Entomologica Basiliensia	20	57–80	1997	ISSN 0253-2484

Midgut Structure and Contents in some Higher Moths, specially in Eye-frequenting Taxa

by **W. Büttiker**

Summary

The midgut of several eye-frequenting Lepidoptera was compared with that of certain other fruit-sucking, sweat- and nectar-feeding insects. Strict eye-frequenters (e.g. *Arcyophora* spp. and *Lobocraspis griseifusa*) imbibe a considerable number of leucocytes and epithelial cells with the lachrymation. No pollen grains have been found in any ophthalmotropic moths. The suspected eye-frequenting sphingids *Nephele peneus* and *N. comma* showed no traces of leucocytes or other particles except for some ''erythrocyte'' – like plasmatic balls. The gut of the nectar-feeding moth *Noctua pronuba* contained the pollen of the host plant at which the moths were collected. The sweat-feeding noctuid *Hypocala rostrata* had an amorphous eosinophilic substance in the midgut. Finally the tabanid *Haematopota pluvialis* represented as an example of a typical blood-sucking insect; it was the only species producing a peritrophic membrane after blood-feeding.

Key words: higher moths – midgut structure – stomach content – microtome study.

1. Introduction

Ophthalmotropic Lepidoptera have been recorded from Africa*, Asia* and South America, the host animals belonging to the Artiodactyla, Perissodactyla and Proboscidea (fig. 1). Occasionally humans have been noted as hosts. A review of the literature up to 1972 was given by BÜTTIKER (1973). It has been shown that these Lepidoptera exhibit the behaviour of feeding nocturnally on the lachrymation and pus from the host's eyes (BÜTTIKER, 1964, 1967, 1970b, 1973; BÜTTIKER & BÜTTIKER 1988; BÄNZIGER, 1972ff.; BÄNZIGER & BÜTTIKER, 1969). During investigations in Asia, BÄNZIGER (1968) showed that there are skinpiercing blood-sucking noctuids, viz. *Calyptra eustrigata* (Hampson), in Thailand and Malaysia and additional species in New Guinea, Nepal and India (e.g. BÄNZIGER, 1986).

The approximate total number of eye-frequenting species now known is shown in table 1.

Fruit-licking and fruit-piercing moths have long been known. A preliminary review of the literature was given by BÜTTIKER (1962, 1970a), and BÄNZIGER (1969, 1982).

---

* Most of early investigations by the author were supported by the Swiss National Fund for the Advancement of Science (grants Nos 2669, 3707, 4655, 3.88.69 and 3.503.71).

Fig. 1. *Lobocraspis griseifusa,* a *eulacryphagous noctuid,* on the purulent eye of a young water buffalo. Note the flow of lachrymation due to keratoconjunctivitis epidemica. Chiengmai (N. Thailand), 1963.

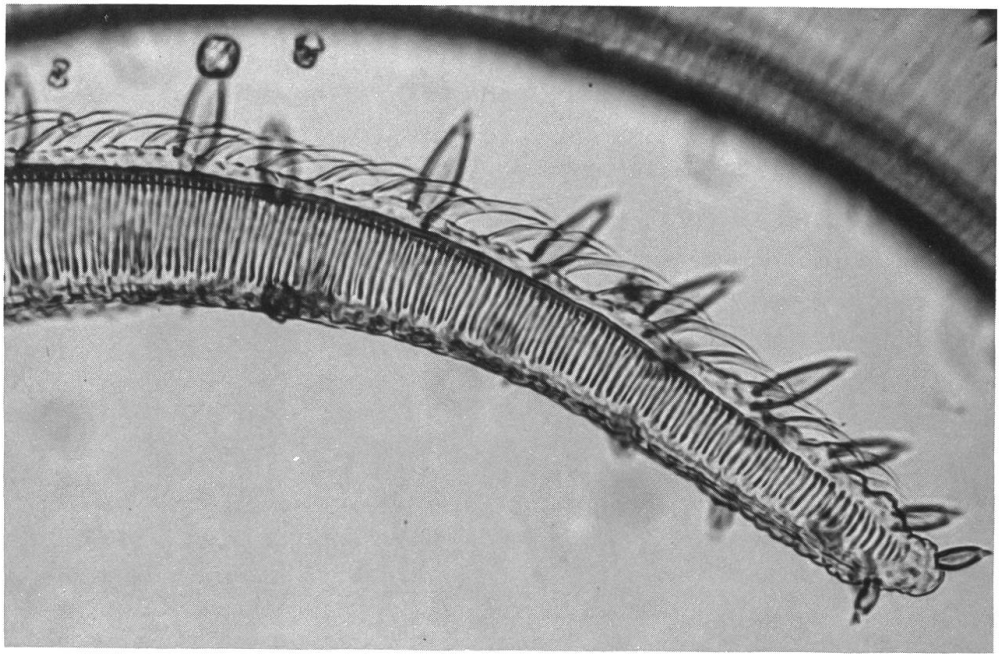


Fig. 2. Proboscis of *Lobocraspis griseifusa*..

Table 1: Families and numbers of species of ophthalmotropic Lepidoptera according to zoogeographical regions (compiled from Büttiker & Nicolet (1975), Büttiker & Büttiker (1988) and Bänziger (1972–1988)).

Regions/ Subregions / Families	Afrotropical		Oriental		Australian		Neotropical
	Africa South of Sahara	Southern Arabian peninsula	Indo-Himalayan Indo-Malaysian	Sumatra	Papua New Guinea	Australia mainlad	South America (Büttiker, in press)
Noctuidae	7	2	4	0	0	0	3
Notodontidae	0	0	11	0	0	0	1
Geometridae	3	1	30	4+	0	0	20
Pyralidae	5	0	19	3+	1 (imported)	0	4
Thyatriridae	0	0	2	0	0	0	0
Sphingidae	(2)*	0	(1)*	0	1	0	1
Total	**15** (+2)*	**3**	**66** (1)*	**7+**	**1**	**0**	**29**

*questionable NB: No recorded eye-frequenters in the Holarctic Region.

Comparative studies on the anatomy, morphology and mechanism of the proboscis of eye-frequenting and fruit-piercing noctuids have been made by BÜTTIKER (1962) and also of skin-piercing blood-sucking species by BÄNZIGER (1970, 1972, 1983, 1986), who have shown that there are considerable morphological differences among the various groups according to their feeding mechanism.

The probosces of eye-frequenting species examined (fig. 2), e.g. *Arcyophora sylvatica* Büttiker and *Lobocraspis griseifusa* Hampson (Noctuidae), have a rough surface which increases the irritation. It was also assumed that the insect is able to take up lachrymation and pus, sometimes erythrocytes from purulent host tissues (BÜTTIKER 1959a, 1962, BÜTTIKER et al. 1996). However, similarly shaped probosces have been found in the related fruit-piercing noctuids, e.g. *Ophiusa (Achea) lienardi* Boisduval, *Serrodes (Ophideres) partita* Fabricius and *Oraesia provocans* Walker. Extremely well developed hooks and spines are present on the proboscis of skin-piercing blood-sucking moths of the genus *Calyptra,* as discovered by BÄNZIGER (e.g. 1968, 1970).

