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## Investigations on the Anatomy and the Behaviour of the Fur Mite *Listrophorus leuckarti* (Acari: Listrophoridae)

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With 77 figures and 1 table

### Summary

1.) The internal and external anatomy of *Listrophorus leuckarti* Pagenstecher, 1861 was investigated by means of light and electron microscopy. Observations on movement patterns and behaviour were carried out to supplement and verify the anatomical findings.

2.) For description of the body architecture the pneu concept by OTTO (1984) was used. A pneu is considered a natural or artificial structure consisting of a flexible layer encasing a pressurized filling. It is analyzed in which way this principle causes or influences construction and function of particular organs (chapter 5.).

3.) The body musculature is described in detail and its functional roles are discussed (6.).

4.) The supracoxal glands consist of seven cells each, which are connected by a branched afferent duct. At their proximal ends each branch is closed by a porous cap. In their ultrastructure these cells display numerous mitochondria and an extensive network of membrane plications. The element microanalysis of the crystallized gland secretions revealed a high amount of potassium and chlorine. As for the function of the gland cells it is suggested that potassium is pumped into the cytosol along the membranes of the foldings. The cytosol is filtered through the cap and released to the outside. This leads to the conclusion that the supracoxal glands, besides their role as salivary glands, serve for taking up water from the ambient air osmotically as proved for other astigmatic mites (WHARTON & FURUMIZO 1977). The genital papillae are strongly reduced. Their participation in water uptake is very unlikely (7.).

5.) The arrangement of the legs and the different kinds and orientation of the leg joints are described in general (8.1.). The locomotory apparatus of *L. leuckarti* shows strong alterations and reductions. In all legs two segments (legs I and II: tibia and tarsus; legs III and IV: femur and genu) are fused. This can be explained by the fact that the mites do no longer walk on highly variable substrates but on smooth and identically shaped hairs. As the clasping flaps are located between legs I these legs have ceased to participate in normal walking. They are now mainly used as feelers. Their contribution to locomotion is confined to pulling the mite to another hair (8.2.).

6.) For the extension of certain leg joints by means of haemolymph pressure as it occurs in many Chelicerata a detailed model is proposed: the displacement of haemolymph during bending expands the cuticle. The potential energy thereby stored in the body wall is transformed into kinetic energy when the flexor muscle slackens and the haemolymph flows back exten-

ding the joint. Thus with each bending the flexor muscle has to provide additionally the energy for the extension. This mechanism might at the same time serve as a partial substitute for a missing or poorly developed circulatory system (8.4.).

7.) The clasp apparatus at the rostral end of the mite is opened and closed by the movements of the gnathosoma. The gnathosoma articulates via two endoskeletal rods with the apodemes of legs I. This allows rotations only in the vertical plane. The clasp flaps are a derivative of the body wall and are joined with the palp coxae which serve as a lever to move the flaps. By lifting the gnathosoma the palp coxae press onto the clasp flaps which rotate inwards and press the hair against the distal ends of the palps. When the gnathosomal musculature is relaxed the clasp flaps take a medial position which allow the mite to walk on the hair. In order to leave the hair the clasp flaps have to be forced apart. For doing this the gnathosoma is lowered. Now the palp coxae pull at the flaps and open the apparatus (9.).

8.) The investigation of gut contents and hairs of the host suggests that *L. leuckarti* is saprophagous and randomly grazes off the hairs. Large amounts of food are likely to be turned over (10.2.).

9.) The structure of the digestive tract conforms in its main aspects with the situation in other Acaridida. Within the stomach elements of the peritrophic membrane are secreted and mingled with the food particles. The formation of a continuous peritrophic membrane during the passage of the gut contents to the colon could not be observed (10.2.).

10.) The cells of the postcolon possess a strongly folded apical plasmalemma and numerous vacuoles. Obviously the vacuoles contain water and dissolved substances which have been resorbed pinocytotically (10.2.).

11.) Oviducts and vasa deferentia are bent forward. The sexes display a remarkable sexual dimorphism. In the male the opisthosoma is dorsoventrally flattened which allows a tight contact between the sexes during copulation. The formation of attachment pairs was never observed (11.).

### Zusammenfassung

1. Die innere und äußere Anatomie von *Listrophorus leuckarti* Pagenstecher, 1861 wurde mittels licht- und elektronenmikroskopischer Methoden untersucht. Durch Beobachtung von Bewegung und Verhalten wurden die anatomischen Befunde ergänzt und abgesichert.

2. Zur Beschreibung der Körperarchitektur wurde das Pneu-Konzept nach OTTO (1984) genutzt. Danach ist ein Pneu ein (natürliches oder technisches) Gebilde, das aus einer zugbeanspruchten Schicht besteht, die eine unter Druck stehende Füllung umhüllt. Davon ausgehend wird analysiert, inwiefern dieses Konstruktionsprinzip den Bau und die Funktion verschiedener Organe beeinflusst (Kapitel 5.).

3. Die Körpermuskeln werden detailliert beschrieben und deren unterschiedliche Funktionen erörtert (6.).

4. Die Supracoxaldrüsen bestehen aus jeweils sieben Zellen, die durch einen verzweigten ableitenden Gang verbunden sind. Die proximalen Enden der Verzweigungen werden durch poröse Deckel verschlossen. Die Drüsenzellen enthalten zahlreiche Mitochondrien, die von umfangreichen Membraneinfaltungen umgeben sind. Die Elementaranalyse von eingetrocknetem Drüsensekret ergab einen hohen Anteil von Kalium und Chlor. Als Funktionsweise der Supracoxaldrüsen wird vorgeschlagen, daß entlang der Membranen Kalium in die Zelle gepumpt wird. Das Cytosol wird durch den porösen Deckel filtriert und die Lösung nach außen abgegeben. Somit dient die Supracoxaldrüse – neben ihrer Rolle als Speicheldrüse – der osmotischen Wasseraufnahme aus der Atmosphäre, wie es bereits für andere astigmaten Milben nachgewiesen wurde (WHARTON & FURUMIZO 1977). Die Genitalpapillen sind stark reduziert. Ihre Beteiligung an der Wasseraufnahme erscheint sehr unwahrscheinlich (7.).

5. Die Anordnung der Beine sowie die verschiedenen Typen von Gelenken und deren Ausrichtung werden allgemein dargestellt (8.1.). Der Lokomotionsapparat von *L. leuckarti* zeigt starke Veränderungen und Vereinfachungen. Bei allen Beinen sind zwei Glieder verwachsen (Bein I und II: Tibia und Tarsus; Bein III und IV: Femur und Genu). Dies kann durch die Tatsache erklärt werden, daß die Milben nicht mehr auf variablem Untergrund laufen, sondern auf relativ glatten und gleichmäßig geformten Haaren. Da sich die Klammerlappen zwischen den Beinen I befinden, können diese Beine nicht mehr am normalen Lauf teilnehmen. Sie fun-

gieren hauptsächlich als Fühler. Ihr Beitrag zur Fortbewegung ist darauf beschränkt, die Milbe zu anderen Haaren hinüberzuziehen (8.2.).

6. Für die Streckung bestimmter Beingelenke mittels Hämolymp-Druck, wie sie bei vielen Chelicerata vorkommt, wird ein detailliertes Modell vorgeschlagen: Durch Verlagerung von Hämolymphe während der Beugung des Beines wird die Cuticula gedehnt. Dabei wird potentielle Energie gespeichert, die in kinetische Energie umgewandelt wird, sobald der Flexor-Muskel erschlafft und die Hämolymphe in das Gelenk zurückfließt. Folglich hat der Flexor mit jeder Beugung zusätzlich die Energie zur Gelenkstreckung aufzubringen. Dieser Mechanismus könnte zugleich als Teilersatz für ein fehlendes oder gering entwickeltes Kreislaufsystem dienen (8.4.).

7. Der Klammerapparat am Rostralende der Milbe wird durch die Bewegungen des Gnathosomas geöffnet und geschlossen. Das Gnathosoma artikuliert mittels zweier Skelettstäbe mit den Apodemen der Beine I, was Bewegungen nur in der Vertikalebene erlaubt. Die Klammerlappen sind ein Derivat der Körperwand. Mit ihnen verbunden sind die Palpencoxen, die wie ein Hebel auf die Klammerlappen einwirken und diese bewegen. Beim Anheben des Gnathosomas drücken die Palpencoxen auf die Lappen, was zu einer Einwärtsdrehung führt. Befindet sich ein Haar im Klammerapparat, wird es dabei gegen den Distalteil der Palpen gepreßt. Ist die Gnathosoma-Muskulatur entspannt, nehmen die Klammerlappen eine mittlere Position ein, die es der Milbe erlaubt, auf dem Haar zu laufen. Um das Haar zu verlassen, müssen die Lappen auseinandergespreizt werden. Dazu wird das Gnathosoma abgesenkt, wobei die Palpencoxen an den Klammerlappen ziehen und damit den Klammerapparat öffnen (9.).

8. Die Untersuchung von Darminhalt und Wirtstier-Haaren läßt darauf schließen, daß *L. leuckarti* ein Saprophage ist, der wahllos die Haare abweidet. Dabei werden vermutlich große Nahrungsmengen umgesetzt (10.2.).

9. Der Aufbau des Verdauungstraktes stimmt in wesentlichen Zügen mit den Verhältnissen bei anderen Acaridida überein. Im Magen werden Elemente der peritrophischen Membran abgeschieden und mit der Nahrung vermischt. Die Bildung einer durchgehenden peritrophischen Membran beim Übergang der Nahrung in das Colon konnte nicht beobachtet werden (10.2.).

10. Die Zellen des Postcolon haben ein stark aufgefaltetes apikales Plasmalemma und zahlreiche Vakuolen. Die Vakuolen enthalten offensichtlich Wasser und gelöste Substanzen, die pinocytotisch resorbiert wurden (10.2.).

11. Die Ovidukte und die Vasa deferentia sind nach rostral umgebogen. Die Geschlechter zeigen einen auffallenden Sexualdimorphismus. Beim Männchen ist das Opisthosoma dorso-ventral abgeflacht, was einen engen Kontakt zwischen den Geschlechtern während der Paarung ermöglicht. Die Bildung von Attachment-Paaren wurde nicht beobachtet (11.).

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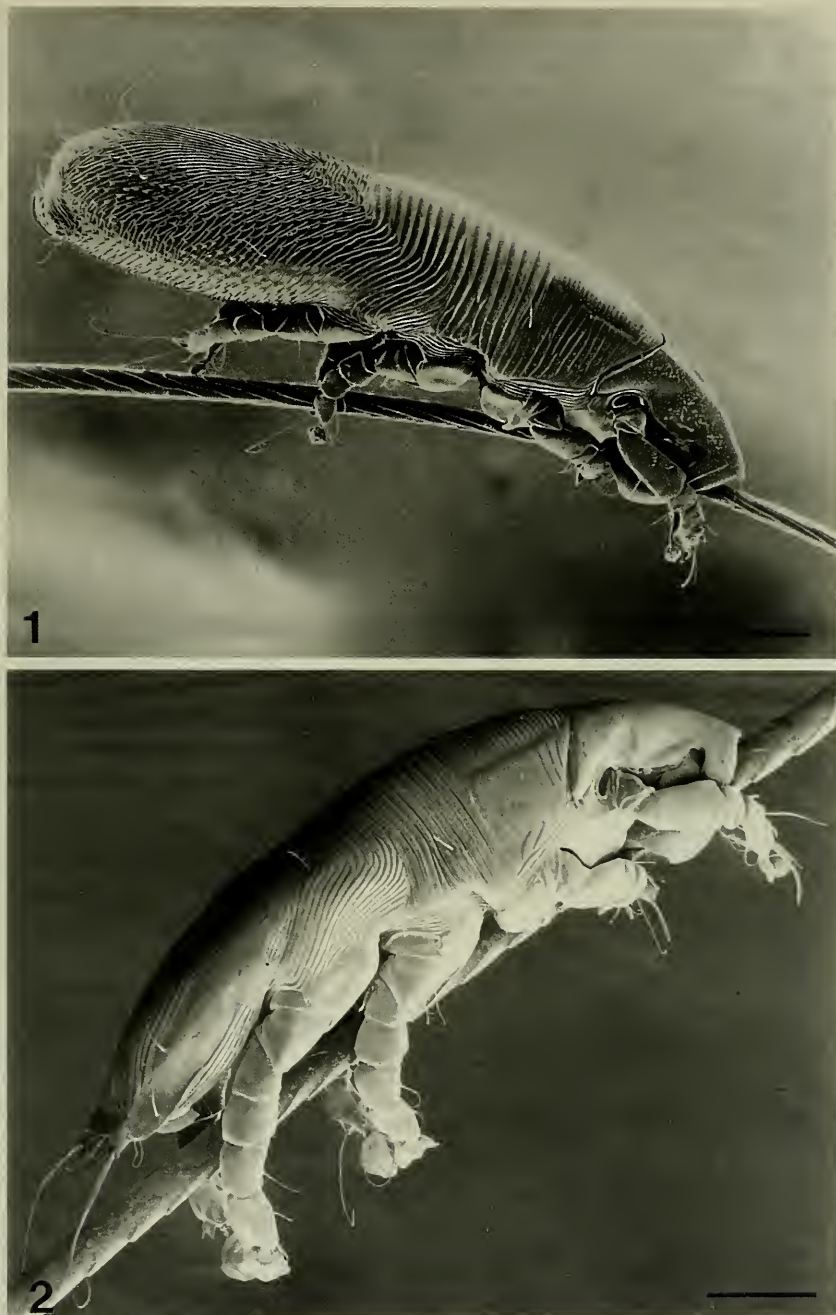
## 1. Introduction

In spite of their widespread occurrence in a great variety of habitats our knowledge of mites of the suborder Acaridida is underdeveloped in comparison to other groups of arthropods. This concerns both taxonomy as well as anatomy, physiology and ecology.

This situation improved slightly with the discovery, that some astigmatic mites are the main producers of house-dust allergens (VOORHORST et alii 1964). This discovery initiated a huge number of investigations on the biology of the main allergen producers (*Dermatophagoides* spp.). Today *Dermatophagoides farinae* and *D. pteronyssinus* can be regarded as the best known astigmatic mites.

Yet, studies on other Astigmata were sporadic and often confined to a few aspects. This applies especially to parasitic Acaridida. Up to now merely species of medical or veterinary importance were studied more in detail.

The present work on *Listrophorus leuckarti* is an attempt to create a solid picture of the anatomy and behaviour of this species and to contribute to a better understanding of this large and important group of parasitic arthropods.

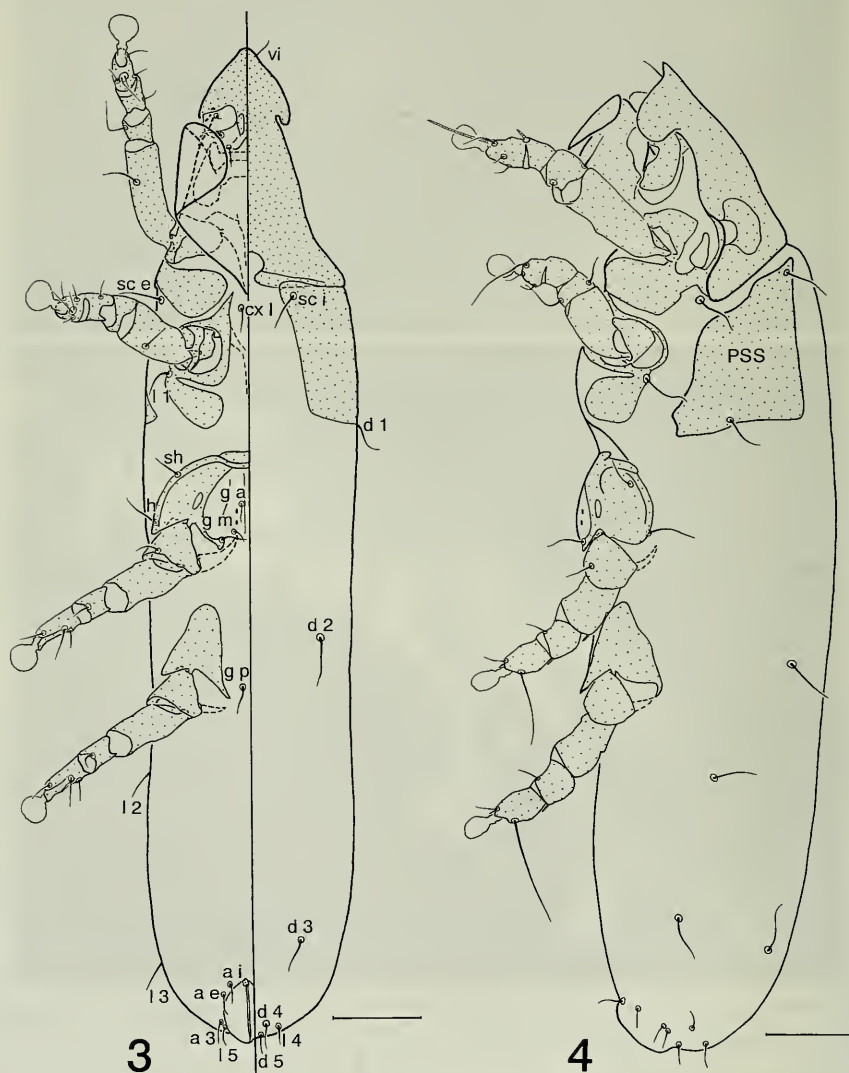


Figs. 1-2. *Listrophorus leuckarti*, on a hair of its host *Arvicola terrestris*. — 1. Female; — 2. male. — Scale bars: 50  $\mu$ m.

## 2. The Systematic Position of *Listrophorus leuckarti* Pagenstecher, 1861

*L. leuckarti* belongs to a larger group of pilicole Acaridida which were combined by FAIN (1971) to form the superfamily Listrophoroidea. This taxon comprises the following families:

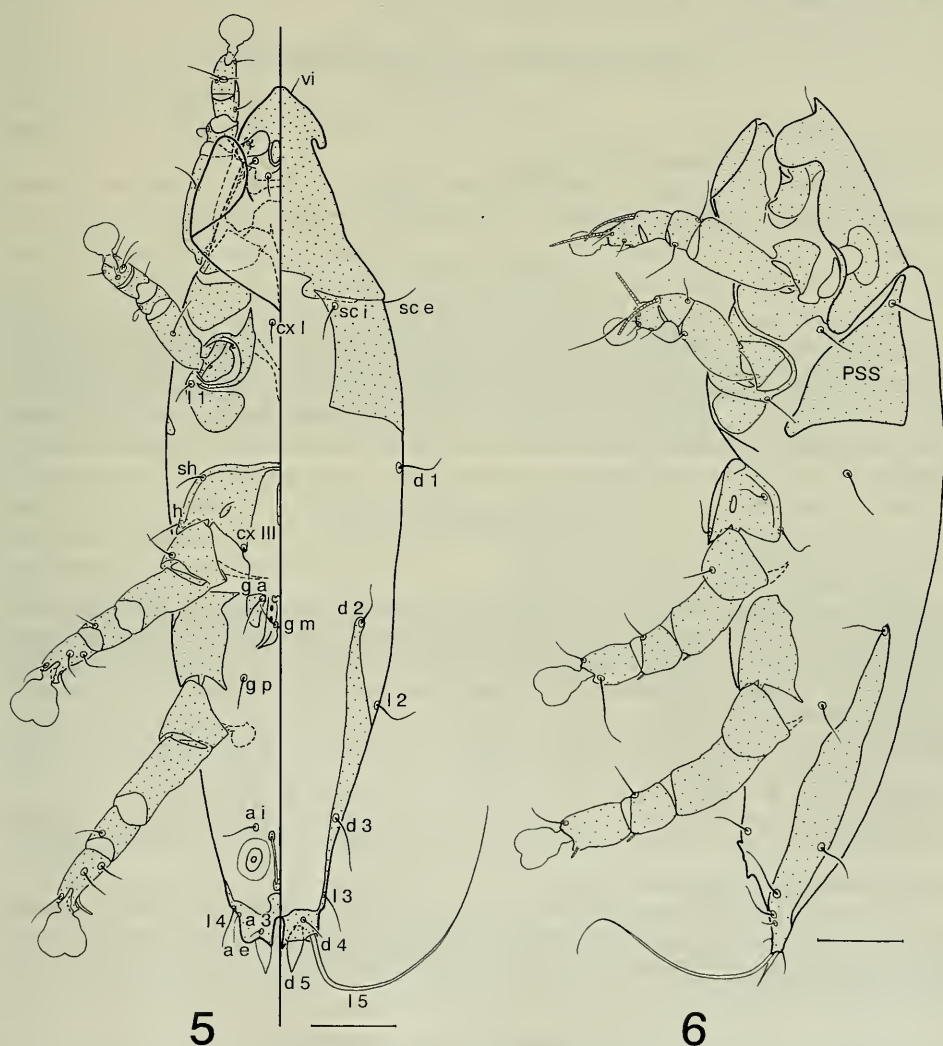
Listrophoridae,  
Atopomelidae,  
Chirodiscidae,  
Myocoptidae.



Figs. 3–4. *Listrophorus leuckarti*. — 3. Female, ventral and dorsal view combined; — 4. female, lateral view. — Abbreviation: PSS = postscapular shield. — Scale bars: 40  $\mu$ m.

This classification traces back to McDANIEL (1968) who additionally included the Rhyncoptidae in the Listrophoroidea. Most of the present authors agree with FAIN's classification. OCONNOR (1982) on the other hand takes a different view. In his opinion all the families of stationary mammal parasites constitute the single superfamily Psoroptoidea (for the history of classification of pilicole Acaridida see McDANIEL 1968; FAIN 1971, 1973a, 1976).

Most probably the members of the families Listrophoridae, Atopomelidae and Chirodiscidae feed exclusively on material they find on the hairs of their hosts (sebum, shedded tissue particles, fungal spores and hyphae, pollen etc.). Consequently they must be regarded rather as saprophagous epizoots than as parasites. In contrast to them the Myocoptidae are true parasites. They feed on the soft parts of epidermis and cause irritations (BÖHME & SUPPERER 1958; FAIN et alii. 1970).



Figs. 5–6. *Listrophorus leuckarti*. — 5. Male, ventral and dorsal view combined; — 6. male, lateral view. — Abbreviation: PSS = postscapular shield. — Scale bars: 40  $\mu$ m.

Today the family Listrophoridae comprises 21 genera (for overview see KIM 1985). The genus *Aplodontochirus* with its single species *A. borealis* was included into the Listrophoridae by FAIN & HYLAND (1974). This, however, does not seem to be very suitable since *A. borealis* differs considerably from the other listrophorids (e. g. the absence of the clasping apparatus).

The hosts of the Listrophoridae belong to the following orders of mammals: Rodentia, Insectivora, Lagomorpha, Carnivora, Scandentia and Marsupialia. Listrophorids occur world wide with the exception of Madagascar, New-Guinea and Australia (*Leporacarus gibbus* was imported into Australia together with the rabbit) (for geographic distribution see FAIN 1976, 1981). The genus *Listrophorus* is restricted to the holarctic.

The host of *L. leuckarti* is exclusively the water vole (*Arvicola terrestris*). Figs. 1 to 6 show both sexes of *L. leuckarti*. Striking features are the cylindric body shape, the proterosomal clasping apparatus, the strongly sclerotized tegmen which covers the mouth parts and the reduced length of legs II to IV in the female. Adults measure about 460 µm (female) and about 380 µm (male).

### 3. Materials, Methods and Acknowledgements

#### 3.1. Materials

Eight individuals of the water vole *Arvicola terrestris* (Rodentia: Muridae) were trapped (23. 10. 90; Stuttgart-Büsnau, SW-Germany).

For comparisons *Caloglyphus berlessei* Michael, 1903 (Acari: Acaridae) from own cultures (collected 9. 1. 89; Hemmingen, near Ludwigsburg, SW-Germany) was used.

#### 3.2. Methods

##### 3.2.1. Light Microscopy

Chitinous structures: Whole mounts of mites and coarse sections (razor blade) in Hoyer's fluid. — Chitinous structures and soft tissues: Fixation in Bouin (at least one day), piercing of cuticle to allow penetration of subsequent fluids, 90% ethanol, 70% eth., distilled water, staining after SCHÖNFELD (1980), differentiation with 70% and 90% ethanol, 94% eth., 100% eth., xylol, Malinol. — Semi-thin sections were stained with toluidine blue and embedded in Entellan.

##### 3.2.2. Electron Microscopy

###### 3.2.2.1. Transmission electron microscopy

Two modes of preparation were applied:

(A) Mites were pierced and fixed in a solution containing 2% formaldehyde and 2.5% glutaraldehyde in 0.1 M Na-cacodylate buffer (pH 7.2). After washing in buffer the mites were post-fixed in 2% osmium tetroxide in 0.1 M Na-cacodylate buffer (pH 7.2) for two hrs. and washed again in buffer. The specimens were dehydrated in a graded series of ethanol and embedded in Araldite via propylene oxide.

