Reproduction, progenesis, and embryogenesis of thrips (Thysanoptera, Insecta)

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Abbreviations

AGA	“stretching solution“ (ethanol-glycerol-acetic acid)
BF	bright field (light microscopy)
D.E.R.	liquid epoxy resin
DIC	differential interference contrast (light microscopy)
ERL	vinylcyclohexene dioxide
FBS	fetal bovine serum
Fig.	figure
GLY	glycine
HE	Haematoxylin-Eosin-staining
L1	first instar larva
L2	second instar larva
LD	light density
n	number
NSA	nonenyl succunic anhydride
P	pupa
PBS	phosphate buffered saline
PIPES	piperazine-1,4-bis(2-ethanesulphonic acid)
PLT	progressive lowering temperature
PO	propylene oxide
PP	propupa
S1	dimethylaminoethanol
SD	standard deviation (used in this study always with the same unit like the mean value)
TEM	transmission electron microscopy
TSWV	tomato spotted wilt virus
w/v	weight per volume

Abbreviations used for plates

A	antenna
Abd	abdomen
AbdG	abdominal ganglion
AbdS	abdominal segment
AbGl	abdominal gland
Ae	aedeagus
AGl	accessory gland
Am	amnion
AmPo	amniotic pore
Bl	blastoderm
BM	basal membrane
Ca	calyx
Ch	chorion

Con	connective
Cp	cytoplasm
Cy	cyst
DO	dorsal organ
En	energid
FoC	follicle cell
GA	germ anlage
GC	germ cells
Germ	germarium
GT1	prothoracic ganglion
GT2	mesothoracic ganglion
GT3	metathoracic ganglion
H	head
Hg	hindgut
HL	head lobe
Le	leg
Le1-3	pro-, meso-, and metathoracic leg (leg 1-3)
Lb	labium
LE	larval eye
M	musculature
Md	mandible
Mg	midgut
MT	Malpighian tubule
Mthp	mouthparts
Mv	microvilli
Mx	maxilla
My	mycetome
NOpt	nervus opticus
Nu	nucleus
Oe	oesophagus
Og	oogonium
Ooc	oocyte
Ov	ovary
OvdLat	oviductus lateralis
Ovp	ovipositor
Ovr	ovariole
Ovrp	oviruptor
Pc	protocerebrum
Pl	pleuropodium
Protoce	protocephalon
Protoco	protocorm
ReP	rectal papilla
SerC	serosal cells
SG	suboesophageal ganglion
SGl	salivary gland
Sp	sperm

SpB	sperm bundle
Spg	spermatogonium
SpG	supraoesophageal ganglion
Spth	spermatheca
SpthD	spermathecal duct
Te	testis
TFil	terminal filament
VaD	vas deferens
Vit	vitellarium
Vitph	vitellophage
Yo	yolk
Z1-3	zone 1-3
Zo II	zone II
Zo IIIa-IIIc	zone IIIa-IIIc

1. Introduction

The order Thysanoptera (common name: thrips) encompasses minute insects which are usually only a few millimeters long. The majority of the species has fringed, banded wings as well as asymmetrical sucking and piercing mouthparts (only the left-hand side mandible is developed) (HEMING 1978; MOUND *et al.* 1980; MORITZ 1989b, 1997). Thrips also have a protrusible sac-like arolium at the apex of each leg (HEMING 1971; MOUND *et al.* 1980; MORITZ 1989c).

These insects were first described by DE GEER in 1744 (Physapus), later LINNEAUS placed the species which were known at this time in a genus called Thrips, and in 1836 HALIDAY ranked these insects to the Thysanoptera order.

Thysanoptera are distributed worldwide predominating in tropical, subtropical, and temperate regions (LEWIS 1973, 1997).

Currently about 5500 thrips species are described (10000 species estimated) (LEWIS 1997; MOUND 1997). Within Thysanoptera there are two suborders, Terebrantia and Tubulifera. Females of the Terebrantia possess an external ovipositor composed of four valves (HEMING 1970a; BODE 1975; MORITZ 1989d, 1997). In the tubuliferan species the ovipositor displays a flexible internal structure which is evertable (HEMING 1970a; MORITZ 1997). There are nine families within the Thysanoptera (MORITZ *et al.* 2001). Eight of these (Uzelothripidae, Merothripidae, Aeolothripidae, Melanthripidae, Adiheterothripidae, Fauriellidae, Heterothripidae, and Thripidae) belong to the Terebrantia. The suborder of Tubulifera includes only a single family, the Phlaeothripidae (MOUND 1997). 93 per cent of all known thrips species are placed in either the Thripidae or Phlaeothripidae (MOUND 1997) and of these two major families the Phlaeothripidae is the largest with about 3100 currently described species (MOUND *et al.* 1980).

Most thrips feed either on flowers or leaves of green plants, fungi, and a few feed on mosses and detritus (MOUND & PALMER 1983b; LEWIS 1997). There are only a few species known as thrips predators (SELHIME *et al.* 1963; DERBENEVA 1967; MORITZ 1982d; ARAKAKI & OKIJIMA 1998; MOUND & MARULLO 1998; WATSON *et al.* 1998) and thus are interesting for biological pest management (ZUR STRASSEN 1984; RAMAKERS *et al.* 2000), while others are useful as pollinators of host plants (SCHLIEPHAKE & KLIMT 1979; APPANAH & CHAN 1981). About 300 species of thrips (belonging to 57 genera) are known to form galls (CRESPI *et al.* 1997). The feature of gall induction has evolved a number of times in different species of Phlaeothripinae with no obvious pattern of relationship between the genera (MORRIS *et al.* 1999). In Australia, gall inducing thrips species show a number of characteristics which are interesting in the evolutionary sense, including connections with diverse host plants (CRESPI *et al.* 1997), a wide range of habitation types and life histories (CRESPI & MOUND 1997), and complex behaviour comprising caste systems (MOUND *et al.* 1996; CRESPI & MOUND 1997) and at least six eusocial species (CRESPI 1992b).

Only a few thrips species are known as serious crop pests and most belong to the family Thripidae (LEWIS 1973, 1997; MORITZ 1988a; MOUND 1997). There are several features of thrips biology predisposing them to become pests, e.g. the ability to cause direct damage by feeding which often leads to growth damage (MORITZ 1982e, 1988a, 1989b; PALMER 1992; DE JAGER *et al.* 1997), they reproduce rapidly in favourable environments (BRØDSGAARD 1994a; GAUM *et al.* 1994; TSAI *et al.* 1995; LESKEY *et al.* 1997; EKESI *et al.* 1999; MURAI 2000; TRDAN & MILEVOJ 2000), and their ability to spread and colonize in broadly geographical ranges. The ability to spread and colonize broadly is provided with natural flight and by plant distribution worldwide through imported and exported plant material (MOUND 1983; LEWIS 1997). Thrips are also known as vectors of bacterial (BAILEY 1935), fungal (SCHLIEPHAKE

& KLIMT 1979; ZUR STRASSEN 1984; ADIS *et al.* 1985; FARRAR & DAVIS 1991), and viral (DAY & IRZYKIEWICZ 1954; SAKIMURA 1963; ROSELLO *et al.* 1996; BOISSOT *et al.* 1998; ADKIN 2000; GARCIA *et al.* 2000; NAGATA & DE AVILA 2000) diseases.
About ten thrips species, all members of the Thripinae, have demonstrated the ability to breed and transmit plant viruses (ULLMAN *et al.* 1997). Four virus groups are transmitted by thrips. The most common are “prunus necrotic ringspot ilavirus“ (GREBER *et al.* 1991, 1992), “tobacco streak ilavirus“ (KAISER *et al.* 1982; SDOODEE & TEAKLE 1993), “sowbean mosaic sobemovirus“ (HARDY & TEAKLE 1992), and the most common “tomato spotted wilt virus“ (CHO *et al.* 1986; BROADBENT *et al.* 1990; MARCHOUX *et al.* 1991). Thrips are the only known transmitters of tospoviruses which belong to the family Bunyaviridae (GERMAN *et al.* 1992; ULLMAN *et al.* 1997). Tospoviruses possess a very close and complex relationship with their thrips vectors (ULLMAN *et al.* 1992, 1993, 1995; BANDLA *et al.* 1998). Thrips merely facilitate mechanical transmission in other cases (ULLMAN *et al.* 1997).

The postembryonic development of terebrantian species encompasses two active feeding larval instars, and two relatively inactive non-feeding pupal or metamorphic instars called propupa and pupa. Individuals of the Tubulifera have an additional pupal stage (MORITZ 1989a, 1997). The complete life cycle ranges between ten and 30 days, depending on temperature, day length, and available food (BRØDSGAARD 1994a; GAUM *et al.* 1994; RIJN *et al.* 1995; TSAI *et al.* 1995; MURAI 2000). Adults live for additional 10 to 30 days (LEWIS 1997). In warm regions and in greenhouses where breeding may be continuous, up to 12 or 15 generations could be completed each year. In cooler regions only one or two generations are possible and thrips overwinter as larva in the soil, or as adults among plant litter or under tree bark (LEWIS 1973, 1997).
Although the Thysanoptera are classified within the Hemimetabola, they do not have typical hemimetabolous stages. TAKAHASHI (1921) called the postembryonic development in thrips “remetaboly“ since the larval structures appear to become reconstructed in the adult. Metamorphosis is a way of indirect development linked to at least one larval stage that reaches the adult stage through more or less intense transformation processes (FIORONI 1973, 1985). NÜESCH (1987) described three different processes of metamorphosis: (1) the reduction (or degradation) of imaginifugal structures, (2) development of imaginipetal features, and (3) the taking over of larval-adult structures.
Point (1) serves as an indicator for the degree of metamorphosis. There are few structures known in Thysanoptera which appear to be present only during larval stages. Imaginifugal structures are the anal tube of terebrantian larvae (HEMING 1970a), numerous larval muscle groups (DAVIES 1969; HEMING 1975; MORITZ 1982b, c, d, 1988b, 1989a, b, c, d), and the larval eyes or stemmata (KUMM 1997; KUMM *et al.* 1997; KUMM & MORITZ 1998).
LEWIS (1973), HEMING (1973, 1975), and MOUND *et al.* (1980) describe the type of metamorphosis as intermediate between holometabolous and hemimetabolous. Several studies (MORITZ 1995) indicate that the metamorphosis of thrips does not fit into either of these categories, and that following NÜESCH (1987) it is preferable to place the Thysanoptera together with Coccina and all Endopterygota in a group called Holometamorpha.

Since knowledge about reproduction, progenesis, and embryogenesis of thrips is rare, this study aims on collecting data of these topics, creating a solid foundation for further molecular and biochemical investigations as well as for applied questions like virus transmission ability and reproduction rates.
This study mainly focuses on two thrips species, *Frankliniella occidentalis* and *Suocerathrips linguis*, representatives of the two suborders Terebrantia and Tubulifera, respectively. These species were chosen because they are readily available throughout the year in the laboratory. Thus, allowing

collection of both embryonic and postembryonic developmental stages with an exact age.
Western flower thrips, *F. occidentalis*, was a local pest in the western USA until 1980 (MOUND 1997) and quickly spread worldwide becoming a major pest (BRYAN & SMITH 1956; YUDIN *et al.* 1986; BRØDSGAARD 1994a; GAUM *et al.* 1994; RIJN *et al.* 1995). In the Netherlands it has become the most important pest in many ornamental and vegetable crops in greenhouses (MOUND 1997). *F. occidentalis* shows a very broad host plant range (YUDIN *et al.* 1986; EPPO 1988) damaging at least 59 genera and 219 species of vegetable and ornamental crops (BRØDSGAARD 1989). Currently chemical and biological control are used to control this pest and, unfortunately, *F. occidentalis* has become resistant to many chemical insecticides (IMMARAJU *et al.* 1992; BRØDSGAARD 1994b; KOGEL *et al.* 1997). *F. occidentalis* is now a quarantine pest species in the European Union (EPPO 2001).
Thus, data on the biology, development, and reproduction are essential to create strategies aimed at, e.g., interrupting reproduction.
Echinothrips americanus, another terebrantian species, is becoming a more important pest species (OPIT *et al.* 1997; COLLINS 1998; BILLEN 1999; RAMAKERS *et al.* 2000) and has been included in this study to show the variety of similarities and differences in the biology of the two pest species (*F. occidentalis* and *E. americanus*) in the family Thripidae.
S. linguis was first described by MOUND & MARULLO (1994) and belongs to the subfamily Phlaeothripinae (Phlaeothripidae). This species exhibits a subsocial lifestyle (MORITZ *et al.* 1998; SCHÄFER 1998).

Much research on thrips has focused on pest-management strategies and little is known about their reproductive biology, mating behaviour, or population dynamics. Data on thrips biology are important to control pests in long term (HIGGINS & MYERS 1992; MOUND 1992). Modern agriculture leads to serious environmental problems, human health problems and a dramatic reduction in biodiversity, as a result of monocropping, intensive fertilizer use and frequent application of chemical pesticides. Pure scientific research for instance in insect reproduction helps to find unexpected solutions for crop protection problems in current agriculture (VAN LENTEREN 1999). Studies on thrips behaviour and ecology are making it possible to understand patterns of structural variation within the order (MOUND 1997). Thus, reproduction studies on sex ratio, life tables, mating behaviour, and oviposition behaviour are examined in *F. occidentalis* and *E. americanus* in this study. Results should provide fundamental knowledge to help manage these pests.
Female thrips are diploid and males are always haploid (WHITING 1945; STANNARD 1968). Unfortunately, karyotype data are available for scarcely ten of the 5500 described species of Thysanoptera (RISLER & KEMPTER 1961), and of those ten the published date are contradictory. Arrhenotoky (where unfertilized eggs develop parthenogenetically into males and fertilized eggs develop into females) generally yields a sex ratio which deviates from 1 : 1 (female : male) value (HAMILTON 1967) and, according to LEWIS (1973), thrips species which reproduce by haploid facultative arrhenotoky often produce females : males in a ratio of 1 : 0.25.
Thrips also often produce by thelytoky, females giving birth only to further females. In some thrips species (e.g., *Heliothrips haemorrhoidalis*, *Hercinothrips bicinctus*, *Heliothrips errans*, *Scirtothrips longipennis*, *Leucothrips nigripennis*, and *Chaetanaphothrips orchidii*) males are very rare if ever recorded (LEWIS 1973). These species must therefore be assumed to produce more or less wholly parthenogenetically (obligate thelytoky). Other species (e.g., *Thrips tabaci*, *Taeniothrips inconsequens*, and *Haplothrips tritici*) reproduce by thelytoky in some geographical areas, whereas the sex ratio values indicate arrhenotoky in other areas (LEWIS 1973).
Wolbachia was discovered in two thelytokous thrips species, *H. haemorrhoidalis* and *H. femoralis*,

using PCR and ftsZ gene primer (PINTUREAU *et al.* 1999). The maternally inherited *Wolbachia*-bacteria are responsible for various modifications in host reproduction, including cytoplasmic incompatibility (HOFFMANN 1988; BREEUWER & WERREN 1990; O'NEILL & KARR 1990; WERREN 1997), parthenogenesis (STOUTHAMER *et al.* 1993), feminization of genetic males (ROUSSET *et al.* 1992), and altered male fertility or female fecundity (WERREN 1997; BOURTZIS & O'NEILL 1998).
The reproduction strategy adopted by a species is determined by the natural selection acting upon that species and the local species population (CHARNOV 1982). Environmental factors will influence the strength and evolutionary consequences of the selection. Therefore, the influence of different rearing conditions on developmental time and sex ratio of thrips species was examined in this study.
Thysanoptera is the only insect order other than Hymenoptera where all females are diploid and males are haploid (STANNARD 1968; LEWIS 1973; CRESPI 1991; CHAPMAN & CRESPI 1998). Haplodiploidy plays a main role in shaping the evolution of sociality in Hymenoptera (TRIVERS & HARE 1976). Therefore, the study of these insects helps to understand the relationship between haplodiploidy and kin selection in social evolution.
Six species of tubuliferan thrips that induce galls on Australian *Acacia* have been identified as eusocial (CRESPI 1992a; CRESPI & MOUND 1997). These thrips have a morphologically distinct soldier caste (enlarged forelegs, reduced wings, antennae, and melanisation) which fight invaders. Gall-inducing thrips are of particular interest in evaluating the roles of ecology and genetics in the evolution of social behaviour in haplodiploid species. Their life cycle is remarkably different from many other social insects (KRANZ *et al.* 1999). Thrips feed on the cell contents of the gall and thus do not forage or nurse their young as do eusocial Hymenoptera (RAMAN 1987).
Thrips show a broad variety of different behaviours ranging from non-social, subsocial to eusocial forms (TERRY 1997). Thrips offer a unique chance to understand the evolution of sociality. A couple of thrips species exhibit a subsocial lifestyle (MOUND & PALMER 1983a; CRESPI 1990). *S. linguis* displays a subsocial behaviour on *Sansevieria trifasciata* plants (MORITZ *et al.* 1998; SCHÄFER 1998). Data about the biology especially reproduction, mating and oviposition behaviour can reveal detailed information important for the understanding of the evolution of sociality.

Important for the understanding of the observed reproductive behaviour of the species is the knowledge of the morphological structures performing this kind of behaviour. In this connection, the outer and inner morphology of the female and male genitalia is important and also the progenesis of these structures. The observed reproductive behaviour is not possible without the anatomical structures or features and opposite, i.e. these structures are responsible that the species can act in the described manner. Conclusions are just possible considering both the structures and the behaviour.

As mentioned above, the morphology of the inner genital organs is important for understanding reproductive mechanisms and embryogenesis of the species.
A few embryological studies exist for thrips species. Tubuliferan embryogenesis was examined by BOURNIER (1966) on *Hoplothrips buffai*. ANDO & HAGA (1974) described the genesis of pleuropodia in *Bactrothrips brevitubus* and HEMING (1979, 1980) investigated the development of the mouthparts and gonads in *Haplothrips verbasci*. Terebrantian species were examined by KIRK (1985b) and by MORITZ (1988a).
The aim of this study is to show the similarities and differences in the embryology of both suborders of Thysanoptera (Terebrantia and Tubulifera) and to collect data on the embryogenesis, e.g., the duration of embryogenesis, morphology of eggs, and the mechanisms causing parthenogenesis in thrips. These data help to provide better control of the pest and to understand the adaptations under different

environmental conditions. Fundamental knowledge about thrips embryology is also important for the understanding of the evolutionary situation of Thysanoptera.

This study aims on adding more facts to the knowledge of reproduction, progenesis and embryogenesis in thrips to provide a better understanding of their biology, to help to develop new strategies to fight against pest species, and to explain the evolutionary differences of social behaviour in thrips.

2. Material and methods

2.1. Thrips species and culture

2.1.1. Thrips species

Table 1: Thrips species used in this study.

Species	Author and year	Suborder	Family	Origin
Aeolothrips intermedius	BAGNALL 1934	Terebrantia	Aeolothripidae	Wittenberg, Germany
Frankliniella occidentalis	(PERGANDE 1895)	Terebrantia	Thripidae	Lab culture
Frankliniella fusca	(HINDS 1902)	Terebrantia	Thripidae	Raleigh, USA
Echinothrips americanus	MORGAN 1913	Terebrantia	Thripidae	Lab culture
Parthenothrips dracaenae	(HEEGER 1854)	Terebrantia	Thripidae	Lab culture
Suocerathrips linguis	MOUND & MARULLO 1994	Tubulifera	Phlaeothripidae	Lab culture
Bactrothrips brevitubus	TAKAHASHI 1935	Tubulifera	Phlaeothripidae	Tokyo, Japan

2.1.2. Insect rearing methods

A. intermedius:
A. intermedius was collected in 1999 on *Silene vulgaris*. Specimens were collected from the plants, mounted for identification and prepared for further examination (see Chapter 2.3.).

F. occidentalis:
The *F. occidentalis* colony (original from Switzerland) was kept in a breeding room. The insects were reared on beans (*Phaseolus vulgaris* L.) under a temperature of 23 °C ± 1 K, a relative humidity of 80 %, and a light regime of LD = 16 : 8 (light on: 6.00 am).

F. fusca:
Specimens of *F. fusca* were prepared for electron microscopic examination at the University of Raleigh in North Carolina and were kindly provided by Dr. George Kennedy.

E. americanus:
E. americanus was reared in separated cages made of acryl glass (50 cm x 50 cm x 50 cm) on *Phaseolus vulgaris* under standard conditions (23 °C ± 1 K, 80 % relative humidity, light regime LD = 16 : 8, light on: 6.00 am).

P. dracaenae:
The laboratory stock culture was maintained on different indoor plants, for example, *Dieffenbachia maculata*, *Cyperus albostriatus*, *Phoenix canariensis*, *Ficus benjamina*, in cages under standardized conditions (temperature: 23 °C ± 1 K, relative humidity: 80 %, light regime: LD = 16 : 8, light on: 6.00 am).

S. linguis:
S. linguis was cultured on *Sansevieria trifasciata* (different cultivars) under a constant light regime of LD = 16 : 8 (light on: 6.00 am), a temperature of 23 °C ± 1 K, and a relative humidity of 80 %. The population originally came from England and was kindly provided by Phill Griffiths and Alison Scott-Brown from the Royal Botanical Garden, Kew, London.

B. brevitubus:
Samples (preserved in 70 % acetone) of viviparous and oviparous individuals were kindly sent us from Brenda Kranz (Laboratory of Insect Resources, Tokyo University of Agriculture, Japan). Fixation was carried out with glutaraldehyde and osmium tetroxide in phosphate buffer. The samples were further processed for light and electron microscopy (see Chapter 2.3.).

