exposed to their attacks except when a smoke-producing fire is lit near the host by man.

The population breakdown of adult *Calyptra* during the cold season in N. Thailand, when no individuals fly from December through to February, parallels that of the fruit-piercing moths but is in marked contrast to population patterns of lachryphagous moths. *Lobocraspis griseifusa* feeds upon lachrymation throughout the year and is particularly common during the cold season. Lachryphagous geometrids and pyralids are also active during essentially the same period. This is yet another indication that *Calyptra*'s haematophagy is more closely connected to the fruit-piercing than to the lachryphagous habits. It represents a further argument in favour of the view discussed previously (BÄNZIGER, 1980) that skin-piercing blood-sucking habits derived from the fruit-piercing way of feeding rather than from lachryphagy.

A number of facial, morphological, genitalic, and behavioural aspects indicate that the four *Calyptra* species treated here belong to two different species groups, with *eustrigata, minuticornis* and *orthograpta* on one side and *fasciata* on the other. The fore wing of *fasciata,* among other peculiarities with often extremely faint or altogether missing diagonal line (Figs. 17, 19, 21), is so unusual for the otherwise confusingly uniform pattern of *Calyptra,* that at one time the genus *Hypocalpe* BUTLER, 1883 was used especially for this species. Besides this, it was also shown (BERIO, 1956; BÄNZIGER, 1983) that in males the androtheca is missing on tibia II (present in the other three species), the antenna is bipectinate (unidentate to unipectinate in the other three) and, among other genitalic differences, the aedeagus's cornuti have quite another configuration. Moreover, as pointed out in the present study, *fasciata* has, when compared with the other three species, a somewhat modified proboscis armature and finally, while engorging, the moth keeps the wings in a wholly different position.

The above finding has interesting implications as to the phylogeny of some *Calyptra,* as well as about the time when adult haematophagy evolved in the genus. All the evidence is that many *Calyptra* species (e.g. *albivirgata* (HAMPSON), *lata* (BUTLER), *thalictri* (BORKHAUSEN), belonging to yet other species groups) are frugivorous only. Seemingly present in all species, fruit-piercing, as has been shown repeatedly (l. c.), is the more primitive and blood-sucking the derived feeding habit, hence haematophagy must have appeared after the genus was already established. On the other hand, unless blood-sucking was developed at least twice in *Calyptra* – which is of course possible though the author is inclined to think less probable – haematophagy must have evolved before *fasciata* separated from the other species group. This is earlier than what the author had thought until recently.

But the conclusions would appear, at first, to be quite different if the two subspecies of *C. minuticornis* are considered. Unlike the Indomalayan *C. m. minuticornis*, the Papuan *C. m. novaepommeraniae* is not haematophagous. This would favour the assumption that blood-sucking developed much later, after the subspeciation of *minuticornis,* i.e. polyphyletically at least 3 times as a parallel evolution. This is particularly tempting as lachryphagy, for instance, developed at least four times in Lepidoptera: in the Noctuidae, Notodontidae, Geometridae, and Pyralidae. However, there may be a more plausible explanation; namely, that haematophagy was secondarily lost in *novaepommeraniae.* In this hypothesis, the original, not yet subspeciated but already haematophagous, *C. minuticornis* found no adequate mammal hosts upon crossing the Wallace Line into the Papuan Region. The only eutherian land mammals to reach the region on their own are the Rodentia and the Chiroptera, all non-hosts of *Calyptra.* The wild pig is obviously feral there (WHITMORE, 1975), resident for some 10000 years (BULMER, 1966), arriving much later than man who seems to have first appeared on the New Guinea Island about 25000 years ago, and possibly as early as 50000 years ago (POWELL, 1976). As the moth differentiated into *novaepommeraniae* the blood-feeding habits were lost. This reduction probably presented no major difficulty as haematophagy does not seem to be obligatory in *minuticornis,* at least adults of both subspecies can live and reproduce in captivity on a fruit diet alone. From the above it could be speculated that haematophagy in *Calyptra* may have evolved more, possibly much more, than 15000 years ago, when due to the low sea level during the last glatiation, the sea between New Guinea and Mainland S.E. Asia was narrow for the last time (CHAPPELL & THOM, 1981). This is possibly the time when *minuticornis* spread to the Papuan Region or, if the moth was already there, when there was the last contact with the S.E. Asian populations, and the moth's subspeciation started.