Investigations of stomach swabs and precipitin tests have shown that *Lobocraspis griseifusa* in Cambodia is an occasional blood-feeder on cattle and water buffalo (BÜTTIKER, 1959b; b). Subsequent field obser-

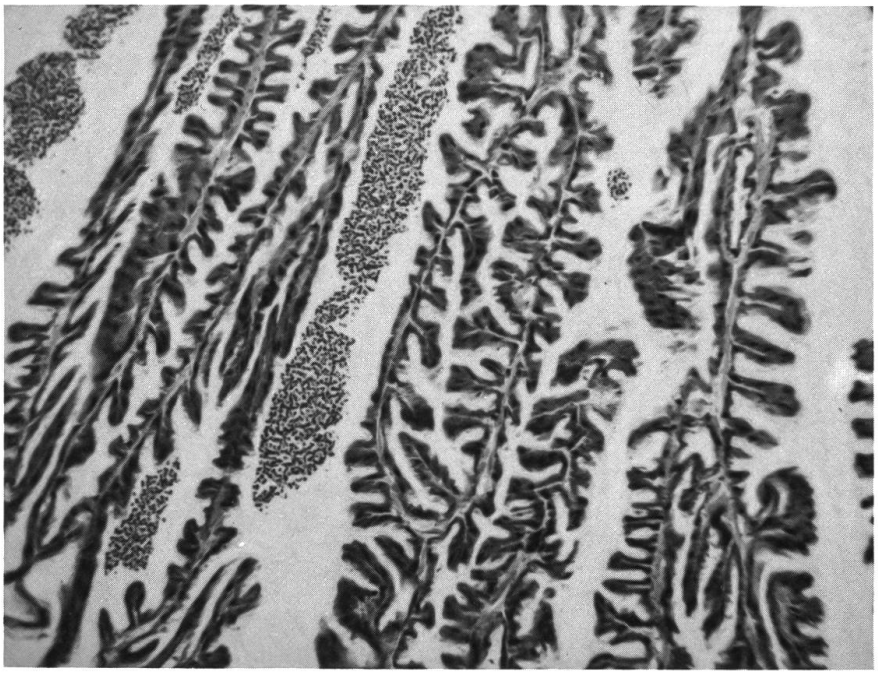


Fig. 3. Cross-section through the midgut of the *eulacryphagous Lobocraspis griseifusa* with midgut (= mesenteron) epithelium, masses of leucocytes and scattered epithelial cells. Chiengmai (N. Thailand), 1963.

vations on ophthalmotropic species by BÄNZIGER (1972) in Thailand and Malaya and later elsewhere produced no evidence of an uptake of blood by an active licking or even skin-piercing action in this species. It is very likely, however, that the specimens investigated by BÜTTIKER in Cambodia imbibed blood from open wounds or purulent, inflamed tissue or even perhaps from droplets of blood excreted by mosquitoes. The latter process of blood uptake has been photographed by BÄNZIGER (1972) for *Pionea damastesalis* Walker. Although investigations on the various possibilities of ''blood-feeding'' by eye-frequenting Lepidoptera are incomplete, there remains no doubt that a considerable amount of lachrymal fluid and pus, the latter mainly consisting of leucocytes, is eagerly ingested by species with strictly eye-frequenting behaviour.

The internal anatomy of adult Lepidoptera of several families has been the subject of various investigations (DAUBERSCHMIDT, 1933; SNODGRASS, 1935; MORTIMER, 1965; SMITH, 1985; KERKUT & GILBERT, 1985; CHAPMAN, 1985; PETERS, 1992), and KRENN (1990) covers the literature on the proboscis. More recently a SEM study on the proboscis of eye-frequenting and piercing Lepidoptera was published (BÜTTIKER et al., 1996).

In higher Lepidoptera the oesophagus is a long tube of very narrow caliber, expanding distally into a crop. In the majority of taxa the crop forms a large food reservoir connected with the anterior intestine by a short narrow duct. The stomach or midgut is usually a straight tube of variable volume, depending on a fed or unfed condition. Little is known about the microscopic anatomy of the midgut of adult Lepidoptera; in the present study the emphasis is on the food content of the midgut, and the presence or absence of symbionts and of the peritrophic membrane. Finally, the hind gut consists of the ileocolon*, a distended chamber or colon, and a short muscular rectum.

The normal amount of time spent feeding at a single eye may vary from five to 20 minutes or more when undisturbed, and many observations indicate that considerable quantities of lachrymation are taken up, as shown by the almost simultaneous and regular flow of droplets of fluid excreted from the anus of the moth.

New contributions on the feeding behaviour and food requirements of Lepidoptera have recently been reviewed by PETERS (1992).

---

* The coiling of this section is not of general occurence even among higher Lepidoptera, but it is pronouced in noctuids (DAUBERSCHMIDT, 1933).

The present study addresses the following problems:

- Is it possible to trace and describe the actual food taken up by the moths in the intestinal canal?
- Which exogenous cell types can be found in the midgut of eye-frequenting Lepidoptera that have fed on the eyes of mammalian hosts?
- What kind of other exogenous elements or organisms (bacteria, pollen) can be traced in any section of the gut in eye-frequenting and other Lepidoptera with special feeding habits?
- Can we identify symbionts in a particular part of the gut?
- What are the special features, if any, of the intestinal tract of eye-frequenting moths compared with nectar-feeding and/or fruit-sucking Lepidoptera, as well as with other insects exhibiting special feeding habits?

Abbreviations used:

Am = amorphous eosinophilic material
Ep = epithelial cell(s) of the host
Er = erythrocyte-like cell
Erd = erythrocyte(s) being digested
Le = leucocyte(s)
Me = mesenteron (midgut) epithelium
Pb = plasmatic ball(s)
Pe = flat epithelial cell of the host
Pm = peritrophic membrane
Po = pollen

2. Material and methods

Microtome sections of *Lobocraspis griseifusa* were studied earlier, but the results were not published except for an illustration (fig. 3) in BÜTTIKER (1970b). As an additional element of the field and laboratory studies, it was decided in 1963 to collect fixed material during expeditions in Asia and Africa for the eventual preparation of series of microtome sections of several species belonging to groups with different feeding behaviour.

All the specimens examined are listed in table 2. The moths were fixed either in Carnoy's fluid or in Helly's fixation fluid, dehydrated in ethyl alcohol and embedded in paraffin. Serial sections were cut at a thickness of 4 to 8 µm and using approximately every thirtieth section. In most cases the moths were cut along the longitudinal axis, but some transverse sections were made as well. The following histological stains were used: Mayer's heamalaun-eosin or Boehmer's heaematoxy-

lin-orange G as a general stain, PAS to visualize mucopolysaccharides, Feulgen's stain for the detection of nucleic acids, and a combined May-Grünwald method to demonstrate the blood cells. In some cases, the contents of the midgut* of the moths and of the conjunctival sac of the host animals were studied by means of swabs. For this purpose, the combined May-Grünwald stain and the haemalaun-eosin stain were used. In addition to the qualitative examination of the cell shape and its staining reactions, a quantitative evaluation was also made. The size measurements were made from on enlarged photographs. This study confirmed the considerable effect of the histological processing of the preparations on the size parameters of the cells: generally the samples embedded in paraffin exhibited shrinkage, i.e. the cells were smaller compared with those from swab preparations (tables 3 and 4). The cell size figures given in this report are therefore only rough estimates.

Caution also needs to be exercised when estimating relative midgut volumes and performing differential cell counts in the same species. The relative midgut volume was defined as the proportion of the midgut volume to the total volume of the abdomen. To estimate this volume, the histological sections were projected at a scale 1:10, the outlines of the midgut and of the abdomen were drawn and cut out of sheets of paper. These paper cuttings were then weighed on an analytical balance and the relation of their weights was taken as the relation of the midgut/abdomen volumes. The results of this are summarised in table 5. Specimens of each group with the largest midguts were selected for measurement.

---

* The expression ''midgut'' is used here in the sense of the *mesenteron* of SNODGRASSS (1935) and therefore describes the ''stomach'' of the moths.