(B) Without piercing the mites were submerged in a solution containing 3% glutaraldehyde in 0.1 M phosphate buffer (pH 7.4). After washing in buffer they were postfixed in 1% osmium tetroxide in 0.1 M buffer for one hour. Further procedure like given in (A).

Electron micrographs which are based on method (A) are indicated. For sectioning a LKB ultra microtome with a diamond knife was used. Energy-filtering TEM CEM 902 (Zeiss).

###### 3.2.2.2. Scanning electron microscopy

Mites were killed by freezing and washed with a tenside. Preparation after BOCK (1987): fixation in modified Carnoy (acetic acid: chloroforme: abs. ethanol = 1 : 1 : 3) (at least 4 hrs.), abs. ethanol (5–10 min), hexamethyldisilazane (5 min), air-drying and sputtering with gold. SEM DSM 940 (Zeiss).

##### 3.2.3. Electron-Probe Microanalysis

In order to obtain indications on the composition of the secretions of the supracoxal glands a microanalysis was carried out. The range of detectable elements started at fluorine ( $Z = 9$ )

and ended at uranium ( $Z = 92$ ). Mites were maintained in a vessel until they desiccated. Sputtering with gold. SEM JXA 50A (JEOL).

### 3.2.4. Life Observations

The behaviour of the mites was observed by means of a stereo microscope (40x). For a more detailed study of particular movements mites were fixed by a small coverslip and filmed with a video camera. In spite of the strong light the animals survived longer than one hour and were active for most of the time.

### 3.3. Acknowledgements

I would like to thank the following individuals for their kind help. Prof. Dr. B. LOOS-FRANK (Stuttgart) supported this study from its beginning and gave valuable comments on the manuscript. Prof. Dr. R. LUCIUS and Prof. Dr. H. RAHMANN (Stuttgart) kindly gave permission to use institute facilities. P. VÖHRINGER, E. BECK and B. AICH (all in Stuttgart) gave very helpful technical assistance in sectioning and electron microscopy. I also thank Dr. K.-H. KÖRTJE for his continuous interest and help in the transmission electron microscopic investigations, S. HENNIG and B. CURTH for their help with the SEM-examinations and Dr. R. WURSTER (all in Stuttgart) who carried out the microanalysis.

## 4. Historical Record

*Listrophorus leuckarti* was described by H. A. PAGENstecher in 1861. From the beginning the investigators' attention was focused on the curious clasping apparatus at the rostral end of the mite. This is also reflected in the name of the newly discovered animal: the form of the clasping apparatus reminded the author of a shovel (Greek: *listros*) and induced him to choose the name "*Listrophorus*" (shovel bearer). But despite of many attempts to explain the structure and function of the clasping organ little understanding was achieved.

PAGENstecher in his description gives the first interpretation of the diverse elements of the clasping apparatus. Furthermore he describes partly the internal anatomy of both sexes. The function of the proterosomal clasping apparatus, however, remained enigmatic to him, since almost all of the mites he received were dead and had been separated from their host.

The first author who realizes that the clasping apparatus is used for grasping hairs and thereby enables the mite to stay on its host is CLAPARÈDE (1868). He also corrects some misinterpretations by PAGENstecher (1861a) concerning the sexual organs. But with regard to the anatomy of the clasping organ CLAPARÈDE follows PAGENstecher's opinion.

MÉGNIN (1878) figures the mouth parts and the clasping apparatus of *Leporacarus gibbus* (syn.: *Listrophorus gibbus*) without further comment. His drawings imply a completely different view of these structures.

HALLER (1880) essentially agrees with MÉGNIN. In his description of *Metalistrophorus pagenstecheri* (syn.: *Listrophorus pagenstecheri*) he gives a very detailed drawing of the gnathosoma.

In BERLESE (1897) a minute illustration of the clasping apparatus can be found. In most aspects it confirms the opinion of MÉGNIN (1878) and HALLER (1880).

The later publications on listrophorids are exclusively descriptions of new species and only repeat the opinions of the former authors (for taxonomic literature of that period see DUBININA 1967; FAIN 1971, 1973b, 1976; FAIN & HYLAND 1974). Only HUGHES (1954) presented again a very comprehensive study on the anatomy of *L. leuckarti* which includes to that time the most detailed description of the clasping apparatus.

Since then most of the publications on listrophorids deal with the description of new species (mostly by A. FAIN). If there are any informations on the form and function of the clasping organ they mostly refer to HUGHES (1954) (e. g. WOOLLEY 1988: 96).

### 5. The Mite Construction: A Pneu

From the constructional point of view the body architecture of mites constitutes a pneu. "Pneu" here means a (natural or engineered) structure consisting of an easy to bend layer, loaded only in tension, encasing a pressurized filling (OTTO 1984). Since the mite cuticle is partly sclerotized and muscles, fibres and skeletal rods are fixed to its inner surface a mite can be regarded as a partially hardened pneu with internal bracing.

For physical reason it is obvious that every loaded elastic body adopts at least one possible equilibrium configuration. It follows for the mite cuticle that its energy under given forces and pressure is at minimum. In the static case every combination of hydrostatic pressure and muscular contraction can be associated with a particular body shape.

In general this can be written as

$$A = A(p_{\text{hyd}}, F_1, F_2, \dots, F_n)$$

$A$  = surface form of the mite

$p_{\text{hyd}}$  = hydrostatic pressure

$F_1 \dots F_n$  = forces on the body surface (e. g. due to muscle contraction)

Since  $p_{\text{hyd}}$  and the body-volume  $V$  are not independent (by altering  $V$  the hydrostatic pressure changes) it follows that

$$A = A(V, F_1, F_2, \dots, F_n)$$

$V$  = body-volume

These relationships are valid both for the whole animal and for parts of it.

Fig. 7 shows how pressure and body-volume affect some structural elements and vice versa. The equivalency of pressure and volume in the present sense is symbolized by a double-headed arrow.

**Body-shape:** Some vitally important parts of the body can only function if their form is maintained by hydrostatic pressure (e. g. ambulacra, rims of adanal suckers in the male, rim of sucker plate in the deutonymph). Proterosoma, gnathosoma, chelicerae, penis and adanal suckers are extruded by hydraulic pressure.

**Locomotion:** The following joints are extended by hydrostatic pressure: femur-genu, genu-tibia, tibia-tarsus (8.1.).

**Digestive tract:** As a result of haemolymph pressure, gut contents might be squeezed out. Therefore efficient closing systems at both ends and a powerful pump at the rostral end of the gut are necessary (10.1.).

**Genital system:** Analogous to the gut contents the discharge of sexual products must be controlled by suitable closing systems (11.2.1., 11.3.1.).

**Regulator musculature (dorsovental musculature):** This compensates alterations of volume (mainly due to transpiration, feeding, defecation and deposition of eggs) by changes of cuticle shape and maintains the internal pressure at the required level (6.1.).

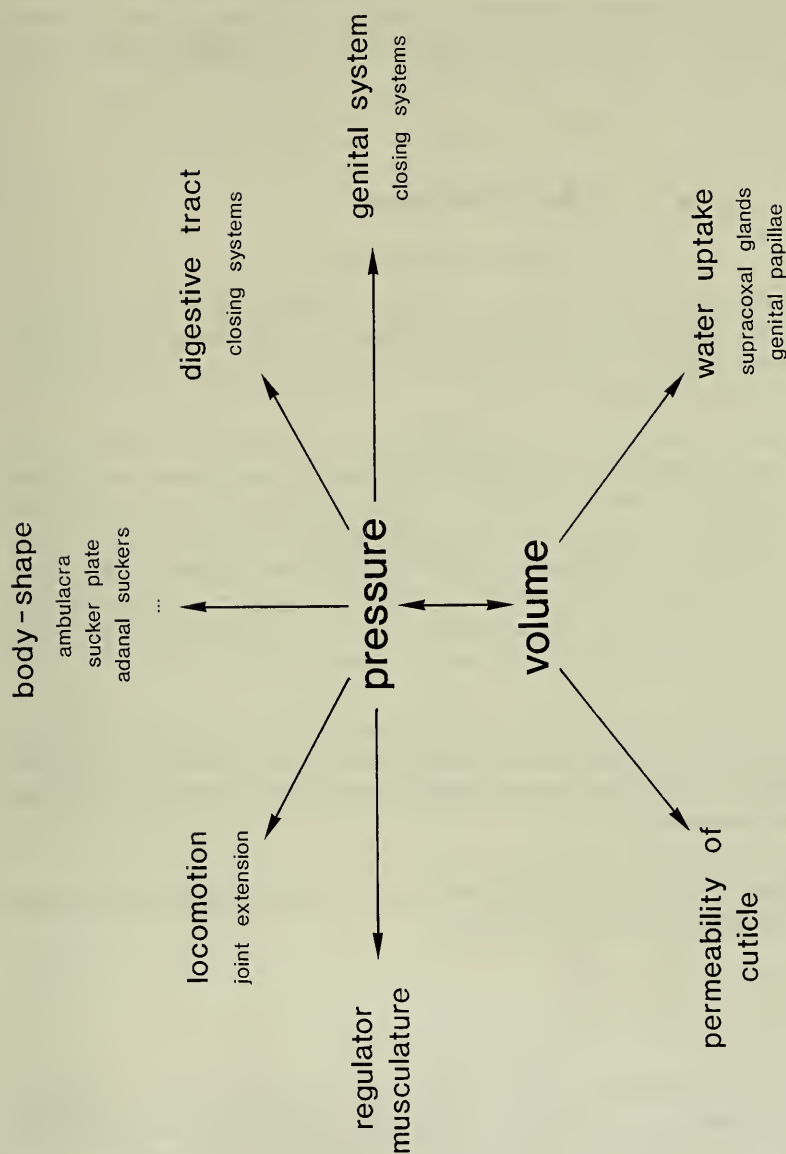


Fig. 7. Influence of haemolymph pressure and body volume on particular organs.

**Permeability of cuticle:** Transpiration through the cuticle results in water loss which reduces the body volume. ARLIAN & WHARTON (1974), however, demonstrated that in *Dermatophagoides farinae* the permeability of the cuticle decreases with a reduction in atmospheric humidity.

**Water uptake:** This is accomplished by the supracoxal glands which enable the mite to take up water from the atmosphere. According to some authors (ALBERTI 1979, WITALINSKI et alii 1990) the genital papillae might be regarded as another organ for water uptake (7.1.).

## 6. Body Musculature

### 6.1. Previous Knowledge

Up to now the musculature of Astigmata has been insufficiently described. At present the only attempt to describe and figure the body musculature of an astigmatic mite in more detail is made by KUO & NESBITT (1970). HUGHES (1954) does not mention the body musculature.

All Astigmata have strong muscles which are serially arranged on both sides of the body more or less perpendicular to the long axis (dorsoventral musculature). This musculature essentially serves to maintain the physiologically necessary internal pressure (KUO & NESBITT 1970; WOOLLEY 1988: 101). This can be shown very simply by the following experiment: mites which have been exposed to an atmosphere of low humidity show deep grooves in their cuticle after a relatively short period. These grooves mark the points of insertion of the dorsoventral muscles which now are contracted and thereby compensate the decrease in pressure that results from water loss.

Additionally astigmatic mites have maximally four pairs of longitudinal muscles which move the proterosoma. These are located at the dorsal side of the prosoma and their anterior tendons are inserted on the sejugal furrow. They allow the bending and redrawing of the proterosoma.

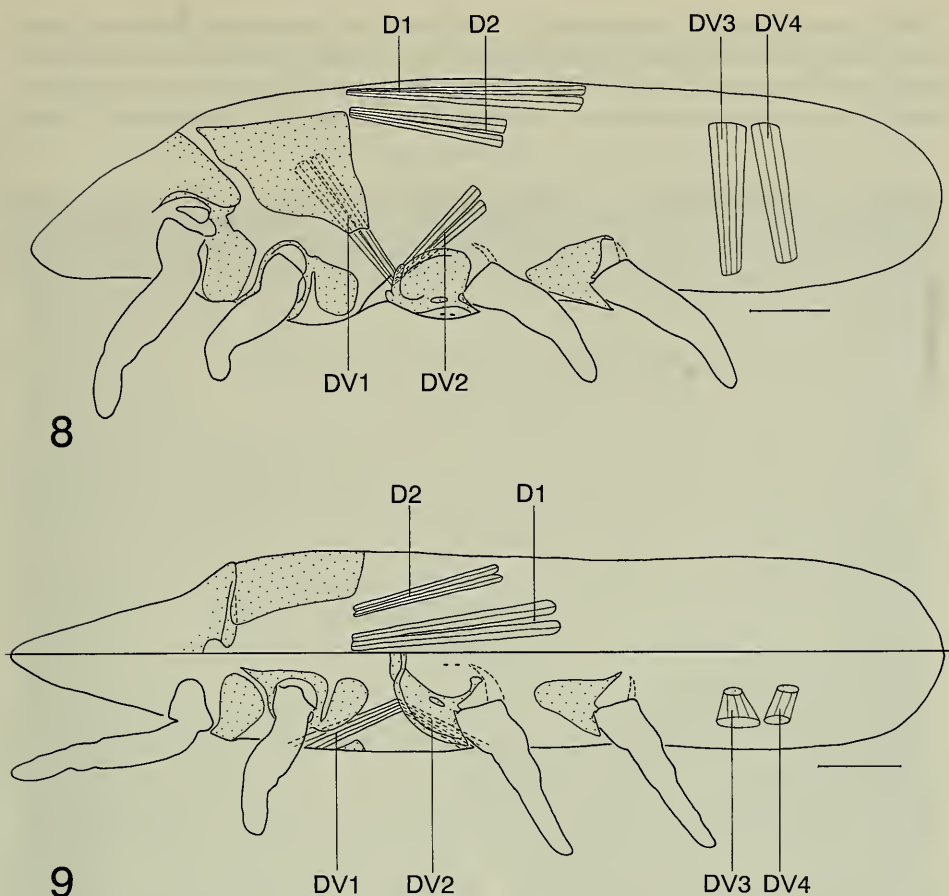
For the gnathosomal musculature see 9.2.2.

The nomenclature for the body musculature used below is inspired by KUO & NESBITT (1970) without supposing homology.

### 6.2. Results

**Female:** Two muscles (DV1, DV2) run inside the prosoma from the ventral to the lateral wall, two muscles (DV3, DV4) inside the opisthosoma from the ventral wall to the dorsum. DV1 passes through the supracoxal gland between the gland cells 4 and 5. Two pairs of muscles (D1, D2) pass parallel to the dorsum (table 1; figs. 8–9).

**Male:** The prosomal muscles correspond in position and size to the female's. The muscles of the opisthosoma will be described together with the reproductive system (see chapter 10.).



Figs. 8–9. *Listrophorus leuckarti*; schematic presentation of the body musculature. — 8. Female, lateral view; — 9. female, ventral and dorsal view combined. — Scale bars: 40  $\mu$ m.

Table 1. Body musculature.

Muscles	Insertion points
DV1	from apodeme of leg III to the postscapular shield
DV2	from apodeme of leg III to the lateral wall above leg III
DV3, DV4	in the middle of the opisthosoma; both muscles are inserted on the body wall
D1, D2	obliquely from dorsolateral to dorsomedian; both fillets are inserted anteriorly on the sejugal furrow

### 6.3. Discussion

DV2 to DV4 certainly can be regarded as muscles for the regulation of the internal pressure. Between their insertion points the body is not movable. In living mites above leg III and in the opisthosoma dents could repeatedly be observed.

DV1 cannot clearly be attributed to a single function. Sometimes lowering of the proterosoma was accompanied by an inward movement of epimer III as a result of strong contraction of DV1. Thus DV1 might serve as depressor of the proterosoma. Additionally the inward motion of epimer III accomplishes a decrease in body volume and thereby an increase in hemolymph pressure.

D1 and D2 are the levators of the proterosoma.

The number of body muscles in *L. leuckarti* is strongly reduced compared with free living Astigmata even of similar size. Homologization of every muscle, however, is impossible since a sufficient description of the body musculature of free living Astigmata is still lacking.

## 7. Supracoxal Glands and Genital Papillae

### 7.1. Previous Knowledge

Lateral to esophagus and stomach there is a paired group of cells designated as "supracoxal glands". Each gland has a chitinous duct that opens to the outside dorsal to coxa I. Recent investigations unanimously showed that one gland is composed of seven cells of different size into each of which projects a branch of the chitinous duct (PRASSE 1968a; BRODY et alii 1976). In addition PRASSE (1968a) found in *Caloglyphus* spp. a complex of several cells which constitute a cavity filled with secretory products. These products also are released into a chitinous duct which communicates with the common duct.

In his lighth microscopic analysis of the supracoxal glands (here named as "Große Lateraldrüse") of *Caloglyphus berlesii* and *C. michaeli* PRASSE (1968a) described the seven cells as "im Zentrum schaumartig, ansonsten aber fibrillär strukturiert" ("foamlike in the center but otherwise fibrous").

The first electron microscopic investigation of the supracoxal glands was carried out by BRODY et alii (1976) on *Dermatophagoides farinae*. They found three units each combined of two different cells one cell (type A cell) enveloping the other (type B cell) completely. In both cells the end of a branched duct projects that are covered by a porous cap from inside. The type A cell shows an extremely folding of plasma-lemma whereas the folding of the cell membrane of type B cell is less elaborate. The foldings are filled with numerous mitochondria. At the penetration point of the chi-

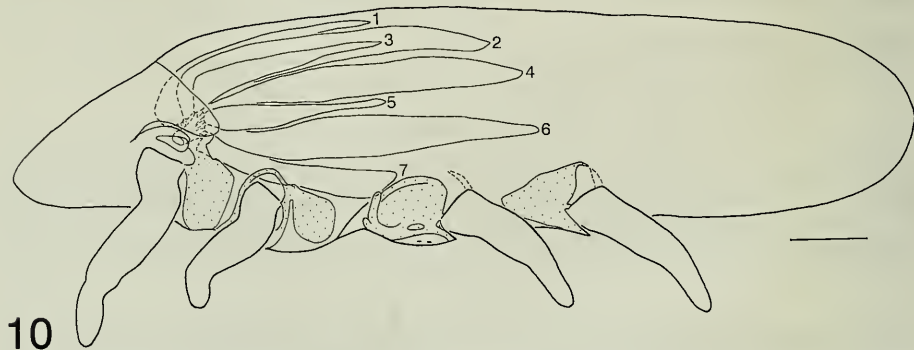
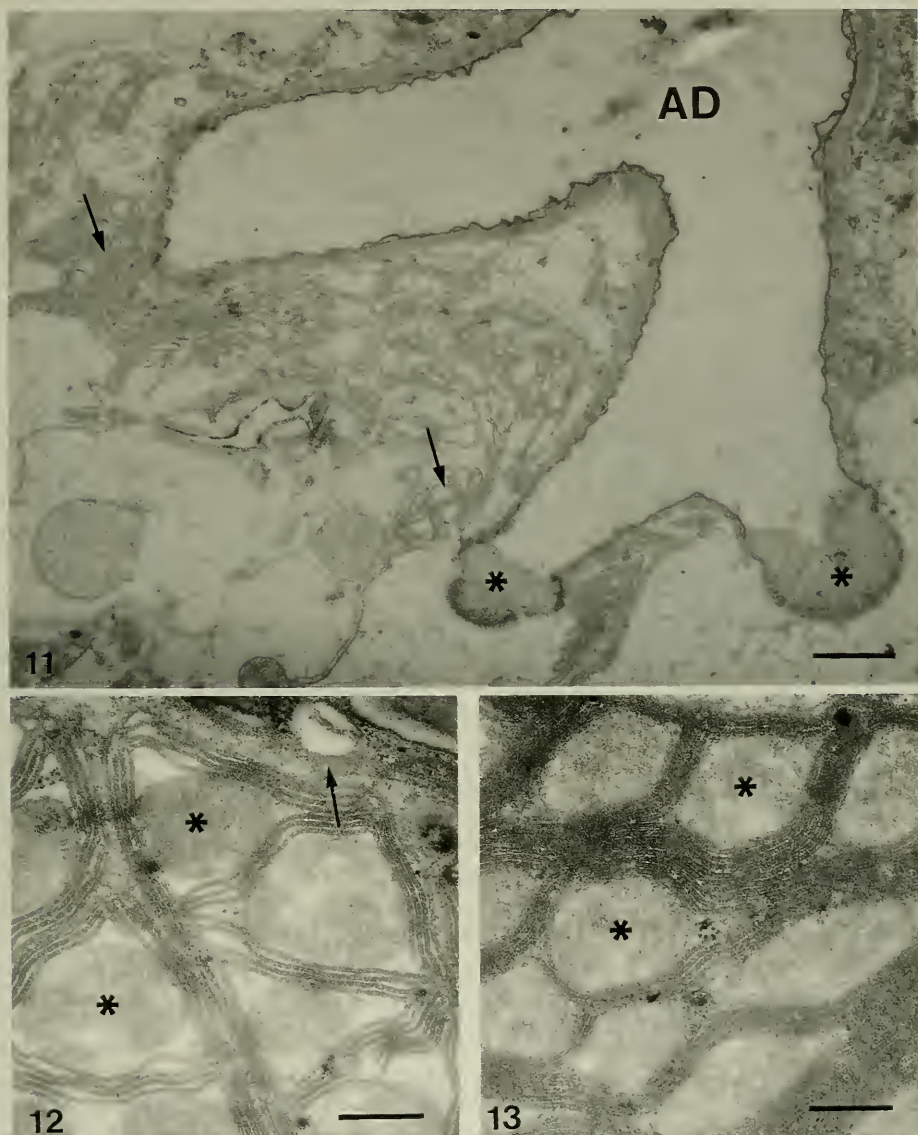


Fig. 10. *Listrophorus leuckarti*, female; schematic presentation of the left supracoxal gland. The numbers indicate the gland cells. — Scale bar: 40  $\mu$ m.

tinous duct into type B cell the plasmalemma folds back upon itself several times. The smaller seventh cell (type C cell) is characterized by numerous vesicles and mitochondria, lysosomes and an extensive rough endoplasmic reticulum which may indicate the synthesis of proteins. All cell products are brought together by the system of chitinous ducts and released to the outside.



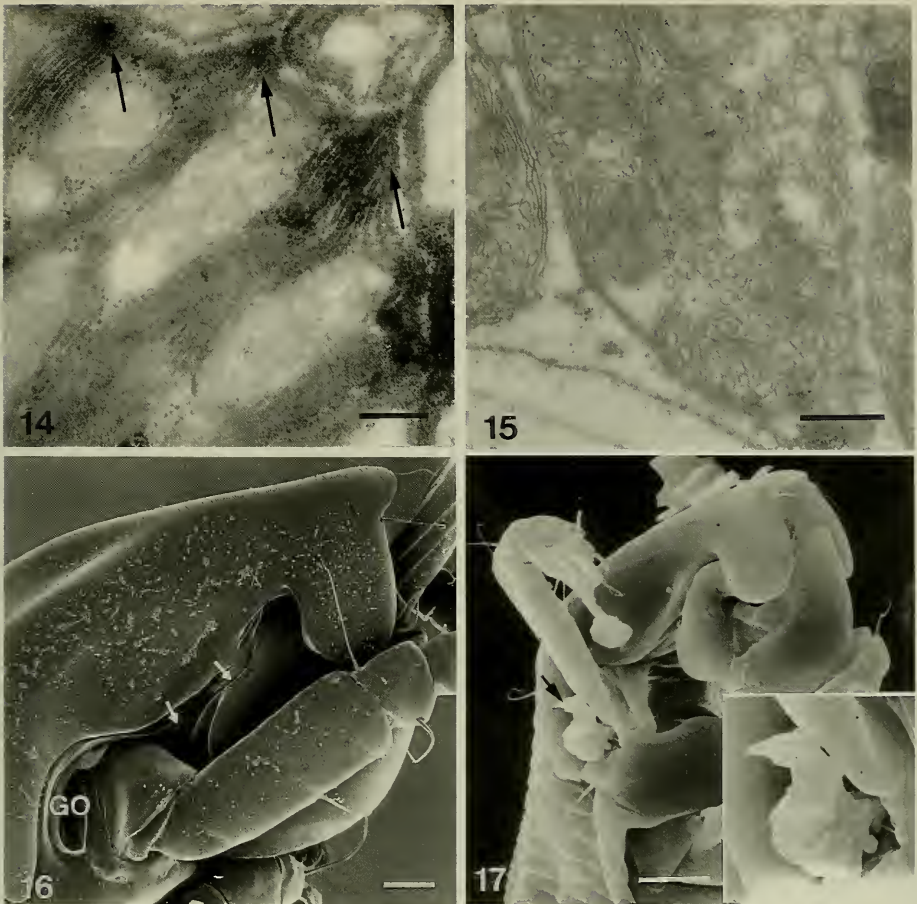
Figs. 11–13. *Listrophorus leuckarti*, female; supracoxal gland. – 11. Longitudinal section, contact zone between the afferent chitinous duct (*AD*) and gland cells; *asterisk* = porous cap, *arrow* = folded plasmalemma of gland cell (scale bar: 1.1  $\mu\text{m}$ ); – 12. transverse section, cell 6; mitochondria (*asterisks*) surrounded by plasma membrane plications; *arrow* = cell border (scale bar: 0.4  $\mu\text{m}$ ) (fixation mode A; see 3.2.2.1.); – 13. transverse section, cell 3, as in fig. 12 (scale bar: 0.4  $\mu\text{m}$ ) (fixation mode A).