2.2. Culturing of the different developmental stages

2.2.1. Embryonal stages

1. *F. occidentalis*:
It was difficult to collect eggs of *F. occidentalis* laid in natural substrate, because they are embedded in the plant tissue. However, *F. occidentalis* could be induced to lay eggs in agar through a thin membrane.
For this reason, adult individuals were kept in cages made of acryl glass cylinders (diameter: 80 mm; thickness of the wall: 3 mm; height: 50 mm; VINK-Kunststoffe GmbH & KG). After transferring adult thrips to the cage, the cage was enclosed with parafilm. Pine pollen served as food.
An agar-block was placed on top of the parafilm. Females laid their eggs within the agar (agar-agar: 1.3 % (w/v) in distilled water). Eggs could carefully be removed from the agar block with a fine brush.

2. *S. linguis*:
Female *S. linguis* lay their eggs at the ground level making egg collection difficult. Therefore, young *Sansevieria trifasciata* leaves were dissected from whole plants. They were moved to plastic beakers (Saarstedt, Germany), glued to the bottom of the beaker, and surrounded by moist cotton.
20 to 30 adult thrips were transferred to one leaf and kept in cylindrical glass containers (height: 20 cm; diameter: 10 cm) covered with gauze. Egg laying began between 14-21 days.
Experiment A:
Eggs were collected from plants every 12 h and positioned on *Sansevieria trifasciata* leaf in a greiner chamber plate (Greiner Labortechnik, Germany). Greiner plates were covered with a glass lid. Eggs were stored in a climatic chamber under standardized conditions (temperature: 23 °C ± 1 K, relative humidity: 80 %, light regime: LD = 16 : 8).
16 mm time-lapse motion pictures were taken for analysing the morphogenetic movement of developing embryos.

Experiment B:
Experiment B was prepared using a 15 x 15 mm field marked on a microscope slide with dental wax (Plano, Wetzlar) and covered with a microscope slide cover slip forming a chamber. Eggs were positioned in the chamber. Thus, eggs could be observed individually. The slides were kept in petri dishes in a climatic cabinet (temperature: 23 °C ± 1 K, relative humidity: 80 %, light regime: LD = 16 : 8).

2.2.2. Postembryonal stages

1. *E. americanus*, *F. occidentalis*:
All postembryonal stages were reared in chambers made from greiner-plates with glass lids in a climatic cabinet (Sanyo, Japan) at a temperature of 23 °C, 80 % relative humidity, and a light regime of LD = 16 : 8. Chambers were filled with 0.4 % (w/v) agar to a height of approximately 3 mm. A bean leaf disc was placed on top of the agar on which the eggs were positioned.
To get larvae with a definite age, eggs at the "red eye" stage were transferred to greiner plates and their developmental status was monitored every 4 h under a stereo microscope.

2. *S. linguis*:
S. linguis larvae develop only in the presence of adults, and, therefore, the above postembryonal methods are not successful. Adults probably provide food (fungus spores which have to become established on the leaf first). Larvae seem to need the adults for more than providing food, because larvae do not survive on leaves on which adults are absent.
Therefore, larvae were kept with adults on *Sansevieria trifasciata* leaves and reared using the methods described in the *S. linguis* embryonal stages above. Leaves were glued in a plastic box containing moist absorbent cotton. The plastic box with the *Sansevieria trifasciata* leaf was positioned in a glass cylinder covered with gauze. Thus, leaves could be taken out of the cylinder for observation and control of thrips developmental stages.
Exact developmental times of single individuals, however, could not be determined due to difficulty in marking single individuals.

2.3. Histology

2.3.1. Light microscopy

2.3.1.1. Whole mounting

Embryonal stages of *F. occidentalis* and *S. linguis* could be examined *in-vivo*. Once eggs were enclosed in paraffin oil, their chorion became transparent making an *in-vivo* observation possible. However, early embryonal stages died after several hours (before anatrepsis) in *F. occidentalis* probably due to an insufficient uptake of water (MORITZ 1988a).
Larval, propupal, and pupal stages were incubated with lactic acid**,** dehydrated with ethanol, and embedded in canada balsam for mounting onto microscope slides (Table 2).

Adults were treated with a “stretching solution“ (AGA, composition: 60 % ethanol : glycerol : acetic acid = 10 : 1 : 1), dehydrated and after transferring in isopropanol and xylol, embedded in canada balsam on microscope slides.

Table 2: Preparation of whole mounts of thrips.

Larva 1, Larva 2, Propupa, Pupa				Adult			
	Concen-tration	Tempera-ture	Time		Concen-tration	Tempera-ture	Time
Lactic acid	90 %	60 °C	30 min	AGA		20 °C	1 h
Water		20 °C	10 min	Ethanol	60 %	20 °C	24 h
Distilled water		20 °C	10 min	Ethanol	70 %	20 °C	20 min
Ethanol	60 %	20 °C	24 h	Ethanol	80 %	20 °C	5 min
Ethanol	70 %	20 °C	1 h	Ethanol	95 %	20 °C	5 min
Ethanol	80 %	20 °C	20 min	Ethanol	100 %	20 °C	5 min
Ethanol	90 %	20 °C	5 min	Canada balsam			
Ethanol	100 %	20 °C	5 min				
Canada balsam							

2.3.1.2. Paraffin

Carnoy (1 h at 20 °C, composition: ethyl alcohol : chloroform : acetic acid = 6 : 3 : 1) was used as a fixation solution for all developmental stages. After fixation, the samples were dehydrated in an ethanol series, gradually infiltrated with isopropanol, and embedded in paraffin (Table 3). Polymerization was carried out at room temperature.

Transfer of the samples from one solution to the next was done using Pasteur-pipettes (Saarstedt, Germany) which were enclosed on one side with gauze (modified after MORITZ 1982a). Serial sections were cut on a microtome in three different directions (frontal, sagittal, transversal). Each section was 6 -8 µm thick.

Sections were stained with either Azan-novum (LEUTERITZ 1969) (Table 4) or Haematoxylin-Eosin (SMITH & BRUTON 1979) (Table 5) and they were examined with a light microscope (Leitz DMRBE, Leica, Germany). Documentation was either on Kodak film or images were captured directly from the microscope using a colour video camera (Sony, Japan).

Table 3: Time schedule for paraffin-embedding.

	Concentration	Time
Ethanol	70 %	1 h
Ethanol	80 %	1 h
Ethanol	90 %	1 h
Ethanol	100 %	1 h
Isopropanol I	100 %	1 h
Isopropanol II	100 %	12 h
Isopropanol III	100 %	1 h
Isopropanol : Paraffin	1 : 1	24 h
Paraffin I	100 %	24 h
Paraffin II	100 %	24 h
Paraffin III	100 %	24 h

Table 4: Azan-novum staining.

	Time
Kernechtrot	1 min
Distilled water	1 min
Differentiation solution	5 min
Distilled water	1 min
Anilin-orange-glacial acetic acid	10 min
Distilled water	1 min
Ethanol (96 %)	2 min
Isopropanol	2 min
Xylol	2 min
Canada balsam	
Differentiation solution: 100 ml 50 % acetic acid, 5 g phosphorous-tungsten-acid	

Table 5: Haematoxylin/Eosin staining.

	Time
Haemalaun	6 min
Water	10 min
Distilled water	1 min
Eosin	5 min
Ethanol (96 %)	≥ 1 min
Isopropanol	2 min
Xylol	2 min
Canada balsam	

2.3.1.3. Semithin sections

Samples of the different developmental stages were embedded in epoxide-resin (SPURR 1969) (see Chapter 2.3.2.2.). Semithin sections (1 µm thick) were cut at ultramicrotoms of different types, Ultratom I (LKB, Sweden), Ultracut R (Leica, Germany). Both glass knifes and a diamond knife (Diatome, Switzerland) were used for sectioning.
Sections were fixed at 80 °C. Afterwards, they were stained with 1 % (w/v) Toluidinblue in distilled water, 0.5 % (w/v) Safranin in 50 % ethanol, or Methylenblue-Fuchsin-staining.
A solution of 1 % boric acid was prepared in a mixture of methanol, glycerol, PBS (pH 7.4), and distilled water (relation 1 : 1 : 3 : 5) to provide Methylenblue-Fuchsin-staining (modified after SCHREITER *et al.* 1994). When the boric acid was solved totally, Methylenblue was added until a concentration of 0.13 % (w/v). The solution was immediately ready to use and stable for a couple months. Sections were stained with 0.13 % (w/v) Methylenblue for 2 min at 55 °C, rinsed with distilled water and then the slides were dried. Sections were stained with 0.05 % (w/v) basic fuchsin in 2.5 % ethanol and washed several times with distilled water.
Sections were examined under a compound microscope and photographed on Kodak film.

2.3.2. Transmission electron microscopy

1. Fixation and embedding

Postembryonal stages were decapitated under a microscope in either a drop of the fixative or physiological insect saline [composition: 0.2 M sodium chloride (NaCl); 0.003 M potassium chloride (KCl); 0.002 M calcium chloride ($CaCl_2$); 0.002 M magnesium chloride ($MgCl_2$); 0.003 M sodiumhydrogencarbonat ($NaHCO_3$); 0.01 M glucose ($C_6H_{12}O_6$); ph 7.5].

Paraformaldehyde/osmium tetroxide fixation:
Samples were fixed with 2 % paraformaldehyde (w/v) in 0.1 M Soerensen's buffer (pH 7.2) (ROBINSON *et al.* 1987) for 3 h at 4 °C followed by 1 h at room temperature. Samples were rinsed four times for 20 min and once overnight in buffer, postfixed with 1.5 % osmium tetroxide in 0.1 M Soerensen's buffer (pH 7.2) for 2 h at room temperature, and rinsed four times with distilled water for 20 min. Dehydration with acetone was followed by infiltration with propylene oxid and epoxide resin (Table 6). Polymerization was carried out at 65 °C for 16 h.

Paraformaldehyde fixation:
Samples were fixed in 2 % paraformaldehyde (w/v) in 0.1 M PIPES (pH 7.2) for 1 h at room temperature followed by two 10 min washes in buffer. Dehydration and infiltration was carried out after the PLT-method (progressive lowering temperature) (Table 7).
Gelatine capsules (Plano, Wetzlar) were used as embedding forms. A UV-sensitive accelerator (Benzoinmethylether) was added to the LR-White resin.
Samples were polymerized under air conclusion using UV-treatment for 12 h at -20 °C from below and 24 h at 4 °C from above.

Paraformaldehyde/glutaraldehyde fixation:
Samples were fixed in a mixture of 0.2 % (w/v) glutaraldehyde and 4 % (w/v) paraformaldehyde in

0.1 M Soerensen's buffer (pH 7.2) at 37 °C for 30 sec in a microwave oven (Ted Pella, USA). Specimens were rinsed four times for 2 min in buffer at room temperature following dehydration with ethanol and infiltration with LR-White (Table 8).
Polymerization was carried out in the microwave at 95 °C for 30 min and without restricted temperature for 1 h.

Table 6: Time schedule for Spurr-embedding.

	Concentration	Time
Acetone	10 %	15 min
Acetone	30 %	15 min
Acetone	50 %	30 min
Acetone	70 %	30 min
Acetone	90 %	30 min
Acetone, water free	100 %	30 min
Acetone, water free	100 %	30 min
Acetone : PO	3 : 1	30 min
Acetone : PO	1 : 1	30 min
Acetone : PO	1 : 3	30 min
PO	100 %	30 min
PO	100 %	30 min
Resin - PO	10 %	24 h
Resin - PO	30 %	24 h
Resin - PO	50 %	48 h
Resin - PO	70 %	24 h
Resin - PO	80 %	24 h
Resin - PO	90 %	24 h
Resin	100 %	12 h
Resin	100 %	16 h (65 °C)
Composition of the resin: D.E.R. 15 g, NSA 52 g, ERL 20 g, S1 0.8 g		

Table 7: Time schedule for LR-White embedding (PLT-method).

	Concentration	Temperature	Time
Ethanol	10 %	20 °C	10 min
Ethanol	20 %	20 °C	10 min
Ethanol	30 %	0 °C	1 h
Ethanol	50 %	- 20 °C	1 h
Ethanol	70 %	- 20 °C	1 h
Ethanol	90 %	- 20 °C	1 h
Ethanol	100 %	- 20 °C	1 h
Ethanol	100 %	- 20 °C	1 h
Ethanol : LR-White	2 : 1	- 20 °C	24 h
Ethanol : LR-White	1 : 1	- 20 °C	24 h
Ethanol : LR-White	1 : 2	- 20 °C	24 h
LR-White	100 %	- 20 °C	48 h
LR-White	100 %	- 20 °C	24 h
LR-White	100 %	- 20 °C	36 h (UV-light)

Table 8: Time schedule for LR-White embedding using a microwave.

	Concentration	Temperature restriction set point	Processing time in microwave
Ethanol	50 %	45 °C	2 x 45 sec
Ethanol	70 %	45 °C	2 x 45 sec
Ethanol	90 %	45 °C	2 x 45 sec
Ethanol	100 %	45 °C	2 x 45 sec
LR-White : Ethanol	1 : 1	40 °C	15 min
LR-White	100 %	40 °C	3 x 10 min
LR-White	100 %	95 °C	15 min
LR-White	100 %	None	1 h

2. Sectioning (Ultramicrotomy)

The polymerized samples were trimmed to a small trapezoid sectioning surface.
Ultrathin sections were cut on ultramicrotoms of different types, Ultratom I (LKB, Sweden) and Ultracut R (Leica, Germany) using a diamond knife (DIATOME, Switzerland) and glass knives. Glass knives were prepared on a 7800 knife maker (LKB, Sweden) using glass stripes (Polysciences, INC). Sections were carefully stretched with chloroform and then transferred onto copper-grids or nickel-grids.

3. Coating of grids

Copper grids and nickel grids of different types (G 100, 150, 200) were used. They were coated with either zaponlack (Roth) or formvar (SERVA).

Preparation of grids coated with zapon:
The stock solution was mixed with amylacetate 1 : 2.7. The thickness of the film could be changed by modifying the ratio mix of amylacetate. 10 µl of the solution were dropped on a clean water surface in a petri dish (from a height of approximately 10 cm). Once the amylacetate evaporated, a film remained which thickness was detected by water interference colours. Grids were placed onto the surface of the film and the film and grid were removed using a filter paper.

Preparation of formvar coated grids:
A solution of 0.5 % (w/v) formvar in either ethylene dichloride or chloroform was used. After dipping a cleaned microscope slide into the solution, the excess was drained off by touching the edge of the slide to a filter paper. The slide was air dried thoroughly. Razor blades were used to scratch the edges of the slide to free the film from the slide. The slide was slowly lowered into the water at a shallow angle to float the film onto the water. A low air current (a breath) facilitated the release of the film and was used to check the thickness of the film (colour should be gold). The grids were placed on top of the floating film and picked up by placing a piece of parafilm over them and carefully lifting it up.

4. Staining of the ultrathin sections

Ultrathin sections were stained with 1 % (w/v) uranyl acetate in distilled water for 30 min at room temperature and then treated with lead citrate (VENABLE & COGGESHALL 1965) for 2 min at room temperature. Carbon dioxide builds precipitates with the lead citrate, therefore, the staining was carried out in a petri dish with sodium hydroxide.
The grids were put with the section-side on a drop of the staining solution on parafilm, washed two times with distilled water for 1 min each, and then air dried.

5. Immunogoldlabeling

The labeling experiments were carried out with thrips material embedded in LR-White (see above). Ultrathin sections (90-100 nm) were transferred on nickel grids coated with formvar.
Grids were floated on 5 % (w/v) fetal bovine serum (SERVA) in 0.05 M phosphate buffered saline with 0.02 M glycine (FBS-PBS-GLY), pH 7.4 for 15 min and then floated on a 6 µl drop of the first antibody (anti TR313) diluted 1 : 10 in 5 % (w/v) FBS-PBS-GLY for 45 min at room temperature. Samples were then washed in 10 % (w/v) FBS-PBS-GLY four times for 5 min followed by an incubation of 30 min at

room temperature on 15 nm protein A-gold (SERVA) diluted 1 : 15 in 5 % (w/v) FBS-PBS-GLY. Samples were washed four times for 5 min each in 0.05 M PBS. The labeling was fixed with 2 % (w/v) glutaraldehyde in distilled water for 15 min and samples were washed four times with distilled water (5 min each). Finally, samples were stained with 2 % (w/v) uranyl acetate in distilled water for 15 min and lead citrate for 3 min and viewed in a Philips 410 LS transmission electron microscope.

List of used stains:

Anilinblue	Merck
Eosin	VEB Laborchemie Apolda
Fuchsin (basic)	SERVA
Haemalaun	Fluka
Kernechtrot	Merck
Lead citrate	SERVA
Methylenblue	SERVA
Orange G	Merck
Safranin	SERVA
Toluidinblue	SERVA
Uranyl acetate	SERVA

3. Results

3.1. Reproduction

In the following chapter, data on the reproduction of different thrips species were collected. They underline the variability of different strategies of reproduction in thrips. Special emphasis was put on *Frankliniella occidentalis*, a major pest in a lot of crops. Data on the reproduction of this species are fundamental for a better understanding of the biology and consequently the control of this pest. In addition, *Suocerathrips linguis* a representative member of the Phlaeothripidae showing a subsocial lifestyle was examined.

3.1.1. Sex ratio, type of parthenogenesis

Sex ratio of four different thrips species was determined (*F. occidentalis*, *Echinothrips americanus*, *Parthenothrips dracaenae*, and *S. linguis*). Adult thrips of the four different species were collected from their respective host plant. Number of ♂ and ♀♀ were counted and the spontaneous sex ratio was calculated (number of adult thrips per plant per day). Sex ratios (female : male) were 1 : 0.9 for *F. occidentalis*, 1 : 0.3 for *E. americanus*, and 1 : 0.5 for *S. linguis* (Table 9). One ♂ was found in *P. dracaenae*.

Table 9: Sex ratio (female : male) of different thrips species under constant rearing conditions (temperature: 23 °C, relative humidity: 75 %, LD = 16 : 8, light on: 6.00 am).

Thrips species	Sex ratio (female : male)	Number
F. occidentalis (Thripidae, Thripinae)	1 : 0.9	145
E. americanus (Thripidae, Thripinae)	1 : 0.3	123
P. dracaenae (Thripidae, Panchaetothripinae)	one ♂ was found (1 : 0.006)	175
S. linguis (Phlaeothripidae, Phlaeothripinae)	1 : 0.5	197

These findings correspond to the type of parthenogenesis found naturally in these species. *F. occidentalis* and *E. americanus* are haplodiploid. Winged species with a haplodiploid sex determination are assumed to disperse after emergence. Therefore, sex ratio is close to 1 : 1. *F. occidentalis* displays this type of behaviour dispersing immediately after hatching and adults move around frequently. In contrast to this, *E. americanus* does not disperse directly after hatching. Observed specimens did not change their position on bean leaves frequently. The reduced dispersal could explain the female biased sex ratio in *E. americanus*.

P. dracaenae has a thelytokous mode of reproduction. Female populations exist almost exclusively. Males are very rare. One ♂ of *P. dracaenae* was found.

Reproduction mode is still unknown in *S. linguis*. Being haplodiploid as well, however, would support the estimated sex ratio of 1 : 0.5.

In another experiment, the sex ratio of *F. occidentalis* was determined under influence of different temperatures. Females of *F. occidentalis* taken from the lab colony were allowed to lay eggs (see Chapter 2.2.1.). Eggs at the "red eye" stage were transferred on greiner plates filled with agar and a bean leaf disc on top of the agar. Greiner plates were stored in a climatic cabinet at three different temperatures (15 °C, 23 °C, and 30 °C), constant humidity (75 %), and a light regime of LD = 16 : 8. The developmental stage of the thrips was monitored every 12 h under a microscope. The sex ratio of the adults was determined immediately after emergence (Table 10).

Table 10: Sex ratio (female : male) of *F. occidentalis* at three different temperatures (15 °C, 23 °C, 30 °C; relative humidity: 75 %; light regime: LD = 16 : 8; light on: 6.00 am).

Temperature	Sex ratio (female : male)	Number
15 °C	1 : 1.2	238
23 °C	1 : 0.9	145
30 °C	1 : 0.5	424

The sex ratio of examined *F. occidentalis* altered depending on the temperature. Thrips reared at 23 °C had a sex ratio (females : males) of approximately 1 : 1 (75 ♀♀ and 70 ♂). Thrips reared at 30 °C induced a more female biased sex ratio (1 : 0.5). Decreasing temperature in contrast caused a more male biased sex ratio of 1 : 1.2 (Table 10).

To find out more about the sex determination in *F. occidentalis*, the experiment undertaken to determine the sex ratio was continued. It was examined whether unmated females produced exclusively male progeny, and whether females arise from unfertilized eggs. Unmated freshly hatched female adults were collected and kept separately in greiner plates in a climatic cabinet at different temperatures (15 °C, 23 °C, 30 °C). The unmated females were allowed to lay eggs and the sex of their progeny was determined. A few females hatched from unfertilized eggs in each replicate (Table 11). The same experiment was performed with *E. americanus* at 23 °C. Here the progeny of unmated females consisted exclusively of males. No females hatched from unfertilized eggs (Table 11).

Table 11: Sex of the progeny of unmated females of *F. occidentalis* reared at three different temperatures (15 °C, 23 °C, 30 °C) and *E. americanus* reared at 23 °C (relative humidity: 75 %, light regime: LD = 16 : 8, light on: 6.00 am).

	Progeny of unmated females of *F. occidentalis*		**Progeny of unmated females of *E. americanus***	
Temperature	Number of males	Number of females	Number of males	Number of females
15 °C	360	2	-	-
23 °C	116	1	262	0
30 °C	540	2	-	-

3.1.2. Copulation behaviour

F. occidentalis: *F. occidentalis* showed short copulation times lasting only a few minutes (between two and six minutes) with an average of 3.5 min. Females retracted further copulations after mated with one male.

S. linguis: Copulations in *S. linguis* took (compared with *F. occidentalis*) very long and often lasted for several hours (up to six hours was observed). Both male and female individuals were noticed possessing shortened wings. The wings were often observed to break during copulation while the smaller male fixes the female with his legs.