Table 2: Data for the specimens examined

A. Lepidoptera used for microtome sections

Species	Place of collection	Country	Year	Host
1. Nectar-feeding Lepidoptera				
Noctua pronuba Linné (Noctuidae)	Magden	Switzerland	15.8.1973	*Buddleja davidii* (flower)
Autographa gamma Linné	Magden	Switzerland	15.8.1973	*Buddleja davidii* (flower)
2. Fruit-sucking Noctuidae				
Scolyopteryx libatrix Linné	Magden	Switzerland	4.7.1973	*Rubus idaeus* (fruit)
3. Eye-frequenting moths 3.1. – Noctuidae				
Arcyophora particula Hmps.	Aboukouamékro Bouaké Wararíene	Ivory Coast Ivory Coast Ivory Coast	1970 1970 1972	Cattle Cattle Cattle
Arcyophora longivalvis Gn.	Aboukouamékro Bouaké Wararíene	Ivory Coast Ivory Coast Ivory Coast	1970 1970 1972	Cattle Cattle Cattle
Arcyophora sylvatica Bütt.	Chiengmai	Thailand	1963	Water Buffalo
Arcyophora zanderi Feld.	Taouara Bouaké	Ivory Coast Ivory Coast	1970 1970	Cattle Cattle
Lobocraspis griseifusa Hmps.	Chiengmai	Thailand	1963	Cattle

3.2 Pyralidae

Pionea damastesalis Wlk.	Chiengmai	Thailand	1963	Cattle

3.3 Suspected eye-frequenting Sphingidae

Nephele peneus Cr.	Tauara	Ivory Coast	1970	near Cattle
Nephele comma Hpffr.	Bouaké	Ivory Coast	1970	near Cattle

4. Sweat-feeding Noctuidae

Hypocala rostrata Fabr.	Taouara	Ivory Coast	1970	Man (arm)
	Bouaké	Ivory Coast	1970	Man (arm)

5. Blood-sucking Tabanidae (Diptera)

Haematopota pluvialis L.	Magden	Switzerland	15.8.1973	Man (arm)

B. Eye surface swabs from mammalian hosts
Swabs from the purulent eye surfaces of cattle for microscopic examination were taken in India in 1966, and in the Ivory Coast in 1972.

C. Swabs of the midgut content of eye-frequenting moths
From *Arcyophora patricula* collected from cattle at Karakoro, Ivory Coast in 1972.

Table 3: Size diferences of albino rat leucocytes caused by different methods of histological preparation.

Preparation	Average diameter of the leucocytes (μm)*
Microtome section (paraffin embedding)	4.9 ± 1.0
Smear (no embedding)	11.4 ± 2.5

* This estimate was made by measuring 20 neutropic granulocytes each on one histological section and one smear preparation.

Table 4: Size differences in leucocytes and flat epithelial cells observed on histological sections and swab preparations from the midgut of *Arcyophora longivalvis*. (Karakoro, Ivory Coast, 1972).

Preparation	Average diameter (μm)	
	leucocytes	flat epithelial cells*
Microtome section (paraffin embedding)	5.4 ± 0.1	16.5 ± 7.7
Swab (no embedding)	9.9 ± 2.2	33.9 ± 15.1

* 20 cells of each kind were measured in one histological section and one swab preparation.

Table 5: Relative volume of midgut in relation to total volume of adomen.

Category	Species	Relation of midgut volume to total volume of abdomen
Nectar-feeding moths	*Noctua pronuba* *Autographa gamma*	4.8 3.4
Fruit-sucking moth	*Scolyopteryx libatrix*	1.1
Sweat-feeding moth	*Hypocala rostrata*	1.7 ± 0.2
Eulachryphagous eye-frequenters	*Arcyophora patricula*	27.4 ± 7.1
	Arcyophora longivalvis	41.6 ± 2.7
	Arcyophora sylvatica	10.5
	Arcyophora zanderi	33.7 ± 14.0
	Lobocraspis griseifusa	22.4
Hemilachryphagous eye-frequenter	*Pionea damastesalis*	2.9
Suspected eye-frequenter	*Nephele peneus*	2.9 ± 0.3
Blood-feeder	*Haematopota pluvialis,* unfed *Haematopota pluvialis,* fed	3.2 30.4

3. Results

Table 6 shows the figures obtained from differential cell counts of the midgut contents of several species. The figures express the relative numbers of different cell types observed in three fields of view with a light microscope at a magnification of × 1000. In addition to these overall results detailed observations from each single species are given as follows:

Table 6: Number and percentage of the cells in mid-gut microtome sections of some eulachryphagous noctuids.

Species	Cell group Number and %	Number of cells/3 fields (10 × /100 ×)		
		Epithelial cells	Lymphocytes	Granulocytes and leucocytes*
Aryophora patricula (n = 9)	Total percentage	184 35.3 %	40 7.7 %	298 57.0 %
Arycyophora longivalvis (n = 3)	Total percentage	49 30.1 %	16 9.8 %	98 60.1 %
Arcyophora zanderi (n = 2)	Total percentage	90 43.7 %	9 4.4 %	107 51.9 %

* cell fragments difficult to identify are included here

3.1. Nectar-feeding Noctuidae

In *Noctua pronuba* Linnaeus, the relative midgut volume is 4.8 % of the volume of the entire abdomen, and the midgut wall is partly slightly stretched and partly folded. The epithelium is flattened in the stretched areas and columnar in the folded areas. The midgut content consists of several pollen grains (i.e. from *Buddleja davidii* (Buddlejaceae), an ornamental bush where the moths were feeding), occasional plasmatic balls and some amorphous eosinophilic material. There is no peritrophic membrane.

In *Autographa gamma* Linnaeus, the relative midgut volume is 3,4 %, and the midgut wall is folded and consists of a columnar epithelium. In the midgut there is little amorphous eosinophilic material, and a few plasmatic balls. No peritrophic membrane is present. A detailed description of the midgut was given by MORTIMER (1965).

3.2. Sweat-feeding Noctuidae Fig. 17.

Hypocala rostrata Fabricius has a relative midgut volume of about 2 %. The midgut wall is folded and consists of a columnar epithelium. Microscopic examination of the midgut contents showed only some amorphous eosinophilic material and several plasmatic balls. No peritrophic membrane is seen.

3.3. Fruit-sucking Noctuidae

In *Scolyopteryx libatrix* Linnaeus, the relative midgut volume is about 1,1 %, and the midgut wall is folded and covered with a columnar epithelium. The midgut content consists of a minute amount of an amorphous eosinophilic material. No peritrophic membrane is evident.