By most of the former authors as well as by HUGHES (1954) the supracoxal glands are regarded as the salivary glands (for a literature review see PRASSE 1968a). WHARTON & FURUMIZO (1977) were the first who proved that the supracoxal glands additionally constitute an important organ for water supply. According to them the glands secrete a solution of high osmolarity which is directed by the podocephalic canal to the mouth and imbibed by the mite. If the water vapour activity  $a_v$  (= relative atmospheric humidity/100%) is above the activity of water in the gland fluid  $a_w$ , a net transfer of water from the atmosphere into the solution occurs. In the other case ( $a_v < a_w$ ) the solution loses water to the ambient air. Finally the water loss leads to crystallization of the solutes. Thus a plug is formed at the gland orifice which prevents further release of the solution. If the atmospheric humidity increases again the plug deliquesces. MCDANIEL (1981) describes a small cuticular flap-like lid dorsal to the gland opening in *Geomylicus thomomys*. He assumes that the lid serves to close the gland orifice and may replace the plug. The value of atmospheric humidity at which the mite shows a net loss of water is called "critical equilibrium activity" (CEA) (KNÜLLE & WHARTON 1964). It is specific for each species and is for example in nonfed *Tyrophagus putrescentiae* between 0.75 and 0.84 (25°C) (CUTCHER 1973). Among the osmotically active substances in *Tyrophagus putrescentiae* and *Dermatophagoides farinae* WHARTON & FURUMIZO (1977) traced potassium chloride as a significant component. Furthermore they found macromolecules with >30,000 Dalton. The close vicinity of the supracoxal glands to the stomach suggests the following circulation of the dissolved salts: supracoxal glands — podocephalic canals — esophagus — stomach — haemocoel — supracoxal glands (WHARTON & FURUMIZO 1977).

As another organ for managing water balance the genital papillae (also: genital suckers) are discussed (ALBERTI 1979). They consist of one (protonymph) or two (deuto-, tritonymph, adulti) pairs of fingerlike structures which are normally hidden between the genital folds. Instead of them the larva bears a pair of similarly shaped so called "CLAPARÈDE organs" which protrude completely unprotected from coxal fields I. The genital papilla is filled with the extensions of one or several cells. In the latter case the cells seem to fuse in their apical parts (WITALINSKI et alii 1990). The cells contain an extensive network of vesicular tubules or numerous vesicles as well as numerous mitochondria and microtubuli. Their apical plasmalemma is deeply folded. Between the apical cell membranes and the surrounding cuticle a cell-free space filled with a liquid occurs. The apical dome-shaped part of the papilla consists of a special material (FASHING 1988; WITALINSKI et alii 1990). The ultrastructure of CLAPARÈDE organs is nearly identical. In terrestrial forms both organs are supposed to function in water uptake whereas in aquatic species they might be utilized for ion exchange (ALBERTI 1979; FASHING 1988).

## 7.2. Results

The supracoxal gland in *L. leuckarti* consists of seven elongated cells, four of them considerably smaller in size (fig. 10). Each cell possesses a nucleus. The branched duct is cuticle-lined and its proximal ends are closed by a porous cap (fig. 11). All cells contain numerous mitochondria which are surrounded by membranes. In the larger gland cells this arrangement is restricted to the periphery of the cell (fig. 57). The smaller gland cells are densely filled with mitochondria and membrane plications (fig. 13), whereas the larger gland cells appear highly variable: in some specimens the



Figs. 14–17. *Listrophorus leuckarti*, female; supracoxal gland. – 14. Transverse section, cell 1, rostral part; contact zone between membrane plications and cell membrane (arrows) (scale bar: 0.25  $\mu\text{m}$ ) (fixation mode A); – 15. longitudinal section, at the level of DV1; membranes with vesicular extensions (scale bar: 0.6  $\mu\text{m}$ ); – 16. opening (GO) of supracoxal gland and probable podocephalic canal (arrows) (scale bar: 10  $\mu\text{m}$ ); – 17. dried specimen with a plug (arrow, inset) formed by the crystallized gland secretion at the orifice (scale bar: 25  $\mu\text{m}$ ).

system of mitochondria and membranes is scanty (fig. 57), in others it is more elaborate (fig. 12). In its extreme form the membranes form vesicular extensions which fill the space between the mitochondria (fig. 15). In the rostral part of the cells the membrane plications run towards the cell membrane (fig. 14) whereas in the more caudal parts they bend and parallel the plasmalemma (fig. 12).

At the point of penetration of the chitinous duct into the cell the cell membrane is folded back upon itself several times (fig. 11). Fig. 16 shows the gland orifice and the probable course of the podocephalic canal. In all dried mites a plug had been formed in the gland opening (fig. 17). By microanalysis of the plug material a high amount of potassium and chlorine was detected (fig. 18).

The genital papillae appear as small chitinous rings or bowls that open to the outside (fig. 64).

7.3. Discussion

The densely packing with mitochondria is a measure for high consumption of energy, probably as a result of work of concentration. Though in none of the sections an indication for an inflection of the plasmalemma was seen the system of membranes in all probability represents an infolding of the cell membrane.

Under these assumptions the following model for the function of the supracoxal glands in *L. leuckarti* is proposed: like a sponge a continuous network of membrane plications passes from the rostral to the caudal end through the cell. At the cell ends the system of foldings opens to the haemocoel. Potassium is pumped across the membrane of the plications into the cell. By realizing the principle of counter current the ratio of concentrations in cytosol and haemolymph along the membrane is relatively constant. The cytosol is filtered through the cap and released to the outside in order to take up water from the ambient air. The different structural appearances of the same gland cells may indicate the ability of the supracoxal glands for adaptation to changes in the water need and/or the humidity of the ambient air.

HUGHES (1954) erroneously believed the supracoxal glands (here named as salivary glands) of *L. leuckarti* to open into the buccal cavity.

In their electron microscopic appearance the supracoxal gland cells are very similar to the cells that fill the CLAPARÈDE organs and the genital papillae in *Naiadacarus arboricola* (FASHING 1988).

The difference in the organization of the supracoxal gland of *Dermatophagoides farinae* is most astonishing. Common features are the following: the number of seven cells with a common duct, the great number of mitochondria, the closing of the

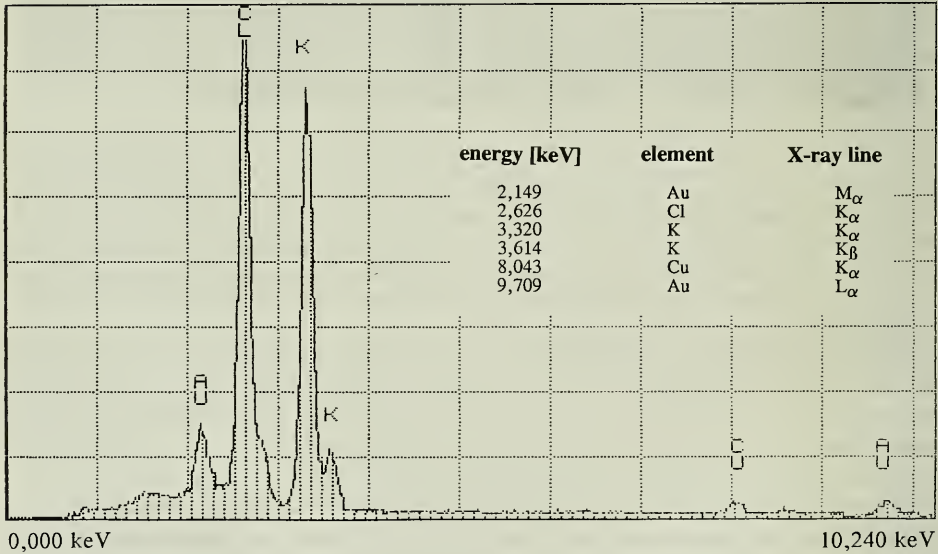


Fig. 18. Microanalysis of the plug material of fig. 17; energy dispersive X-ray spectrum for elements with Z≥9.

proximal duct ends with a porous cap and the folded cell membranes at the point of contact with the duct.

The genital papillae appear to be reduced. Their participation in water uptake seems very unlikely.

## 8. Locomotion Apparatus

### 8.1. Previous Knowledge

Up to now a satisfying investigation of the anatomy and kinematics of the locomotion apparatus of astigmatic mites has not yet been presented. Only in KUO & NESBITT (1970) some leg muscles are described and illustrated. Considering the high number of muscles moving the leg segments as one can see even in whole specimens simply stained their informations are completely insufficient. HUGHES (1954) describes in extenso the leg musculature of *L. leuckarti* and gives several drawings. On the value of his description see below.

The following introduction is an attempt to sketch the situation in free-living Astigmata. The informations are based exclusively on my own observations mainly of *Caloglyphus berlesei*.

The legs of free-living Astigmata normally articulate ventrally along an oval line (fig. 19). The coxa-trochanter joints of all legs are monocondylic<sup>1)</sup>, trochanter and femur are connected by two condyles. The other joints are hinge joints without condyli. In each leg the joint axes run nearly parallel to each other except in the trochanter-femur joint.

In forward locomotion it is most suitable if all legs (leg segments) swing in the direction of progression. In other words: the rotational axes should be orientated perpendicular to the direction of locomotion. Under these conditions all pulling and thrusting forces the leg exerts to the ground contribute to progression. All deviations lead to force components that do not contribute to progression.

In astigmatic mites only the first pair of legs complies with these requirements. But as the joint between trochanter and femur runs obliquely to the long axis of the leg and the leg therefore can be bent obliquely to the long axis, a transmission of force parallel to the long axis of the mite body is also possible for the other legs. Consequently the leg movement in straight forward walking is a combination of flexing and extending as well as obliquely bending of the trochanter-femur joint. By this the first two pairs of legs act in pulling, the other two pairs in thrusting. Thus the contribution of the joints for the scheme of movement is different for each leg:

leg I: almost exclusively flexing and extending;

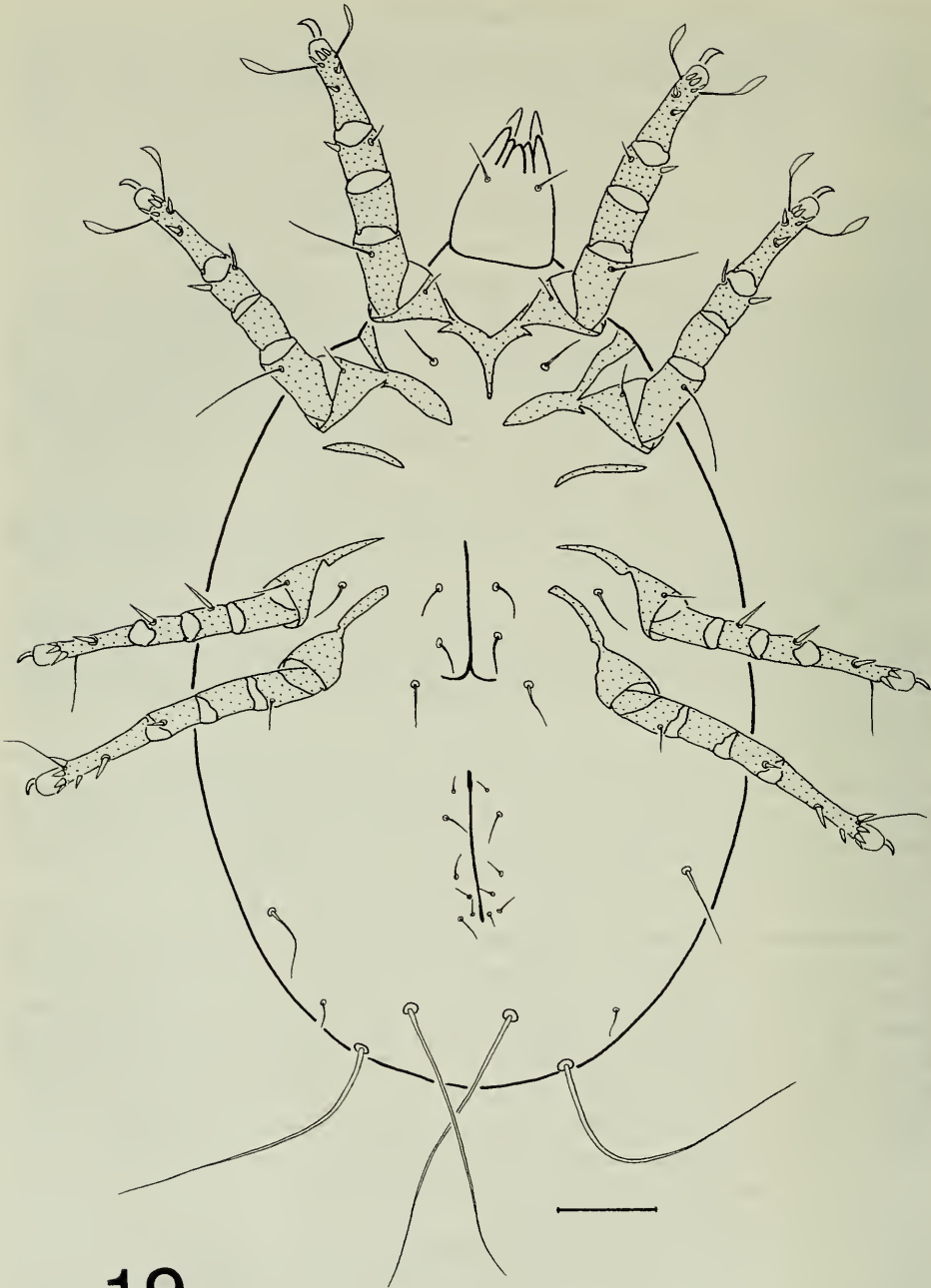
leg II: flexing and extending, little bending;

leg III: almost exclusively bending;

leg IV: flexing and extending, little bending.

The pattern of leg movement in astigmatic mites is very similar to the one in spiders (FOELIX 1979: 132).

<sup>1)</sup> In fact the term "condylus" is wrong, since in Astigmata condyli do not occur. The junctures consist of narrow bridges of flexible chitin. This bridge is provisionally designated here as "condylus".



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Fig. 19. *Caloglyphus berlesei*, female; ventral view. — Scale bar: 100  $\mu$ m.

Trochanter and femur possess an antagonistic musculature. Genu, tibia and tarsus are equipped only with flexors, the extension of their joints is performed by hydraulic pressure. Ambulacra are again moved by antagonistic musculature which originates from the distal end of the tibia.

## 8.2. Results

### 8.2.1. Skeletal System

The coxa-trochanter joints of *L. leuckarti* cannot be linked by an oval line as described for most of the free-living species. The legs II to IV are arranged in a straight row (figs. 3, 5, 20). Despite of these modifications the orientation of the axes of coxa-trochanter joints in respect to the long axis of the mite, however, remained nearly constant.

Contrary to free-living Astigmata trochanter I to IV articulate via two condyles.

The coxa-trochanter joints of leg I and II are surrounded by skeletal rings (figs. 3–6). The rings of leg I are interrupted ventrally in order to make room for the clasping flaps originating here. Thus the rings are missing between this site and the articulation of the endoskeleton of leg I with the skeletal rods (fig. 21; S) establishing the connection with the gnathosoma (see below).

The skeletal rings of the first two pairs of legs are connected by a well developed endoskeleton each (fig. 21). The endoskeleton consists of inwards arched chitinous plates arising from the dorsal border of the skeletal rings. These plates pass ventro-medially and fuse via a caudal extension ("sternum"). This extension serves as surface for attachment of several leg muscles. In addition to the caudal extension two rostral extensions arise at the endoskeleton of leg I. Ventrally the chitinous plates and the extensions fuse with the internal surface of the body cuticle. This arrangement demonstrates that the endoskeletons are derived from the apodemes of legs I and II which are named here as "endoskeleton I and II". One of the two condyli of trochanter I and II is located at the outer face of the chitinous plates. The other one is attached to the posterior half of the skeletal ring.

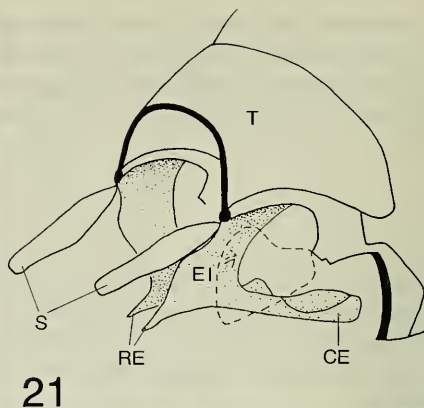
Two sclerites are located posterior to leg I and II, both connected with the skeletal ring.

The coxal fields of legs III and IV are strongly sclerotized. The coxal fields III are joined by a strong apodeme at their anterior border. Only the legs IV are completely separated from each other. Posterior to trochanters III and IV there is a crescent sclerite each, at which the posterior condylus of the coxa-trochanter joint is fixed.

The length of legs is about 120  $\mu\text{m}$ , 85  $\mu\text{m}$ , 100  $\mu\text{m}$ , 100  $\mu\text{m}$  (female) and 115  $\mu\text{m}$ , 85  $\mu\text{m}$ , 115  $\mu\text{m}$ , 135  $\mu\text{m}$  (male). All leg segments are present but an alteration in their proportions and a fusion of several podomeres occurred.

In free-living Astigmata normally the tarsus is the longest segment in each leg. In *L. leuckarti*, however, in leg I and II the femur is the longest podomere. Especially femur I is exceptionally elongated (fig. 22). Femur and genu of legs III and IV are fused. Regarded as one leg segment they constitute the longest leg section and are the analogy to the femur of leg I and II. The length of tarsi differs only slightly from the length of the other leg segments, but tibia and tarsus of legs I and II are fused which is equivalent to an elongation of the last leg section.

For comparison of the legs of *L. leuckarti* and *Caloglyphus berlesei* see (figs. 23–26).



Figs. 20–22. *Listrophorus leuckarti*. – 20. Female (scale bar: 50  $\mu$ m); – 21. propodosoma, integument removed in the region of leg I; CE = caudal extension of endoskeleton I ("sternum"), EI = endoskeleton I, RE = rostral extension of endoskeleton I, S = skeletal rods articulating with the gnathosoma, T = tegmen; – 22. female; leg I, medial view; F = femur (scale bars: 10  $\mu$ m).

Altogether in *L. leuckarti* a limitation in the motility of legs has taken place. The number of joints in all legs has been reduced from five like in free-living forms to four. – The legs II are extremely bent medially.

#### 8.2.2. Musculature

For the arrangement of the leg musculature see (figs. 27–33). The adductors of trochanter I and II are better developed as the corresponding muscles of legs III and IV.

Like in all Astigmata extensors of the trochanter-femur joints are inserted outside the leg tube, the flexors extend from the dorsal side of trochanter to the ventral border of the femur. As a result of fusion the musculature of the other leg segments is strongly simplified.

In spite of an articulation between femur and genu of legs I and II the genu is not provided with musculature. Flexion is performed passively by strong flexion of the last two segments, when the ventral border of the tibia presses on the genu.

### 8.2.3. Ambulacra

The structure of the ambulacra is very uniform. The nomenclature of component parts used here follows ATYEO (1978).

The tarsus ends in a short stalk (ambulacral stalk) to which the ambulacral disc is attached (fig. 34). The disc is not a massive structure but is kept in form by filling with haemolymph. Internally there are several sclerites (fig. 35). The sclerites are dominated by the basilar piece (BP) and the modified claw (Cl) which are both obviously fused. Additionally a condylophore guide (CG) and a pair of small sclerites (unguiform sclerites US) occur. The latter probably serve to stabilize the disc (ATYEO 1978). The basilar piece articulates with two condylophores (C). The ambulacral disc can be tilted over this axis. In SEM-preparations the position of the joint is clearly recognizable as a furrow traversing the disc.

Two pairs of muscles (two levators, two depressors), originating at the tibia, send tendons (one for each muscle) into the ambulacral disc. In free-living Astigmata the tendons of levators terminate dorsally in the cuticle of the pretarsus, the depressors at the proximal end of the basilar piece. In *L. leuckarti* the course of the tendons could not be observed.

On its distal end the ambulacral disc bears two semicircular flaps that contain no sclerites. (In light microscopic observation they can easily be overlooked. Thus they are missing in the drawings of PAGENSTECHER 1861a and WILSON & LAWRENCE 1967.) The flaps are divided into two parts by a fan-shaped structure (FSS) that narrows proximally and appears to run into the ambulacral stalk. With the aid of these structures the ambulacral disc is folded in itself immediately before lifting the leg.

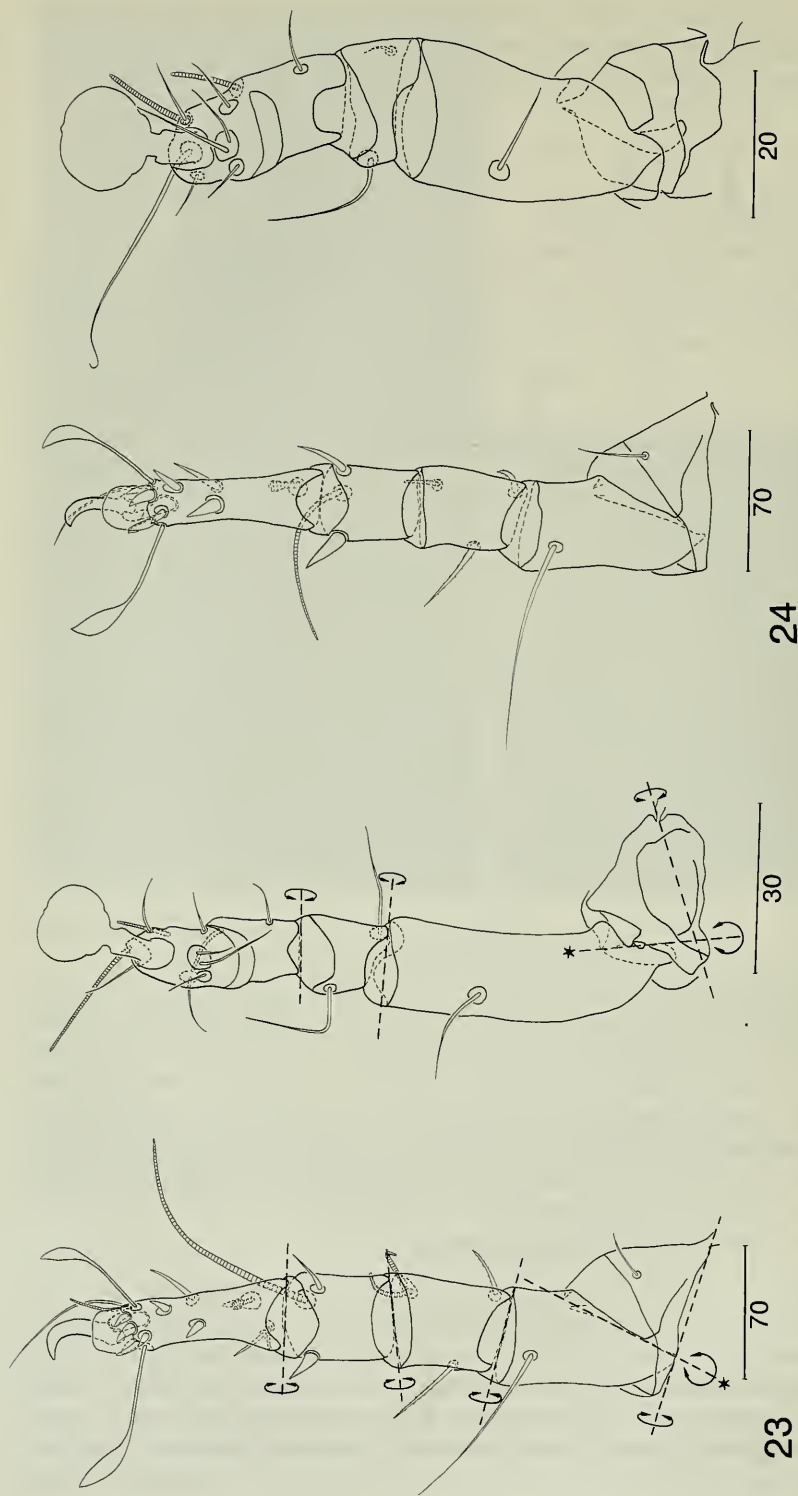
The ventral face of the ambulacral disc is irregularly corrugated (fig. 34).