3.1.3. Oviposition behaviour

F. occidentalis: Newly hatched females of *F. occidentalis* were reared in separated greiner plates on bean leaf discs and stored in a climatic cabinet under constant conditions (temperature: 23 °C; relative humidity: 75 %; LD = 16 : 8) (see Chapter 2.2.1.). They were allowed to lay eggs.
The first larvae hatched after day five or six of the adult's lifetime (Fig. 1). This suggests a preoviposition period within the female of approximately one day, since embryogenesis takes about four days (90 h - 102 h) in *F. occidentalis*.
In this experiment, the mean lifetime of females was found to be 9.8 days ± 6.5 (SD, standard deviation used in this study always with the same unit as mean value) (n = 90). The oldest females were 32 days old.
Females started to lay eggs almost immediately after they emerged. It was no distinct postoviposition period observable. The oviposition period amounting to approximately 90 % of the females entire lifetime.
Females of *F. occidentalis* laid on average 75.6 eggs ± 52.24 during their entire lifetime. The average number of eggs laid by one female was 4.9 eggs ± 2.4 per day.

S. linguis: Females of *S. linguis* lay their eggs on leaves at the soil level of the *Sansevieria trifasciata* plant. Video observations revealed that individual eggs were moved by the females. They push the eggs with their legs into one group. It could not be determined whether the female who laid the egg transported it to the batch or whether other females or males moved the eggs.
An experiment was conducted to determine how many eggs *S. linguis* females lay per day. Adults were difficult to rear individually in chambers dying after a couple days. Therefore, groups of adult thrips were placed on single *Sansevieria trifasciata* leaves positioned in a glass cylinder (see Chapter 2.2.1.). Each group consisted of ten ♀♀ and five ♂. Females began to lay eggs after 14 to 18 days and on average two to three eggs were laid per day. It was not determined if all females laid eggs.

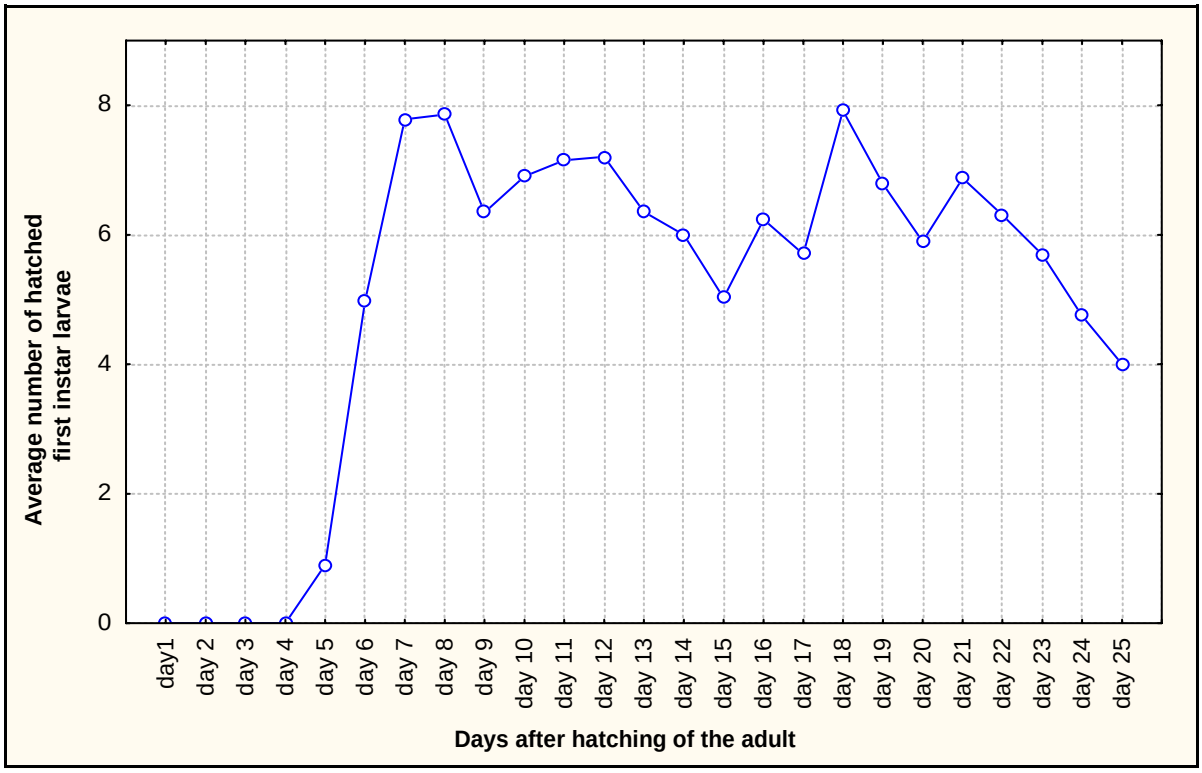


Fig. 1: Average number of eggs laid by *F. occidentalis* females during their entire lifetime. Reared in constant conditions (temperature: 23 °C, relative humidity: 75 %, light regime: LD = 16 : 8), number of examined females, n = 23.

3.1.4. Morphology of inner and outer genitalia of females and males

3.1.4.1. Morphology of the outer female genitalia

The differences in the morphology of the ovipositor of the examined terebrantian and tubuliferan thrips species result in a different oviposition behaviour of the observed representatives of the two suborders of thrips.

F. occidentalis and *E. americanus*:
In females examined from the suborder Terebrantia, *F. occidentalis* and *E. americanus*, the appendages of the eighth and ninth abdominal segments have been modified to form the egg-laying organ (ovipositor). The ovipositor (Fig. 2-4) is composed of the basal apparatus (valvifers and basalvalvulae) and the shaft (valvulae). It lacks the third valvulae. A protective cavity for the ovipositor is formed from the abdominal tergites IX to X.
The females are able to insert their eggs into the plant tissue with the ovipositor.

S. linguis:
The morphology of the ovipositor of tubuliferan females of *S. linguis* differs from the structure of the described terebrantian species *F. occidentalis* and *E. americanus*. The ovipositor in females of *S. linguis* has the structure of a simple tube and is situated at the eighth abdominal segment. In the retracted position it is contained within the ovipositor sheath of abdominal segment nine (Fig. 7).
Females of *S. linguis* lay their eggs on the surface of the *Sansevieria trifasciata* plant.

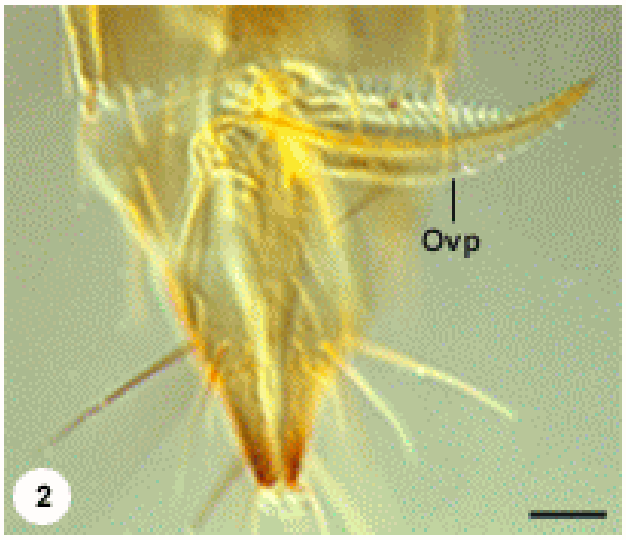
3.1.4.2. Morphology of inner female genitalia

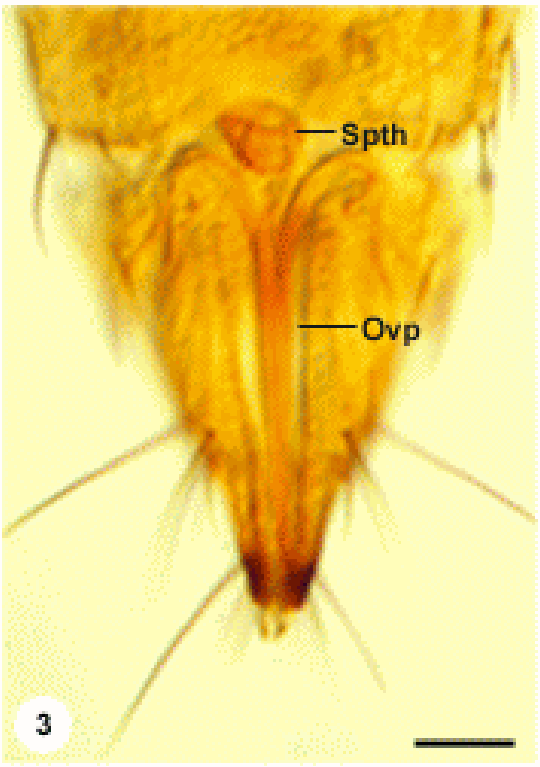
The inner female genital organs of investigated terebrantian and tubuliferan species consist of a pair of ovaries which connect with a pair of lateral oviducts. They join to form a median oviduct. The females examined in this study possess one spermatheca.
The observed thrips species have one pair of secondary panoistic ovaries since all oogonia develop into oocytes and follicle cells. Each ovary contains four ovarioles.

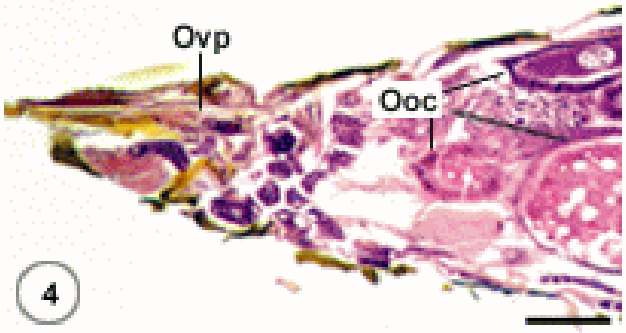
F. occidentalis and *E. americanus*:
Ovaries are situated underneath the midgut and in the oviposition phase the ovarioles reach the first abdominal segment. Each ovary is connected via a ligament with the thorax.
Five different zones are identifiable in one ovariole. Depending on the age and ovulatory stage, each zone develops differently.
Zone I is the terminal filament. The germarium, zone II (Fig.8, 9, 13), is located just below the terminal filament and above the vitellarium (zone III). The germarium contains somatic prefollicular cells, oogonia, and early (primary) oocytes.
Three different zones are distinguishable within the vitellarium (Fig. 8, Table 12). Zone IIIa contains small oocytes (Table 12). In zone IIIb the oocytes are recognizable on the previtellogenic growth of the oocytes, the yolk appears basophil.
The vitellogenetic growth of the oocytes takes place in zone IIIc (Table 12), which is distinguishable from zone IIIa and IIIb of the acidophil yolk (Fig. 8, 10-12).
Microscope counts of the average number of oocytes per ovariole for *F. occidentalis* is 8.6 ± 0.8 and 5.9 ± 0.2 for *E. americanus* (Table 13).
Lateral oviducti become unified in abdominal segment VII. The oviductus communis leads to the vagina. The spherical spermatheca (Fig. 14-17) is situated at the top of the vagina.
Unfertilized females show a small spermatheca without a big cavity. The spermatheca of fertilized females is filled with sperm (Fig. 14-17) and appears larger.

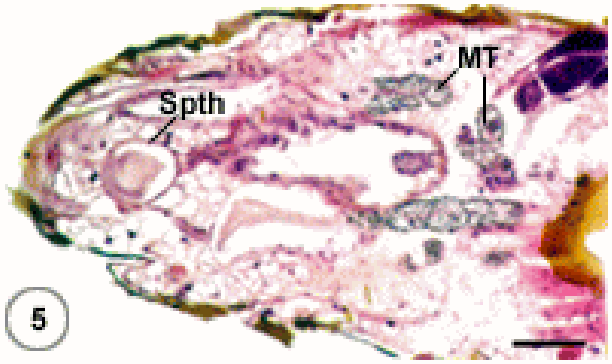
Plate I, II: **Fig. 2.** *F. occidentalis*, adult female, saw-like ovipositor composed of paired first and second valvulae, whole mounting, DIC, Bar = 50 µm. **Fig. 3.** *F. occidentalis*, adult female, ovipositor and spermatheca, whole mounting, DIC, Bar = 50 µm. **Fig. 4.** *E. americanus*, adult female, section through ovipositor, sagittal section, HE-staining, BF, Bar = 50 µm. **Fig. 5.** *S. linguis ,* adult female, section of last abdominal segments, frontal section, HE-staining, BF, Bar = 50 µm. **Fig. 6.** *S. linguis*, adult female, spermatheca and last abdominal segments, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 7.** *S. linguis*, adult female, abdomen, whole mounting, DIC, Bar = 150 µm. **Fig. 8.** *F. occidentalis*, ovariole of adult female, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 9.** *F. occidentalis*, germarium of a newly hatched adult female, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 10.** *E. americanus*, adult female, oocytes at different developmental stages, sagittal section, HE-staining, BF, Bar = 50 µm. **Fig. 11.** *F. occidentalis*, adult female, oocytes at stage IIIb and IIIc in the vitellarium, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 12.** *F. occidentalis*, adult female, oocytes at different developmental stages in the vitellarium, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 13.** *F. occidentalis*, adult female, germarium and oocytes in the vitellarium, frontal section, HE-staining, BF, Bar = 25 µm. FoC = follicle cell, Germ = germarium, Hg = hindgut, Mg = midgut, MT = Malpighian tubule, Nu = nucleus, Ooc = oocyte, Ovp = ovipositor, Spth = spermatheca, Vit = vitellarium, Yo = yolk, Zo II = zone II, Zo IIIa = zone IIIa, Zo IIIb = zone IIIb, Zo IIIc = zone IIIc.

Plate I









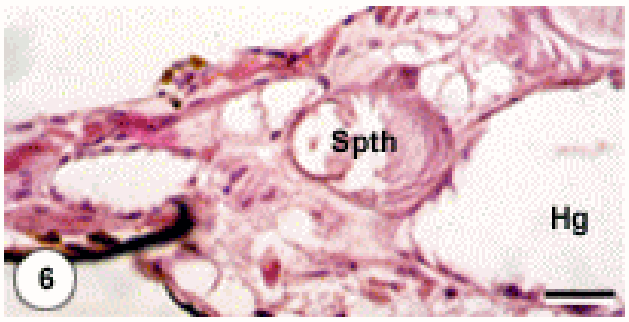
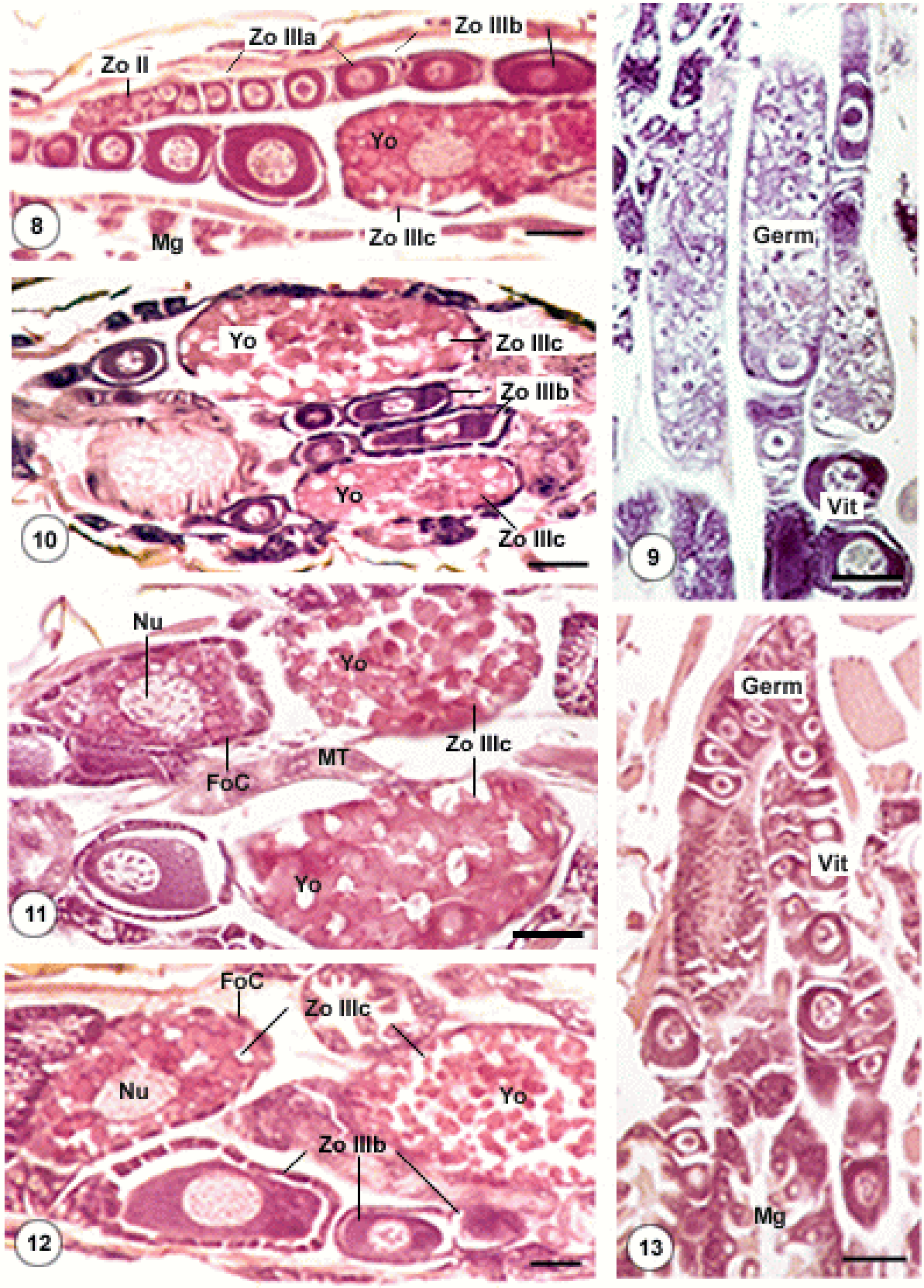
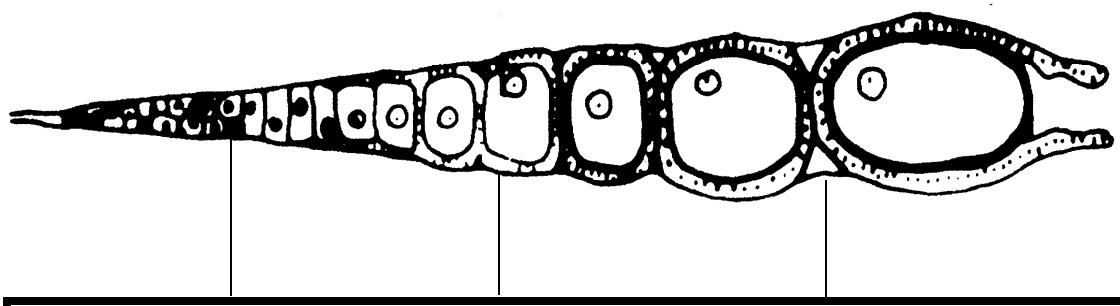


Plate II


Zo II
Zo IIIa
Zo IIIb
Yo
Mg
Zo IIIc
8
Yo
Zo IIIc
Zo IIIb
Yo
Zo IIIc
10
Germ
Vit
9
Nu
Yo
FoC
MT
Zo IIIc
Yo
11
Germ
Vit
FoC
Zo IIIc
Nu
Yo
Zo IIIb
12
Mg
13

Sperm is assembled within the spermatheca, which functions as a storage organ, as a spherical mass (Fig. 14-17). The spermatheca is surrounded by a thin sheath.
Whether the assemblage of sperm in the spermatheca should be considered to be a spermatophore is unclear. The sheath around sperm bundles in fertilized females of *F. occidentalis* is not visible in unmated females. There are two possibilities to explain the sheath covering of the sperm. One is that a spermatophore is made by the male and then transferred to the female during copulation. The second possibility is that the female produces the sheath around the sperm.
The spermathecal duct has a valve which could play a role in controlling fertilization of the eggs. Fertilization takes place when the valve is open, and through which the egg passes into the vagina regulated by thin muscles.

Table 12: Length and width of oocytes in the vitellarium of *F. occidentalis*.