ACKNOWLEDGEMENTS

Sincerest thanks are due to Dr. A. GEATER, Fac. Science, Prince of Songkla University, Thailand, for criticizing and correcting the manuscript; to Dr. A. PONT, Dept. Entomology, British Museum (Nat. Hist.), London, for identifying *Musca* sp. and giving crucial reference information, as did Dr. P. GIANOLA, Library, Swiss Fed. Inst. Technology, Zürich; to Dr. J. D. HOLLOWAY, Commonw. Inst. Entomology, London, and especially to Dr. R. DE JONG, Rijksmuseum, Leiden, for comments on aspects concerning evolution; to Mr. J. SUTHERLAND, formerly of the Bubia Res. Station, Lae, for invaluable help extended during the study in Papua New Guinea; to Dr. W. RIETSCHEL for offering important suggestions about what the elephant skin lesions might be. Last but not least, to the author's Dept. colleagues, Mr. P. SUKUMALANAN, Mr. U. ARITAJAT, Dr. S. RATANABHUMMA, Dr. V. HENGSAWAD, Dr. M. TITAYAVAN, Mrs. J. VISITPANICH, Dr. S. BUDHARUGSA and Mr. C. SIWASIN for their continuous support.

BÄNZIGER, H. 1973 (1972). *Biologie der lacriphagen Lepidopteren in Thailand und Malaya.* Rev. Suisse Zool. *79:* 1381–1469.

BÄNZIGER, H. 1975. *Skin-piercing blood-sucking moths I: Ecological and ethological studies on Calpe eustrigata (Lepid., Noctuidae).* Acta trop. (Basle) *32:* 125–144.

BÄNZIGER, H. 1979. *Skin-piercing blood-sucking moths II: Studies on a further 3 adult Calyptra [Calpe] sp. (Lepid., Noctuidae).* Acta trop. (Basle) *36:* 23–38.

BÄNZIGER, H. 1980. *Skin-piercing blood-sucking moths III. Feeding act and piercing mechanism of Calyptra eustrigata (Hmps.) (Lep., Noctuidae).* Mitt. Schweiz. Ent. Ges. *53:* 127–142.

BÄNZIGER, H. 1982. *Fruit-piercing moths in Thailand: A general survey and some new perspectives.* Mitt. Schweiz. Ent. Ges. *55:* 213–240.

BÄNZIGER, H. 1983a. *Lachryphagous Lepidoptera recorded for the first time in Laos and China.* Mitt. Schweiz. Ent. Ges. *56:* 73–82.

BÄNZIGER, H. 1983b. *A taxonomic revision of the fruit-piercing and blood-sucking moth genus Calyptra OCHSENHEIMER [= Calpe TREITSCHKE] (Lepidoptera: Noctuidae).* Ent. scand. *14:* 467–491.

BÄNZIGER, H. 1986. *Lachryphagous Lepidoptera recorded for the first time in Papua New Guinea and Indonesia.* Heteroc. Sumatr. (in press).

BERIO, E. 1956. *Appunti su alcune specie del genere Calpe Tr. (Lep., Noctuidae).* Mem. Soc. ent. Ital. *35:* 109–119.

BERIO, E. 1970. *Diagnosi di alcune specie esotiche di Noctuidae (Lepidoptera).* Boll. Soc. ent. Ital. *102:* 21–29.

BUBBERMAN, C. & KRANEVELD, F. C. 1933. *Over een dermatitis squamosa et crustosa circumscripta bij het rund in Nederlandsch-Indië, genaamd cascado. I. Onderzoekingen over aard en wezen der cascado.* Ned. Ind. Bl. v. Diergeneesk. *45:* 239–278.

BUCKLEY, J. J. C. 1937. *On a new species of Stephanofilaria causing lesions in the legs of cattle in the Malay Peninsula.* J. Helminth. *15:* 233–242.

BULMER, S. 1966. *Pig bone from two archaeological sites in the New Guinea Highlands.* J. Polynesian Soc. *75:* 504–505.

BUTLER, A. G. 1883. *On a collection of Indian Lepidoptera received from Lieut.-Colonel Charles Swinhoe; with numerous notes by the collector.* Proc. Zool. Soc. Lond.: 144–175.

BÜTTIKER, W. 1962a. *Notes on two species of Westermanninae (Lepidoptera: Noctuidae) from Cambodia.* Proc. R. ent. Soc. Lond. *31:* 73–76.

BÜTTIKER, W. 1962b. *Biological and morphological notes on the fruit-piercing and eye-frequenting moths.* Verh. Int. Kongr. Ent. Wien, 1960. *2:* 10–15.