### 8.2.4. Life Observations

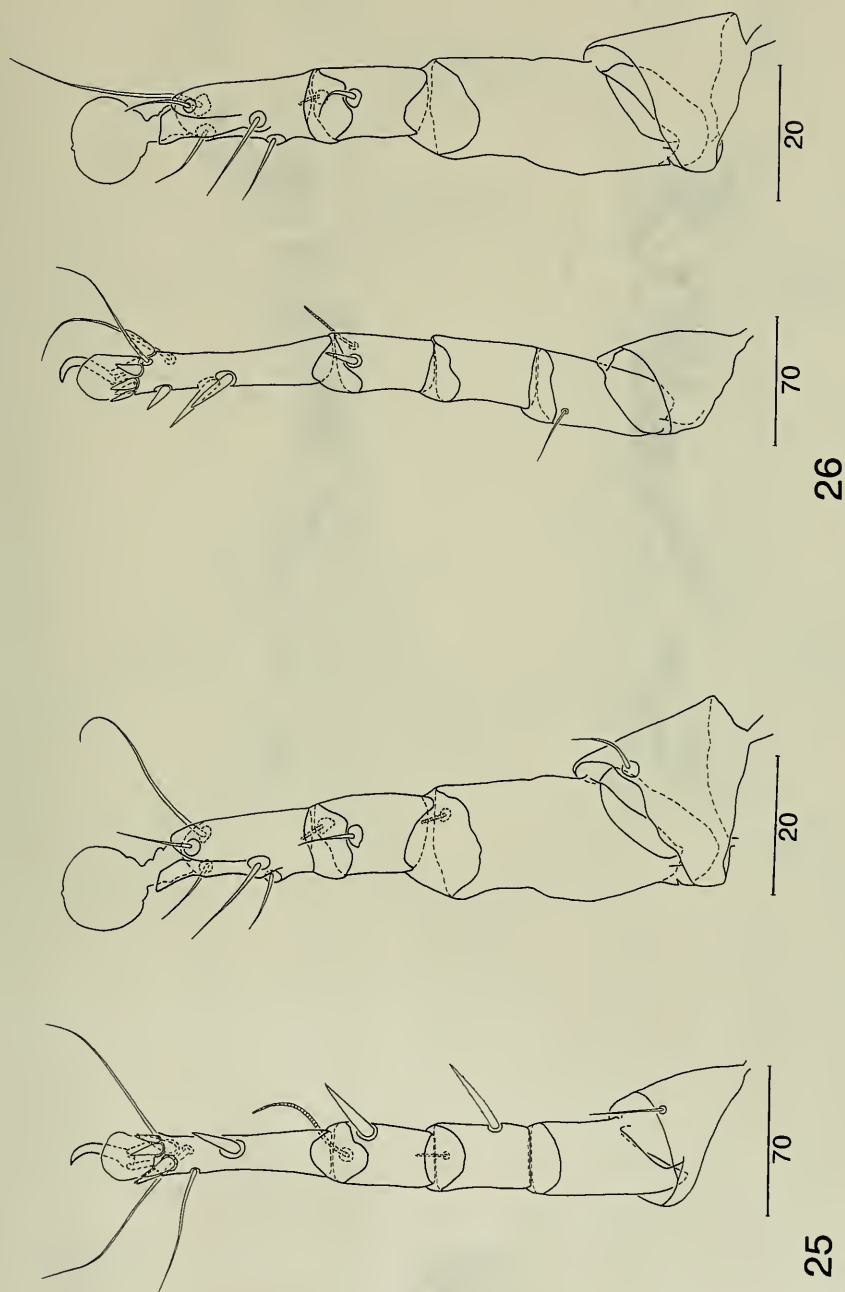
The mites live exclusively on the hairs of their host. When staying or moving on a hair the gnathosoma always points towards the root of the hair. In this orientation the animals walk back and forth. By doing so the hair is loosely embraced by the clasping flaps so that the hair is practically "threaded" through the clasping apparatus. Since the clasping flaps are located between coxae I, legs I can not reach the surface of the hair and have ceased to participate in normal walking. They are now mainly used as feelers and are permanently moved up and down. Additionally, with the aid of legs I, the mites pull themselves to another hair. If the mite walks on smooth surfaces (glass, paper) all legs are used.

## 8.3. Discussion

Since the mites are moving exclusively on the hairs of their host several heavy modifications and simplifications of the locomotion apparatus took place during their evolution. In the course of the formation of the clasping apparatus legs I could no longer participate in walking. Finally their contribution to locomotion was confined to pulling the mite to another hair. This is the reason why the ambulacra of legs



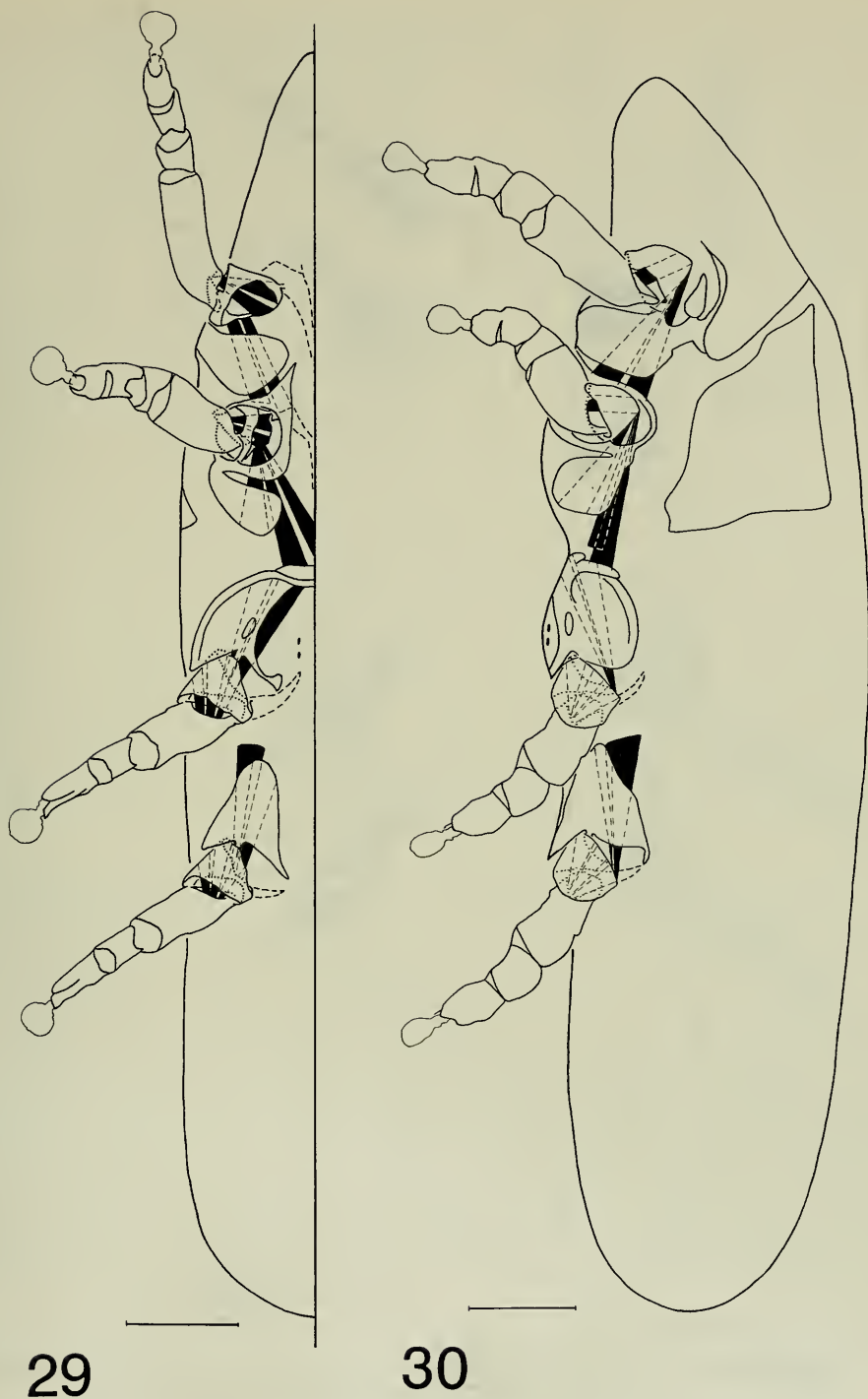
Figs. 23–24. *Caloglyphus berlessei*, female (left) and *Listrophorus leuckarti*, female (right), legs in comparison. — 23. Legs I; — 24. Legs II. — The legs are drawn to the same size. — *Explications*: Broken lines = rotational axes, the axes marked with an asterisk traverse obliquely the paper plane. — Scale bars in  $\mu\text{m}$ .



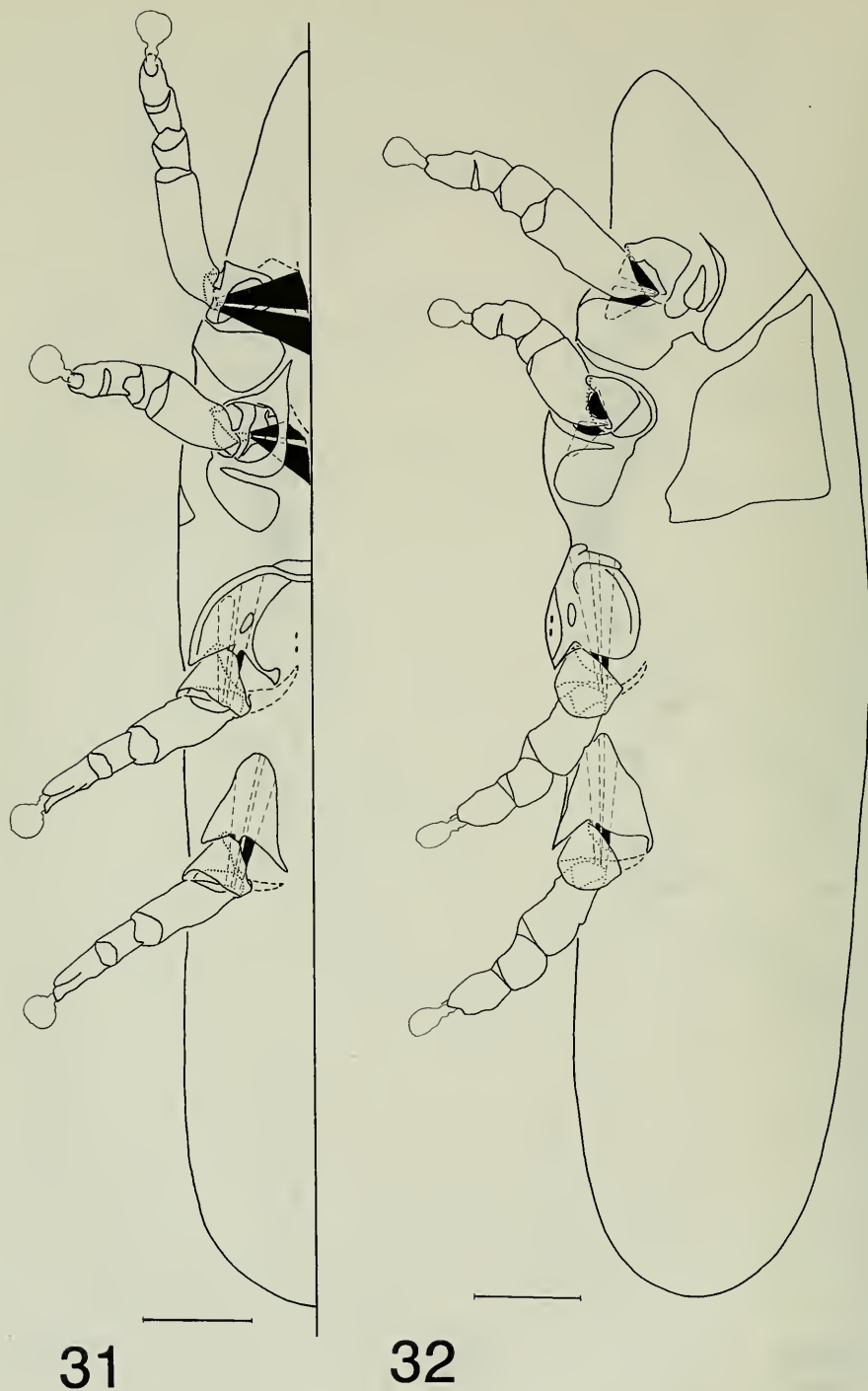
Figs. 25-26. *Caloglyphus berlesei*, female (left) and *Listrophorus leuckarti*, female (right), legs in comparison. — 25. Legs III; — 26. Legs IV. — The legs are drawn to the same size. — Scale bars in μm.



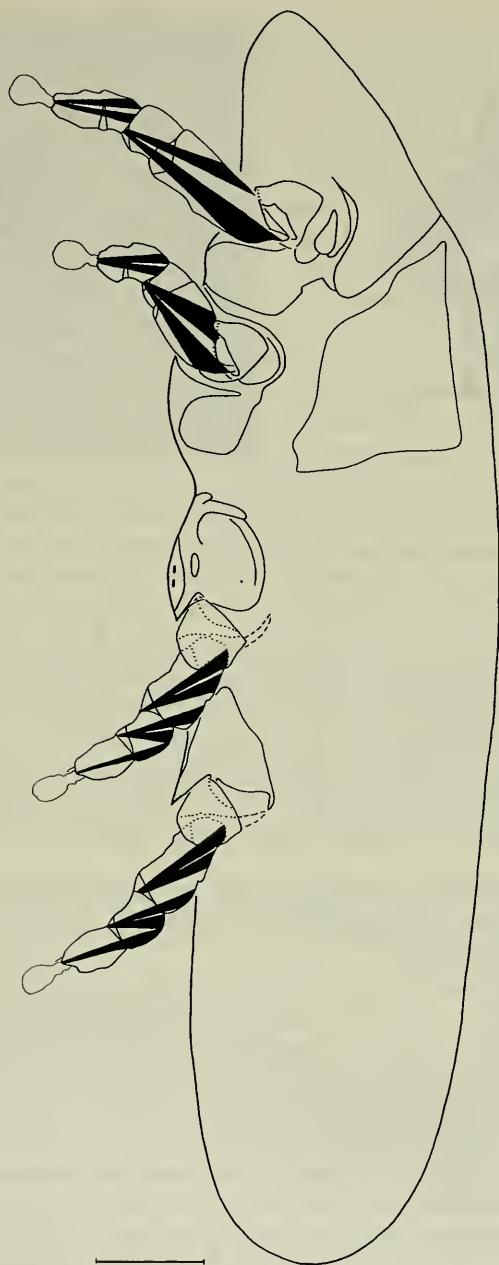
Figs. 27–28. *Listrophorus leuckarti*, female; adductors of trochanter I–IV. – 27. Ventral view; – 28. lateral view. – Scale bars: 40  $\mu$ m.



Figs. 29–30. *Listrophorus leuckarti*, female; abductors of trochanter I–IV, flexors of femur I–IV. — 29. Ventral view; — 30. lateral view. — Scale bars: 40 μm.



Figs. 31–32. *Listrophorus leuckarti*, female; extensors of femur I–IV. — 31. Ventral view; — 32. lateral view. — Scale bars: 40  $\mu$ m.



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Fig. 33. *Listrophorus leuckarti*, female, lateral view; flexors of tibia I-IV and tarsus III and IV; musculature of ambulatory discs. — Scale bar: 40  $\mu$ m.

I were not reduced. On the other hand it opened the possibility to change their function. They took now the role of feelers. For the new function long legs were advantageous since in this way a larger surrounding could be reconnoitred. This may explain the extreme elongation of femur I.

By the orientation of the mite in the long axis of the hair, and even more by grasping of the hair by the clasping apparatus, the position of the hair relative to the mite is precisely determined. Only the diameter of the hair can vary. This led to a shift of the articulation points of legs II to IV towards the median line. Finally these legs articulated along a line parallel to the hair.

As during walking the hair is directed through the clasping apparatus the distance between the body and the hair at the level of leg II is necessarily very small. Therefore, legs II are bent inwards and are shorter than the following legs.

Since the mites do not walk on highly variable substrates but on smooth and identically shaped hairs subtle movements of correction were no longer required. This led to the fusion of leg segments and to the reduction of leg musculature.

Most authors believe the ambulacral discs to act like suckers (FAIN 1971, 1973a; MIRONOV 1987). This, however, is not consistent with their anatomy. Neither the ambulacral disc is formed like a sucker, nor there are any devices (muscles, tendons) to produce a negative pressure between cuticle and the ground surface. The observations made by ATYEO (1978) in SEM-preparations that the ventral side of the disc is always shaped concave, are probably due to an artifact. Moreover, the ventral corrugating reaching the edge of the ambulacral disc makes the generating of a vacuum unlikely. More plausible is the assumption that adhering to the substrate is accomplished by adhesion. Because of the adsorption of water from the air all surfaces are covered by a thin layer of water. The tight contact between cuticle and ground can probably be achieved by this thin water film. Another possibility may be the secretion of a sticking fluid, as it occurs in insects (NACHTIGALL 1974; BAUCHHENS 1979).

Immediately before lifting the leg, the area of contact is minimized by folding of the ambulacral disc. By this mechanism the energy costs for detaching the leg is obviously kept at a minimum.

A comparison with the informations given by HUGHES (1954) on the locomotion apparatus is impossible and one has the impression that the author describes a completely different species. To give an example: in his fig. 19 he shows leg III including its musculature. According to his drawing all segments are not only connected by joints but also are provided with musculature. Even more uncomprehensible is that he depicts extensor musculature for genu, tibia and tarsus. These muscles, however – if they existed – would act as flexors. This is not surprising since in a hinge joint extensors are possible only in a certain configuration (an example is shown by MANTON 1956). WOOLLEY (1988: 101) adopts this slip without criticism. FAIN (1971) even takes "cinq articles libres" in all legs as part of his definition of the family Listrophoridae.

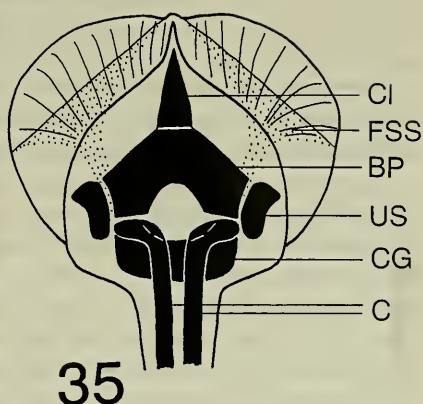
#### 8.4. Some Remarks on the Hydraulic Mechanism of Joint Extension in Chelicerata

The extension of certain leg joints by filling the space which is surrounded by the articular membrane with haemolymph is widespread among the Chelicerata (PARRY



Fig. 34. *Listrophorus leuckarti*, female; ambulacra of legs I. — Scale bar: 5  $\mu$ m.

Fig. 35. *Listrophorus leuckarti*; schematic drawing of the ambulacrum. — Abbreviations: BP = basilar piece, C = condylophores, CG = condylophore guide, Cl = claw, FSS = fan-shaped structure, US = unguiform sclerite.



1960). Up to the present quantitative investigations on this mechanism were carried out only in spiders (PARRY & BROWN 1959a, b; WILSON & BULLOCK 1973; STEWART & MARTIN 1974; ANDERSON & PRESTWICH 1975; BLICKHAN & BARTH 1985). The joints in question are the femur-patella joint and the tibia-metatarsus joint. Most of the previous studies are confined to pure measuring without introducing any quantitative model to explain the results. Only PARRY & BROWN (1959a, b) and BLICKHAN & BARTH (1985) attempt to link the relevant quantities in a quantitative way.

The haemolymph pressure of spiders is mainly determined by the muscoli laterales (WILSON 1970; ANDERSON & PRESTWICH 1975). They run from the carapax to the lateral pleura. Three levels of pressure are unanimously recorded by all investigators in all animals used for study (ANDERSON & PRESTWICH 1975):

- 13–67 hPa: the spider is resting;
- 40–80 hPa: the spider walks normally;
- 600–640 hPa: the spider is agitated.

Many authors draw the conclusion that for each joint-extension the muscoli laterales have to contract ("pressure pump") (ANDERSON & PRESTWICH 1975; FOELIX 1979: 19; analogous suggestions also for Gamasina in AKIMOV & YASTREBTSOV 1988). ANDERSON & PRESTWICH (1975) even see an advantage in the extension of legs by hydraulics, arguing that since there was no need for extensors in the legs the flexors could be enlarged which might facilitate the overcoming of prey. This view, however, is inconsistent with the normal gait of spiders. Here during the bending of one leg another leg is simultaneously straightened (FOELIX 1979: 132). Under these conditions the flexors would always have to work against increased pressure and no advantage is evident (MANTON 1973).

For the extension mechanism therefore the following model is proposed which would be valid in principle also for mites (fig. 36):

During flexion the haemolymph content  $v$  of the joint is pressed into the prosoma (reservoir). If the contraction state of muscles in the prosoma (thread) remains unchanged the cuticle (elastic wall) is expanded and potential energy stored. The pressure in the whole system increases. If the flexors slacken the haemolymph flows

from the prosoma into the joint. By doing this the potential energy of the cuticle is transformed into kinetic energy. With each bending the flexor muscle has thus to provide additionally the energy for the joint extension.

If the hydrostatic pressure in the system increases by contraction of the body musculature the pre-stressing of the cuticle is higher. Straightening now is faster since with the higher level of pressure the haemolymph flows faster into the joint. At equal  $v$  a larger amount of energy is made available (a technical analogy can be seen in the bow and arrow: by increasing the pre-stressing of the string the same maximal elongation which is determined by the length of the arm generates a greater accelerating force on the arrow).

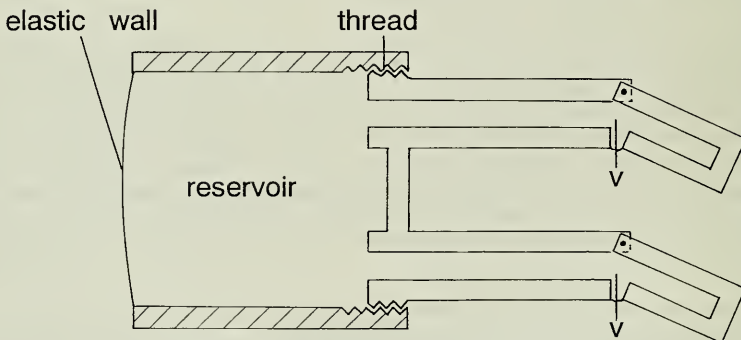
In the resting spider the haemolymph pressure will be decreased, probably to allow the legs to lie against the body without muscle activity.

Whether mites are also able to regulate their walking speed by altering the hydrostatic pressure must be a subject for future research.

At first sight this mechanism of straightening the legs seems energetically very inefficient since by displacing of haemolymph over long distances through the crevices between muscles, nerves and body wall energy losses occur as a result of fluid friction. By insertion of extensible cuticle areas in close vicinity to the joint suitable for taking up the displaced haemolymph, these flows could be minimized to a great extent. The flows during leg movement, however, have the side effect that the flexor musculature is bathed by the haemolymph. The hydraulic mechanism therefore might at the same time serve as a partial substitute for a missing or poorly developed circulatory system. This assumption is supported by the fact that precisely the distal leg segments are straightened by this principle.

In this way the activity of musculature and the supply of nutrients would be coupled, walking speed and pumping power would be co-ordinated at all times.

In view of its possible double function the hydraulic mechanism no longer seems to be inefficient but to be an extremely elegant "biological design".



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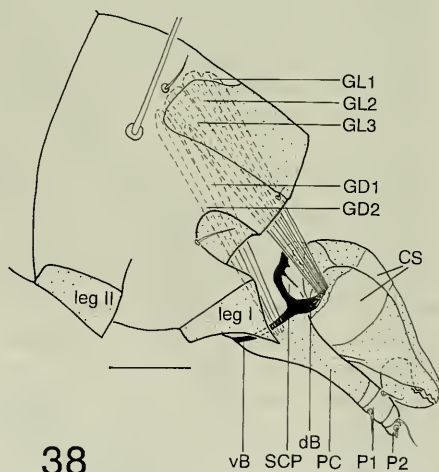
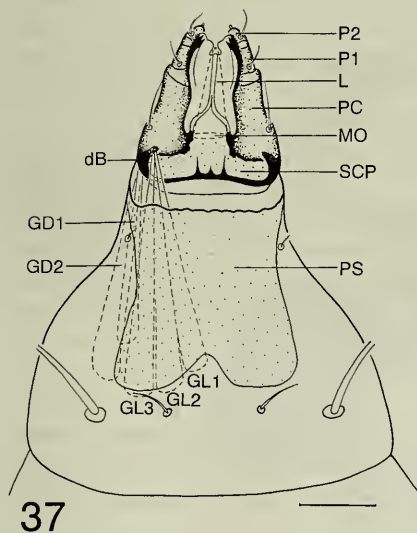
Fig. 36. Model of the joint extension in chelicerata, longitudinal section; the analogy to the flexor musculature is omitted. — Abbreviation:  $v$  = joint volume.