3.4. Eulachryphagous eye-frequenting Noctuidae

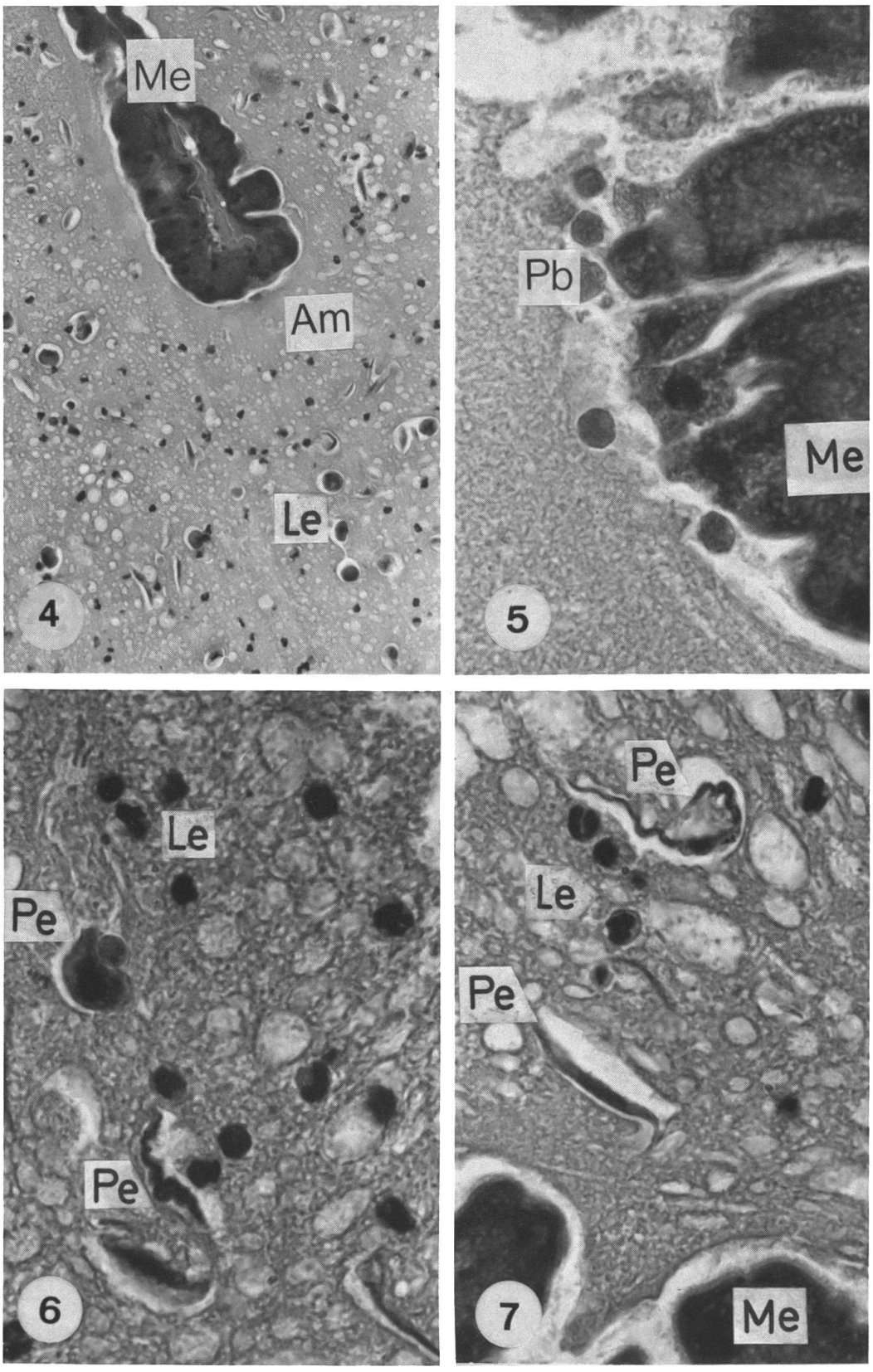
Arcyophora patricula Hampson, *A. longivalvis* Guénée, *A. sylvatica* Büttiker, *A. zanderi* Felder, and *Lobocraspis griseifusa* Hampson all have relative midgut volumes from 10 to 40 %. Microscopic examination revealed some food in each midgut. The folding and the thickness of the midgut wall corresponded to the amount of food present. In full midguts the wall was stretched and its epithelial layer flattened, whereas midguts containing little food had a folded wall composed of high columnar epithelial cells. In no case could a peritrophic membrane be seen. In specimens of the African species, microscopic examination of the midgut content revealed single cells or small groups of cells scattered within an eosinophilic amorphous material (fig. 4). The following cell types could be discerned: ephithelium cells, leucocytes, and round fragments of cytoplasma from the midgut wall epithelium (the so–called ''plasmatic balls'') (fig. 5). Apart from these structures there were also some unidentifiable cell fragments. The flat epithelial cells were

Fig. 4. *Arcyophora longivalvis* (No 1/1972). Ivory Coast; paraffin, haemalaun-eosin, 250 ×. The midgut content consists of cells (leucocytes, Le) loosely scattered within an eosinophilic mass.

Fig. 5. *Arcyophora longivalvis* (No 1/1972). Ivory Coast; paraffin, haemalaun-eosin, 1000 ×. Some plasmatic balls (Pb) are near the epithelial cells of the midgut wall (Me).

Fig. 6. *Arcyophora longivalvis,* (No 1/1972). Ivory Coast; paraffin, haemalaun-eosin, 1000 ×. Composition of the midgut contents: flat epithelial cell (Pe), leucocytes (Le).

Fig. 7. *Arcyophora longivalvis* (No 1/1972). Ivory Coast; paraffin, haemalaun-eosin, 1000 ×. Flat epithelium (Pe), leucocytes (Le), epithelial cell of the midgut wall (Me).


Me
Am
Le
4
Pb
Me
5
Le
Pe
Pe
6
Pe
Le
Pe
7
Me

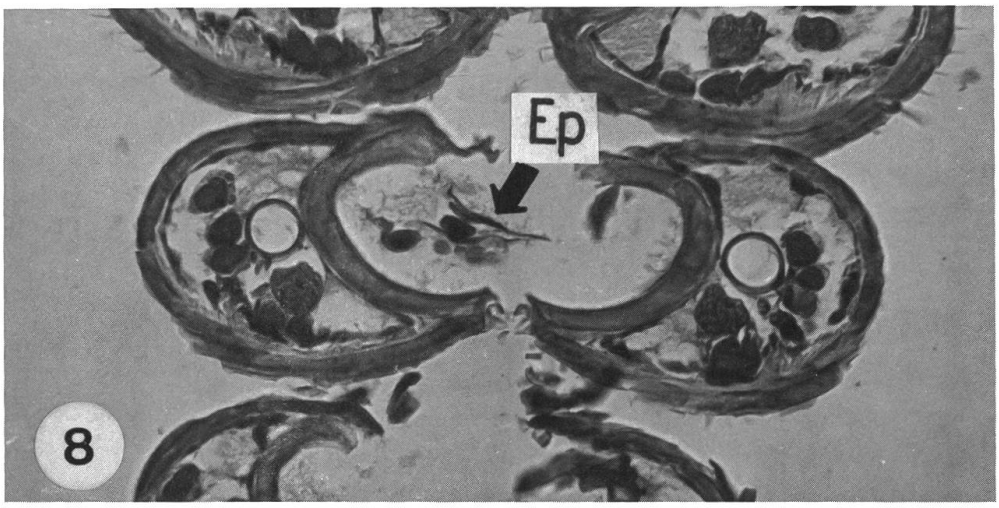


Fig. 8. *Arcyophora longivalvis* (No 6/1972). Ivory Coast; paraffin, haemalaun-eosin, 250 ×. Cross-section of the proboscis with epithelial cells (Ep with arrow).

sectioned parallel to their surface or across it. They therefore appeared in some instances as large flat discs, whereas in others narrow long stripes were seen (figs 6 and 7). Within the group of leucocytes there were mainly older phagocyting granulocytes, some younger forms of granulocytes (with non-segmented nuclei), and some lymphocytes (figs 7 and 8). The differential cell counts showed that in the samples of African species the propotion of granulocytes (plus some unidentifiable cell fragments) was about 50 to 60 %, whereas the epithelial cells made up some 30 to 40 % (table 6). These figures are an average taken from several specimens.

The flat epithelial cells were not only found in the midgut. They were also seen in transverse sections of the proboscis. They are therefore considered to be an exogenous component of the midgut content ingested with the food (figs 8 and 9).

An examination of the midgut content of *Arcyophora sylvatica* and *Lobocraspis griseifusa* generally showed a much higher cell density than the African eye-frequenting species. The most frequent cell type in the Asian specimens were the leucocytes. Epithelial cells of the host were found only very rarely (figs 10 and 11).

A comparison of histological sections of the midgut content of eye-frequenting Noctuidae with swab preparations from the eye of the host animals shows that the same cell types are present in both. The flat epithelium seems to be identical with the superficial layer of the conjunctival epithelium and the leucocytes clearly form part of the inflammatory exudate of the eye, including the conjunctival sac. Examination

of the swab preparations of the eye exudate of host animals confirmed the difference between the African material on the one hand and the Asiatic material on the other, which had previously been observed in the midgut sections. In the Asiatic eye-swab there were (as in the Asiatic midgut sections) many leucocytes and only very few epithelial cells (fig. 14). On the other hand, the African eye-swabs showed scattered leucocytes and rather frequently epithelial cells too (fig. 13). This compared well with the findings in the African midgut sections. Finally, an