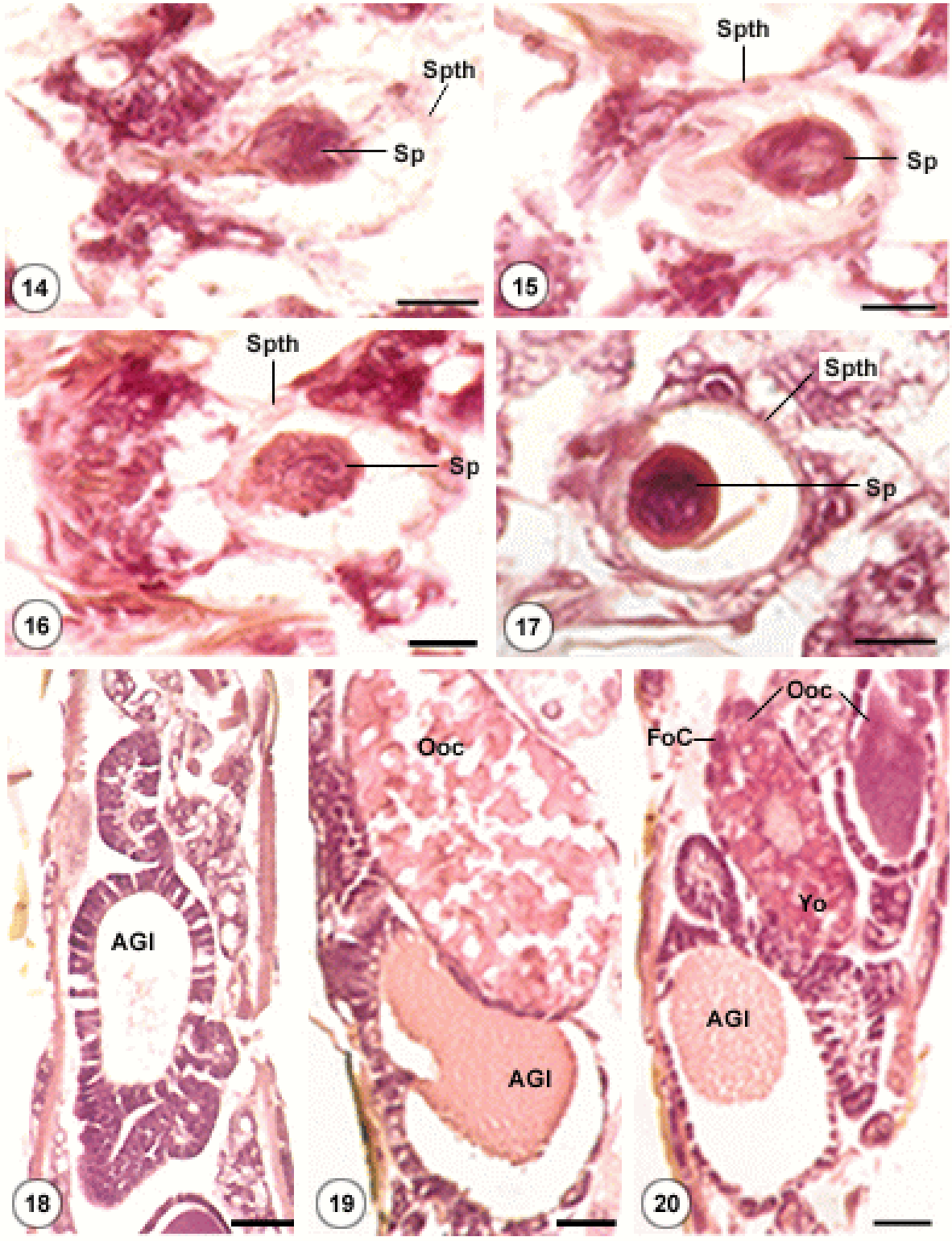


	Zone IIIa		Zone III b		Zone III c	
	Minimum	Maximum	Minimum	Maximum	Minimum	Maximum
Length in µm	15.0	37.5	45.0	120.0	125.0	225.0
Width in µm	12.5	20.0	25.0	40.0	50.0	100.0

The accessory gland (Fig. 18-20) is situated at the left side of the abdomen dorsally in segments VII and VIII.
The shape is different in newly hatched females versus ovipositing females. The gland of the latter group (Fig. 19), because of increased secretion, is fuller and appears larger.
An acidophil secretion product is visible in the accessory gland of ovipositing females (Fig. 19, 20).

Plate III: Fig. 14 - 17. Spermathecae of different terebrantian species, sperm assembled in a spermatophore-like structure. **Fig. 14 - 16.** Serial sections through a spermatheca of *E. americanus*. **Fig. 14.** *E. americanus*, adult female, frontal section, HE-staining, BF, Bar = 15 µm. **Fig. 15.** *E. americanus*, adult female, frontal section, HE-staining, BF, Bar = 10 µm. **Fig. 16.** *E. americanus*, adult female, spermatheca and associated muscles, frontal section, HE-staining, BF, Bar = 10 µm. **Fig. 17.** *F. occidentalis*, adult female, spermatheca, sagittal section, HE-staining, BF, Bar = 15 µm. **Fig. 18 - 20.** Sections of the accessory gland of female terebrantian species. **Fig. 18.** *F. occidentalis*, adult female, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 19.** *E. americanus*, adult female, accessory gland and oocyte at stage IIIc in the vitellarium, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 20.** *F. occidentalis*, adult female, accessory gland and oocytes of the vitellarium, sagittal section, HE-staining, BF, Bar = 25 µm. AGl = accessory gland, FoC = follicle cell, Ooc = oocyte, Sp = sperm, Spth = spermatheca, Yo = yolk.

Plate III


Spth
Sp
14
Spth
Sp
15
Spth
Sp
16
Spth
Sp
17
AGl
18
Ooc
AGl
19
Ooc
FoC
Yo
AGl
20

S. linguis:

The morphology of the inner female reproductive organs is similar to the terebrantian species examined in this study. Ovarioles are constructed from the terminal filament, the germarium, and the vitellarium (Fig. 21-24, 26). Because of the smaller amount of oocytes within the ovarioles, only two different zones were distinguishable within the vitellarium (zone IIIa and IIIb, Fig. 22, 23). In contrast to *Bactrothrips brevitubus* (Fig. 25), another representative of the family Phlaeothripidae, oocytes of *S. linguis* do not show a mycetome.

The ovarioles of *S. linguis* contain on average 4.5 ± 0.3 oocytes (Table 13).

The spermatheca (Fig. 5, 6, 27-29, 31) is situated in abdominal segments VI and VII. The spermatozoa within the spermatheca are not contained in a spermatophore-like structure as in *F. occidentalis* or *E. americanus*, but instead are loosely disposed and mixed with a granular basophil material (Fig. 27-29). Compartmentalization of the sperm bundles in the spermatheca could indicate that the female remated. *S. linguis* has long copulation times (see Chapter 3.1.2.). It is not known how the males transfer their sperm, as a bundle, a spermatophore, or one by one.

The prolonged copulation in *S. linguis* might be one strategy males use to make sure that the female is using their sperm for fertilization.

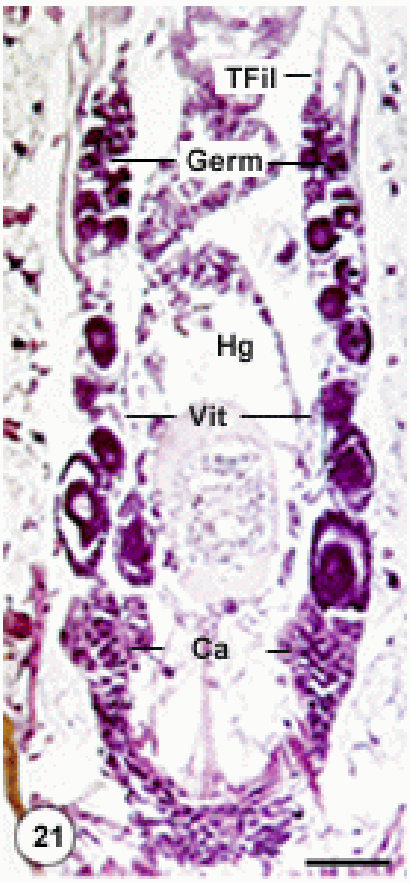
Females of *S. linguis* do not possess an accessory gland as described for *F. occidentalis* or *E. americanus*. There is a gland-like structure which has a connection to the spermatheca (Fig. 30, 31).

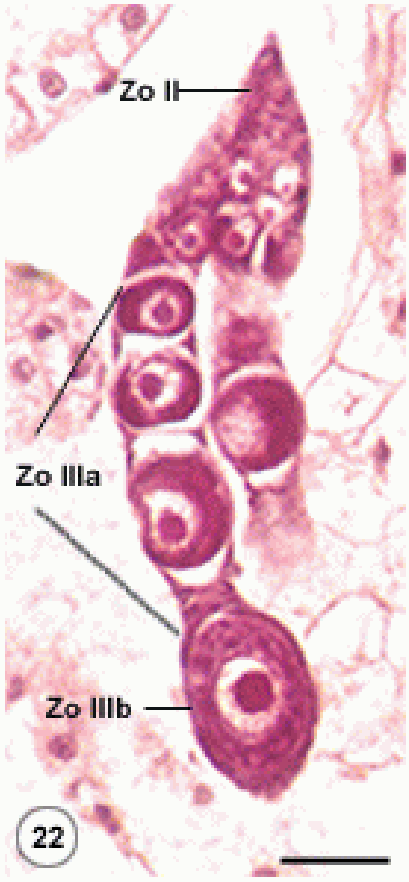
Table 13: Average number of oocytes per ovariole in different thrips species.

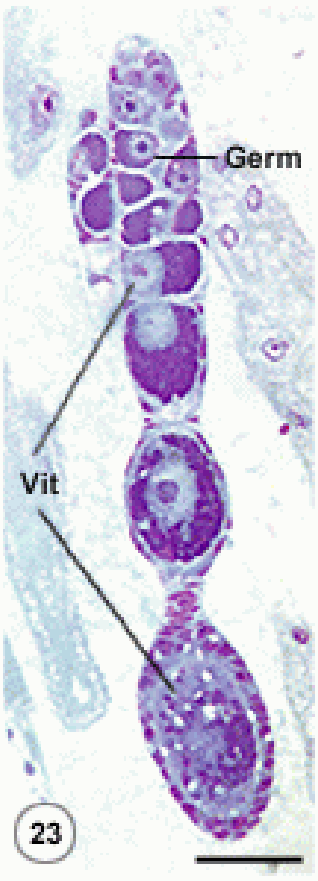
Species	Number of oocytes per ovariole (± SD)
A. intermedius	11.3 ± 0.7
E. americanus	5.9 ± 0.2
F. occidentalis	8.6 ± 0.8
S. linguis	4.5 ± 0.3

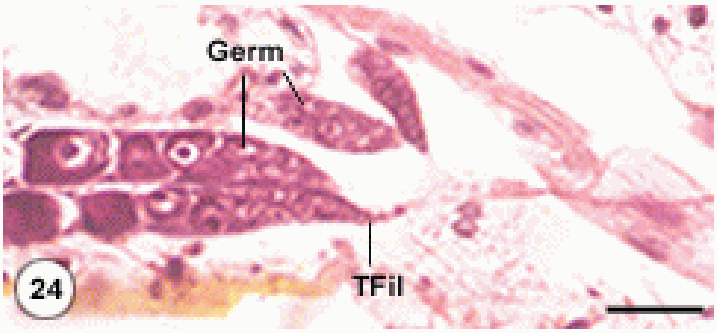
Plate IV, V: Fig. 21. *S. linguis*, adult female, paired ovaries consisting of ovarioles, frontal section, HE-staining, BF, Bar = 50 µm. **Fig. 22 - 23.** Different zones of ovarioles in ovaries of *S. linguis*. **Fig. 22.** *S. linguis*, adult female, sagittal section, HE-staining, BF, Bar = 20 µm. **Fig. 23.** *S. linguis*, adult female, sagittal section, Methylenblue-Fuchsin-staining, BF, Bar = 25 µm. **Fig. 24.** *S. linguis*, adult female, germarium and terminal filament of ovarioles, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 25.** *B. brevitubus*, adult female, oocytes showing a mycetome, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 26.** *S. linguis*, adult female, oocytes at different developmental stages, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 27 - 29.** Sections through spermatheca of *S. linguis*, sperm assembled in a loose order. **Fig. 27.** *S. linguis*, adult female, spermatheca and spermathecal duct, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 28.** *S. linguis*, adult female, spermatheca filled with sperm, sagittal section, HE-staining, BF, Bar = 15 µm. **Fig. 29.** *S. linguis*, adult female, spermatheca with sperm arranged in a loosely order, sagittal section, HE-staining, BF, Bar = 15 µm. **Fig. 30.** *S. linguis*, adult female, gland-like structure containing a secretion, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 31.** *S. linguis*, adult female, spermatheca filled with sperm and gland-like structure, sagittal section, HE-staining, BF, Bar = 25 µm. Ca = calyx, FoC = follicle cell, Germ = germarium, Hg = hindgut, My = mycetome, Nu = nucleus, Ooc = oocyte, Sp = sperm, Spth = spermatheca, SpthD = spermathecal duct, TFil = terminal filament, Vit = vitellarium, Zo II = zone II, Zo IIIa = zone IIIa, Zo IIIb = zone IIIb.

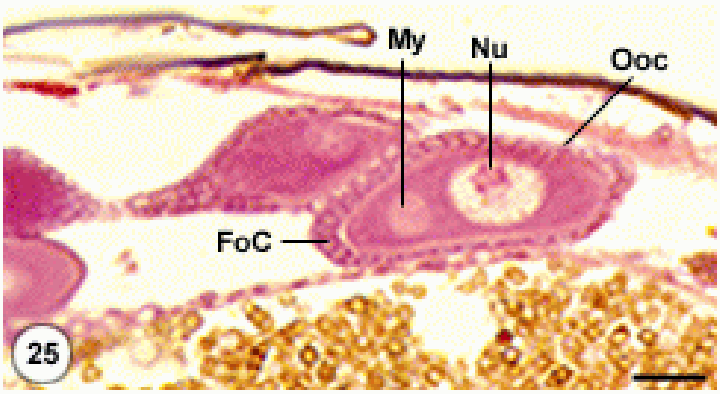
Plate IV


TFil
Germ
Hg
Vit
Ca
21


Zo II
Zo IIIa
Zo IIIb
22


Germ
Vit
23


Germ
TFil
24


My
Nu
Ooc
FoC
25

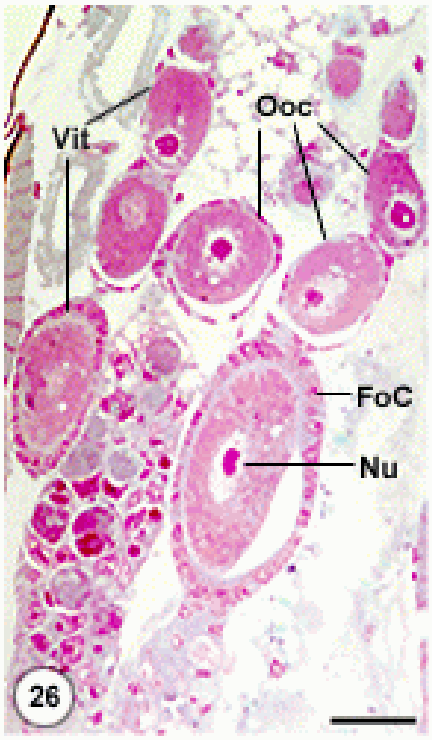
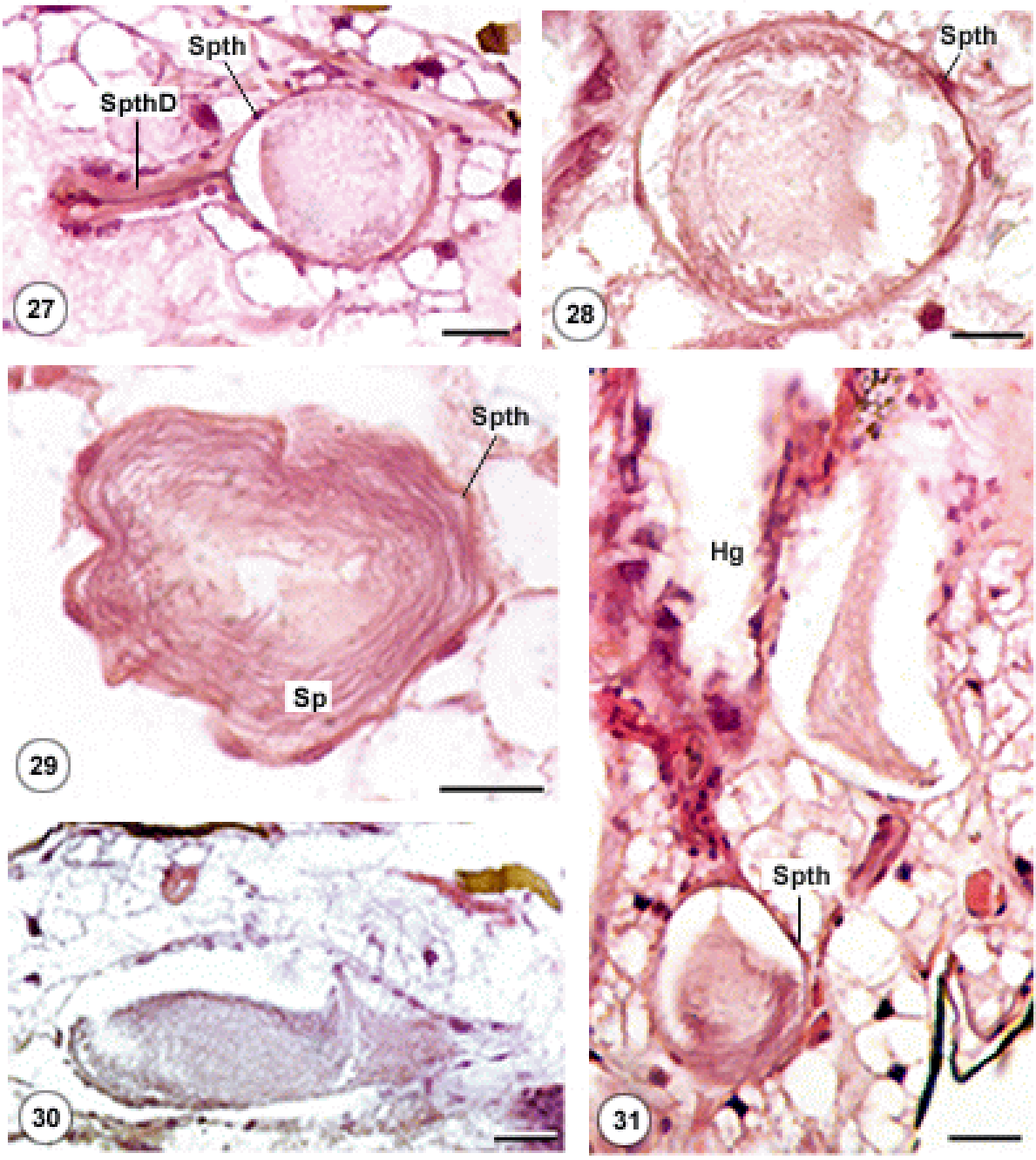

Vit
Ooc
FoC
Nu
26

Plate V



Determination of the quantity of oocytes within the vitellarium resulted in a different number in ovarioles of the following species: *Aeolothrips intermedius*, *E. americanus*, *F. occidentalis*, and *S. linguis* (Table 13). Considering these findings conclusions can be drawn of a connection between different reproduction strategies and the number of oocytes within an ovary. *F. occidentalis* possesses on average 8.6 ± 0.8 oocytes per ovariole and has a shorter generation time than *S. linguis*. *A. intermedius* shows approximately the same developmental time as *F. occidentalis* and *E. americanus* but has almost twice as many oocytes as *F. occidentalis* or *E. americanus.*
S. linguis has relatively long developmental times. Females of this species do not lay as many eggs as those of the Thripidae. *S. linguis* expresses a subsocial lifestyle investing more in parental care and less in egg production than *F. occidentalis*. By contrast, *F. occidentalis* favours laying as many eggs as possible in a relatively short period of time.

3.1.4.3. Morphology of outer male genitalia

All examined thrips species possess an extrusible phallus contained within a genital chamber (above the ninth sternum) at the ninth abdominal segment.

F. occidentalis and *E. americanus*:
The phallus of the adult male consists of a sclerotized phallobase which supports caudally a primitive aedeagus and two parameres situated more laterally. When the phallus is at rest, it is invaginated within the endotheca, a membranous protrusible vesicle at the phallotheca.

S. linguis:
In the adult male of *S. linguis* the phallus (Fig. 39) is composed of a sclerotized phallobase, having laterally a pair of sclerotized parameres and continues with the phallotheca. Posteriorly connected to the sclerotized phallotheca is the endotheca. The phallus is invaginated within this membranous vesicle when it is at rest. The aedeagus is also sclerotized and fixed to the apex of the endotheca.

3.1.4.4. Morphology of inner male genitalia

The male reproductive system consists of paired testes, two vasa deferentia each enlarged at its posterior end into a seminal vesicle, and an unpaired ejaculatory duct.

F. occidentalis and E. americanus:
Each testis of both *F. occidentalis* (Fig. 32) and *E. americanus* contains a single cyst of germ cells (Fig. 33). The testes of the adult are usually smaller than they were in the propupa and pupa. The mature spermatozoa are fine and basophilic and are twisted about one another in no particular order (Fig. 33). Testes of *P. dracaenae*, a species which also belongs to the family Thripidae, are divided into two chambers both containing sperm arranged in the same manner as described for *F. occidentalis* and *E. americanus* (Fig. 35).
The posterior end of each vas deferens (Fig. 33) expands into a seminal vesicle before contacting the wall of the ejaculatory bulb. The two accessory glands are filled with a nonstaining secretion. The wall of each gland is two-layered with a thin nonpigmented peritoneal sheath and an inner secretory epithelium. The glands are connected with the ejaculatory bulb via a small duct.

The ejaculatory duct is lined with a cuticle and penetrates the copulatory organ above the base of the aedeagus which forms the floor of the phallobase.

S. linguis:

Spermatogenesis still continues during the adult stage (Fig. 38). The testes contain cysts or follicles with different stages of spermatogenesis (Fig. 38). Another examined phlaeothripid species (*B. brevitubus*) did not show this arrangement of cysts with differently developed spermatogonia. Testes contained only mature sperm and no different stages of spermatogenesis were visible in the adult. The sperm showed an arrangement of longitudinal bundles which overlap one another and refers to an order of cysts during the immature stages (Fig. 36, 37).

The wall of a follicle is a thin epithelium. The follicles are bound together by a peritoneal sheath. Testes lead caudally into the vasa deferentia. Each vas deferens expands posteriorly into a seminal vesicle. The individual spermatozoa of a single sperm bundle become released when a sperm bundle moves into the vas deferens. Spermatozoa are found singly in the lumina of the exit ducts and aedeagus.

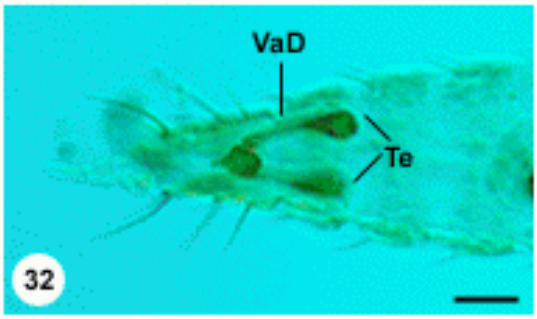
The proximal ends of the two pairs of accessory glands and of the vasa deferentia converge and merge in segment VIII with the anterior end of the ejaculatory duct. The first pair of glands is smaller and the product of these glands does not take stain and is homogenous. Each of the second pair of glands is large and bottle-shaped. These contain a basophilic secretion.