## 9. Gnathosoma and Clasping Apparatus

### 9.1. Previous Knowledge

Up to now the gnathosoma of astigmatic mites was most exactly described by HUGHES (1953), PRASSE (1967) and BRODY et alii (1972). Supplemented by my own observations at *Caloglyphus berlesei* the following general picture can be given (figs. 37–38).

The rigid frame for the whole gnathosoma is constituted by the hypognathosoma (subcapitulum) which has arisen from the fusion of the palp coxae (PC) in their proximal parts. Ventrally the hypognathosoma is continuous with the hypostome which forms most of the ventral face of the gnathosoma and lies between the distal portion of the palps. The palp coxae continue in two movable podomeres (P1, P2). They are moved by musculature originating in the palp coxae. Dorsally there are the chelicerae which are inserted into a short cuticular tube known as the cheliceral sheath (CS). Anteriorly the sheath is attached to the cheliceral shaft which is the proximal hollow part of the chelicera. Posteriorly the sheath fuses with the idiosoma. At the cheliceral shaft strong retractor musculature is inserted. It originates at the sejugal furrow and between the sejugal furrow and the propodosomatal sclerite (PS). Protraction of the chelicerae is accomplished by haemolymph pressure. Between the chelicerae the labrum (L) is located which is a long tongue-like structure tapering anteriorly. The space between the labrum and the hypostome is called "buccal cavity". It merges into the pharynx. Dorsal to the pharynx there is the subcheliceral plate (SCP) (epistome) which is a posterior elongation of the dorsal wall of the palp coxae. Its posterior edge



Figs. 37–38. *Caloglyphus berlesei*, female; proterosoma, integument removed in the rostral region; sclerotized parts dotted. — 37. Dorsal view, chelicerae omitted; — 38. lateral view. — Abbreviations: CS = cheliceral sheath, dB = dorsal branch of stabilizing ledge, GD = gnathosomal depressors, GL = gnathosomal levators, L = labrum, MO = mouth opening, P1, P2 = podomeres of palp, PC = palp coxa, PS = propodosomatal shield, SCP = subcheliceral plate, vB = ventral branch of stabilizing ledge. — Scale bars: 50  $\mu$ m.

is accompanied by a ledge which branches at the posterior margin of each palp coxae. One branch runs dorsally and frames the chelicera for a short distance the other branch follows the posterior border of the palp coxa. The gnathosoma is moved by two groups of muscles at each side. Three fillets (GL1, GL2, GL3) extend between the posterior margin of the propodosomatal sclerite and the dorsal branch of the ledge mentioned above. Two muscles (GD1, GD2) take a course from the lateral margin of the propodosomatal sclerite to the proximal end of the palp coxae. These muscles allow bending and retraction of the gnathosoma. Protraction is performed by hydraulic pressure.

## 9.2. Results

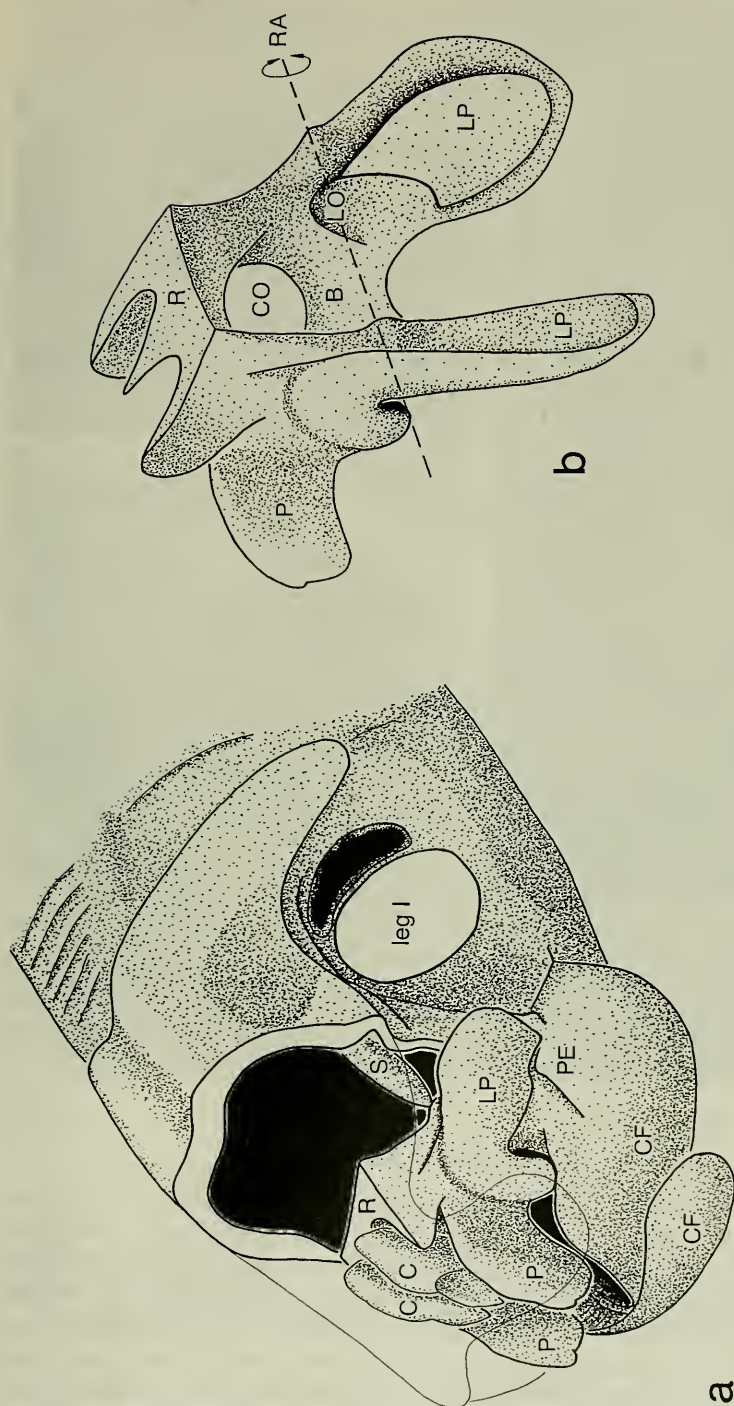
### 9.2.1. Skeletal System

Most part of the gnathosoma is hidden under the heavily sclerotized tegmen (fig. 40). It has a well developed endoskeleton (fig. 39) which is formed by a chitinous frame on which two arched structures (lateral plates LP) are laterally attached. The lateral plates on the one hand are connected with the bottom (B) of the gnathosomal frame, on the other hand via a strong strut with the lateral walls of the gnathosomal frame. In frontal aspect this results in a structure with a large opening (CO) in its center and two smaller lateral breaches (LO). The caudal ends of the lateral plates pass beyond the gnathosomal frame. This caudal part is hollow and slightly bent ventromedially. The wall which follows the outline of the lateral plate is thickened. In the roof (R) of the gnathosomal frame there are two openings serving as guides for the chelicerae (C). At its rear edge there is a narrow projection to which the pharynx musculature attaches. The anterior borders of the two lateral openings are continuous with the soft walled palps (P). Distally they are bent outwards so that adjoined they result in a broad piston (fig. 40). The gnathosoma articulates with two skeletal rods (S) which themselves articulate with the endoskeleton I.

The clasping flaps (CF) are a derivative of the integument (fig. 42). They extend from the posterior end of the sternum of legs I to the anterior border of the gnathosomal frame. Their outer surface is partly sclerotized, their inner surface is soft. TEM-sections reveal that the material of the flaps contains fibres to a great extent (figs. 44–45). The cuticle of the inner surface sits upon these fibres via small pillars. In their distal part the orientation of these fibres follows in its course the form of the flaps. At their ends the fibres fuse with the outer sclerotized wall of the flap or with apodemes originating there, respectively. At the outer face of the flap a small peg (PE) is easily seen (figs. 43, 49). It projects into a similarly formed groove at the ventral border of the lateral plate. The anterior arch of the lateral plate projects behind the clasping flap (fig. 49). Lateral plate and clasping flap are fused by elastic cuticle.

In regions which are often in tension fibres could be detected repeatedly. They occur:

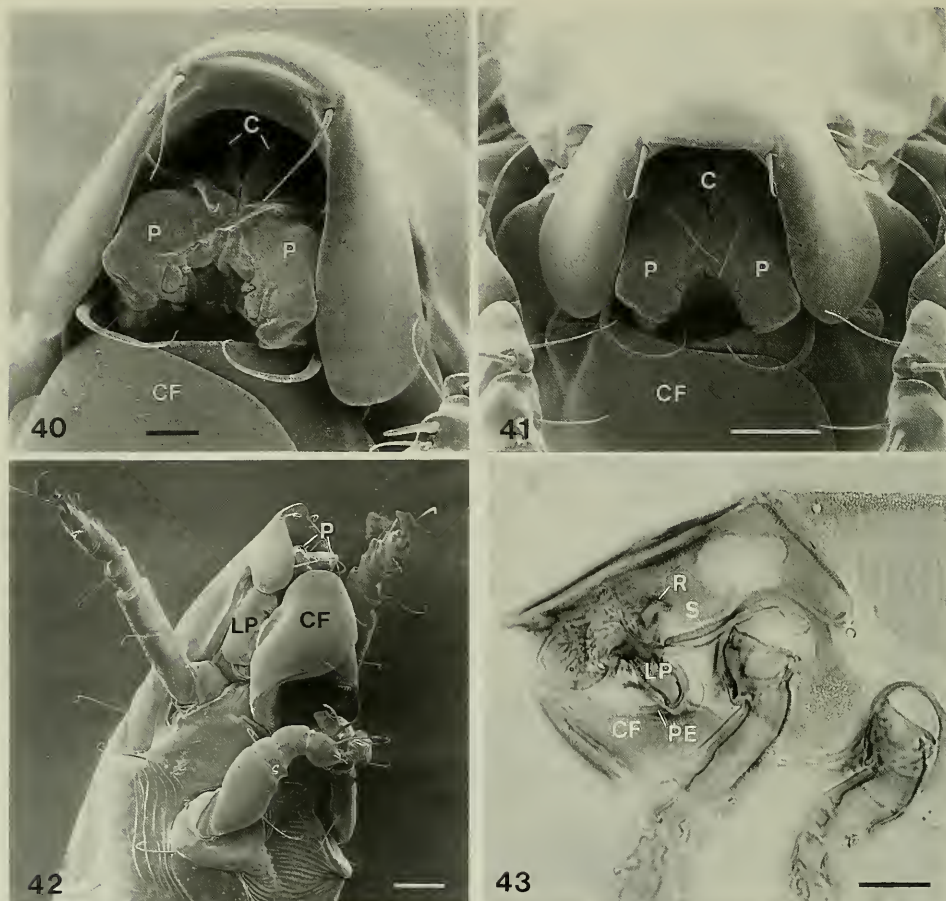
- 1.) between the bottom of the gnathosomal frame and the clasping flaps (fig. 46);
- 2.) between the endoskeleton I and the origin of the flaps as well as between the bases of the flaps;
- 3.) between the tegmen and the gnathosomal frame in close vicinity of the articulation of the gnathosomal frame (fig. 55).



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Figs. 39a-b.

*Listrophorus leuckarti*, clasper apparatus. - a. Anterior view, tegmen partly removed, leg I removed; - b. gnathosoma, posterior view, chelicerae omitted. - Abbreviations: B = bottom of gnathosomal frame, C = chelicera, CF = clasper flap, CO = central opening of gnathosomal frame, LO = lateral opening, LP = lateral plate, P = palp, PE = peg, R = roof of gnathosomal frame with guides for the chelicerae, RA = rotational axis of gnathosoma, S = skeletal rod.

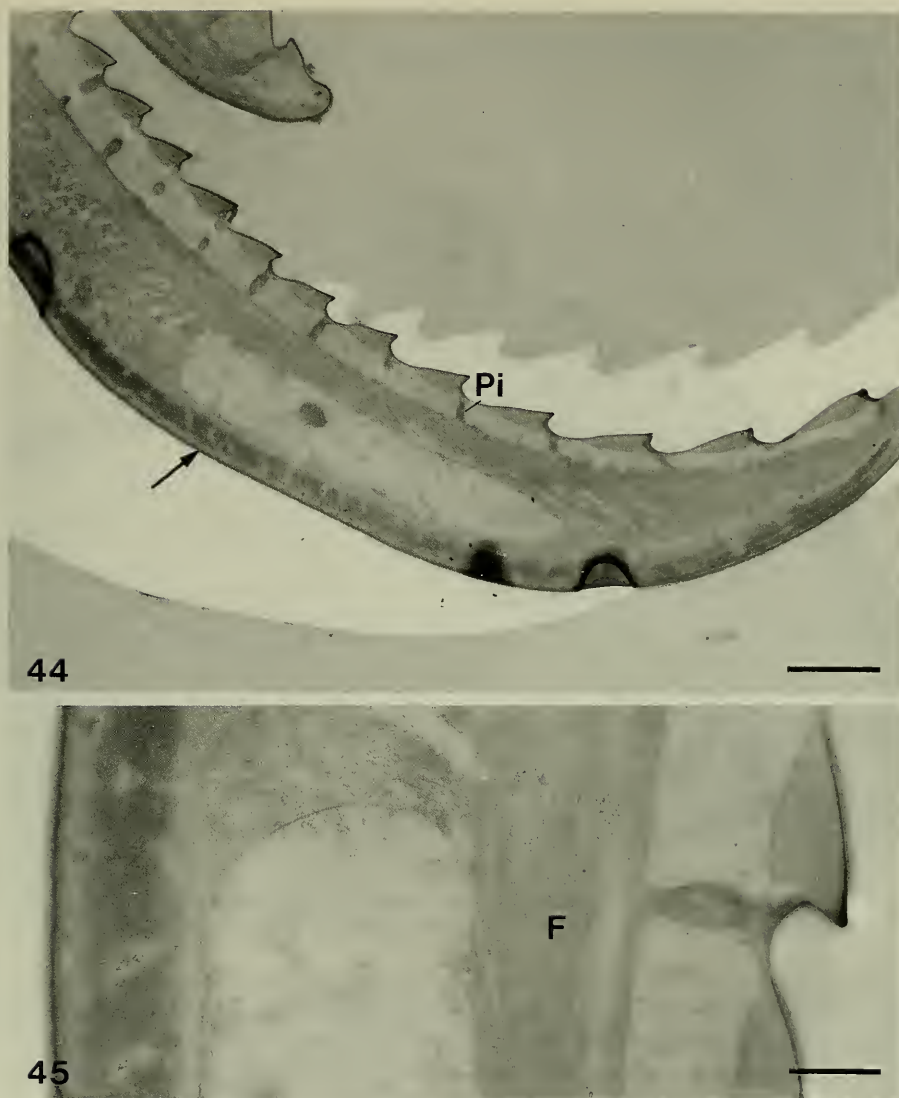


Figs. 40–43. *Listrophorus leuckarti*, female. – 40. Rostral end with mouth parts (C = chelicerae, CF = clasp ing flap, P = palp) (scale bar: 5  $\mu$ m); – 41. as in fig. 40 (scale bar: 10  $\mu$ m); – 42. proterosoma (CF = clasp ing flap, LP = lateral plate, P = palp) (scale bar: 20  $\mu$ m); – 43. proterosoma, whole mount in Hoyer's fluid (light micrograph; CF = clasp ing flap, LP = lateral plate, PE = peg, R = roof of gnathosomal frame, S = skeletal rod) (scale bar: 20  $\mu$ m).

### 9.2.2. Musculature

As mentioned in 8.2.1. the gnathosoma articulates with the idiosoma via two skeletal rods (S) (figs. 47–48). The joint allows only vertical movements. Lowering of the gnathosoma is accomplished by two depressors at each side of the body (GD1, GD2). GD2 is inserted laterally at the posterior margin of the tegmen. Its tendon turns around the articulation of leg I and ends at the ventral border of the lateral plate immediately anterior to the groove. GD1 arises from the tegmen dorsal to leg I and passes straight-lined to the same insertion point as GD2. Two levators (GL1, GL2) run from the posterior border of the tegmen to the roof of the gnathosomal frame.

The chelicerae are turned dorsally by two small muscles (CL1, CL2) which run in the middle of the tegmen. Three little bands of muscles (CD1, CD2, CD3) have their



Figs. 44–45. *Listrophorus leuckarti*, female. – 44. Claspings flaps; transverse section; outer surface sclerotized (arrow), the inner face shows the corrugation. The inner cuticle is connected via small chitinous pillars (*Pi*) with a layer of longitudinal fibres (scale bar: 2.5  $\mu$ m); – 45. detail; *F* = fibres (scale bar: 0.6  $\mu$ m).

origin at each side of the soft-walled region between the postscapular shields. They follow a course ventral to GL1, CL1 and CL2 and are inserted at the chelicerae.

The musculature of the palps is attached to the caudal part of the lateral plates.

### 9.2.3. Life Observations

The movement of the claspings flaps is always coupled with the movement of the gnathosoma. When the gnathosoma is lifted the caudal parts of the lateral plates press on the peg of the claspings flaps. As a result the flaps rotate medially and the claspings

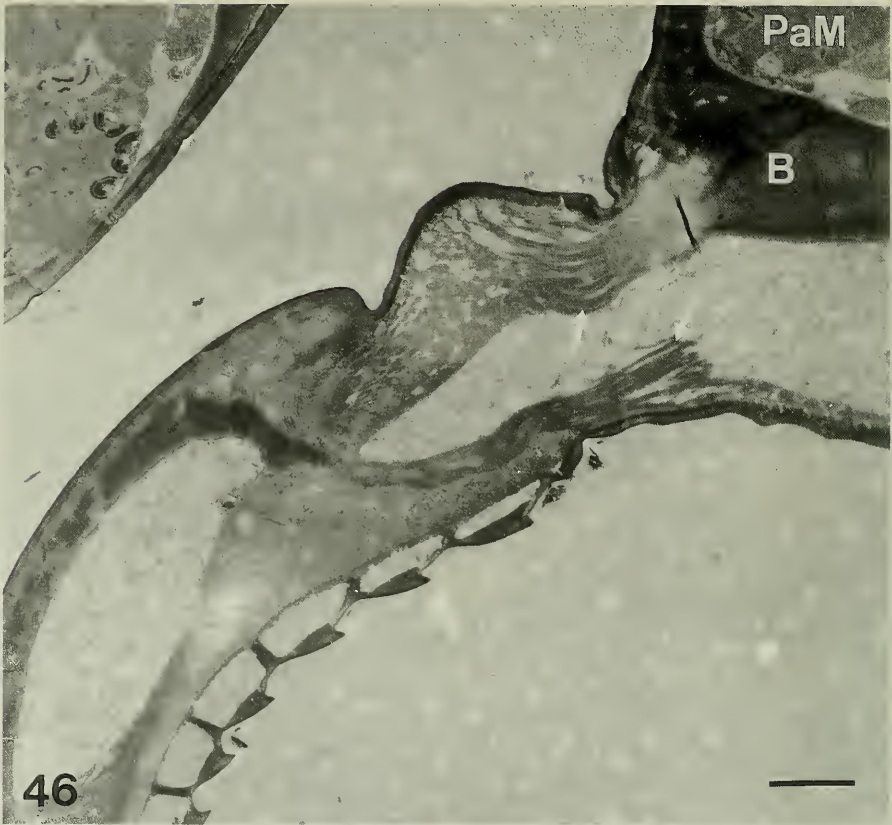


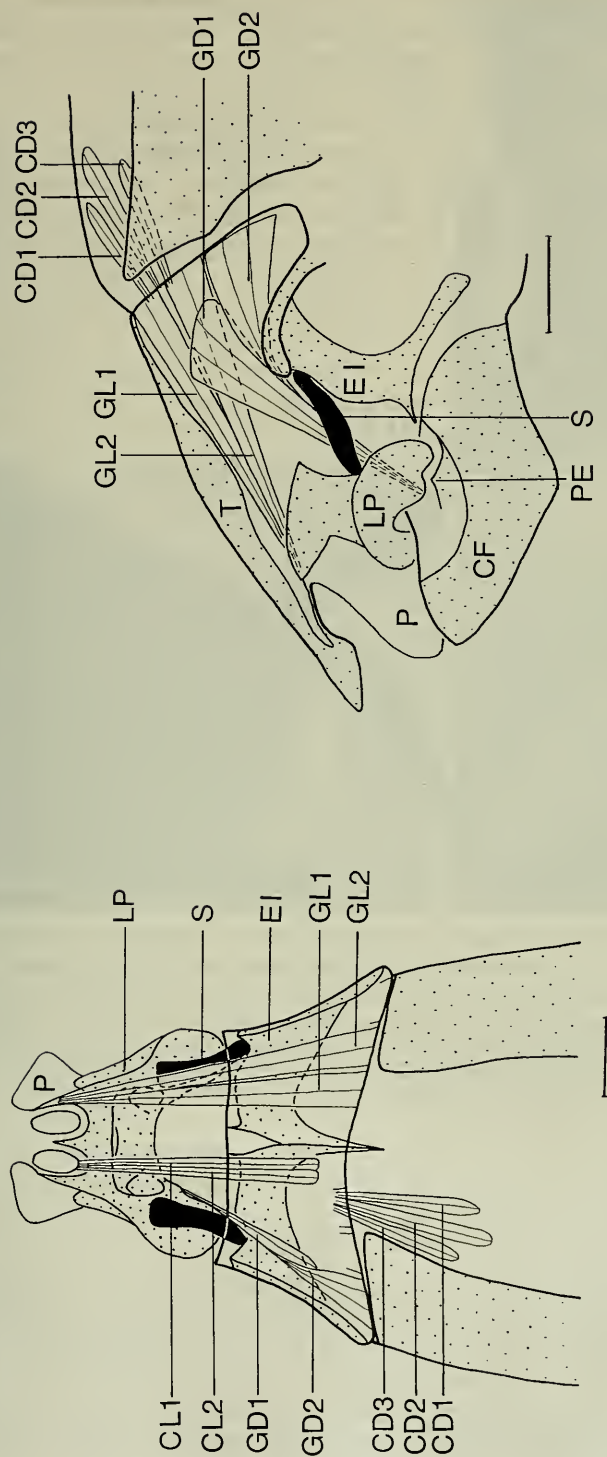
Fig. 46. *Listrophorus leuckarti*, female; gnathosoma with clasp flap; transverse section; stress fibres (arrows) run from the outer face of the clasp flap to the bottom (B) of the gnathosomal frame (PaM = palpal musculature) (scale bar: 2.5  $\mu$ m).

apparatus closes. Are the muscles relaxed the gnathosoma takes a median position at which the hair is embraced by the clasp flap without pinching it. Opening of the clasp flap is always combined with the lowering of the gnathosoma.

During the rotations of the gnathosoma the skeletal rods follow the movements by slight rotations around its articulation point with the endoskeleton I.

Immediately after entering a hair the mite tries to put the hair between the clasp flaps. If the animal is not disturbed it grasps the hair loosely. In this posture it can walk along the hair. This possibly corresponds to the relaxed state of the gnathosomal musculature. As a reaction on mechanical stimuli the gnathosoma is suddenly lifted and the hair thereby tightly embraced by the clasp apparatus. During this, legs I hang down laterally to the clasp flaps, the other legs lie alongside to the body. Shortly after the end of the stimulation the clasp apparatus is slackened and the mite continues to move.

As mentioned above the animals are always orientated towards the root of the hair. If they are disturbed (e. g. by light or heat) the mites try to evade the adverse condition and often take the opposite position. If one smoothes back the fur and watches them after a few minutes all mites are positioned again in the „right” manner.