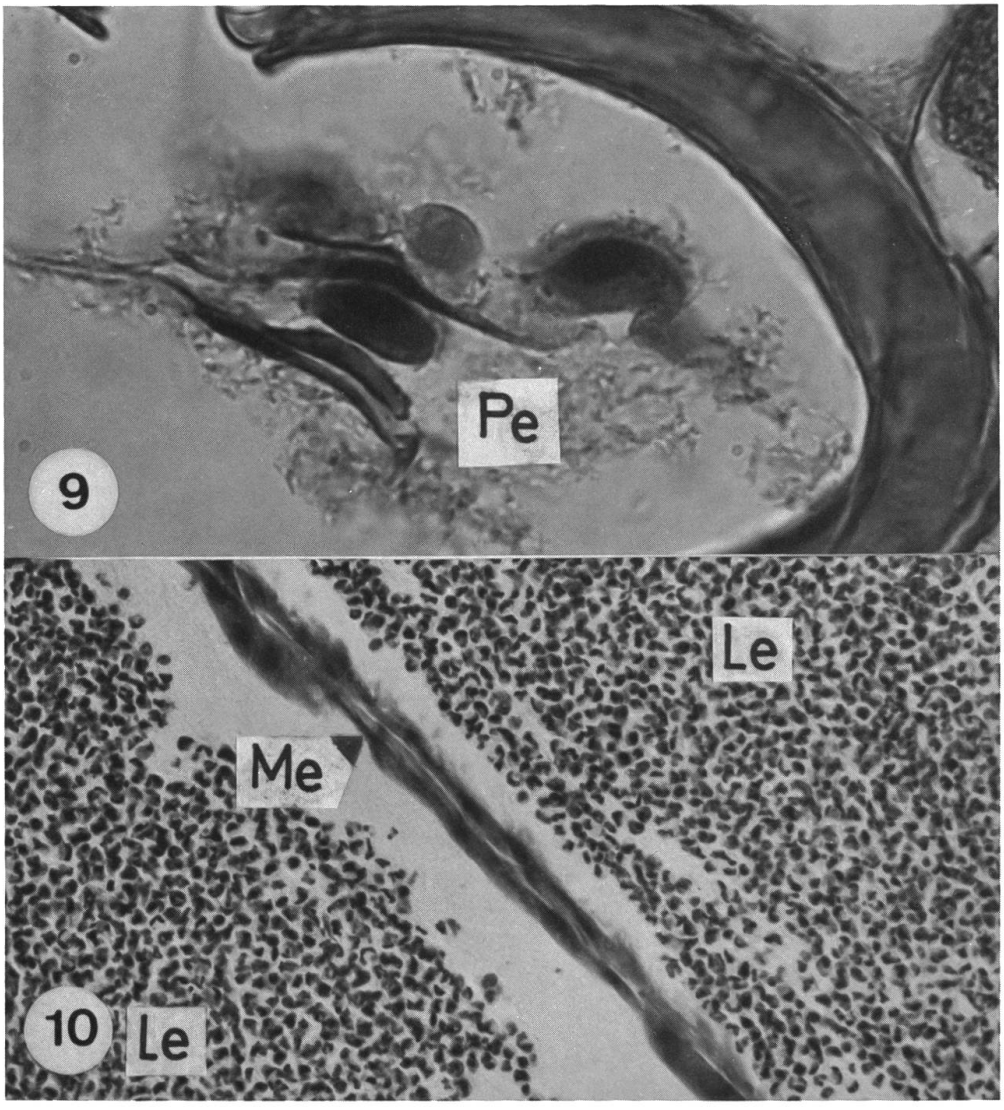
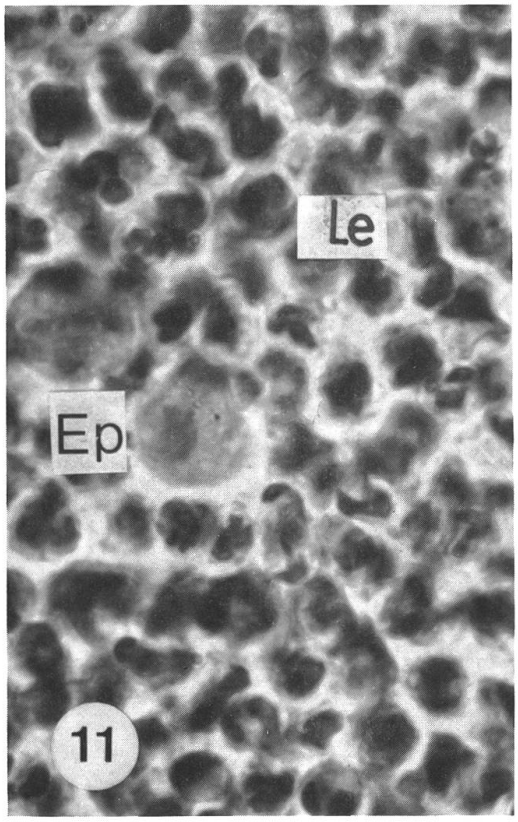
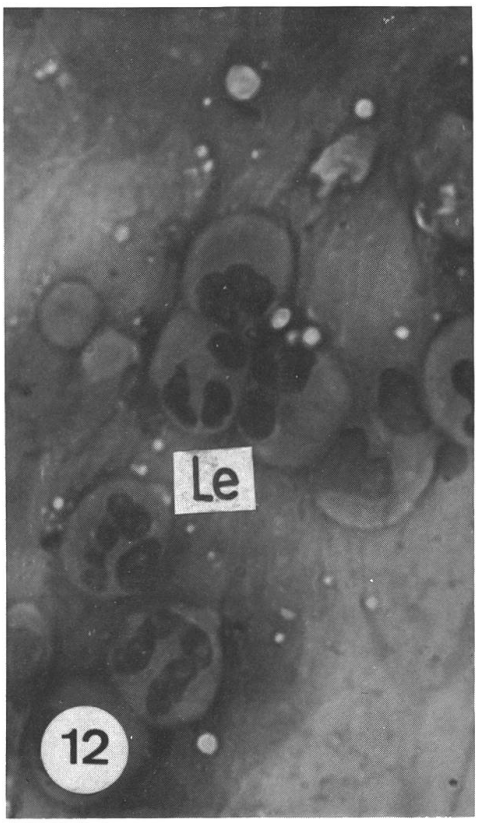
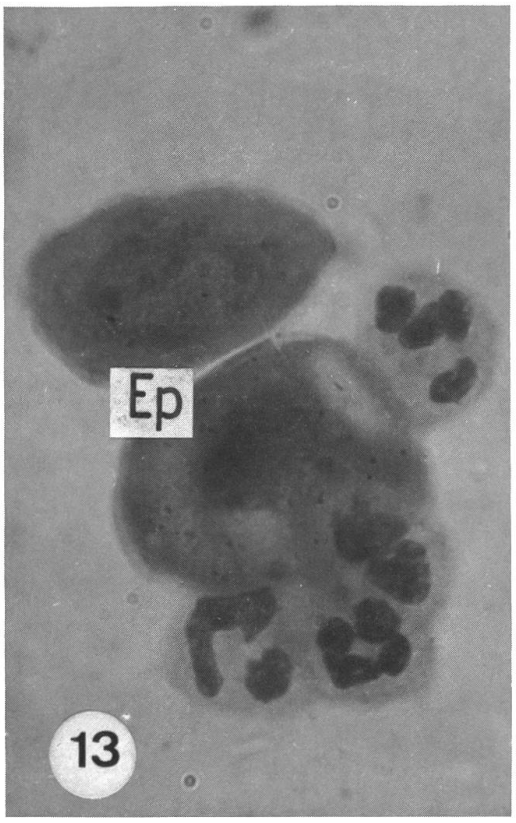
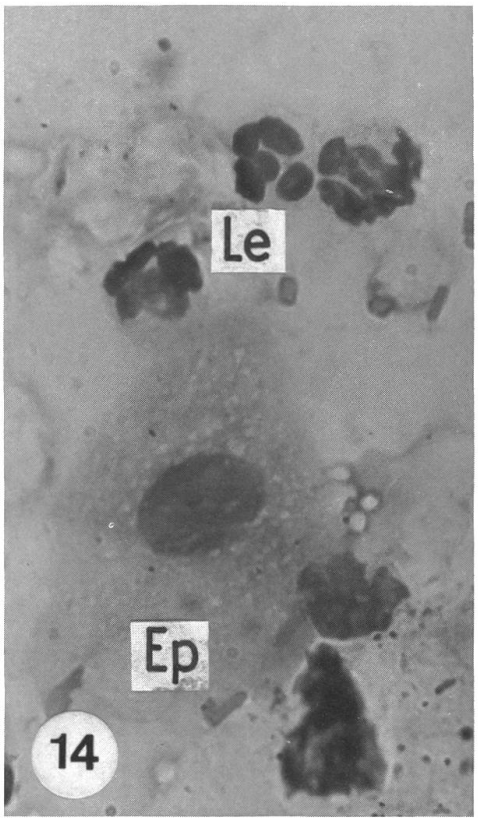


Fig. 9. *Arcyophora longivalvis* (No 6/1972). Ivory Coast; paraffin, haemalaun-eosin, 1000×. Cross-section of the proboscis with epithelial cells (Pe).
Fig. 10. *Lobocrospis griseifusa* (F 69/1963). Thailand; paraffin, haematoxylin-orange G, 250×. The content of the midgut consists mainly of leucocytes (Le). Midgut wall epithelium (Me).