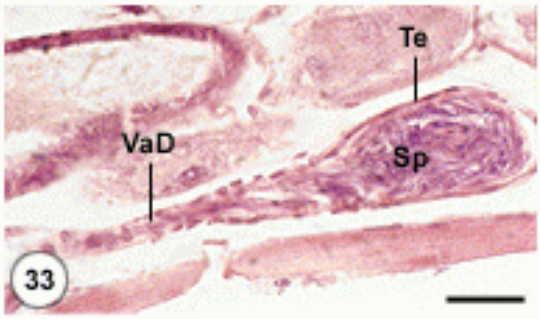
Terebrantia males have ventral abdominal glands, which are not found in *S. linguis* (Fig. 34).

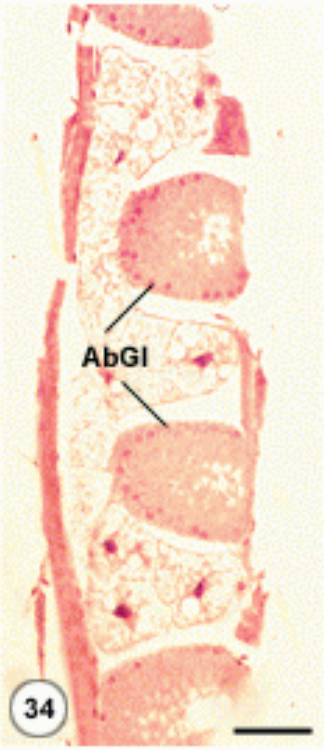
Both *F. occidentalis* and *E. americanus* possess five ventral abdominal glands. They open ventrally through an elliptical pore plate (Fig. 34).

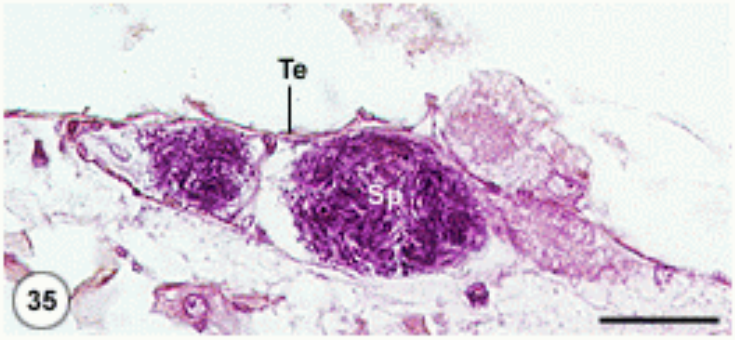
Plate VI: Fig. 32 - 39. Showing the outer and inner male reproductive organs. **Fig. 32.** *F. occidentalis*, adult male, paired testes, whole mounting, DIC, Bar = 50 µm. **Fig. 33.** *F. occidentalis*, adult male, testis containing sperm and vas deferens, sagittal section, HE-staining, BF, Bar = 15 µm. **Fig. 34.** *F. occidentalis*, adult male, abdominal glands, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 35.** *P. dracaenae*, adult male, testis subdivided into two chambers both containing fully differentiated sperm, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 36.** *B. brevitubus*, adult male, testis contains numerous sperm bundles, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 37.** *B. brevitubus*, adult male, testis with sperm and surrounding pigmented sheath, sagittal section, HE-staining, BF, Bar = 15 µm. **Fig. 38.** *S. linguis*, adult male, paired testes with numerous cysts containing spermatogonia at different developmental stages, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 39.** *S. linguis*, adult male with extrusible phallus, whole mounting, DIC, Bar = 50 µm. AbGl = abdominal gland, Ae = aedeagus, Cy = cyst, MT = Malpighian tubule, Sp = sperm, SpB = sperm bundle, Te = testis, VaD = vas deferens.

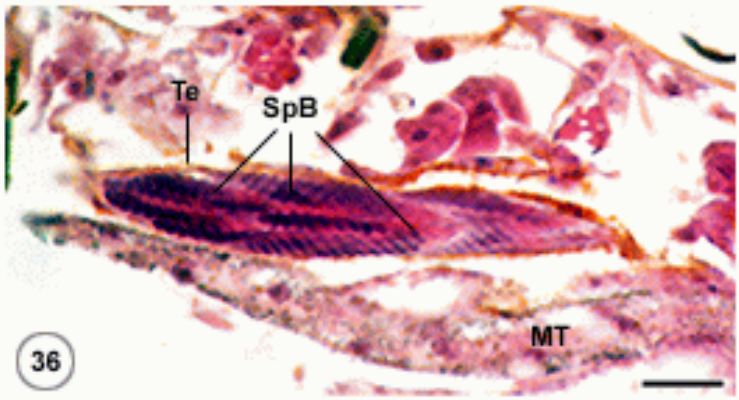
Plate VI

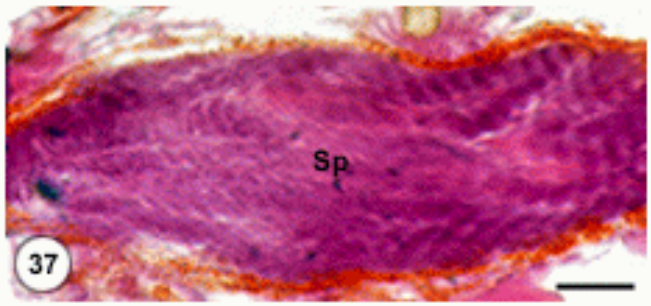

VaD
Te
32

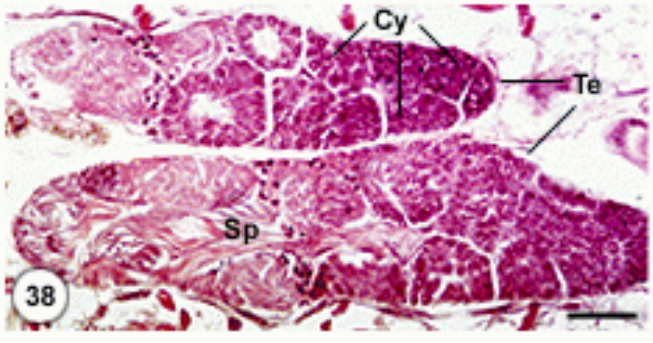

Te
VaD
Sp
33

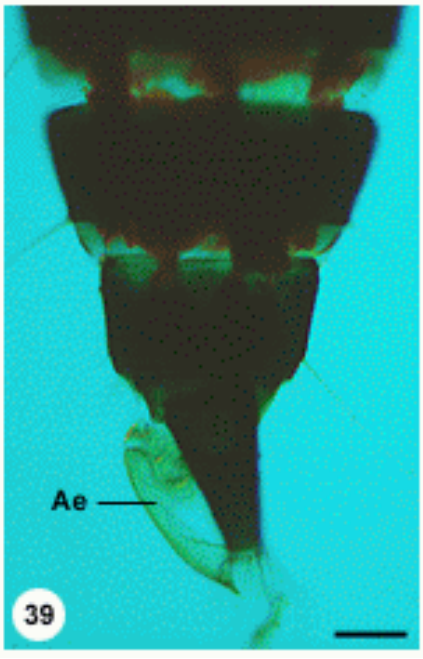

AbGl
34


Te
Sp
35


Te
SpB
MT
36


Sp
37


Cy
Te
Sp
38


Ae
39

3.1.5. Life tables

The developmental times of two different populations of *F. occidentalis* from Halle (Germany) and Perth (Australia) were tested at three intervals during one year. Differences in the developmental times between populations and whether seasonal changes exist was examined.
Experiments were performed in March 1996, September 1996, and November 1996. Eggs of both populations were collected at the same time intervals and positioned in chambers filled with agar and a bean leaf disc. Every chamber contained one egg (see Chapter 2.2.2.). The developmental stage was monitored every four hours under a stereo microscope. Greiner plates were kept in a climatic chamber under constant conditions (temperature: 23 °C, relative humidity: 75 %, LD = 16 : 8).

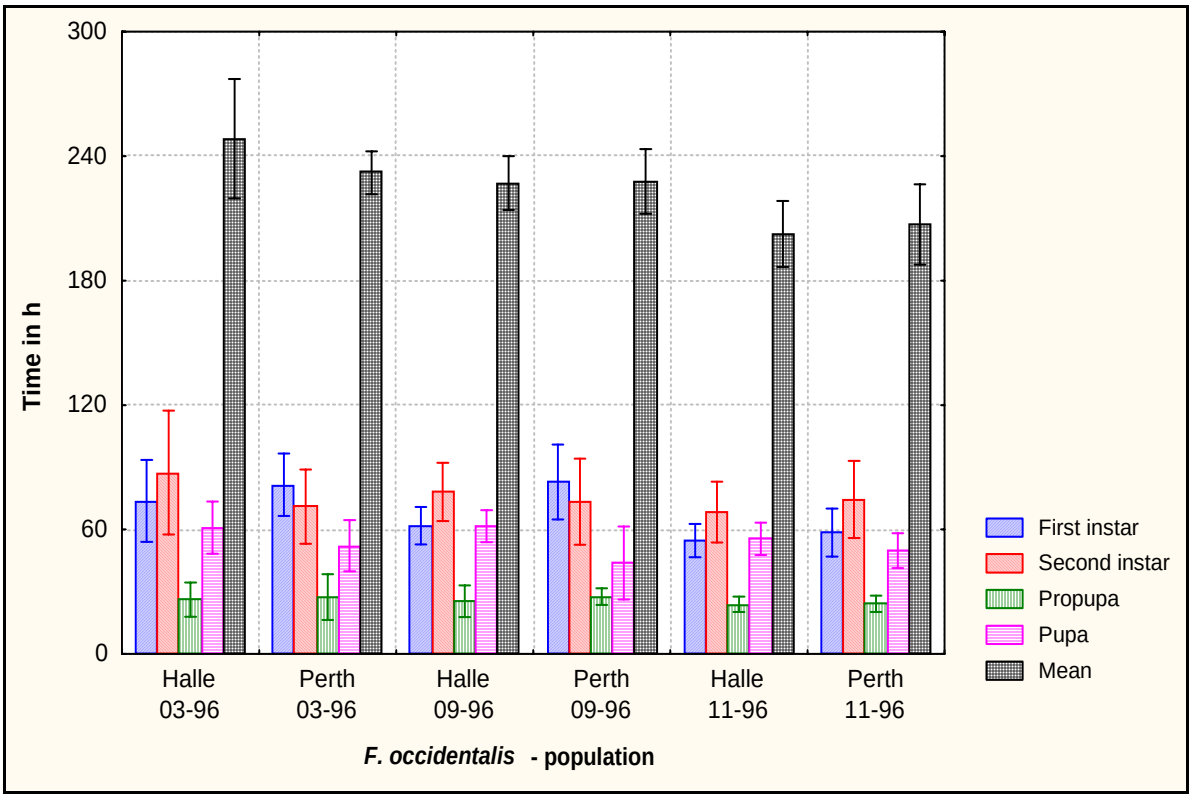


Fig. 40: Average developmental times of postembryonic stages of two different populations of *F. occidentalis* from Halle and Perth reared under constant conditions (temperature: 23 °C, relative humidity: 75 %, LD = 16 : 8) and tested at three intervals during one year (03-96 = March 1996, 09-96 = September 1996, 11-96 = November 1996).

No important changes of the mean developmental time occurred between the two different populations at the different time points during the year (Fig. 40, Table 14). The average developmental time decreased in both populations from March 1996 to November 1996 about 18.5 % (population from Halle) respectively 10.8 % (population from Perth).
The second instar larva was the postembryonic stage with the greatest variability. Relatively stable was the developmental time of propupa and pupa in both populations during all time intervals.

Table 14: Life table characteristics of two different populations of *F. occidentalis* reared in the laboratory under constant conditions (temperature: 23 °C, relative humidity: 75 %, LD = 16 : 8).

Population	Mean ± SD					n
	L1	L2	PP	P	Total	
Halle March 1996	73.8 h ± 19.7	87.4 h ± 29.8	26.2 h ± 8.2	61.0 h ± 12.5	248.4 h ± 28.7	29
Perth March 1996	81.6 h ± 15.1	71.0 h ± 17.9	27.4 h ± 11.0	52.2 h ± 12.3	232.2 h ± 10.4	39
Halle September 1996	61.9 h ± 9.1	78.1 h ± 14.1	25.4 h ± 7.6	61.6 h ± 7.8	227.1 h ± 12.9	27
Perth September 1996	82.9 h ± 18.1	73.4 h ± 20.8	27.7 h ± 4.1	43.8 h ± 17.6	227.8 h ± 15.6	26
Halle November 1996	54.6 h ± 8.0	68.4 h ± 14.7	24.0 h ± 3.7	55.5 h ± 7.8	202.5 ± 15.9	74
Perth November 1996	58.6 h ± 11.6	74.5 h ± 18.6	24.3 h ± 3.9	49.8 h ± 8.4	207.1 h ± 19.4	45

The influence of temperature on the development of the postembryonic stages of *F. occidentalis* was tested in another experiment. Eggs at the “red eye“ stage were placed on bean leaf discs in greiner plates (see Chapter 2.2.2.). Plates were stored in a climatic cabinet at three different constant temperatures (15 °C, 23 °C, 32 °C; relative humidity: 75 %; LD = 16 : 8).

The developmental times at the different temperatures showed differences. Mean developmental times (± SD) were 518.2 h ± 46.0 (15 °C), 217.1 h ± 27.5 (23 °C), and 173.3 h ± 13.2 (32 °C) (Table 15, Fig. 41-44). The mean developmental time at 15 °C was approximately three times longer than the developmental time at 32 °C. The time decreased about 58.1 % from 15 °C to 23 °C and 20.2 % from 23 °C to 32 °C.

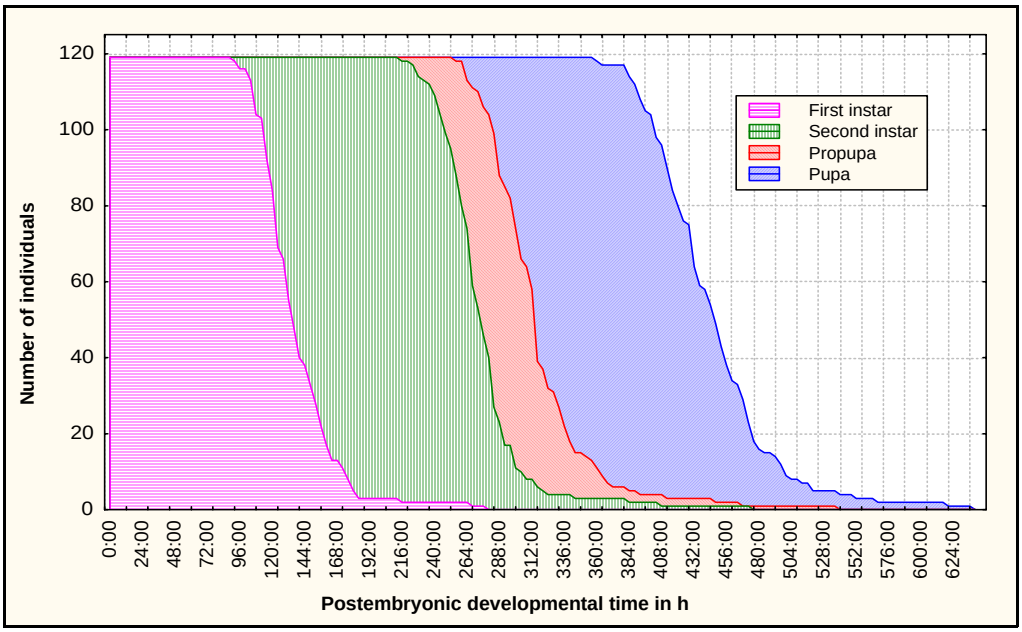


Fig. 41: Postembryonic developmental time of *F. occidentalis* reared at 15 °C (relative humidity: 75 %, light regime: LD = 16 : 8) (n = 119).

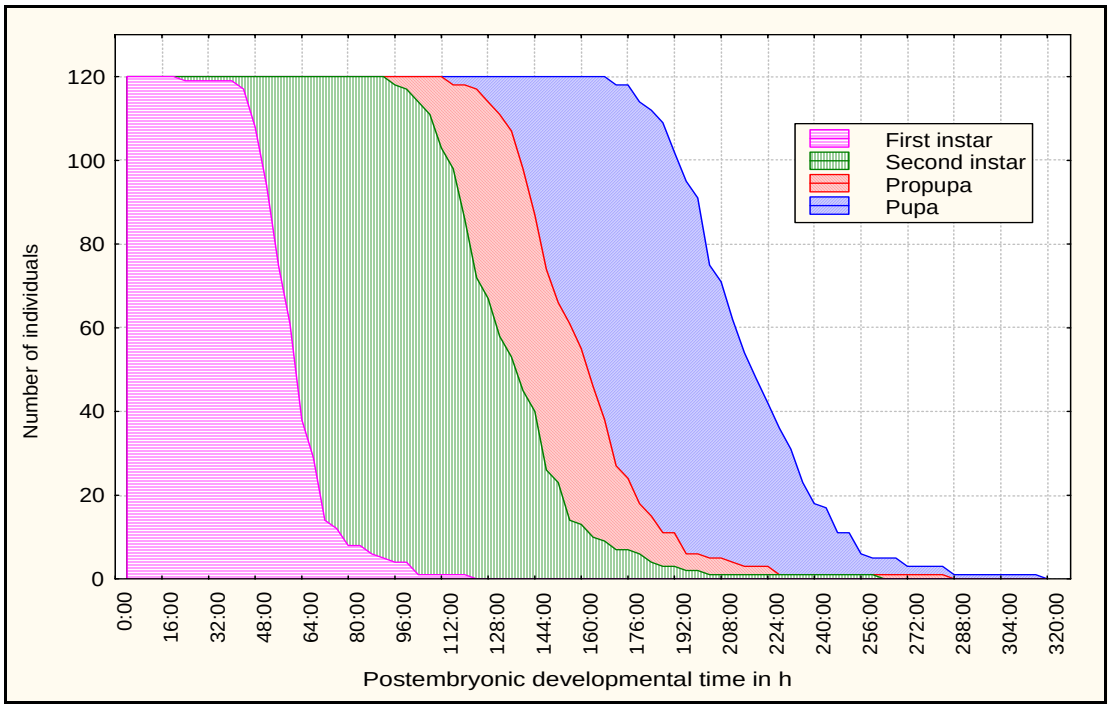


Fig. 42: Postembryonic developmental time of *F. occidentalis* reared at 23 °C (relative humidity: 75 %, light regime: LD = 16 : 8) (n = 120).

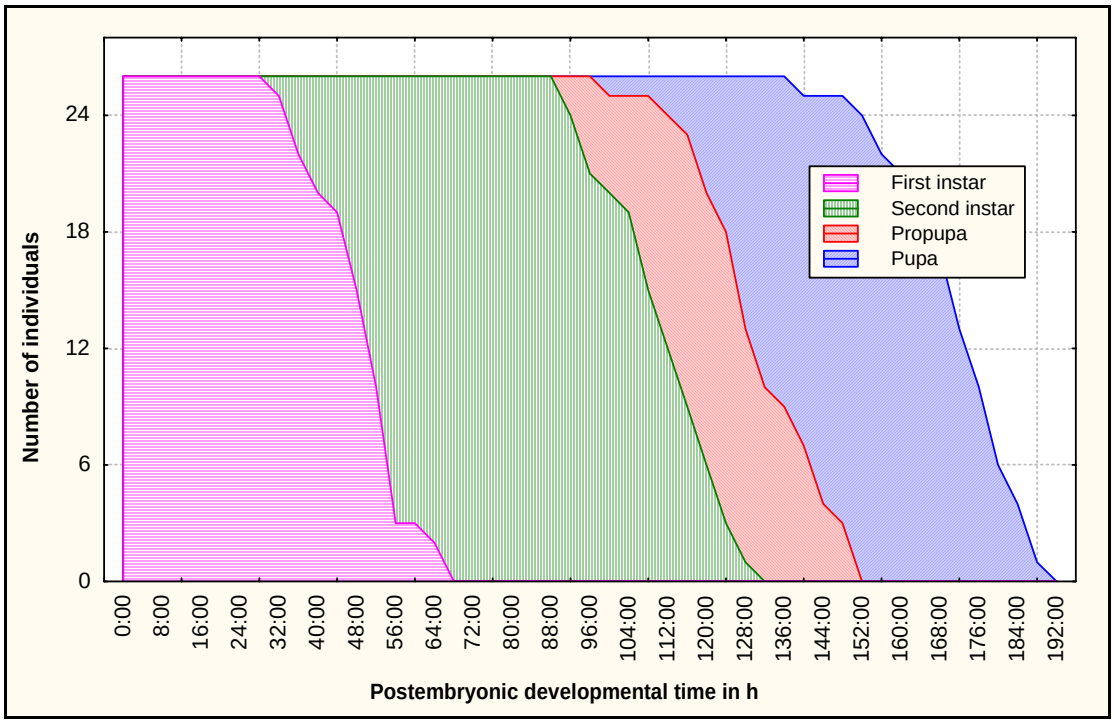


Fig. 43: Postembryonic developmental time of *F. occidentalis* reared at 32 °C (relative humidity: 75 %, light regime: LD = 16 : 8) (n = 26).

Table 15: Life table characteristics of postembryonic stages of *F. occidentalis* reared at different temperatures.