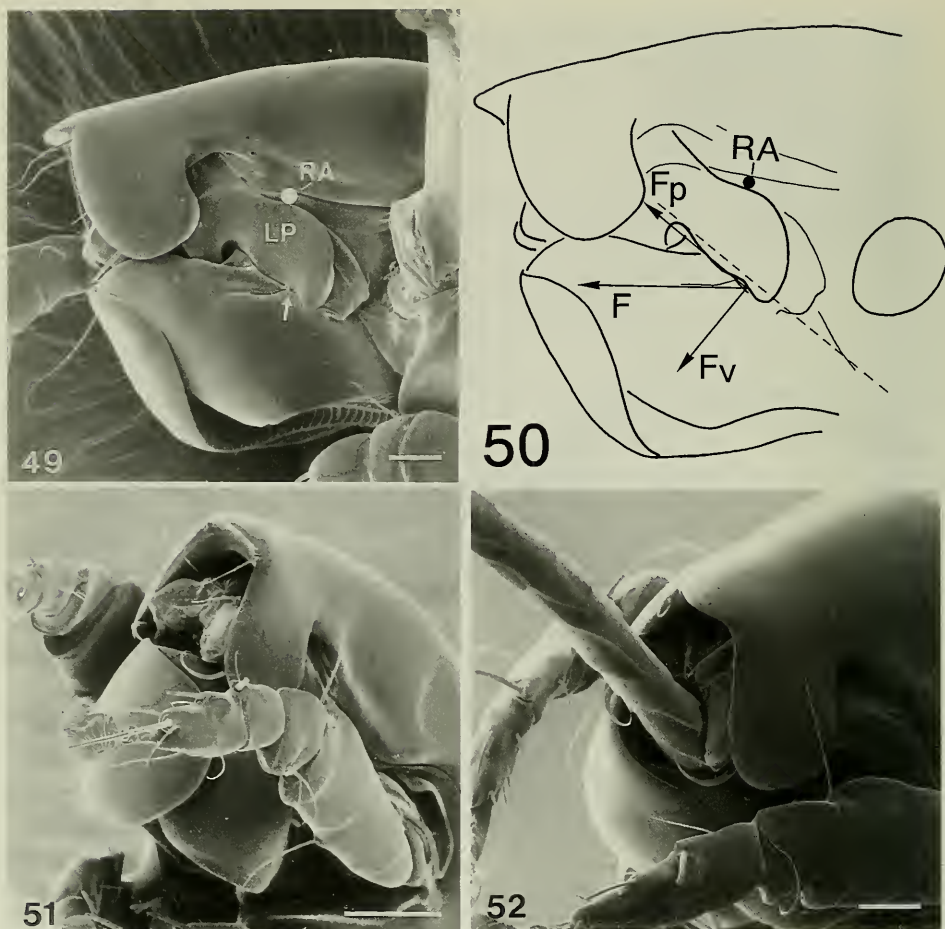


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48

Figs. 47-48.

*Listrophorus leuckarti*; propodosoma. - 47. dorsal view, integument removed in the region of the gnathosoma (CD = depressors of left chelicera, CL = levators of left chelicera, EI = endoskeleton I, GD = left gnathosomal depressors, GL = right gnathosomal levators, LP = lateral plate, P = palp, S = skeletal rod); - 48. lateral view, integument partly removed (CF = clasping flap, PE = tegmen). - Scale bars: 20  $\mu$ m.



Figs. 49–52. *Listrophorus leuckarti*, female. — 49. Lateral view, clasp apparatus ( $LP$  = lateral plate,  $RA$  = rotational axis of gnathosoma, *arrow* = peg) (scale bar:  $10\ \mu\text{m}$ ); — 50. schematic drawing after fig. 49: forces acting from the lateral plate on the clasp flap ( $F$  = force on the clasp flap,  $F_p$  = force component parallel to rotational axis of the clasp flaps,  $F_v$  = vertical force component,  $RA$  = rotational axis of gnathosoma); — 51. clasp apparatus (scale bar:  $20\ \mu\text{m}$ ); — 52. female clasp apparatus clamping a hair ( $10\ \mu\text{m}$ ).

### 9.3. Discussions

#### 9.3.1. Discussion of the Results

The lateral plates are undoubtedly the modified palp coxae. The roof of the gnathosomal frame can easily be derived from the subchelicerar plate, the hypognathosoma and the dorsal branches of the ledge. The tegmen having developed from the propodosomatal sclerite was already recognized by VITZTHUM (1943). The arrangement of the musculature is also compatible with the supposed homologies: GL1 and GL2 extend between the posterior margin of the propodosomatal sclerite (which is the tegmen in *L. leuckarti*) and the dorsal branch of the ledge of the subchelicerar

plate (which is incorporated into the roof of the gnathosomal frame). GD1 and GD2 originate from the lateral margin of the propodosomatal sclerite and end at the palp coxae which conforms with the situation in free-living Astigmata.

The muscles CD1, CD2 and CD3 are the depressors of the chelicerae.

For the two skeletal rods articulating the gnathosoma with the idiosoma no counterpart in other Astigmata is known.

The palp coxae function as levers. By lifting the gnathosoma the posterior border of the groove presses on the peg located at the clasping flap. The force thereby applied to the clasping flap can be resolved in a component  $F_p$  which runs parallel to the rotational axis of the clasping flap and a component  $F_v$  perpendicular to  $F_p$  (fig. 50). Whether there exists a third component perpendicular to  $F_p$  and  $F_v$  cannot be decided.  $F_p$  leads to a shifting of the clasping flaps in the rostral direction. This dislocation probably is limited by the fibres between the bases of the flaps and the endoskeleton I. The component  $F_v$  together with another force (couple!) results in a torque which causes the rotation of the flaps in the medial direction and thus the closing of the organ. This second force could be produced by the stress fibres between the basis of the flaps and the endoskeleton I and/or the fibres running from the bottom of the gnathosomal frame to the flaps.

To guarantee the stability for taking up the forces the borders of the palp coxae are thickened. Contrary to this the sclerotization of the two distal palp segments is strongly reduced. By being bent outwards distally a mould for the hair is formed (fig. 41). When strongly clasped the hair can be completely enclosed by the clasping flaps and the palps (figs. 51–52). By this the clasping flaps press the hair against the palps. As the distal ends of the palps and the inner surface of the clasping flaps are supplied they constitute paddings which closely fit to the surface of the hair and are well suited for taking up the pressure. The intensified insertion of fibres into the clasping flaps increases their stiffness and makes them less deformable. Whether the legs I hanging downwards laterally really help in closing the apparatus by pressing the flaps together as mentioned by FAIR first as a possibility (1971) and later as a fact (1984) must be left in obedience. Apparently O'CONNOR (1982) referred to these statements when he declared that the first pair of legs of listrophorids to be "somewhat modified for holding the hair of the host".

In order to move to another hair the flaps have to be actively forced apart. As described above the clasping apparatus can only be opened if the gnathosoma is lowered. As there exists a cuticular connection between the palp coxae and the flaps the coxae pull at the flaps (fig. 49). A further contribution probably comes from the anterior arch of the coxae. During lowering of the gnathosoma it presses most probably on the inner border of the clasping flap and turns the flap aside. Apart from this there are certainly minor mechanical influences from other regions of the cuticle. During the opening the clasping flaps are stretched apart at their bases. This may explain the fibres occurring there.

By the connection of the gnathosoma with the endoskeleton I via two skeletal rods resistant to compression, shifting of the gnathosoma during its rotation is avoided and it is ensured that the contact of the parts acting on each other is not lost.

The elongated body shape, the clasping apparatus, the enlarged propodosomatal sclerite and the orientation of the mite on the hair prevent the mites from being stripped off while the host cleans its fur. As the mechanical impacts during cleaning mainly come from the direction of the hair root the mites confront with this "threat"

by the strongly sclerotized tegmen. The shape of the tegmen guarantees in the case of a closed clasping organ for a smooth transition between the hair and the mite at its rostral end. In this configuration the forces exerted on the mite have nearly no working surface.

Anatomical comparison by light microscopy with species of the listrophorid genera *Afrolistrophorus*, *Sclerolistrophorus*, *Metalistrophorus*, *Prolistrophorus*, *Spalacarus*, *Leporacarus* and *Lynxacarus* revealed a great uniformity in the design of the clasping apparatus. Differences affect only the form and proportions of the structural elements. It may be concluded that the apparatus functions in the same manner in all listrophorids.

### 9.3.2. Discussion of Previous Investigations of the Clasping Apparatus

Since the first description there were many attempts to understand the form and the function of the clasping organ of listrophorids.

PAGENSTECHER (1861a) gives a first interpretation of the gnathosomal elements. It presents, however, numerous errors. The chelicerae are erroneously regarded as a "pair of oval pits" ("Paar ovaler Grübchen") located at the dorsal surface of the tegmen. From this mistake results a misinterpretation of all other structural parts. As the palps thus become the first gnathosomal appendages PAGENSTECHER believes their distal parts to be "mandibles" (= chelicerae). Their sclerotized portions are supposed to be the "maxillar lobes" which fuse beneath the mouth ("die unter der Mundöffnung verwachsenen Maxillarlappen"). The clasping flaps are the "maxillar palps" ("Maxillartaster"). The position of the mouth, though, is mainly correct.

As previously mentioned the mites which PAGENSTECHER received were mostly dead and had been removed from their host. Despite of his remark that the "mandibles" were found in different positions the motility of the whole gnathosoma thus remained unknown to him. In his description of *Leporacarus gibbus* published in the same year PAGENSTECHER (1861b) persists in his opinion about the anatomy of the gnathosoma (obviously PAGENSTECHER had again received the mites isolated from their host).

The first observations on the function of the peculiar gnathosomal elements in listrophorids are given by CLAPARÈDE (1868). He recognizes the "maxillar palps" as movable clasping organs by which the hair is embraced, but as to the anatomy of the gnathosoma there are no differences between his and PAGENSTECHER's text.

MÉGNIN (1878), however, has another notion of the structure of the mouth parts. Without reference in the text his illustration of *Leporacarus gibbus* shows chelicerae as well as three-segmented palps in front of the clasping flaps separate from them. This describes the situation essentially correct.

With regard to the structure of the gnathosoma of *Metalistrophorus pagenstecheri* HALLER (1880) principally arrives at the same result as MÉGNIN and approves of this author's drawings. The palps and the chelicerae are properly specified the thickened walls in the proximal part of the palps are mentioned and the true site of the mouth is identified. Although HALLER has realized that the clasping flaps are "derivatives of the body wall" ("Derivate der Körperdecke") he believes them to be inserted dorsally.

In BERLESE (1897) two very detailed drawings of the gnathosomal region are given. Concerning the palps and the chelicerae there is no difference from MÉGNIN and HALLER. The clasping flaps, however, are designated as maxillae although they are correctly described and figured.

GUNTHER (1942) also interprets the clasping flaps as modified maxillae.

VITZTHUM (1943) regards the clasping flaps as "malae externae" of the maxillae. Moreover he describes the behaviour of the mites on a hair very well.

In his anatomical investigation on *L. leuckarti*<sup>2)</sup> HUGHES (1954) gives a very detailed description of the clasping organ. In his opinion the gnathosoma is the whole anterior part of the animal terminating at the articulation of legs I. Consequently the gnathosoma sensu HUGHES does no longer articulate with the idiosoma but has a rigid connection with it. Further stiffening of the gnathosomal region is supposed to be achieved by an extension of epimera of leg I which articulates with the "heavily chitinized" palp coxae. By "palp coxae" according to his fig. 1 HUGHES means the space between leg I and the proximal part of the palp which is in fact soft-walled. Additional rigidity is to be realized by "a forward extension from the dorsal walls of the coxae I running obliquely forwards and upwards inside the gnathosoma". This can only be the skeletal rod which articulates with the gnathosoma and the endoskeleton I. Moreover the lateral borders of the tegmen are supposed to articulate with the "palp coxae" and these laterally bear the clasping flaps which are interpreted by him as the endites of palps. From this follows that their basal parts terminate with the posterior arch of the palp coxae and not — as is true — behind the anterior arch. The palp coxae are described to be united dorsally by a narrow bridge of chitin from which the "anterior pair of pharyngeal dilators" arise. Undoubtedly by this he means the posterior border of the gnathosomal frame which is in fact located far away from HUGHES' "palp coxae". According to HUGHES the "posterior second pair of pharyngeal dilators" have their origin at the tegmen but in reality they are the gnathosomal depressors. In his description of the remaining gnathosomal musculature there is also a lot of confusion. Two muscles for moving the clasping flaps are believed to run into both "palp coxae". The pertaining fig. 5, however, shows a traverse section of the posterior region of the gnathosomal frame. Hencefore, doubly wrong becomes right as the musculature mentioned is really palpal musculature and with the aid of it the soft part of the palp is moved. The muscle running from the tegmen to the "median wall of endite" and supposed to represent the "main adductor" is in fact a gnathosomal depressor.

Most surprising, however, is the statement that in life observations the mites were not able to open the clasping apparatus wide enough in order to leave the hair but had to walk off its tip. Even by low magnifications one can see that the opposite is true.

McDANIEL (1968) identifies the clasping flaps with the palps.

FAIN (1971, 1984) regards the clasping flaps as chitinous membranes protruding from the sternum. According to him the hair is clamped between the anterior border of the tegmen and the clasping flaps.

## 10. Digestive System and Nutrition

### 10.1. Previous Knowledge

On the digestive system of astigmatic mites an imposing number of investigations has already been published (HUGHES & HUGHES 1938; HUGHES 1950, 1954; Prasse 1967; ROHDE & OEMICK 1967; KUO & NESBITT 1970; BRODY et alii 1972; AKIMOV 1973; VIJAYAMBIKA & JOHN 1974, 1977; BAKER 1975; BAKER & KRANTZ 1985; TONGU et alii 1986; DESCH et alii 1991). Besides the studies of BRODY et alii (1972), TONGU et alii (1986) and DESCH et alii (1991) who also used electron microscopic techniques, these publications are exclusively based on light microscopic observations. Altogether they show that the alimentary canal of the Acaridida is formed very homogeneously in its basic structure. The differences mainly concern the fine structure of the gut cells and the number and distribution of the different cell types in the respective gut sections. These deviations, however, may also reflect variable phases in the digestive process or different stages of cell development. The nonuniformity in the methods applied complicates the evaluation of the previous findings which is given below.

<sup>2)</sup> According to HUGHES the listrophorids he used were collected from *Apodemus sylvaticus*. On this rodent, however, only *Afrolistrophorus apodemi* has been found. A determination was impossible because of the insufficiency of his drawings.

The digestive system of astigmatic mites can be divided into four sections which are based on the criterion of the presence or absence of a chitinous intima (HUGHES 1950; PRASSE 1967; BRODY et alii 1972; DESCH et alii 1991):

gnathosoma (with buccal cavity),  
foregut (= pharynx and esophagus),  
midgut (= stomach, colon and postcolon),  
hindgut (= rectum and anus).

The foregut and the hindgut are lined with cuticle. Between colon and postcolon malpighian tubules may communicate with the gut. In many species the stomach has two lateral expansions (caeca). All gut sections are accompanied by musculature.

During feeding the food particles are transported into the buccal cavity by the chelicerae by being alternately extruded and retracted. By doing this the subcapitulum serves as a rail. The digitus mobilis of the chelicera is lifted by a pinnate muscle. A smaller muscle opens the chelicera. Within the buccal cavity the food particles mingle with the fluid of the supracoxal glands. Salivary glands are described by BRODY et alii (1972) in *Dermatophagoides farinae* and by DESCH et alii (1991) in *Sarcoptes scabiei*. Their products are said to be delivered between the palp and the leg I into the podocephalic canal. The so-called "salivary glands" of the older descriptions most probably are in fact the supracoxal glands (HUGHES 1950; VIJAYAMBIKA & JOHN 1974). With the secretions of these glands the food becomes more liquid and can be pumped into the body.

With the aid of the strongly chitinized pharynx the food is engorged. In cross section the pharynx is U-shaped, in lateral aspect it is curved dorsally. From the subcheliceral plate and from the palp coxae dilator musculature runs in its main part to the roof of the pharynx. The arrangement of that musculature is very complex and shall not be described in detail (for a minute description see PRASSE 1967). Furthermore, transversal musculature runs between the upwards curved lateral parts of the pharynx. To this latter musculature the function as pharyngeal constrictors is often ascribed (HUGHES & HUGHES 1938; HUGHES 1950; PRASSE 1967; BRODY et alii 1972; VIJAYAMBIKA & JOHN 1974). More plausible, however, is that the tight closing of the pharynx is accomplished by the elasticity of the cuticle. This is supported by the fact that in *Sarcoptes scabiei* DESCH et alii (1991) could find only pharyngeal dilators.

The pharynx merges into the chitinized esophagus. As a result of deep longitudinal plications it looks in transverse sections like a star. It is surrounded by bands of circular muscles which attach solely at the ridges (which in cross section appear as rays) of the esophagus. Waves of contraction run over the bands of musculature in the direction of the stomach. The esophagus enters anteroventrally the stomach.

Stomach and colon possess a monolayer epithelium which rests on a basal lamina. The epithelium consists mainly of two types of cells: flat squamous cells and cuboidal or globular cells. The globular cells project from the epithelium into the gut lumen which gives the epithelium locally a raspberry-like appearance. All cells have a microvillous border.

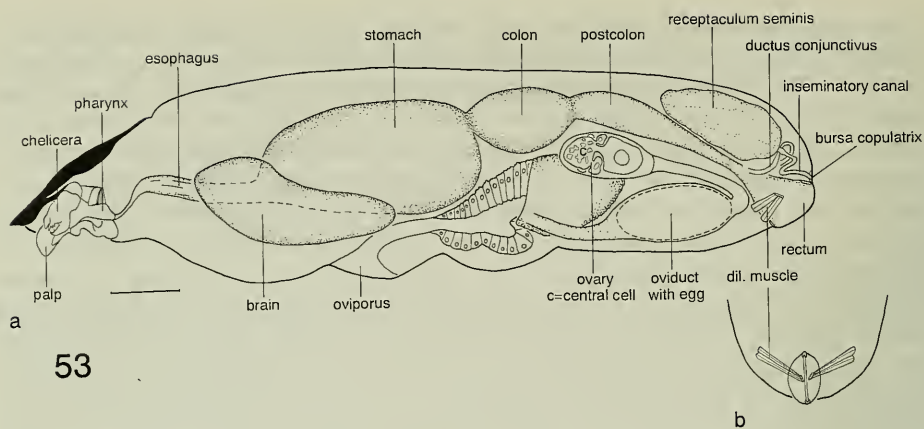
The cuboidal or globular cells of the stomach contain either numerous small or additionally one large vacuole. Repeatedly cells or parts of the cells of this type are detached from the epithelium and released into the gut lumen where they degenerate and are digested. HUGHES (1950) found for the gut contents of the stomach of *Acarus siro* a pH between 5.0 and 6.0.

Between the stomach and the colon the gut tube is strongly narrowed by a sphincter. Within the colon obviously alkaline conditions prevail. According to HUGHES (1950) the pH of the colon fluid is between 7.0 and 8.0. By the muscular constriction between each gut section a mixture of the different fluids is probably avoided. To this the observation of AKIMOV (1973) that within the colon some fluid is squeezed back into the stomach is not necessarily a contradiction. The fluid is likely to be stomach fluid which immediately after entering the colon is regained by this mechanism. While moving through the valve between the stomach and the colon the gut contents are supposed to be wrapped by the peritrophic membrane (WHARTON & BRODY 1972). The food pellet formed in this way remains for some time in the colon (AKIMOV 1973). The cells of the colon are mainly elongated and have conspicuous microvilli (*Caloglyphus mycophagus*, *Aleuroglyphus ovatus*, *Histiogaster carpio*, *Dermatophagoides pteronyssinus*, *D. farinae*, *Sarcoptes scabiei*) or are exclusively flat (*Acarus siro*, *Lardoglyphus konoi*). The transition between colon to postcolon is in most species marked by another narrowing. In contrast to the constriction at the entrance to the colon BRODY et alii (1972) could detect neither musculature nor regular contractions at this region. According to HUGHES (1950) the pH within the postcolon is the same as within the colon. The monolayer epithelium of the postcolon is surrounded by a basal membrane and consists in the Acaridae, Lardoglyphidae and Glycyphagidae of conical and flat cells. Each cell has a brush border (ROHDE & OEMICK 1967; KUO & NESBITT 1970; BAKER 1975; BAKER & KRANTZ 1985).

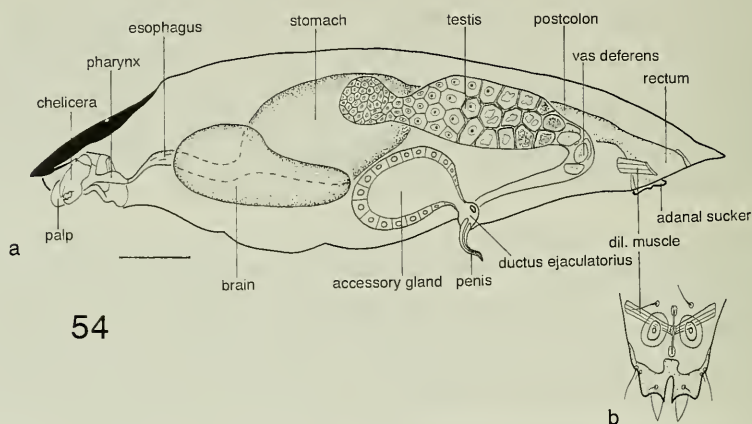
The last gut section (rectum) is lined with cuticle. In *Dermatophagoides farinae* the cuticle is folded in longitudinal direction and has numerous pore canals in order to procure a connection with the underlying epithelium (BRODY et alii 1972; TONGU et alii 1986). The epithelial cells rest on a basal lamina. During their way towards the anus the volume of the food pellets reduces and they become more dense. Several pellets are collected and voided as a clump. The anal slit is opened by a pair of muscles.

Several authors (HUGHES 1950; PRASSE 1967; KUO & NESBITT 1970; BRODY et alii 1972; AKIMOV 1973; BAKER 1975) agree that within the stomach essentially intra- and extracellular digestion and resorption takes place whereas within the colon mainly extracellular digestion and resorption occurs, while the function of the postcolon is restricted to the resorption of water.

Most Acaridida depend in their nutrition on fungi or other microorganisms. This dependency might be indirect, i. e. particles are ingested which are interspersed with microorganisms (mainly fungi) and predigested. It is well known that *Dermatophagoides* spp. can only utilize scales which is their main diet after prefermentation by *Aspergillus repens* (LUSTGRAAF et alii 1978). On colonization of new habitats the necessary or preferred fungi are automatically imported since many spores pass through the digestive tract undestroyed or adhere to the mite body (GRIFFITHS et alii 1959). Some mites exclusively feed on hyphae or spores (Saproglyphidae, Hemisarcopidae; own observations). The mites of several parasitic families, however, seem to be able to digest their food without the support of microorganisms (Sarcoptidae, Knemidocoptidae, Epidermoptidae etc.).



53



54

Figs. 53–54. *Listrophorus leuckarti*; internal anatomy supracoxal glands omitted. — 53 a–b. Female; — a. lateral view, uterus partly dissected, ovary dissected; — b. caudal end of opisthosoma; ventral view. — 54 a–b. Male; — a. lateral view, testis, vas deferens, ductus ejaculatorius and penis dissected; — b. caudal end of opisthosoma; ventral view. — Scale bars: 40  $\mu$ m.

## 10.2. Results

The electron microscopic findings are obtained only from two male and one female specimens. Therefore they probably represent only snapshots of an entire sequence of physiological stages. Fig. 53 and fig. 54 present an overview of the internal anatomy.

Because of the concentration of strongly sclerotized structures (tegmen, chelicerae) only a few sections were obtained from the anterior part of the gnathosoma. According to these sections a labrum seems to be lacking or is at least strongly shortened. The chelicerae are located in their guides in the roof of the gnathosomal frame. The central opening of the gnathosomal frame is the mouth. Posterior to it the chitinized pharynx follows (fig. 55). Between the posterior edge of the gnathosomal frame and the dorsal surface of the pharynx extends the dilator musculature. Transversal musculature could not be detected.