Le
Ep
11


Le
12


Ep
13


Le
Ep
14

examination of swab preparations of the midgut of eye-frequenting Noctuidae confirmed once again that the midgut content was identical with the content of the conjunctival sac or the smears taken from the eye-surface of the host animals (fig. 14).

3.5. Hemilachryphagous eye–frequenting Pyralidae

In *Pionea damastesalis* Walker, the relative midgut volume of one available specimen was 2,9 %. The midgut wall was folded and its epithelium was columnar in shape. Microscopic examination of the midgut sections showed a small amount of an amorphous acidophilic material and several round bodies with an average diameter of 14,1 µm, representing plasmatic balls. No peritrophic membrane could be seen.

3.6. Suspected eye-frequenting Sphingidae

In *Nephele peneus* Cramer and *N. comma* Hopffer, the midgut volume of the specimens examined was approximately 3 %. The midgut wall was folded and equipped with a columnar epithelium. The midgut contained a small amount of an amorphous eosinophilic material and several round bodies with an average diameter of 14,5 µm. Some of them resembled erythrocytes, as they were flattened centrally, but they were too large for erythrocytes (fig. 15). They stained negatively with PAS and Feulgen, and were slightly eosinophilic. They therefore are considered to be plasmatic balls. No peritrophic membrane was found.

3.5. Blood–sucking Tabanidae (Diptera)

Two specimens of *Haematopota pluvialis* Linnaeus were examined: one was unfed and the other was fed with human blood. Both specimens were fixed and embedded in identical fashion for complete com-

Fig. 11. *Lobocrospis griseifusa* (F 69/1963). Thailand; paraffin, haematoxylin-orange G, 1000 ×. The midgut content consists of many densely-packed leucocytes (Le) and some epithelial cells (Ep).
Fig. 12. Eye–swab from domestic cattle. Mudumalai, India 1966. Combined May-Grünwald, 1000 ×. Mainly leucocytes (Le) are present on the slide.
Fig. 13. Eye-swab from domestic cattle. Bouaké, Ivory Coast 1972. Combined May-Grünwald, 1000 ×. Leucocytes and epithelial cells (Ep).
Fig. 14. Midgut-swab from *Arcyophora patricula* (Karakoro No 1). Ivory Coast 1972. Combined May-Grünwald, 1000 ×. Leucocytes (Le) and an epithelial cell (Ep).

parability. The time period between feeding and fixing the blood–fed specimen was 30 minutes. Microscopic examination gave the following results:

– *unfed specimen:*

The relative midgut volume is estimated as 3,2 %; the midgut wall is highly folded and consists of a columnar epithelium. In the midgut there is only a small amount of the amorphous eosinophilic material and several plasmatic balls. No peritrophic membrane is present (fig. 18).

– *fed specimen*:

The relative midgut volume is about 30,4 %; the midgut wall is stretched and its epithelial layer flattened. In the midgut there are large numbers of erythrocytes densely packed together, and a few random scattered leucocytes. This food package is enveloped in a continuous eosinophilic peritrophic membrane. Between this peritrophic membrane and the midgut wall there is a marginal zone of less densely arranged blood cells (fig. 19), disintegrating due to digestion.

The results of this section are summarised in table 7, which is also an easy form of reference for the next section.

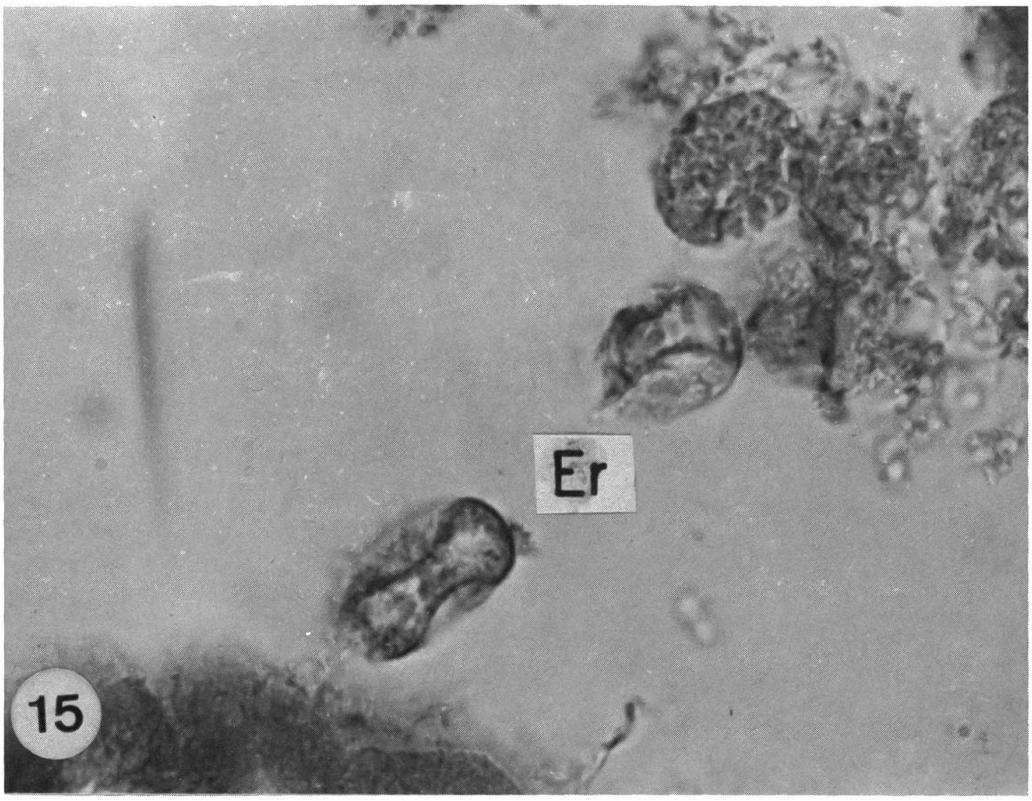
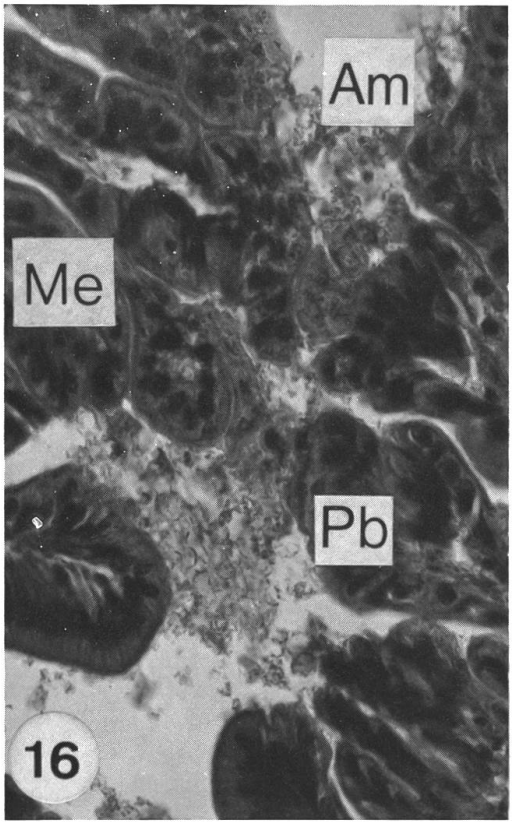