	Mean	Standard deviation	Minimum	Maximum	Number
15 °C					
L1	151.3 h	32.3	108 h	316 h	119
L2	164.4 h	25.2	116 h	264 h	119
PP	62.6 h	8.7	32 h	104 h	119
P	139.9 h	10.2	104 h	176 h	119
Total	518.2 h	46.0	432 h	716 h	119
23 °C					
L1	60.3 h	14.4	24 h	128 h	120
L2	74.4 h	20.8	40 h	208 h	120
PP	24.7 h	5.8	8 h	48 h	120
P	57.7 h	9.5	24 h	96 h	120
Total	217.1 h	27.5	168 h	328 h	120
32 °C					
L1	50.3 h	9.5	32 h	68 h	26
L2	61.7 h	14.4	28 h	92 h	26
PP	19.7 h	3.9	8 h	28 h	26
P	41.5 h	3.8	36 h	48 h	26
Total	173.3 h	13.2	140 h	196 h	26

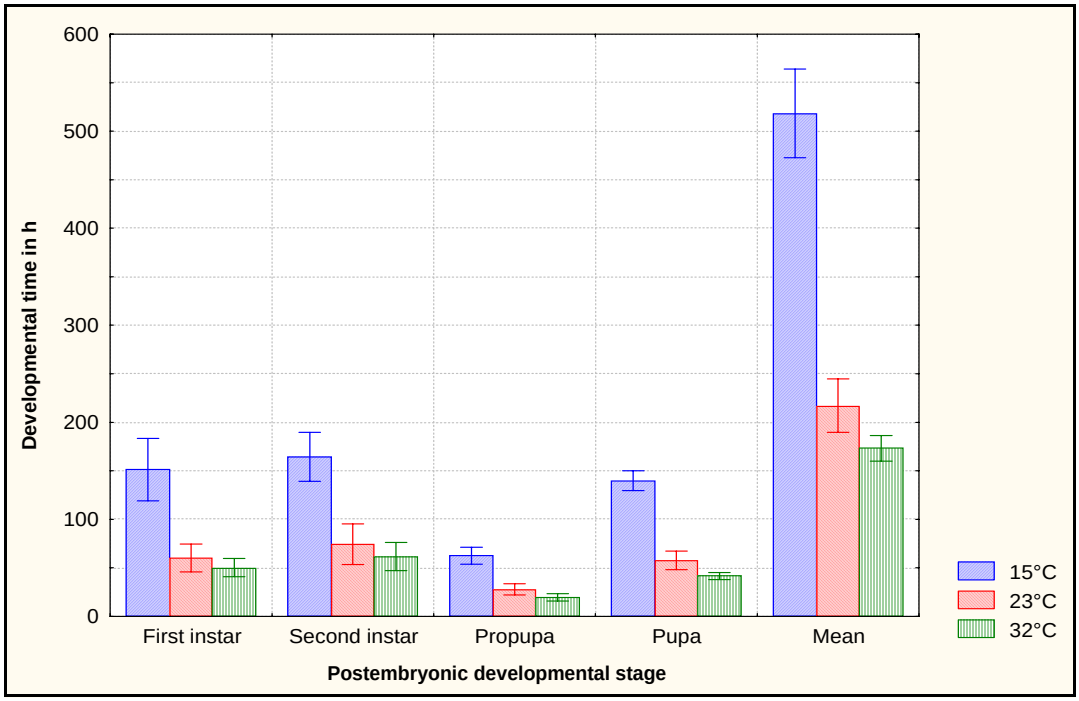


Fig. 44: Comparison of the developmental time of postembryonic stages of *F. occidentalis* reared at different temperatures (15 °C, 23 °C, 32 °C), a relative humidity of 75 %, and a light regime of LD = 16 : 8.

Larval development takes longest at the three temperatures tested, 31.7 % of total developmental time at 15 °C, 34.3 % at 23 °C, and 35.6 % at 32 °C. The second larval stage shows the greatest variability in developmental time. The developmental time of the propupal stage was the shortest time recorded with 11 - 12 % of the total developmental time.

The development of life stages for *E. americanus* was also monitored. To obtain a life table of postembryonic stages of *E. americanus*, the same protocol as described above for *F. occidentalis* was used. It was difficult getting enough eggs from *E. americanus* in the manner described for *F. occidentalis*. Therefore, females of *E. americanus* were separated from the lab colony and kept separately in greiner plates for 24 h to lay eggs. The females were removed after 24 h and the leaf discs were monitored every four hours. Freshly hatched larvae were transferred to chambers of greiner plates (see Chapter 2.2.2.). Greiner plates were stored in a climatic cabinet under constant conditions (temperature: 23 °C; relative humidity: 75 %; LD = 16 : 8). The development was monitored and recorded every four hours using a stereo microscope.
The mean developmental time of *E. americanus* was 185.5 h ± 9.7 (Table 16). The developmental time for *E. americanus* was 13 % reduced from that of *F. occidentalis* reared at 23 °C.
The longest developmental time was recorded in the first instar larva, 63.7 h ± 8.4 or 34.3 % total developmental time. The second instar and pupal developmental time was nearly equal with 51.2 h ± 7.2 for second instar larva and 47.9 h ± 7.4 for pupa (Fig. 45).

Table 16: Life table characteristics of *E. americanus* reared at 23 °C (relative humidity: 75 %, light regime: LD = 16 : 8) (n = 215).

	Mean ± SD	**Minimum**	**Maximum**	**Per cent of total developmental time**
First instar larva	63.7 h ± 8.4	48 h	100 h	34.3
Second instar larva	51.2 h ± 7.2	24 h	64 h	27.6
Propupa	22.7 h ± 4.0	12 h	32 h	12.2
Pupa	47.9 h ± 7.4	24 h	56 h	25.8
Mean	185.5 h ± 9.7	164 h	216 h	100

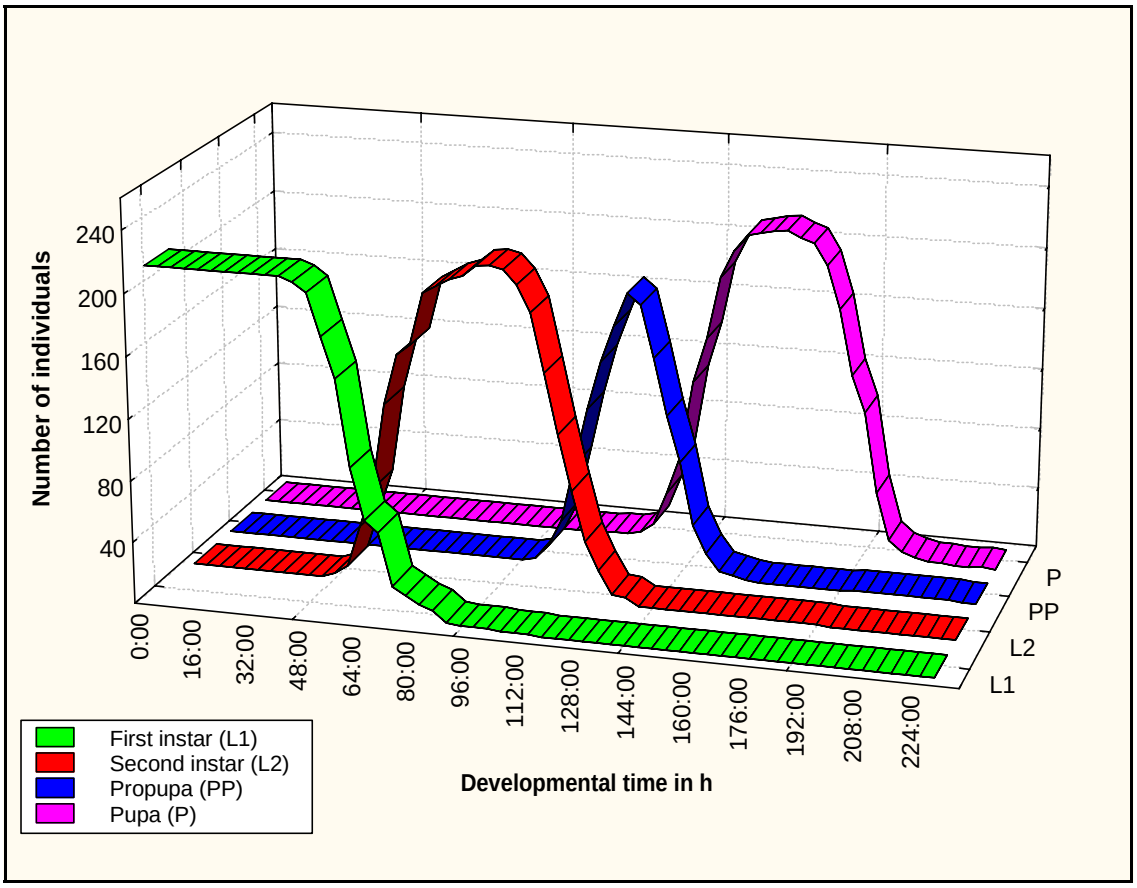


Fig. 45: Life table characteristics of postembryonic stages of *E. americanus* (temperature: 23 °C, relative humidity: 75 %, light regime: LD = 16 : 8) (n = 215).

Mortality rates at different developmental stages:

E. americanus showed the lowest mortality rate over all stages with 10.4% (89.6 % of the individuals developed until the adult stage, n = 240).

The mortality rate over all postembryonic stages was higher in *F. occidentalis* than in *E. americanus*. Mortality rate for *F. occidentalis* was 69.5 % at 23 °C (n = 393) and seven times higher than *E. americanus* with a mortality rate of 10.4 %.

The surviving rate of *F. occidentalis* at different temperatures was also documented. *F. occidentalis* had the lowest mortality (50.4 %) at 15 °C (n = 240). 81.9 % mortality rate at 32 °C (n = 143), thus only 18.1 % of the specimens became adults.

The populations of *F. occidentalis* used in the developmental study were from different regions of the world. The mortality rate for those were 63.7 % (population from Halle) and 75.8 % (population from Perth). There were no striking differences between the two populations. Mortality was slightly higher in March than in November for these populations.

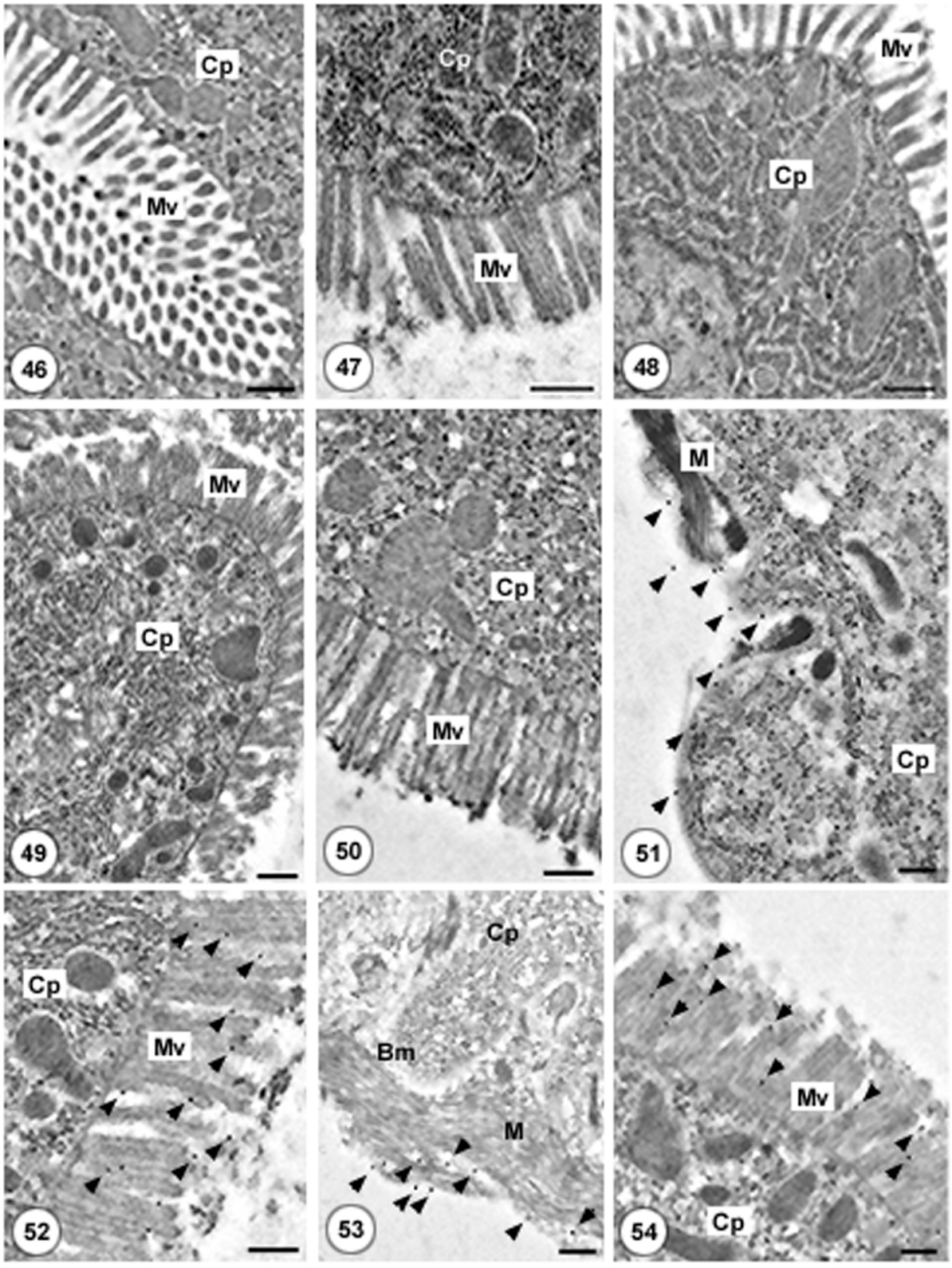
3.1.6. Thrips and tospoviruses

Frankliniella fusca tissue (midgut) was examined from tospovirus-infected and non-infected thrips. The tissue was compared to draw conclusions whether there are histological or structural differences between TSWV infected and non-infected thrips.
Larval and adult thrips of *F. fusca* infected with different virus isolates were prepared for ultrastructural examinations (see Chapter 2.3.2.). Midgut tissue was sectioned and viewed with an electron microscope.
There were no ultrastructural changes found comparing infected (Fig. 47, 48, 50) and non-infected (Fig. 46, 49) tissue of larval and adult stages of *F. fusca*. All the structures necessary for an active metabolism of the cell were well preserved.

In this study also putative receptors for the virus within the thrips were examined. The tests were mainly focused on the binding sites for the virus in the midgut of different developmental stages of *F. occidentalis*. Polyclonal antibodies made against a possible candidate of a receptor protein of the virus (antiTR313) were used for labeling the binding sites in *F. occidentalis*. Labeling was done on ultrathin sections using the polyclonal antibody (antiTR313) and protein A gold as secondary antibody (see Chapter 2.3.2).
Ultrathin sections of the midgut revealed that most labeling was found in the microvilli of the midgut, whereas a few were found in the cytoplasm and basal membrane of the midgut (Fig. 51-54).
A timed series of larval stages and adults of *F. occidentalis* was examined to find out if there are any developmental differences regarding the availability of the TSWV receptor candidate. Larval and adult stages were fixed and embedded every 6 h (see Chapter 2.3.2.), sectioned, and immunolabeled. The tested time series of larval stages and adults of *F. occidentalis* did not reveal any striking difference in the labeling of the examined midgut tissue. Labeling was also found in the salivary glands.

Plate VII: Fig. 46 - 50. Tospovirus-infected and non-infected midguts of different developmental stages of *F. fusca*. **Fig. 46.** *F. fusca*, first instar larva, non-infected, microvilli of the midgut, sagittal section, TEM, Bar = 0.5 µm. **Fig. 47.** *F. fusca*, first instar larva, TSWV-infected, microvilli of midgut, sagittal section, TEM, Bar = 0.5 µm. **Fig. 48.** *F. fusca*, second instar larva, TSWV-infected, midgut with microvilli, sagittal section, TEM, Bar = 0.5 µm. **Fig. 49.** *F. fusca*, adult, non-infected, midgut and microvilli, sagittal section, TEM, Bar = 0.5 µm. **Fig. 50.** *F. fusca*, adult, TSWV-infected, microvilli of the midgut, sagittal section, TEM, Bar = 0.5 µm. **Fig. 51 - 54.** Midgut tissue of larvae and adults of *F. occidentalis* treated with anti TR313 and Protein A gold for labeling of possible binding sites of the tospovirus within the thrips, arrows pointing at immunogold-labeling. **Fig. 51.** *F. occidentalis*, first instar larva (6 h), basal membrane and muscles surrounding the midgut, frontal section, TEM, Bar = 0.5 µm. **Fig. 52.** *F. occidentalis*, first instar larva (12 h), microvilli at the midgut, sagittal section, TEM, Bar = 0.5 µm. **Fig. 53.** *F. occidentalis*, adult (6 h), midgut, basal membrane and muscles, sagittal section, TEM, Bar = 0.5 µm. **Fig. 54.** *F. occidentalis*, adult (24 h), microvilli of the midgut, sagittal section, TEM, Bar = 0.5 µm. BM = basal membrane, Cp = cytoplasm, M = musculature, Mv = microvilli.

Plate VII


Cp
Mv
46
Cp
Mv
47
Mv
Cp
48
Mv
Cp
49
Cp
Mv
50
M
Cp
51
Cp
Mv
52
Cp
Bm
M
53
Mv
Cp
54

3.2. Progenesis

The postembryonic development of *F. occidentalis* and *E. americanus* encompasses two larval stages and two metamorphic stages, propupa and pupa, which do not feed and are inactive. *S. linguis* has an additional pupal stage.
The postembryonic differentiation of female and male genital organs in two terebrantian (*F. occidentalis* and *E. americanus*) and one tubuliferan species (*S. linguis*) are described to show differences and similarities occurring in the two suborders of Thysanoptera, Terebrantia and Tubulifera.

3.2.1. Development of the female genital organs

Ovaries in the larval stages in all three species appear as a pair of sac-like structures and do not show a distinct differentiation into ovarioles. While in *F. occidentalis* and *E. americanus* a first sign of the differentiation of ovarioles is visible in the metamorphic stages, in *S. linguis* it already appears in the late second instar larva. The total differentiation of each ovary into four ovarioles takes place during propupal and pupal stages in the examined species. Shortly before the female hatches, the separation into ovarioles is finished.

3.2.1.1. First and second instar larva

F. occidentalis and *E. americanus*:
Ovaries of the first instar larva are situated dorsally in abdominal segments V and VI in *F. occidentalis* and four and five in *E. americanus*. (Fig. 55, 56). Ovaries measure 35.8 µm ± 2.3 x 13.1 µm ± 2.1 in *F. occidentalis* and 49.1 µm ± 3.7 x 16.1 µm ± 2.3 in *E. americanus*. Each ovary contains germ cells which are at the developmental stage of oogonia (Fig. 56). The oogonia show a lightly basophil cytoplasm and a nuclei containing a single nucleolus. Each ovary is surrounded by a primary epithelial sheath.
Ovaries of second instar larvae are situated within the V. and VI. abdominal segment in *F. occidentalis* and the IV. and V. in *E. americanus* (Fig. 60, 61), and measure 68.3 µm ± 3.8 x 40.8 µm ± 2.9 in *F. occidentalis* and 74.0 µm ± 13.0 x 26.4 µm ± 3.7 in *E. americanus*. At the second instar larval stage, each ovary in both species shows a differentiation into three zones
(Fig. 59, 61). Zone I is the germarium, and zone II and zone III are situated within the vitellarium.

Plate VIII, IX: **Fig. 55.** *E. americanus*, first instar larva, ovary, sagittal section, HE-staining, BF, Bar = 20 µm. **Fig. 56.** *E. americanus*, first instar larva, ovary with oogonia, sagittal section, HE-staining, BF, Bar = 10 µm. **Fig. 57.** *S. linguis*, first instar larva, paired ovaries and oviducti, frontal section, HE-staining, BF, Bar = 50 µm. **Fig. 58.** *S. linguis*, paired ovaries of second instar larva, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 59.** *E. americanus*, second instar larva, differentiation of three zones in the ovary recognizable (Z1 = germarium; Z2, Z3 = vitellarium, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 60.** *E. americanus*, second instar larva, ovary connecting to the oviductus lateralis, sagittal section, HE-staining, BF, Bar = 10 µm. **Fig. 61.** *E. americanus*, second instar larva, paired ovaries joined anteriorly through the terminal filament, sagittal section, HE-staining, BF, Bar = 25 µm. Mg = midgut, MT = Malpighian tubule, Og = oogonium, Ov = ovary, OvdLat = oviductus lateralis, ReP = rectal papilla, TFil = terminal filament, Z1 = zone 1, Z2 = zone 2, Z3 = zone 3.