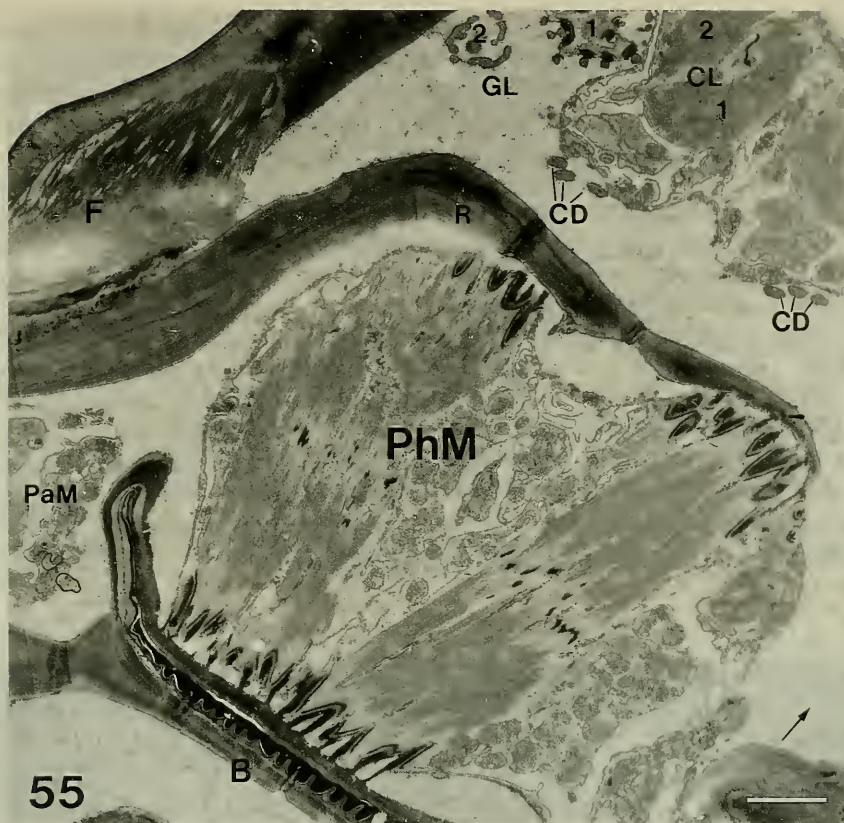


Fig. 55. *Listrophorus leuckarti*, female; posterior end of gnathosoma with pharynx; transverse section. — Abbreviations: arrow = top, B = bottom of gnathosomal frame, CD = tendons of cheliceral depressors, CL = cheliceral levators, F = stress fibres between tegmen and gnathosomal frame, GL = tendons of gnathosomal levators, PhM = pharynx dilators, PaM = palpal musculature, R = roof of gnathosomal frame. — Scale bar: 2.5  $\mu$ m.

The esophagus is bent dorsally and follows a course between the chitinous plates of endoskeleton I and enters ventrally into the stomach at the level of legs II (fig. 56). The esophagus has a chitinous intima. This layer and the adjacent epithelium are surrounded by bands of musculature which are attached to the ridges.

The stomach showed no caeca. A monolayer epithelium rests on a basal lamina (figs. 57–59). The cells besides a nucleus and mitochondria contain free ribosomes, rER and numerous inclusions which cannot be characterized in detail. Within the cells there are large vacuoles. Muscle fibres run beneath the basal lamina (fig. 57). The epithelial cells are of different thickness. The basal and luminal membranes of the cells in the anterior part are smooth. Contrary to them the cells in the posterior section have strongly folded surfaces (fig. 59). Cells which have been shed as well as free cells could not be recognized in any section.

The lumen of the stomach and the food pellets contained bundles of membranes (figs. 59–60).

Dorsal to coxa IV (female) or III (male) the stomach ends in a constriction of the alimentary canal. After passing into the colon the gut contents become more compact (fig. 62). A continuous peritrophic membrane between food and epithelium was never seen. Compared with the posterior section of the stomach there was no difference concerning the histology. Muscle fibres adhere to the basal lamina.

Posterior to another constriction the postcolon begins. It displays a completely different histological picture. On a basal lamina there are resting cells with relatively large nuclei (fig. 61). The luminal surface is extensively folded, the plications filling the gut lumen almost completely. In caudal direction the diameter of the gut tube decreases more and more. The basal plasmalemma of the epithelial cells is folded and the cells show one or a few large vacuoles and numerous smaller vesicles mainly in the vicinity of the gut lumen. Because of the enlarged vacuoles the nuclei are forced to the basal cell margin. The postcolon is surrounded by muscle fibres.

The last section (rectum) is lined with cuticle. The anus is compressed laterally and forms a slit parallel to the long axis of the mite. The ends of the slit are surrounded by small sclerites. In the middle of the anal slit at each side there is an elongated sclerite which parallels the rectum. These are the attachment sites for the musculature that opens the anus. The musculature ends in the body wall.

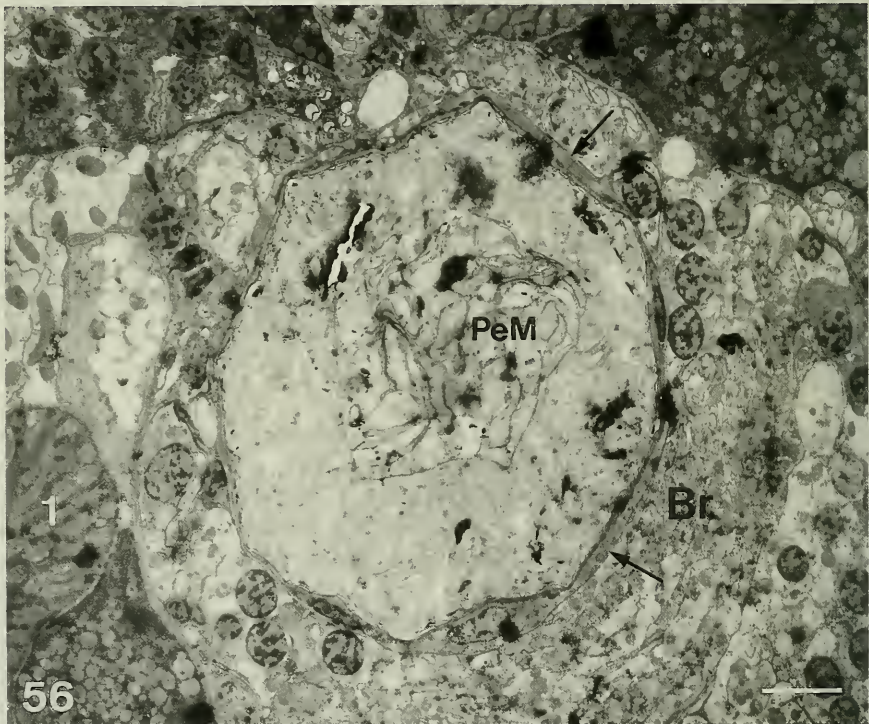


Fig. 56. *Listrophorus leuckarti*, female; esophagus immediately anterior to the stomach; transverse section. The lumen is filled with peritrophic membranes (*PeM*). — Further explanations: *Br* = brain, *1* = supracoxal gland cell 1, arrow = musculature. — Scale bar: 2.5  $\mu$ m (fixation mode A).

In sections of non-chitinized parts of the gut small blebs communicating with underlying cells or the haemocoel via perforations in the basal lamina could be recognized (fig. 58).

No salivary glands were detected.

In specimens of all life stages the gut contents appeared as a brownish, finely granulated mass scattered with different larger particles and fungus spores (fig. 62). In order to clarify if the mites feed on the keratin of the hair some hairs of a highly infested vole were investigated by means of a SEM. The hairs were entirely undamaged.

### 10.3. Discussion

The results of the investigations of the gut contents and the hairs of the host suggest, that *L. leuckarti* is exclusively saprophagous. The diversity of the food components observed within the gut indicates that the mites randomly graze off the hairs. As a result of the poor selectivity it is very likely that large amounts of food have to be turned over.

The anatomical results at *L. leuckarti* agree largely with the general picture presented in 10.1.

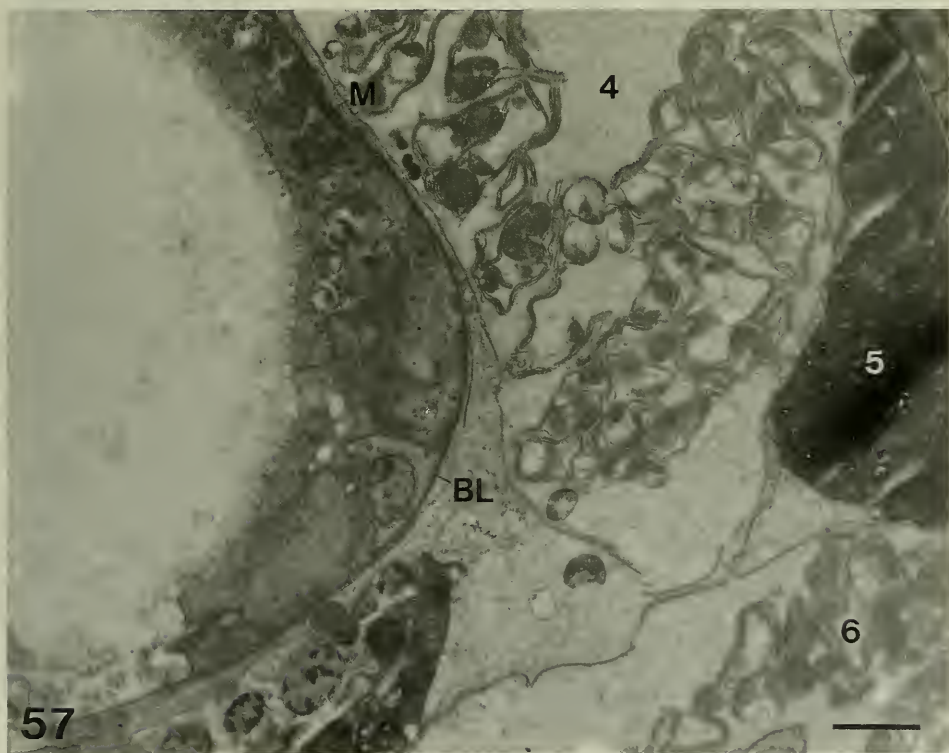


Fig. 57. *Listrophorus leuckarti*, male; anterior part of stomach, epithelium with microvillous border on a basal lamina (BL); transverse section. — Further explanations: M = visceral musculature; 4, 5, 6 = supracoxal gland cells. — Scale bar: 2.5  $\mu$ m.

The esophagus is equipped only with constrictor musculature. This means that the extension of its lumen is generated by the elasticity of the cuticle.

HUGHES (1954) describes in *L. leuckarti* the remnants of two caeca which are said to be located at the posterior part of the stomach. One can surmise that they represent in fact an artifact of fixation (note the heavy deformation of the body contour in fig. 8 in HUGHES).

The small blebs might be one mode of material exchange between the epithelial and the interstitial cells or the haemolymph. Similar interdigitations occur in *Sarcoptes scabiei* (DESCH et alii 1991).

The entangled membranes are elements of the peritrophic membrane which are mingled with food in the stomach and compressed to a pellet in the colon. This mode of formation of peritrophic membranes is widespread (PETERS 1968, 1992). This does not exclude that an additional layer of peritrophic membrane is secreted by the colon which envelops the entire colon contents.

According to a very common view it is the duty of peritrophic membranes to protect the delicate epithelium from damages caused by abrasive food particles. This opinion was first uttered by SCHNEIDER (1887). Doubts about their exclusive protecting function rose when peritrophic membranes were found in many blood- or sap-

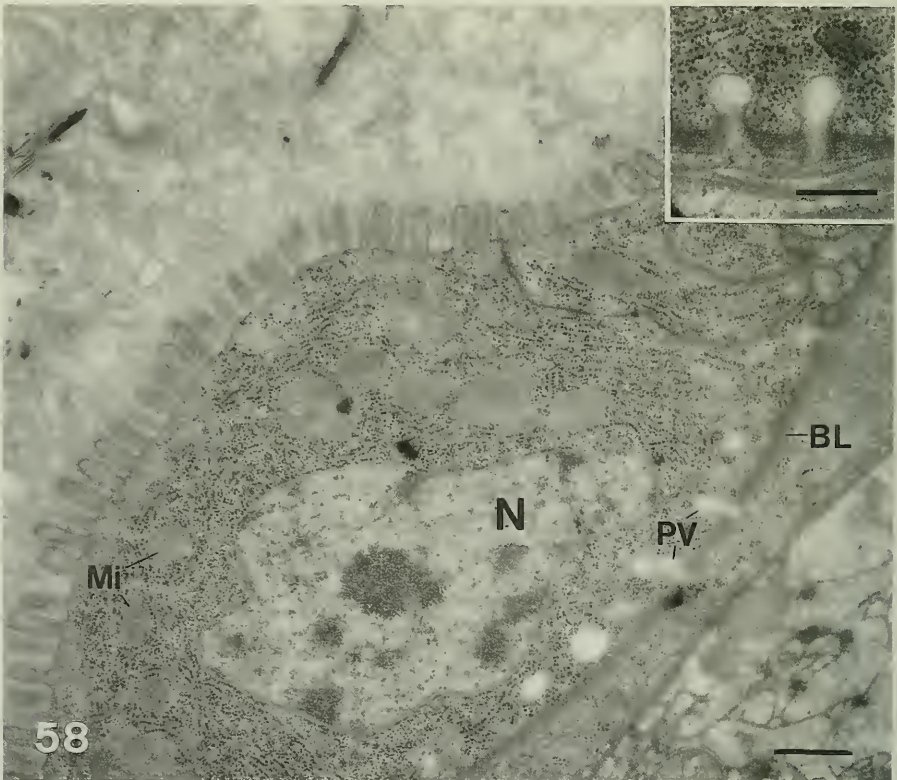


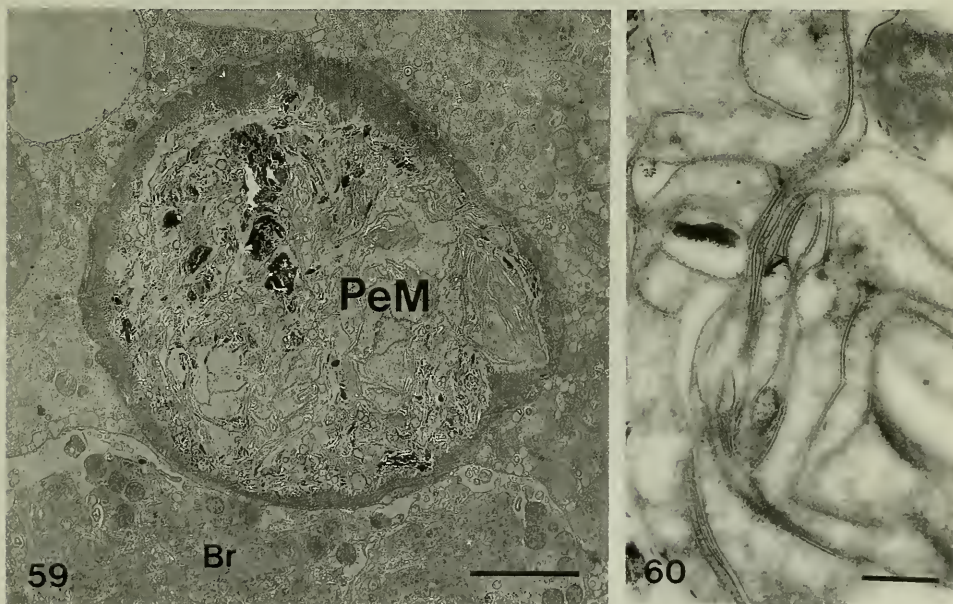
Fig. 58. *Listrophorus leuckarti*, female; anterior part of stomach; transverse section; epithelial cells on a basal lamina (BL) with mitochondria (Mi), small vacuoles, free ribosomes and rER; pinocytotic vesicles (PV, inset) at the basal lamina; N = nucleus. — Scale bar: 0.6  $\mu$ m, inset: 0.4  $\mu$ m (fixation mode A).

feeding insects (PETERS 1969). The results of extensive investigations in representatives of almost all phyla of the animal kingdom by PETERS (1967, 1968, 1969, 1992) supported these doubts. Thus in some species which feed on coarse food (*Gryllotalpa*, *Anthrenus*, *Arenicola*, Sipunculida, *Echinocardium*) peritrophic membranes are lacking. On the other hand they occur in a great number of animals feeding on fluids (*Cicadella*, *Corixa*, several imagines of Lepidoptera and Diptera, Scorpiones, Araneae) (PETERS 1968). The situation in *L. leuckarti* is also in conflict with the traditional doctrine since a continuous wrapping by the delaminated membranes is not attained within the stomach.

PETERS (1968, 1992) therefore presented further possible functions pertaining to the peritrophic membranes:

Compartmentalization of the gut;  
matrix for enzymes either incorporated or adsorbed;  
prevention of feces being carried back into the feeding current of filter feeders;  
enveloping the excretion products (Onychophora);  
barrier for parasites;  
lubricant during the passage through the alimentary canal, also in connection with mucous substances.

Especially the last proposal must be taken into consideration in animals like *L. leuckarti* turning over large amounts of relatively dry food under the conditions of water scarcity. Since mucous binds much water it is hardly suitable as lubricant for the food remnants of these animals.



Figs. 59–60. *Listrophorus leuckarti*. – 59. Male; stomach at the level of the anterior margin of coxa III; transverse section; monolayer epithelium with folded cell membranes; lumen densely filled with peritrophic membranes (*PeM*); *Br* = brain (scale bar: 10  $\mu$ m); – 60. female, stomach; transverse section; peritrophic membranes mingled with gut contents (0.4  $\mu$ m) (fixation mode A).

The greatest differences with the previous studies concern the postcolon. First, in *L. leuckarti* the epithelium of this gut section is not covered with a microvillous border as noticed in all investigations done with the aid of the light microscope. This contradiction, however, might be only putative since the difference between an irregular membrane folding and a brush border is only gradual and is additionally obscured by the limited resolution of the light microscope. Second, BRODY et alii (1972), TONGU et alii (1986) and DESCH et alii (1991) identify the anterior hindgut with the postcolon of the other authors. According to them the entire hindgut is cuticle-lined. Most probably they overlooked the postcolon as a result of the fact that the investigated species are stout and the postcolon very short. Thus fig. 10 in TONGU et alii (1986) shows a section of the rectum of *Dermatophagoides farinae*. The epithelial cells at the lower margin of the figure are free of chitin and display membranous foldings analogous to the findings in *L. leuckarti*.

The findings of HUGHES (1950) in *Acarus siro* are very similar to the ones in *L. leuckarti*. He described for the postcolon "an epithelium with a deep striated border apparently composed of long narrow vesicles". The cytoplasm of the epithelial cells is supposed to contain small vacuoles which became coloured in animals fed on dyed foods.

Within the postcolon most probably water and dissolved substances are resorbed by pinocytosis and collected in the large vacuoles. After the possible chemical modification of these substances they are transported to the basal lamina and discharged.

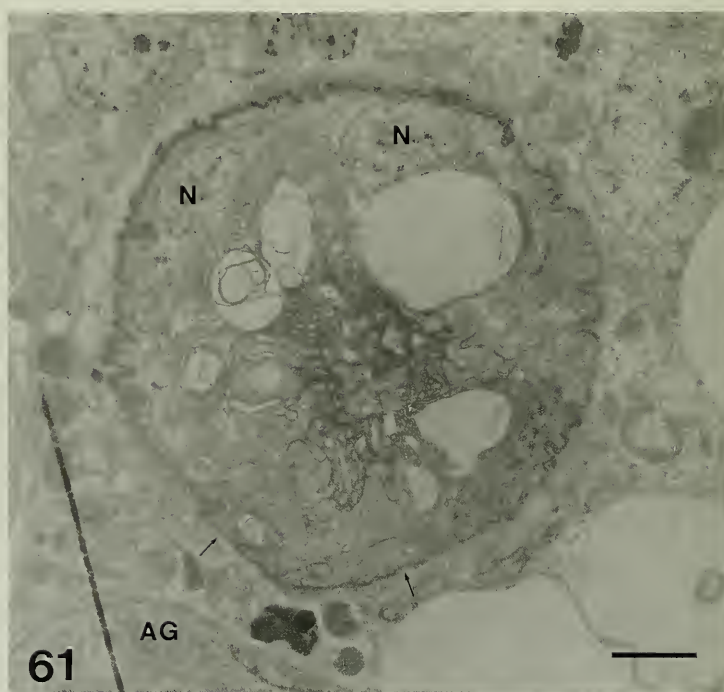


Fig. 61. *Listrophorus leuckarti*, male; postcolon; transverse section; epithelial cells with extensively folded luminal cell membrane, numerous vesicles and a few larger vacuoles. Nuclei (N) forced to the basal parts of cells (AG = accessory gland, arrow = discharging vesicles). — Scale bar: 2.5  $\mu$ m.



Fig. 62. *Listrophorus leuckarti*, female; hysterosoma; whole mount in Hoyer's fluid (light micrograph); contents of stomach (Co) with a fungus spore (arrow); Pe = food pellet within the colon and postcolon. — Scale bar: 20  $\mu$ m.

As pointed out in chapter 5, the animals need efficient closing systems at their gut ends because of the internal pressure. The mouth opening (pharynx) as well as the anus are closed passively by the elasticity of the chitin occurring there. Only for opening muscle work is necessary. In this way the energy effort is kept as low as possible.

## 11. Sexual Organs and Reproduction

### 11.1. Previous Knowledge

In all chelicerata the genital opening is localized ventromedially, an arrangement which is very inapt for an internal fertilization. Therefore many chelicerata transfer the sperm via spermatophores (e. g. Scorpiones, some Gamasina), modified palps (Araneae) or they developed a long penis (Opiliones).

The Acaridida solved this "technical" problem by separating the oviporus and the copulatory opening from each other. The oviporus lies between the third and fourth pairs of legs, the copulatory opening (bursa copulatrix) at the rear end or at the dorsal face of the opisthosoma. In the male a penis developed on the ventrum.

With this arrangement of copulatory organs there are two possible postures the male can adopt for mating and both are realized among the Astigmata: in the proconjugati both sexes point at the same direction, in the retroconjugati they turn away from each other (SAMSINAK 1971). The respective mode of copulation in each group (especially in the males) led to the formation of characteristic structures to ensure a tight connection during mating.

## 11.2. The Female Genital System

### 11.2.1. Previous Knowledge

The bursa copulatrix is connected with the sacculus receptaculum seminis via a chitinous duct, the inseminatory canal. Originating at the receptaculum seminis there run two efferent ducts to the paired ovaries (ductus conjunctivi) which are chitinized in their proximal portion. From the ovaries two oviducts emerge which join medially to form the uterus. The uterus passes into the cuticle-lined preoviporal duct which ends in the genital aperture (oviporus). At the junction of the oviducts with the uterus one accessory gland at each side has been described by several authors (HUGHES & HUGHES 1938; ROHDE & OEMICK 1967; KUO & NESBITT 1970; VIJAY-AMBIKA & JOHN 1975, 1977; BAKER & KRANTZ 1985; WITALINSKI et alii 1990).

The so far only electron microscopic examination of the female reproductive organs was carried out by WITALINSKI et alii (1990). The following introductory remarks are mainly based on their study, keeping in mind that in strict sense they are only valid for *Acarus siro*. Future investigations will show to what extent this picture has general validity. For sketching the gametogenesis and fertilization PRASSE (1968b) and HEINEMANN & HUGHES (1970) are used. Their results are obtained from *Caloglyphus* spp.

The receptaculum seminis at the junction with the inseminatory canal possesses a cup-shaped chitinous structure, the so-called "basal part". From the border of the basal part cuticular lamellae originate which fill the space above the basal part. Outwardly follows a double-layered chitinous sac which envelopes the lamellae. These chitinous structures are surrounded by the wall of the receptaculum seminis formed by 1–3 layers of cells the luminal surfaces of which are covered with numerous long microvilli. The space between the chitinous double layer and the lamellae is filled with a material packed with vesicles and thick fibres. Between the lamellae sperm cells are located. The two ductus conjunctivi leave the receptaculum seminis at the margin of the basal part.

The ovaries contain somatic cells, oogonia, oocytes, spermatocytes and postero-dorsally a large "central cell" with nutritive function which is connected with the oocytes I by cytoplasmic bridges. The oogonia develop from gonial cells which multiply by fission. This phase of proliferation already starts with the tritonymphal stage. The oogonia grow in size and thus become oocytes I (PRASSE 1968b; HEINEMANN & HUGHES 1970). After the oocytes have linked with the central cell they continue to grow. The penetration of the oocytes by the sperm already takes place in the ovary. The nucleic material of the central cell appears in microscopic sections in the form of several lobed patches which has been interpreted by the authors either as a strong ramification of the nucleus (WITALINSKI et alii 1990) or as the nuclei of a syncytium (PRASSE 1968b). As a result of its enormous productivity the central cell contains numerous mitochondria and free ribosomes.

The oocytes I after reaching the maturity for the entrance into the oviduct detach from the central cell. The oocytes migrate one after the other into the oviduct so that oocytes of successive developing stages are lined up in the oviduct. The oviducts are formed by 1–2 cell layers which are accompanied at the periphery by muscle cells. Here the oocytes are supplied with further reserve substances. WITALINSKI et alii (1990) observed small granules within the cells of the oviduct of *Acarus siro*. The cells of empty oviducts contained more granules than compared with the cells of egg-containing oviducts.