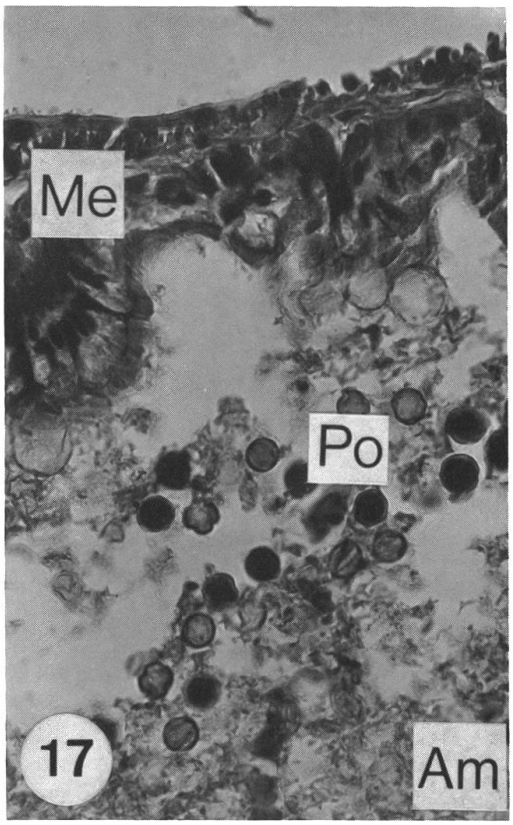
Fig. 15. *Nephele comma,* (No 26/1970). Ivory Coast; paraffin, haemalaun–eosin, 1000 ×. Midgut section with some erythrocyte-like plasmatic balls (Er).

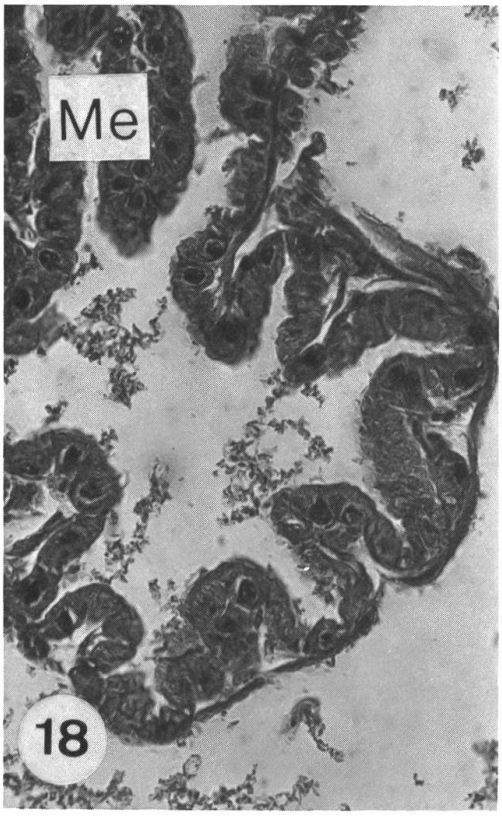
Table 7. Midgut content of different lepidopteran groups compared with one blood-sucking tabanid (Diptera).

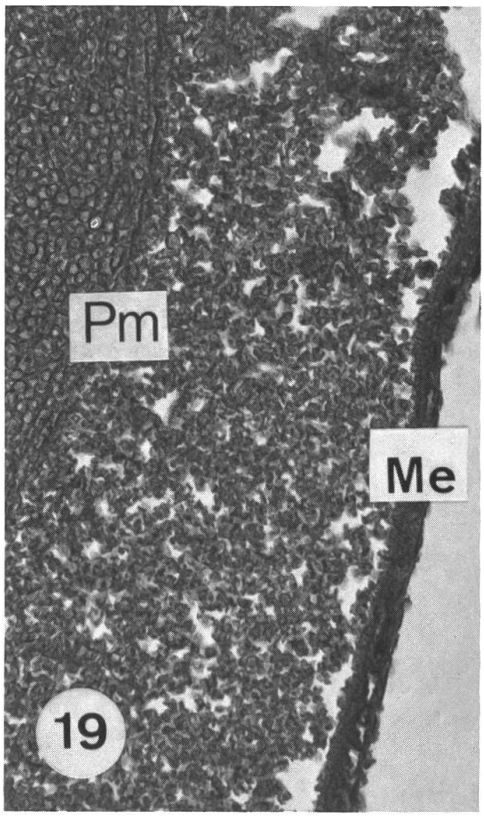
Group of Lepidoptera/Diptera	Midgut content Species	Pollen	Epithelium cells	Leucocytes & granulocytes	Lympho-cytes*	Plasmatic balls**
1. Nectar-feeding moths	*Noctua pronuba*	+	○	○	○	+
	Autographa gamma	○	○	○	○	+
2. Sweat-imbibing moth	*Hypocala rostrata*	○	○	○	○	+
3. Fruit-piercing moth	*Scoliopteryx libatrix*	○	○	○	○	+
4. Eye-frequenting/ophthalmotropic moths						
– Eulachryphagous	*Arcyophora longivalvis*	○	+	++	+	+
	Arcyophora patricula	○	+	++	+	+
	Arcyophora sylvatica	○	++	+++++	+	+
	Arcyophora zanderi	○	+	++	+	+
– Hemilachryphagous	*Pionea damastesalis*	+	+	+++	+	+
– Uncertain eye-frequenters	*Nephele peneus*	○	○?	"Erthrocyte-	○	+
	Nephele comma	○	○?	like cells"	○	+
5. Skin-piercing blood-sucking Diptera – Tabanidae	*Haematopota pluvialis*					
	=fed specimen	○	○	+++++	+	+
	=unfed specimen	○	○	○	○	○

Legend: ○=absent ++ =few ++++ =abundant p=present
+=very few +++=fairly abundant +++++=very abundant
* see also table 6 ** fragments of cytoplasma of the midgut wall epithelium
Symbiontic micro-organisms are absent in all samples, and the peritrophic membrane is present only in fed *H. pluvialis*.


Am
Me
Pb
16


Me
Po
17
Am


Me
18


Pm
Me
19

4. Conclusions

This investigation has shown that food can be traced in the intestinal tract of moths. The degree of filling of the midgut with food was indicated by relative midgut volumes. The relative volume of an empty midgut proved to be about the same in all cases observed, viz. some 2 to 3 % of the abdominal volume. An increase in the relative midgut volume above this level is attributed to the intake of food. This was confirmed by observations on *Haematopota pluvialis,* where there was a tenfold difference in the midgut volume due to blood intake. The stretching of the midgut wall and flattening of its epithelial layer accompanied the increase in midgut volume, whereas in empty midguts the walls were highly folded and the epithelia columnar in form.

Certain specimens had relatively small midguts, containing only some plasmatic balls: *Pionea damastesalis* (Pyralidae), *Nephele peneus* and *N. comma* (Sphingidae), the sweat-feeding *Hypocala rostrata* (Noctuidae), the nectar-feeding *Autographa gamma* (Noctuidae), the fruit-piercing *Scolyopteryx libatrix* (Noctuidae), and also the unfed *Haematopota pluvialis* (Tabanidae, Diptera). All these specimens were evidently collected when starved.

According to SNODGRASS (1935), plasmatic balls appear before the intake of food and in starving insects they may occur in very large numbers. They are ''light-microscopic formations'', i.e. they were discovered and described under the light microscope following previous histological processing of the material. In the present study we were able to distinguish them clearly from other structures.

Fig. 16. *Hypocala rostrata* (No 25/1970). Ivory Coast; paraffin, haemalaun–eosin, 400 ×. Amorphous eosinophilic material (Am) and plasmatic ball (Pb) in the midgut. No peritrophic membrane.

Fig. 17. *Noctua pronuba* (a/1973). Magden, Switzerland; paraffin, haemalaun–eosin, 400 ×. Pollen (Po) of Buddleja davidii in the midgut.

Fig. 18. *Haematopota pluvialis* (15.8.1973). Magden, Switzerland; paraffin, haemalaun-eosin, 400 ×, unfed. Folded midgut wall (Me) and columnar epithelium.