Plate VIII

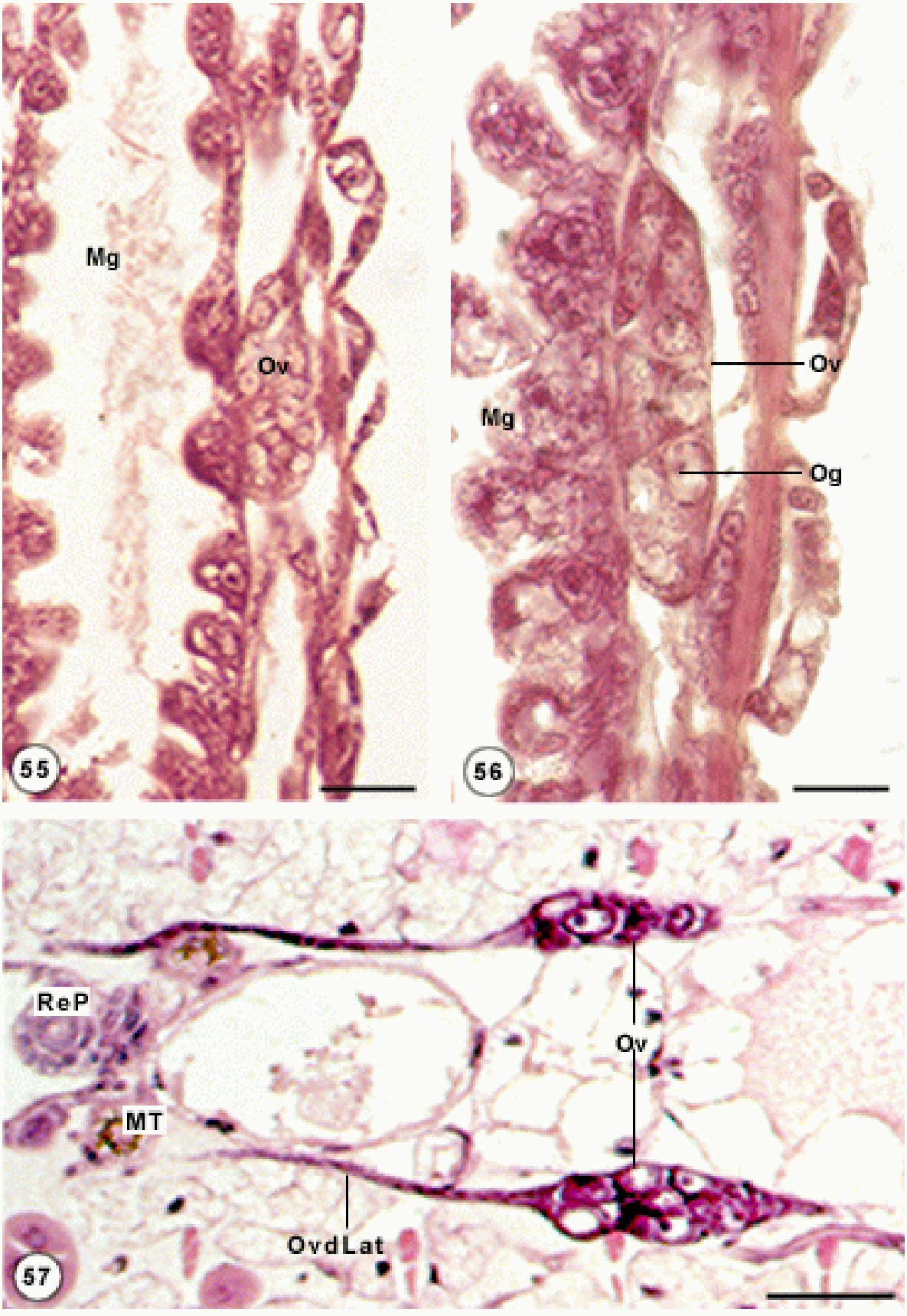
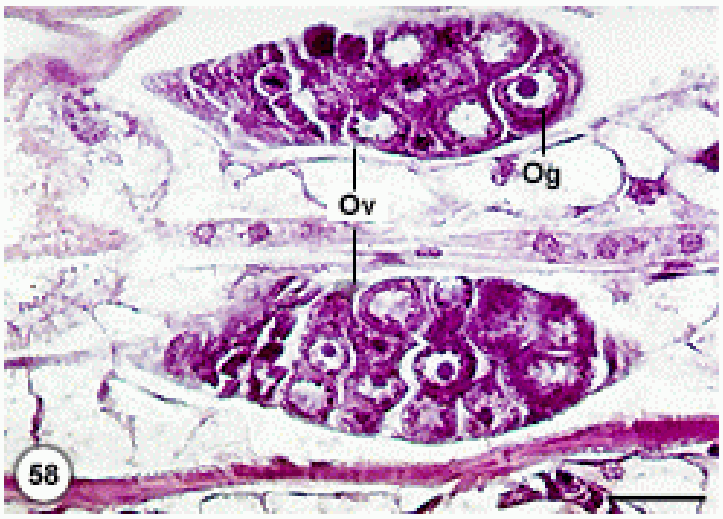
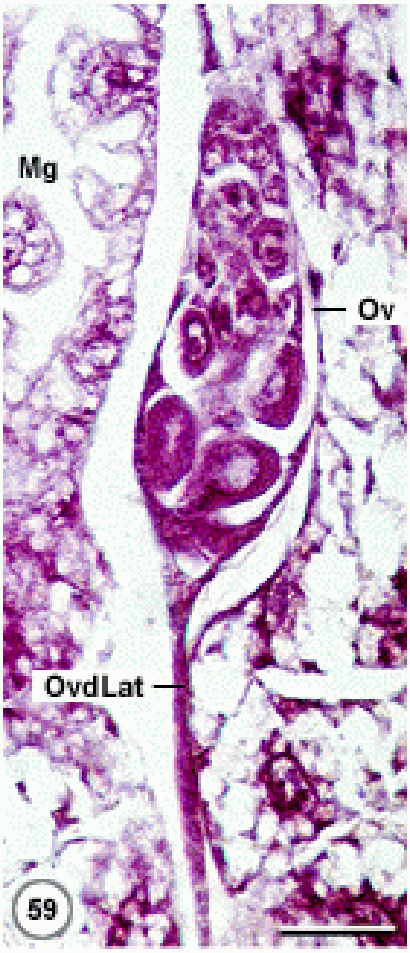
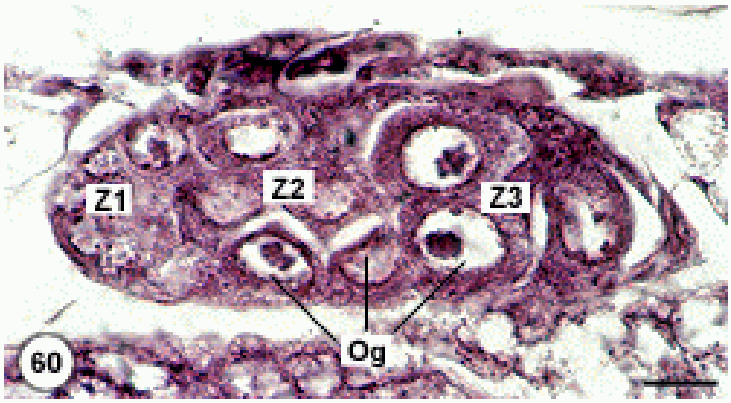
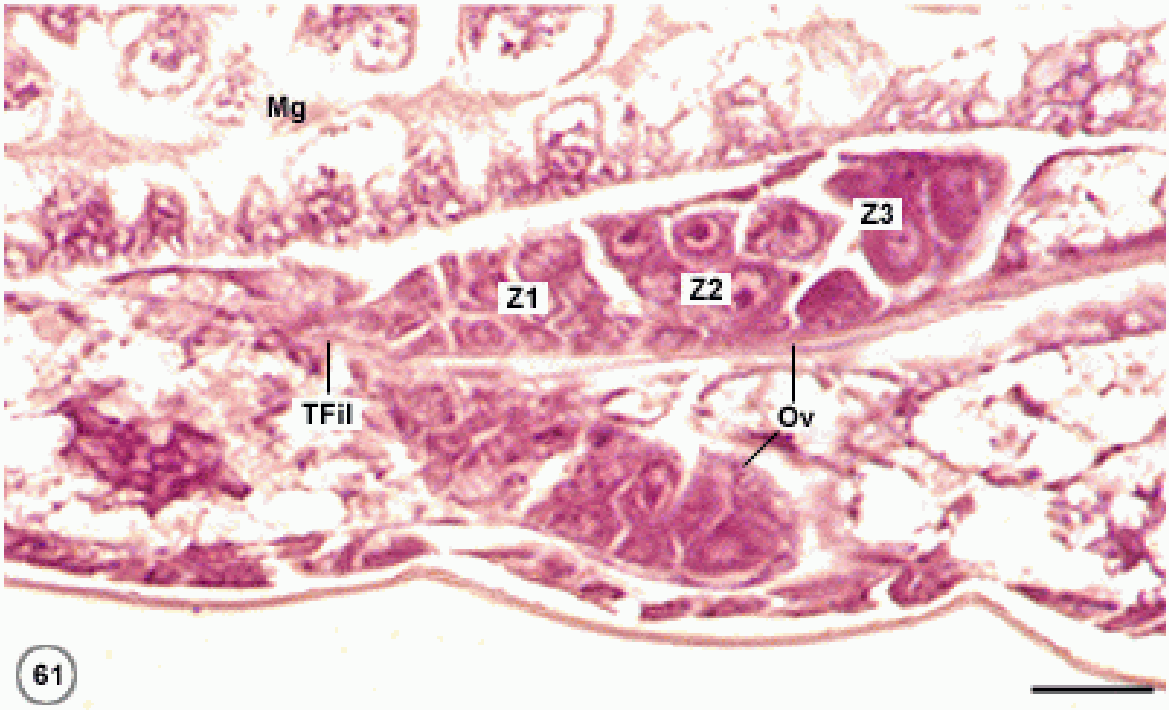


Plate IX









Zone II is situated at the anterior end of the vitellarium and zone III at the posterior end. The oocytes in zone III are further developed and reach the previtellogenic stage. The follicular layer is not fully differentiated yet.
Prefollicular cells, precursors to follicular cells, start to arise approximately in mid development of the second instar. The nuclei of the prefollicular cells are more basophil than those of the oocytes.
The lateral oviduct is visible at the posterior end of each ovary as an extension into a tube-like anlage (Fig. 60).

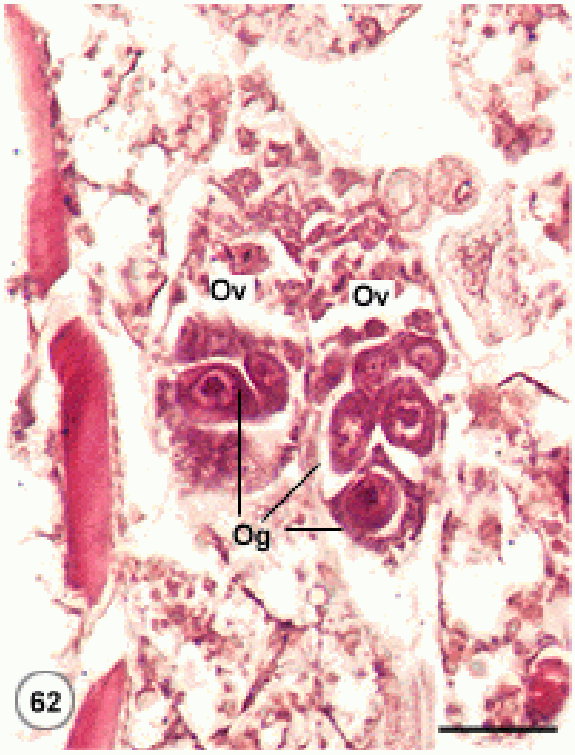
S. linguis:
Larvae of *S. linguis* possess ovaries which are situated in abdominal segments V and VI (Fig. 57, 58). Compared with the examined species of the family Thripidae, in late second instars of *S. linguis*, the cells of the ovarian rudiments already show an arrangement to form columns. These columns are the first sign for the further differentiation of ovarioles. Besides, at the anterior end of the ovary four files of cells are visible shortly before propupa hatches which later develop into the terminal filaments of the ovarioles. Therefore, the situation at the end of the second larval stage is comparable to the propupal stage of *F. occidentalis* and *E. americanus* (see below).

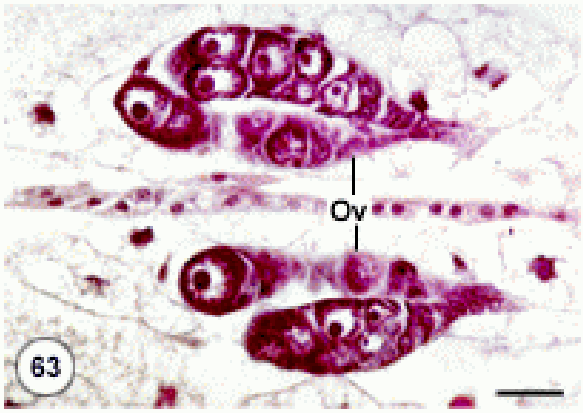
3.2.1.2. Propupa and pupa

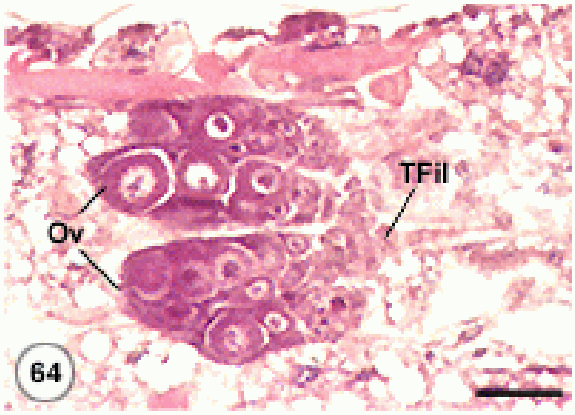
F. occidentalis and *E. americanus*:
The appearance of four distinct longitudinal files of cells at the anterior end in each ovary becomes visible in the propupa (Fig. 62). The files of cells show later an arrangement of eight rows, each row eventually builds a terminal filament of an ovariole (Fig. 64).
During the late propupal stage, each of the two ovaries begins to divide into four ovarioles (Fig. 65, 66). This process continues during the pupal stage (Fig. 67). The separation starts at the anterior end of the ovaries appearing as grooves which intensify caudally and resulting in the dividing ovarioles. In combination with this process, the primary oocytes, which are situated in the posterior region of each ovary, become arranged into four rows (Fig. 67). Prefollicular cells are visible between these oocytes and begin to form a follicular layer around each oocyte.
By the end of the pupal stage, the four ovarioles of each ovary are completely separated from each other.

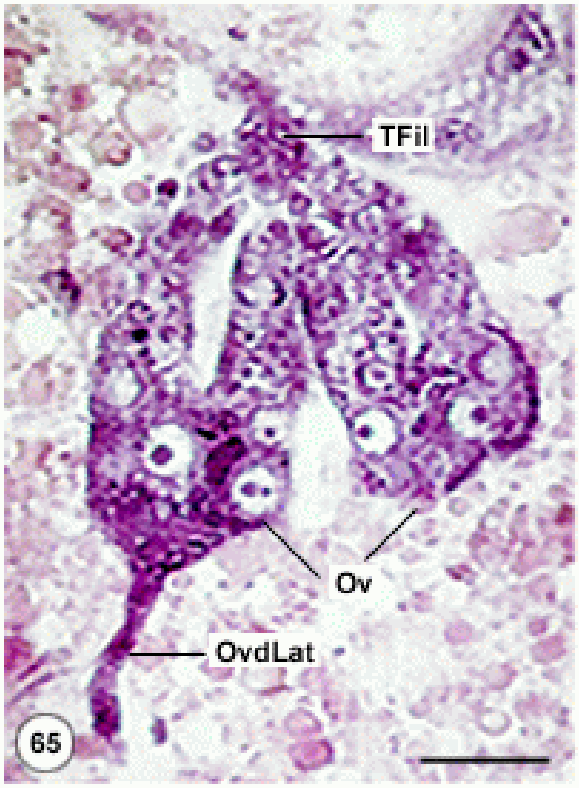
Plate X: Fig. 62 - 67. Progressive development of ovarioles during the metamorphic stages. **Fig. 62.** *E. americanus*, early propupa, no differentiation of ovarioles visible, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 63.** *S. linguis*, propupa, each ovary divides into four ovarioles, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 64.** *E. americanus*, propupa, differentiation of ovarioles starting at the anterior part of the ovary, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 65.** *F. occidentalis*, propupa, further development of ovarioles, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 66.** *E. americanus*, propupa, differentiating ovarioles and oviductus lateralis, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 67.** *F. occidentalis*, pupa, ovarioles are completely divided, frontal section, HE-staining, BF, Bar = 25 µm. Og = oogonium, Ov = ovary, Ovr = ovariole, OvdLat = oviductus lateralis, TFil = terminal filament.

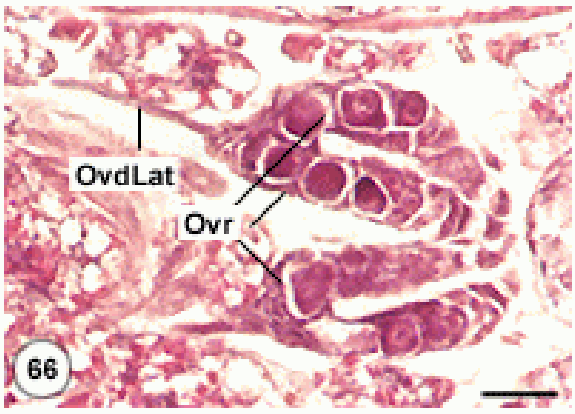
Plate X

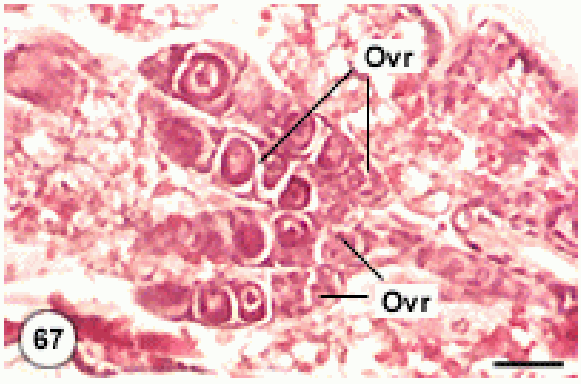

Ov
Ov
Og
62


Ov
63


TFil
Ov
64


TFil
Ov
OvdLat
65


OvdLat
Ovr
66


Ovr
Ovr
67

S. linguis:
In *S. linguis* the division of each ovary into four ovarioles begins in the pharate propupal stage. The procedure of this differentiation process is the same as observed in *F. occidentalis* and *E. americanus*. In the propupal stage of *S. linguis* the approaching division of each of the two ovaries into four ovarioles begins (Fig. 63) and the separation is not completed until the end of the first pupal stage. As in *F. occidentalis* and *E. americanus*, the differentiation of the ovaries is finished a short time before the adult emerges.

3.2.2. Development of the male genital organs

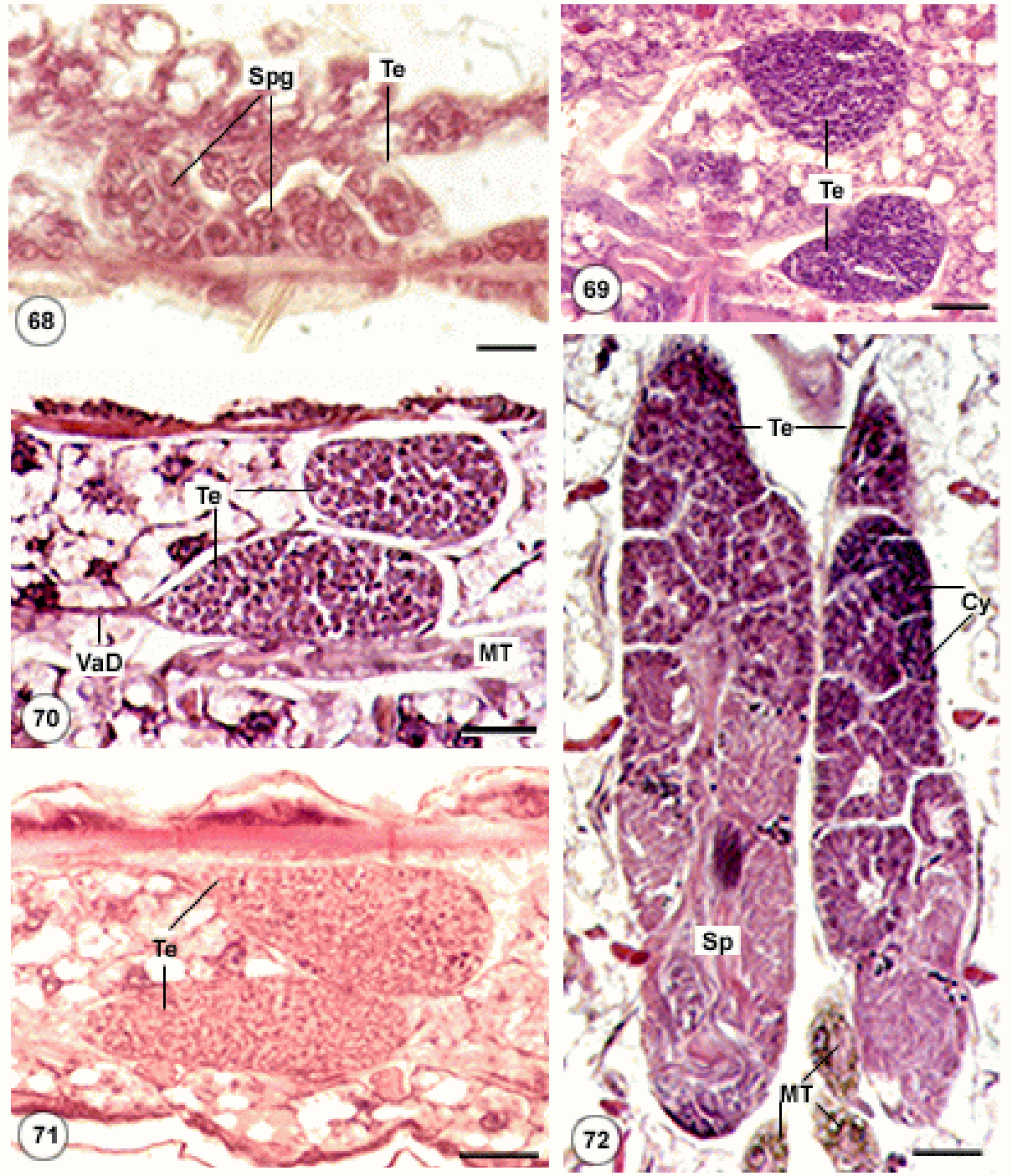
The spermatogenesis of species examined from the suborder Terebrantia and Tubulifera shows several differences. Spermatogenesis starts in both suborders with the immature stages and is finalized before adults emerge in *F. occidentalis* and *E. americanus* (Terebrantia), whereas in *S. linguis* (Phlaeothripidae) sperm production is also found during the adult period.