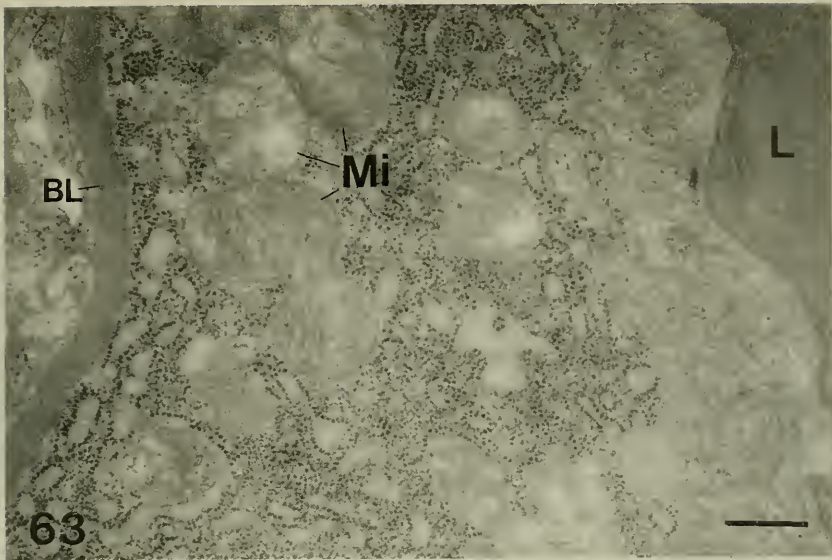


Fig. 63. *Listrophorus leuckarti*, female; receptaculum seminis; transverse section; epithelial cell with mitochondria (*Mi*), free ribosomes and rER. — Further *abbreviations*: *BL* = basal lamina, *L* = lumen of receptaculum. — Scale bar: 0.4  $\mu$ m (fixation mode A).

According to HEINEMANN & HUGHES (1970) meiosis starts before the oocyte comes into cytoplasmic contact with the central cell whereas PRASSE (1968b) states this to happen after detachment from the central cell. The latter, however, reports a temporary condensation and pairing of the chromatin during the connection of the oocyte with the central cell. When the centripetally progressing yolk formation has reached the nucleus the first maturation division takes place. The nuclear envelope disintegrates and the bivalents congregate at the location of the future metaphase plate. After the first maturation division the second meiotic division follows immediately. The eliminated chromatin disappears (PRASSE 1968b). During the second maturation division the chorion is formed (HEINEMANN & HUGHES 1970). Now the male and female chromosomes fuse. Immediately after the fertilization the cleavage of the egg begins.

The uterus consists of a relatively thick band of cells accompanied by numerous muscle cells.

The genital aperture is covered by several cuticular folds (inner and outer paragnyal fold). It is opened by several muscles which run between the paragnyal folds and the body wall.

### 11.2.2. Results

The anatomy of the female genital system conforms in most parts with the general picture given above.

The oviducts with the associated ovaries are bent to the anterior (fig. 53). As a result the spatial relations have rotated by 180 degrees: the distal end of the ovary points to the rear of the mite, the central cell is located anteriorly. In this arrangement the distance between the ovaries and the receptaculum seminis is exceptionally

long. The non-chitinized portion of the ductus conjunctivi were not detectable with the light microscope.

The receptaculum seminis displays a monolayer epithelium on a prominent basal lamina (fig. 63). The cells show an extensive network of rER and numerous free ribosomes. The lumen of the receptaculum contains an electron-dense secretion.

As no electron micrographs of the ovaries and the oviducts were done no informations on their fine structure can be given.

The uterus is composed of two different types of monolayered tissues. The main part consists of conical cells the plasma membranes of which are basally and apically folded. Electron microscopic investigation revealed numerous inclusions (granula, vesicles) which indicates a secretory function. At the ventral face of the uterus there is an extension showing a completely different histological picture. Its cells have smooth surfaces, the nuclei are located basally. By the entry of an egg the wall of the uterus is heavily extended.

Due to the enormous dimension of the egg relatively to the body size of the female (fig. 62) the subsequent oocyte is only released from the ovary immediately before the egg enters the uterus. In the uterus the egg is surrounded by a chitinous shell.

The paragynial folds are pulled aside by two pairs of muscles which originate in the posterior region of the preoviporal canal and end posterodorsally in the body cuticle (figs. 64–65).

The spiny cuticle of the female opisthosoma must be regarded as a secondary sex characteristic (fig. 1). It is lacking in the male and all immature instars.

### 11.3. The Male Genital System

#### 11.3.1. Previous Knowledge

The male reproductive system is composed of a pair of testes, one or two accessory glands and a penis. The products of the testes pass into a pair of vasa deferentia which communicate to form the ductus ejaculatorius. After the ductus ejaculatorius has received the secretions of the accessory gland(s) it passes into the penis (HUGHES &

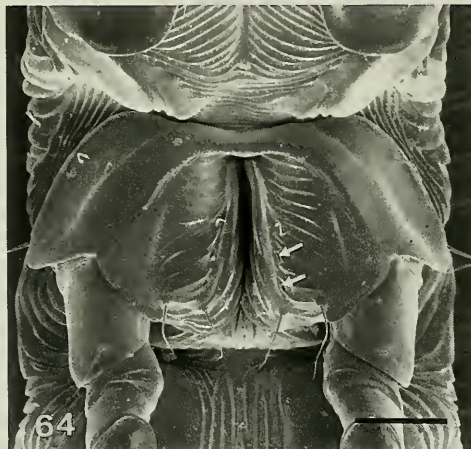


Fig. 64. *Listrophorus leuckarti*, female; oviporus (arrow = genital papilla). — Scale bar: 20  $\mu$ m.

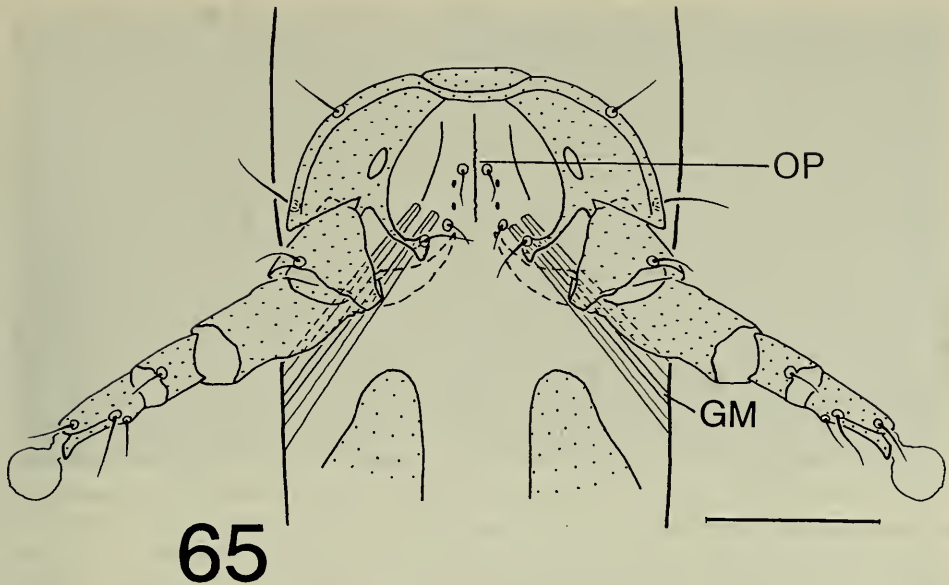


Fig. 65. *Listrophorus leuckarti*, female; oviporus (OP) with genital muscles (GM); ventral view. — Scale bar: 40  $\mu$ m.

HUGHES 1938; ROHDE & OEMICK 1967; KUO & NESBITT 1970; VIJAYAMBIKA & JOHN 1975, 1977; BAKER & KRANTZ 1985; WITALINSKI et alii 1990).

To guarantee the close contact with the female during mating (rivals!) specialized adhering organs developed in the male:

The retroconjugati regularly possess two suckers lateral to the anal opening and two smaller suckers each on the tarsi of legs IV. In the center of each adanal sucker there is a small protuberance (central papilla). It has contact with the projections of a mechano-sensitive organ (WITALINSKI 1990). Frequently the opisthosoma is dorso-ventrally flattened and bears on its margin foliate setae or appendages which by adhesion reinforce the connection between the sexes. The males of the proconjugati mostly show a broadening of the membranous parts of the pretarsi or specially shaped setae at the often enlarged legs I and II which enable the male to hook to the female.

Like in 11.2.1. in the overview given below mainly the results of PRASSE (1968b), HEINEMANN & HUGHES (1970) and WITALINSKI et alii (1990) are utilized.

In analogy to the ovaries somatic cells, besides the gonial cells, are present in the testes. From *Acarus siro*, *Caloglyphus* spp. and *Notoedres cati* a large central cell (WITALINSKI 1988; WITALINSKI et alii 1990) or a syncytium (PRASSE 1968b) with "scattered" nucleic material has been described. In the direction of the vas deferens there follow in concentric layers mitotic spermatogonia, spermatocytes, spermatids and spermatozoa. If present, the central cell is characterized by numerous invaginations containing spermatogonia. Between the central cell and the spermatogonia no cytoplasmic bridges are formed (WITALINSKI et alii 1990).

The spermatogonia have nuclei with normal appearance and undifferentiated cell membranes. The first stage of spermatocyte is marked by an enlargement of the cell and the nucleus. Cisternae of the endoplasmic reticulum and numerous vesicles pro-

duced by the golgi apparatus concentrate beneath the cell surface and fuse with each other and with the plasmalemma. This leads to a spongy marginal zone made of membranous and cytoplasmic material. The mitochondria alter their shape (ALBERTI 1980; WITALINSKI 1988; WITALINSKI & AFZELIUS 1987; WITALINSKI et alii 1986).

At this phase the first maturation division begins with the condensation of chromatin. After the disintegration of the nuclear membrane separation of the chromosomes takes place. The second meiotic division follows immediately without a recognizable interphase (PRASSE 1968b; HEINEMANN & HUGHES 1970).

The spermatids are characterized by lacking a nuclear envelope, scattered chromatin threads and the shedding of the membranous and cytoplasmic material located at the cell margin. Under this peripheral zone the final cell membrane is formed (ALBERTI 1980; WITALINSKI 1988; WITALINSKI et alii 1986). In this way the cell might eliminate useless cell material (WITALINSKI et alii 1986; ALBERTI 1991).

In the spermatozoa the formation of the cell membrane has completed and the superficial membranous layers are lost. The sperms are shaped irregularly and contain free threads of chromatin, modified mitochondria and electron-dense lamellae or vesicular bodies. Centrioles, a flagellum and an acrosome are lacking. The absence of an acrosome may be due to the fact that the spermatozoon penetrates the oocyte before the egg membranes are formed (WITALINSKI et alii 1986). The mature sperms are stored in the vasa deferentia.

The vasa deferentia originate at the anterior end of the testes. Their proximal part serves as a reservoir for the sperms, their distal part has glandular character.

One (chambered organ) (*Acarus siro*, *Aleuroglyphus ovatus*, *Caloglyphus mycophagus*, *Rhizoglyphus robini*) or two (*Lardoglyphus konoi*, *Glycyphagus domesticus*) accessory glands run into the ductus ejaculatorius at its proximal part. The accessory gland of *Acarus siro* consists of relatively large cells. Their cytoplasm contains numerous vesicles, a rich network of rough endoplasmic reticulum and mitochondria. Between the cells there are large vacuoles filled with glandular secretions (WITALINSKI et alii 1990).

The ductus ejaculatorius is lined with cuticle. In *Glycyphagus domesticus* the ductus ejaculatorius can be closed by a sphincter anterior to the point where it passes into the penis (HUGHES & HUGHES 1938).

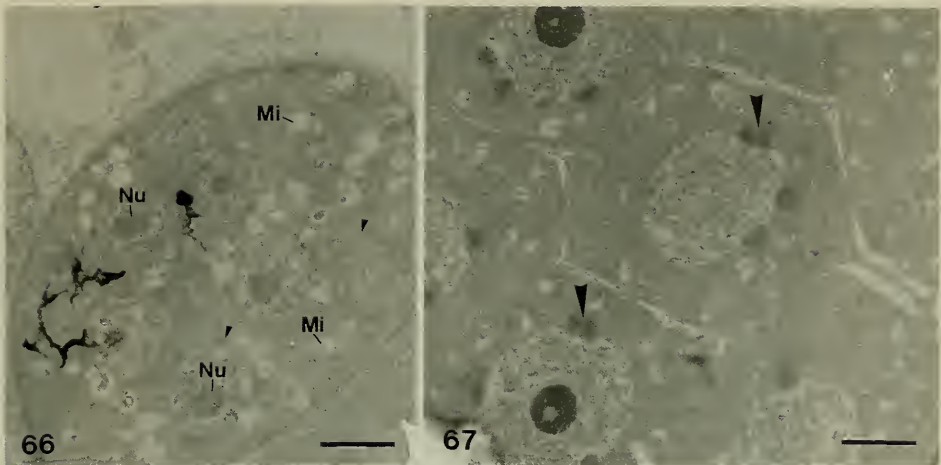
In non-copulating animals the penis is hidden under the genital folds. For copulation the penis is extruded by haemolymph pressure. Several muscles serve as retractors.

In the receptaculum seminis the sperms undergo remarkable alterations. They take a longish or polygonal shape and under the cell membrane are formed fibrillae which run parallel to the plasmalemma (ALBERTI 1980; WITALINSKI 1988; WITALINSKI et alii 1986).

In the ovary of *Notoedres cati* WITALINSKI (1988) found sperms in concavities of somatic cells. Some of them had cell protrusions suggesting an amoeboid mobility of the spermatozoa.

### 11.3.2. Results

In analogy to the oviducts the vasa deferentia are bent anteriorly so that the spermiogenesis proceeds from the rostral to the caudal end (fig. 54). Between the testes and dorsal to the penis there is the accessory gland. Its secretions unite with the



Figs. 66–67. *Listrophorus leuckarti*, male; transverse sections. — 66. Testis with spermatogonia; nuclei with nucleoli (*Nu*); at the nuclear envelope electron-dense bodies (arrowheads) (*Mi* = mitochondrium); — 67. testis with spermatocytes I; alternating layers of cytoplasmic material and membranes located at the cell borders (arrow = electron-dense body). — Scale bars: 2.5  $\mu$ m.

sperms in a short ductus ejaculatorius which is lined with cuticle internally. Since *L. leuckarti* belongs to the retroconjugati the penis points to the rear end.

The anterior section of the testes is densely packed with spermatogonia (fig. 66). A central cell or other somatic cells could not be distinguished. The spermatogonia have large nuclei with a nucleolus in the center. The nuclear envelope is smooth and shows electron-dense bodies on its cytoplasmic surface. The cytoplasm contains many mitochondria.

During the spermatocyte stage the nucleoli vanish, the nuclear membrane appears increasingly frayed and the nucleus takes a ramified shape (figs. 67–68). In the cytoplasm numerous vesicles appear which build up the cytoplasm-membrane layers at the cell periphery.

With proceeding spermiogenesis the spermatocytes drift apart. Finally the nuclear membrane disintegrates and the meiotic divisions take place (fig. 69). As in all species previously examined the nuclear envelope is not rebuilt.

The accessory gland consists of a monolayer epithelium the cells of which contain large nuclei, many mitochondria and are densely packed with relatively small vesicles and inclusions (fig. 70). By light microscope the gland lumen appears to be filled with a material of fine granules. By electron microscope the secretion shows to consist of a matrix of minute vesicles in which more electron dense polygonal bodies are embedded.

Three pairs of muscles allow retraction of the penis (figs. 71–73).

The comparison of the adults with the juvenile instars reveals that the male shows numerous additional sex characteristics. The most obvious difference between the female and the juveniles and the male consists in the body shape. The male opisthosoma is dorsoventrally flattened. The dorsal and ventral body walls merge at the rear end to an acute angle (fig. 75). Due to this the anal opening has shifted rostrally.

In the dorsum of the opisthosoma there are two narrow sclerites which are lacking in the female and the immatures. To these sclerites the muscles DV3 and DV4 attach

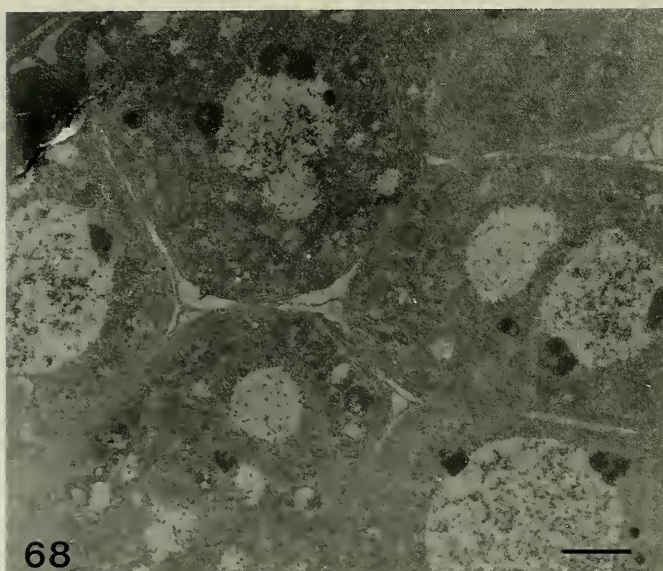


Fig. 68. *Listrophorus leuckarti*, male; transverse section of testis with spermatocytes I, advanced state; nuclei branched and free of nucleoli, nuclear envelope frayed. — Scale bar: 2.5  $\mu$ m.

(fig. 72). At the opisthosomal end two long setae (l5) and a pair of foliate hairs (d5) are inserted (fig. 75).

The legs III and IV are more sturdy in the male compared with the female. This corresponds to an enlarged musculature and a strengthening and multiplication of apodemes and sclerites which are in a functional connection with these legs. The ambulacra of the last two pairs of legs are broadened. The proportions of the internal sclerites deviate only slightly from the picture given in 8.2.3.

The anal slit is flanked by the copulatory suckers (figs. 74–75). They consist of a sclerotized plate which is surrounded by a soft-walled rim. A muscle bundle originates at the plate and runs to the narrow sclerite at the dorsum of the opisthosoma (fig. 72).

#### 11.4. Life Observations

If two sexes meet the male immediately tries to mount the female. It embraces the female opisthosoma with the last two pairs of legs (fig. 76). I could observe several times that the male at first mounted the female in the same orientation as the female. Once positioned correctly on the female the male tries to get the host's hair into the clasping apparatus. Frequently it happened that several males competed for one female, the males clustering around the female and trying to push each other aside.

The formation of attachment pairs (SWEATMAN 1957), i. e. the coupling of males with immature females in order to mate immediately after the last moult of the female, was never seen in *L. leuckarti*.

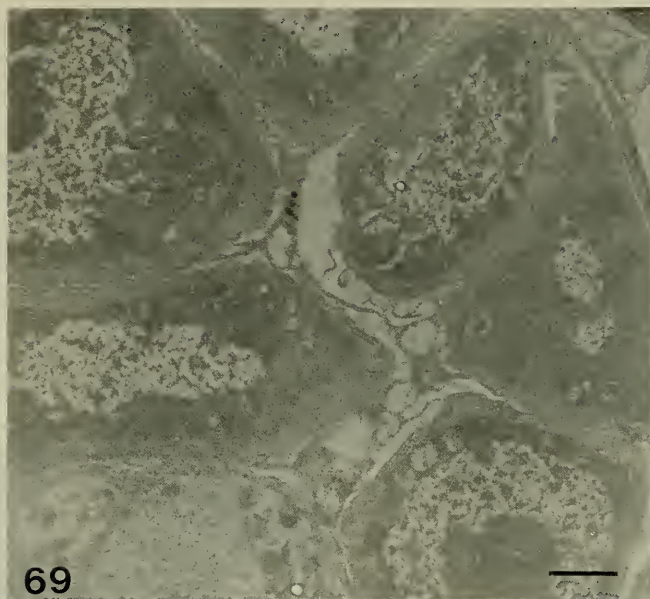


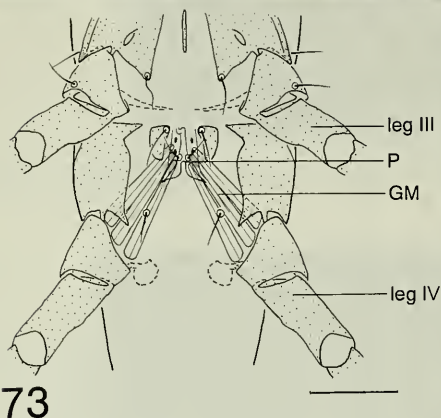
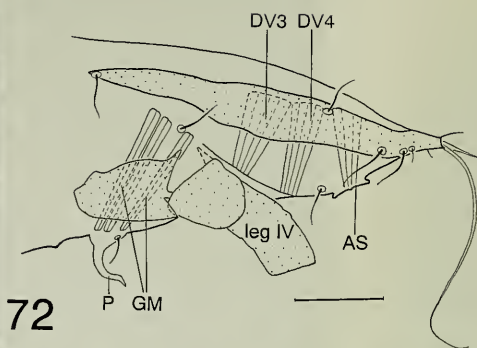
Fig. 69. *Listrophorus leuckarti*, male; transverse section of testis with spermatocytes I; desintegration of the nuclear envelope. — Scale bar: 2.5  $\mu$ m.



Fig. 70. *Listrophorus leuckarti*, male; accessory gland; transverse section; epithelium (E) with mitochondria and numerous inclusions; L = lumen with secretion (partly broken off). — Scale bar: 2.5  $\mu$ m.

### 11.5. Discussion

The most remarkable feature of the genital system is the anterior bending of the oviducts and the vasa deferentia and the resulting reversal of the spatial relations.



Figs. 71–74. *Listrophorus leuckarti*, male. — 71. Penis (scale bar: 5  $\mu$ m); — 72. lateral view (40  $\mu$ m); — 73. ventral view (40  $\mu$ m); — 74. opisthosoma with adanal suckers (20  $\mu$ m). — Abbreviations: AS = adanal sucker, CP = central papilla, GM = genital musculature, P = penis.

Such a "coiling" would have been expected rather in an animal with a stout body. In the moment there is no plausible explanation for this phenomenon.

The electron microscopic appearance of the spermatogonia conforms essentially with the situation in the species which had been previously examined by the same method (*Acarus siro*, *Tyrophagus putrescentiae*, *Notoedres cati*, *Sarcoptes scabiei*). The electron-dense bodies attached to the nuclear membrane were also described in *Acarus siro*, *Tyrophagus putrescentiae* and *Sarcoptes scabiei*.

The vanishing of the nucleoli is noted in none of the previous studies. Concerning the shedding of cell material in the form of alternating membrane and cytoplasmic layers there are no differences to the former investigations.

The accessory gland differs in structure and appearance of its secretion from all analogous glands described before. HUGHES (1954), misled by its granular filling, erroneously interpreted the accessory gland as "vesicula seminalis". This vesicula seminalis is supposed to pass directly into the testes as there is no discrete vas deferrens.

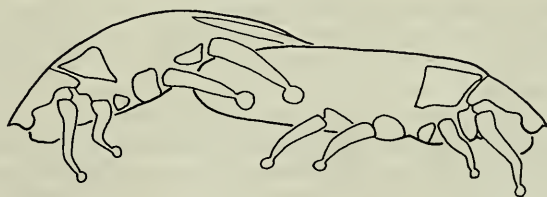


Fig. 75. *Listrophorus leuckarti*, male; opisthosoma, lateral view (AS = adanal sucker, d5 = foliate seta). — Scale bar: 10  $\mu$ m.

During copulation the male is severely endangered as it is orientated towards the tip of the hair. The flattened opisthosoma together with its acute tapering caudal end enables the male to cling to the female during mating. The foliate bristles d5 probably improve the smooth transition between the bodies and strengthen the contact by adhesion. The stronger legs III and IV with their broadened ambulacra may give the most important contribution to the coupling of the sexes. The adanal suckers are extruded and put onto the female opisthosoma. Then the central plate is redrawn. The vacuum necessary for the adherence of the sucker is made possible by its soft-walled rim tightly pressed to the female body surface, probably supported by a secreted fluid.

The spines on the cuticle of the female opisthosoma probably support the recognition of the female by the male and the decision in which way to mount it.

The frequently observed error in the mounting position could be a result of two antagonistic patterns of behaviour since the "right" position on the hair is the "wrong" one on the female.



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Fig. 76. *Listrophorus leuckarti*, mode of copulation (female on the right side).



Fig. 77. *Listrophorus leuckarti*, egg with larva; whole mount in Hoyer's fluid (light micrograph; CF = clasping flaps). — Scale bar: 50  $\mu$ m.

## 12. Ontogenesis

The eggs are glued singly at one end onto a hair (fig. 76). To protect the egg from being removed its free end always points to the tip of the hair.

The postembryonic development has the following sequence:

larva (3 pairs of legs);

protonymph (4 pairs of legs, 1 pair of genital papillae, 1 pair of genital setae);

tritonymph (4 pairs of legs, 2 pairs of genital papillae, 2 pairs of genital setae);

adults (genital opening, bursa copulatrix; penis).

Prior to hatching the animals fall into a state of torpor. During that phase the next instar develops. Before they become rigid the mites clasp to a hair with the aid of their clasping apparatus. The exuvia remains attached to the hair after having been left by the mite.

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