Fig. 19. *Haematopota pluvialis* (15.8.1973). Magden, Switzerland; paraffin, haemalaun-eosin, 1000 ×, blood-fed. Extended wall of midgut, flattened epithelial layer (Me) and peritrophic membrane (Pm). Within the envelope formed by the peritrophic membrane the blood cells are morphologically intact. The blood-cells between the epithelium (Me) and peritrophic membrane (Pm) are being digested and have already been altered morphologically. The specimen was fixed about 30 minutes after the blood meal.

In several species a qualitative and a near-quantitative analysis of food the composition was carried out and correlations with known feeding behaviour were established. It has been shown that eye–frequenting species also imbibe leucocytes and epithelial cells with lachrymation. Specimens of the African eye-frequenting species showed cells rather loosely scattered within the midgut, whereas the Asian specimens had their midguts virtually stuffed with them. It is evident that *Arcyophora sylvatica* agrees more with *Lobocraspis gri- seifusa* in this respect than with the African *Arcyophora* species. It must also be borne in mind that the midgut acts as a filtration appa- ratus in which cells and probably protein coagulates are retained for digestion.

A peritrophic membrane is known to occur in blood-feeding insects. Although it has also been studied by electron microscopy (PETERS, 1992), its fine structural significance is still uncertain. We found a peritrophic membrane only in the midgut of the blood–fed tabanid specimen. Neither in the unfed tabanid nor in any of the fed and unfed Lepidoptera was this particular membrane found. Furthermore, no trace of symbiotic micro-organisms was noted in any lepidopterous species. However, a preliminary microbiological study carried out in parallel on several eye-frequenting species (NICOLET & BÜTTIKER, 1975) isolated various germs from the proboscis, the midgut and other parts of the body. More recent data on the possible transmission of eye and other diseases have been published by GOUWS et al. (1995).

5. Acknowledgements

The author is very grateful to Prof. Dr. J. Nicolet, Berne, for the loan of slides prepared during an expedition to the Ivory Coast in 1972; to Dr. G. Krinke and Mr. A. Schöpfer, Ciba-Geigy Ltd., Basle, for technical assistance and help in the interpretation of the haematological findings; to Dr. W. Rudin, Basle and Dr. N.P. Kristensen, Copenhagen and Dr. A. Pont, London, for reading the manuscript and for valuable comments.

7. References

BÄNZIGER, H., (1968): *Preliminary observations on skin-piercing blood-sucking moth (Calyptra eustrigata (Hmps.) (Lep., Noctuidae) in Malaya.* Bull. Ent. Res. *58(1):* 159–163.

BÄNZIGER, H. (1969): *Erste Beobachtungen über fürchtestechende Noctuiden in Europa.* Mitt. Schweiz. Ent. Ges. *42(1/2):* 1–10.

BÄNZIGER, H. (1970): *The piercing mechanism of the fruit-piercing moth Calpe (Calyptra) thalictri Bkh. (Noctuidae) with reference to the skin-piercing blood-sucking moth C. eustrigata Hmps.* Acta Trop. *27(1):* 54–88.

BÄNZIGER, H. (1972): *Biologie der lacriphagen Lepidopteren in Thailand und Malaya.* Revue suisse Zool., *79(4):* 1381–1469.

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

BÄNZIGER, H. (1983): *A taxonomic revision of the fruit-piercing and blood-sucking moths genus Calyptra Ochsenheimer [= Calpe Treitschke] (Lepidoptera: Noctuidae).* Ent. Scand. *14:* 467–491.

BÄNZIGER, H. (1986): *Skin-piercing blood-sucking moths IV: Biological studies on adults of 4 Calyptra species and 2 subspecies (Lep., Noctuidae).* Mitt. Schweiz. Ent. Ges. *59:* 111–118.

BÄNZIGER, H. & BÜTTIKER, W. (1969): *Records of eye-frequenting Lepidoptera from Man.* J. Med. Ent., *6(1):* 53–58.

BÜTTIKER, W. (1959a): *Blood-feeding habits of adult Noctuidae (Lepidoptera) in Cambodia.* Nature, *184:* 1167.

BÜTTIKER, W. (1959b). *Observations on feeding habits of adult Westermanniinae (Lepid., Noctuidae) in Cambodia.* Acta Trop., *16(4):* 356–361.

BÜTTIKER, W. (1962): *Biological and morphological notes on the fruit-piercing and eye-frequenting moths.* Proc. XI. Int. Congr. Ent. Vienna, 1960, *2:* 10–15.

BÜTTIKER, W. (1964): *New observations on eye-frequenting Lepidoptera from S.E. Asia.* Verhandl. Naturf. Ges. Basel, *75(2):* 231–236.

BÜTTIKER, W. (1967): *Biological notes on eye-frequenting moths from N. Thailand.* Mitt. Schweiz. Ent. Ges. *39(3/4):* 151–179.

BÜTTIKER, W. (1970a): *Erste Beobachtungen an früchtestechenden Noctuiden in Jugoslawien.* Mitt. Schweiz. Ent. Ges. *53(1):* 47–55.

BÜTTIKER, W. (1970b): *Strange parasites of the eye.* Ciba Symposium. *17:* 22–29.

BÜTTIKER, W. (1973): *Vorläufige Beobachtungen an augenbesuchenden Schmetterlingen in der Elfenbeinküste.* Revue suisse Zool. *80(1):* 1–43.

BÜTTIKER, W. & NICOLET, Y. (1975): *Observations complémentaires sur les lépidoptères opthalomotropes en Afrique occidentale.* Rev. Elev. Méd. vét. Pays trop. *28(3):* 319–329

BÜTTIKER, W. (in press): *Field observations on ophthalmotropic Lepidoptera in Brazil.* Rev. suisse Zool.

BÜTTIKER W. & BÜTTIKER, S. (1988): *Further observations on ophthalmotropic Lepidoptera from Oman.* J. Oman Stud., Special Report *3:* 317–320.

BÜTTIKER, W., KRENN, H. & PUTTERILL, J. (1996): *The proboscis of eye-frequenting and piercing Lepidoptera (Insecta).* Zoomorphology *116:* 77–83.

CHAPMAN, R.F. (1985): *Structure of the digestive system.* Pp. 165–212, in: KERKUT, G.A. & GILBERT, L.I. (eds.), *Comprehensive insect physiology, biochemistry and pharmacology.* Vol. 4. Pergamon Press, Oxford.

DAUBERSCHMIDT, K. (1933): *Vergleichende Morphologie des Lepidopterendarmes und seiner Anhänge.* Z. angew. Ent. *20:* 204–267.

GOUWS, J.J., COETZER, J.A.W., HOWELL, P.G. (1995): *A comparative microbiological study of Clinically healthy eyes and those affected by ophthalmia in cattle and the association of noctuid eye-frequenting moths.* Jl. S. Afr. vet. Ass. *66(3):* 160–169.

KERKUT, G.A. & GILBERT, L.I. (1985): *Comprehensive insect physiology, biochemistry and pharmacology.* Vol. *4.* Pergamon Press, Oxford.

KRENN, A.W. (1990): *Functional morphology and movements of the proboscis of Lepidoptera (Insecta).* Zoomorphology *110:* 105–114.

MORTIMER, T.J. (1965): *The alimentary canals of some adult Lepidoptera and Trichoptera.* Trans. R. ent. Soc. Lond. *117(3):* 67–94.

NICOLET J. & BÜTTIKER W. (1975): *Observations sur la kératonjonctivite infectieuse du bovin en Côte d'Ivoire. 1. Aspects microbiologiques.* Rev. Elev. Méd. vét. Pays trop. *28(2):* 115–124.

PETERS W. (1992): *Peritrophic Membranes.* Springer, Berlin. 238pp.

SMITH J.J.B. (1985): *Feeding mechanism.* Pp. 33–85, in: KERKUT G.A. & GILBERT L.I., (eds.), *Comprehensive insect physiology, biochemistry and pharmacology.* Vol. *4.* Pergamon Press, Oxford.

SNODGRASS R.E. (1935): *Principles of insect morphology.* McGraw–Hill, New York & London.

Author's address:
Prof. Dr. W. Büttiker
Lanzenberg 21
CH–4312 Magden