BÜTTIKER, W. 1969. *First records of eye-frequenting Lepidoptera from East Pakistan.* Mitt. Schweiz. Ent. Ges. *42:* 305–312.

CHAPPELL, J. & THOM, B. G. 1981. *Sea level changes, in: Papua New Guinea's prehistory: An Introduction.* In SWADLING, P. & KAIDOGA, K. National Museum, Boroko (Papua New Guinea), 69 pp.

FERRIER, A. J. 1974. *The care and management of elephants in Burma, London, Williams, Lea & Co.*

GOPALAKRISHNAN, V. R. 1948. *Stephanofilariasis among buffaloes in Assam.* Ind. J. Vet. Sci. *18:* 227–231.

HAWKING, F. & WORMS, M. 1961. *Transmission of filarioid nematodes.* Annu. Rev. Entomol. *6:* 413–432.

IHLE, J. E. W. & IHLE-LANDENBERG, M. E. 1933. *Over een dermatitis squamosa et crustosa circumscripta bij het rund in Nederlandsch-Indië, genaamd cascado. II. Stephanofilaria Dedoesi (n. gen., n. sp.), een Nematode uit de huid van het rund.* Ned. Ind. Blad van Diergeneesk. *45:* 279–284.

IVASHKIN, V. M., KHROMOVA, L. A. & SHMITOVA, G. Y. 1963. *Stephanofilariasis in cattle.* Veterinariya *40:* 36–39 (in Russian).

KÜCHLER, A. W. & SAWYER, J. O. 1967. *A study of the vegetation near Chiengmai, Thailand.* Trans. Kans. Acad. Sci. *70:* 281–348.

LOKE, Y. W. & RAMACHANDRAN, C. P. 1967. *The pathology of lesions in cattle caused by Stephanofilaria kaeli Buckley, 1937.* J. Helminth. *41:* 161–170.

MADSEN, D. E., DISSAMARN, R. & CHOMANAN, T. 1956. *Microfilaria in elephants.* J. Parasit. *42:* 552.

MEDWAY, LORD. 1969. *The wild mammals of Malaya (and offshore islands including Singapore).* Kuala Lumpur, Oxford University Press, 127 pp.

MOORE, F. 1882. *Description of new Indian lepidopterous insects from the collection of the late Mr. W. S. Atkinson. Heterocera.* Asiatic Society of Bengal, Calcutta, 299 pp.

PATNAIK, B. & ROY, S. P. 1966. *On the lifecycle of the filariid Stephanofilaria assamensis Pande, 1936, in the arthropod vector Musca conducens Walker, 1859.* Indian J. Animal Health, *5:* 91–101.

POWELL, G. M. 1976. *Ethnobotany,* in: New Guinea Vegetation, K. Paijmans ed., Hong Kong, Australian National University Press, 213 pp.

RAHMAN, M. H. 1957. *Observations on the mode of infection of the hump of cattle by Stephanofilaria assamensis in East Pakistan.* J. Parasit. *43:* 434–435.

Schmidt, M. 1978. *Elephants,* in: Zoo and wild animal medicine, M. E. Fowler ed., W. B. Saunders, Philadelphia, London & Toronto, 951 pp.

Singh, S. N. 1958. *On a new species of Stephanofilaria causing dermatitis of buffaloes' ears in Hyderabad (Andhra Pradesh).* Indian J. Helminth. *32:* 239–250.

Smitinand, T. 1966. *The vegetation of Doi Chiengdao, a limestone massive in Chiengmai, North Thailand.* Nat. Hist. Bull. Siam soc. *21:* 93–128.

Srivastava, H. D. & Dutt, S. C. 1963. *Studies on the life history of stephanofilaria assamensis, the causative parasite of "humpsore" of Indian cattle.* Indian J. vet. Sci. *33:* 173–177.

Strand, E. 1917. *H. Sauter's Formosa Ausbeute: Noctuidae I.* Arch. Naturgesch. *83:* 129–162.

Swadling, P. & Kaidoga, K. 1981. *Papua New Guinea's prehistory: An introduction.* National Museum & Art Gallery, Boroko (Papua New Guinea), Everest Printing Co., Lmtd. Hong Kong, 69 pp.

Whitmore, T. C. 1975. *Tropical rain forests of the Far East.* Oxford University Press, East Kilbride (Scotland), 282 pp.

(received September 10, 1985)