3.2.2.1. First and second instar larva

F. occidentalis and *E. americanus*:
In the first stage larva the two testes are situated dorsally in abdominal segments VI and VII in *F. occidentalis* and IV and V in *E. americanus*, and measure 37.5 µm ± 4.2 x 13.9 µm ± 2.7 in *F. occidentalis* and 49.1 µm ± 5.5 x 23.0 µm ± 6.6 in *E. americanus*. Each testis is surrounded by a primary epithelial sheath and contains numerous spermatogonia (Fig. 68). The cells have a basophil cytoplasm and a nucleus which includes a single acidophil nucleolus.
Testes in second stage larva (Fig. 69-71) vary in size depending on the age of the larva. They measure on average 69.9 µm ± 9.7 x 28.7 µm ± 2.9 in *F. occidentalis* and 86.1 µm ± 14.0 x 28.9 µm ± 5.7 in *E. americanus*.
Meiotic divisions usually appear shortly after the molt into the second stage. Meiosis results in secondary spermatocytes.
In mid development of the second stage larva, the whole of each testis contains functional and pycnotic spermatids. The pycnotic bodies form clusters which move to the periphery of the testis where they disintegrated.

Plate XI: Fig. 68. *E. americanus*, first instar larva, testis with spermatogonia, sagittal section, HE-staining, BF, Bar = 10 µm. **Fig. 69.** *F. occidentalis*, second instar larva, paired testes, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 70.** *E. americanus*, second instar larva, testes consisting of a single cyst, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 71.** *E. americanus*, second instar larva (shortly before propupa hatches), testes, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 72.** *S. linguis*, second instar larva, testes - each testis comprises several cysts with spermatogonia at different developmental stages, frontal section, HE-staining, BF, Bar = 25 µm. Cy = cyst, MT = Malpighian tubule, Sp = sperm, Spg = spermatogonium, Te = testis, VaD = vas deferens.

Plate XI



S. linguis:
Paired testes in the larval stages are situated in abdominal segments V and VI. Each testis is bounded by a primary epithelial sheath and contains numerous spermatogonia.
Scattered among the spermatogonia are small, dark-staining cells possibly of primordial cyst cells origin.
In second instar larvae, several primordial cyst cells aggregate around individual spermatogonia and produce a cyst membrane. Divisions of the spermatogonium result in the formation of a cyst, which is a group of definitive spermatogonia of common origin surrounded by a cyst membrane.
Over time more spermatogonia are enclosed by cyst cells and develop into cysts (Fig. 72).
Meiosis is probably the same as in *F. occidentalis* or *E. americanus*, but was not determined in this experiment. The events of spermatogenesis taking place in each single cyst are equivalent to that occurring in the whole testis of *F. occidentalis* and *E. americanus*.
Shortly before male propupae hatch, merely mature spermatozoa are found in cysts at the posterior end of the testes (Fig. 72).

3.2.2.2. Propupa and pupa

F. occidentalis and *E. americanus*:
Testes in the propupa are centred dorsally in abdominal segments V and VI in *F. occidentalis* and IV and V in *E. americanus*, and measure 95.3 µm ± 8.5 x 39.2 µm ± 4.5 in *F. occidentalis* and 95.6 µm ± 12.7 x 31.9 µm ± 3.5 in *E. americanus*. In the early propupa, the spermatids are uniformly distributed through each testis (Fig. 74). Later the spermatid nuclei move to the periphery of each testis and become nestled against its epithelial sheath (Fig. 75-77).
In pupa the testes are situated dorsally between abdominal segments V and VII in *F. occidentalis* and IV and VI in *E. americanus* measuring 119.1 µm ± 10.7 x 33.9 µm ± 3.1 in *F. occidentalis* and 114.3 µm ± 8.0 x 37.8 µm ± 2.9 in *E. americanus*.
The only change occurring in the pupal stage is completion of the differentiation of the spermatids into spermatozoa (Fig. 78-81).
The size of the testes in late pupal stage is similar to that of the adult. The testes are smaller in adult individuals than in the propupa and pupa, probably due to a contraction and thickening of the testes.

S. linguis:
In propupa the anteriormost cysts contain functional and pycnotic spermatids, while toward the posterior end of each testis are cysts containing spermatids in more advanced stages of

Plate XII, XIII: Fig. 73. *S. linguis*, propupa, paired testes consisting of several cysts, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 74.** *E. americanus*, propupa, paired testes - each testis is single-follicled, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 75.** *F. occidentalis*, propupa, paired testes showing development of sperm, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 76.** *E. americanus*, propupa, testes, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 77.** *F. occidentalis*, propupa, testis, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 78 - 81.** Further differentiation of spermatids. **Fig. 78.** *F. occidentalis*, pupa, testes, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 79.** *E. americanus*, pupa - two days old, testes, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 80.** *E. americanus*, pupa - one day old, testes, frontal section, HE-staining, BF, Bar = 25 µm. **Fig. 81.** *F. occidentalis*, pupa, testes with spermatozoa, frontal section, HE-staining, BF, Bar = 25 µm. Cy = cyst, MT = Malpighian tubule, Sp = sperm, Te = testis, VaD = vas deferens.

Plate XII

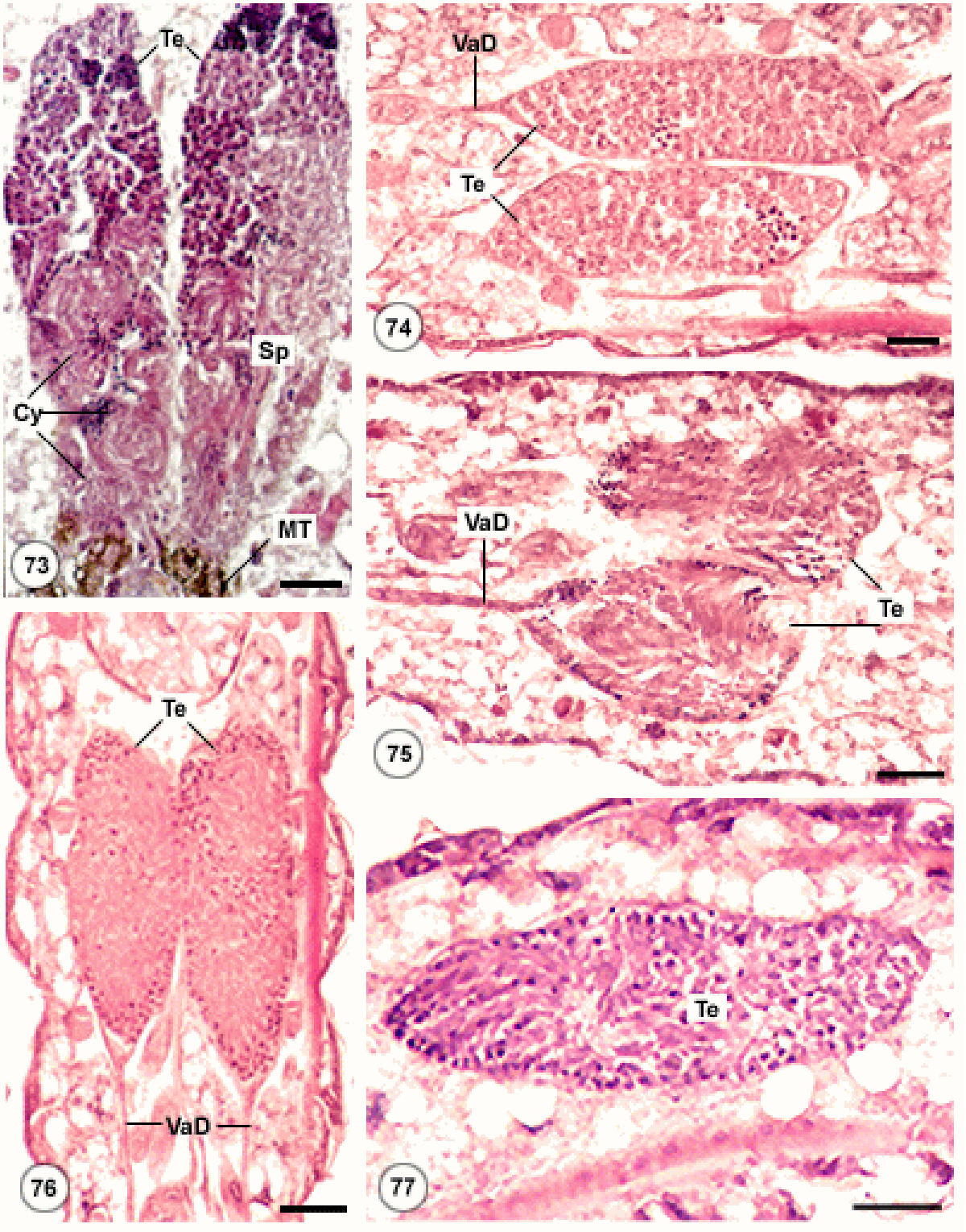
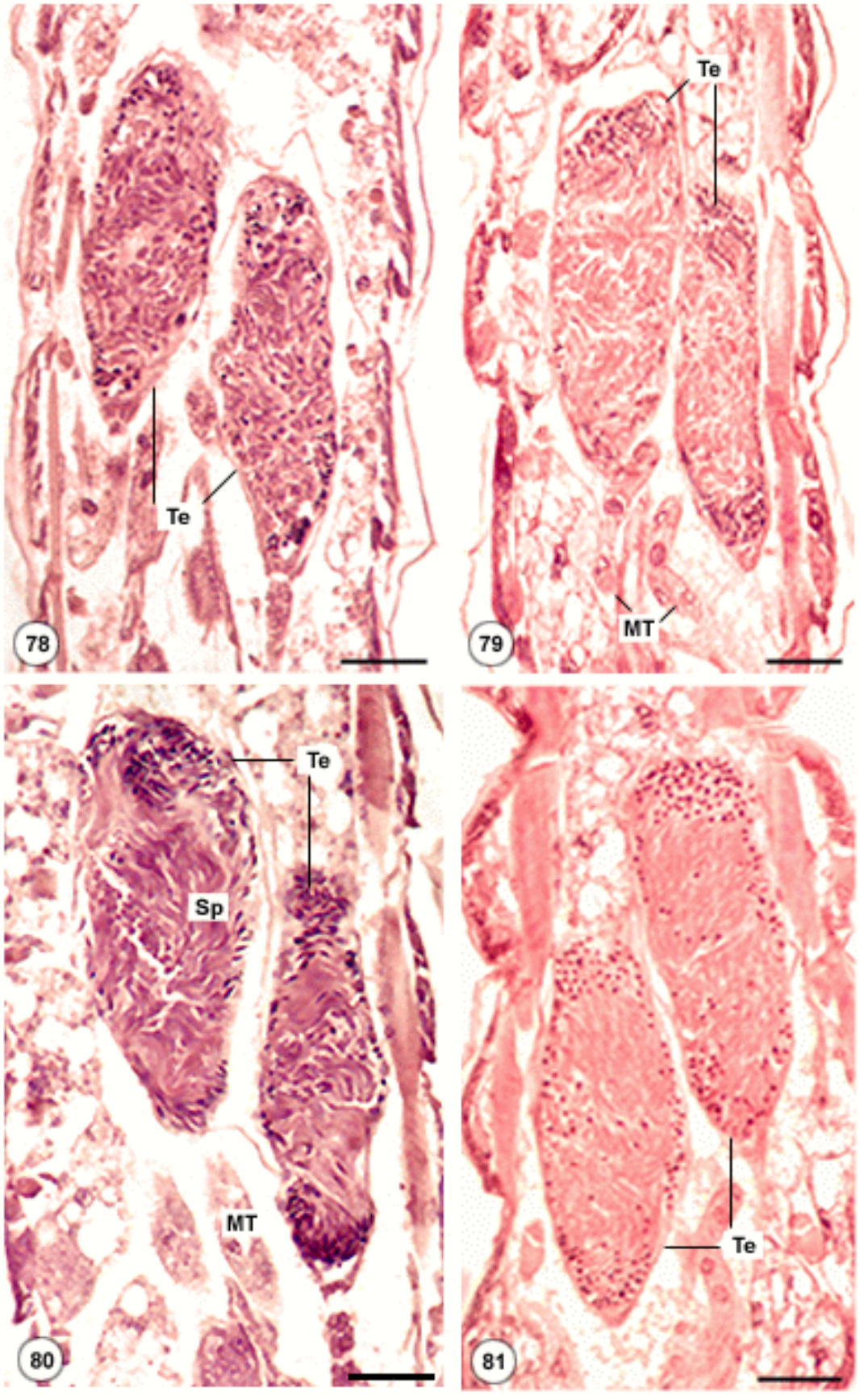


Plate XIII



spermatogenesis (Fig. 73). The testes of the pupal stages are longer and more slender. An increasing number of cysts ruptures and releases sperm bundles.

All the germ cells in the testis of *F. occidentalis* and *E. americanus* are about the same stage of differentiation at any given time, and can be considered single cysts when compared to the testis of *S. linguis*.

3.3. Embryogenesis

The following chapter describes the embryogenesis of *F. occidentalis* and *S. linguis* and aims to compare both species as representatives of the two suborders of Thysanoptera, Terebrantia and Tubulifera. Eggs of both species were obtained as described in Chapter 2.2.1.
The eggs of both *F. occidentalis* and *S. linguis* are relatively large compared to the size of the females that produce them (Table 17).
Containing some cytoplasm and a relatively large amount of yolk (Fig. 86, 121), the eggs are categorized as polylecithale and the yolk distribution is centrolecithale. The zygote nucleus usually occupies a posterior position.
Eggs are enclosed by a shell formed from the vitelline envelope and the chorion (Fig. 86, 121). Two anatomically distinct layers (sometimes called the endochorion and the exochorion) are present in the chorion of the eggs.

Table 17: Comparison of the average length of females and eggs of *F. occidentalis* and *S. linguis*.

Species	Length in µm		Egg length compared with length of female in per cent
	Female Mean ± SD	Egg Mean ± SD	
F. occidentalis	1485.5 ± 98.4	279.5 ± 6.9	18.8
S. linguis	1883.9 ± 71.1	446.0 ± 4.8	23.7

3.3.1. Egg morphology

1. *F. occidentalis*:
After oviposition, eggs of *F. occidentalis* are pale white and later in the development pale yellow. They are kidney-shaped with a flattened anterior egg pole (Fig. 86).
The chorion is smooth. Females lay their eggs singly within the plant tissue. Eggs have an operculum which is removed during the hatching of the first instar larva by an oviruptor.
Neither micropyles nor aeropyles were observed.

Eggs of *F. occidentalis* are averagely 279.5 µm ± 6.9 x 128.9 µm ± 16.5. The length and even more the width of eggs increases during embryogenesis. The length increases slightly from 265.6 µm ± 8.1 at 6 h ± 6 h to 279.1 µm ± 7.5 at 102 h ± 6 h which corresponds to an increase of 5.3 %. The maximum length of 290.9 µm ± 10.9 is achieved at 54 h ± 6 h and the average values from 6 h ± 6 h to 42 h ± 6 h are lower (Table 18, Fig. 82).
The width of the eggs changes more dramatically. Egg width increases from 101.6 µm ± 3.5 at 18 h ± 6 h to 139.2 µm ± 3.7 at 90 h ± 6 h. The total width of eggs increases about 37 % (Table 18, Fig. 82).

Table 18: Documentation of length and width of eggs during embryogenesis of *F. occidentalis*.

Age	Length		Width		Number
	Mean (µm)	Standard deviation	Mean (µm)	Standard deviation	
6 h ± 6 h	265.6	8.1	101.6	3.5	36
18 h ± 6 h	279.0	9.0	104.0	4.6	31
30 h ± 6 h	277.5	8.2	129.4	5.4	36
42 h ± 6 h	281.0	9.9	135.2	4.5	34
54 h ± 6 h	290.9	10.6	140.9	5.8	33
66 h ± 6 h	279.2	8.0	139.2	3.7	36
78 h ± 6 h	283.1	5.5	141.7	4.5	38
90 h ± 6 h	279.2	8.0	139.2	3.7	36
102 h ± 6 h	279.1	7.5	140.2	3.8	30

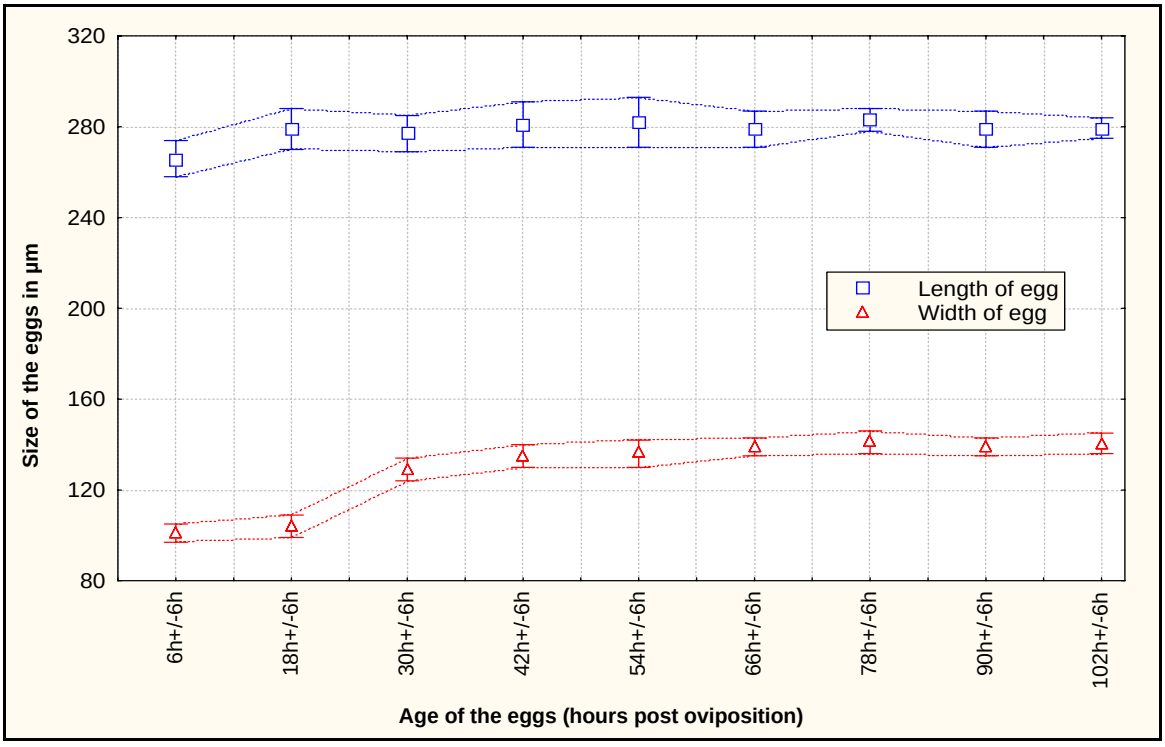


Fig. 82: Changes in the egg size during embryogenesis of *F. occidentalis* (n = 30).

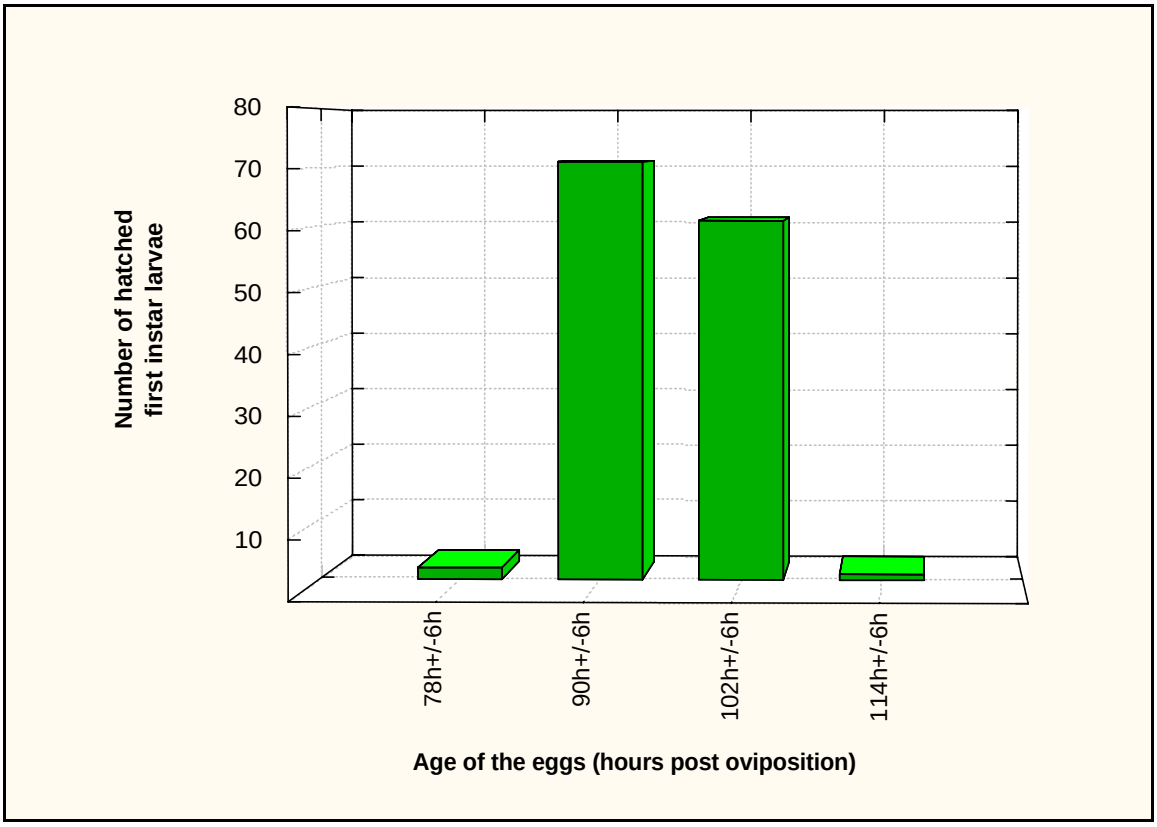


Fig.83: Mean developmental time of eggs of *F. occidentalis* (n = 135).

The average developmental time of a *F. occidentalis* egg is 95.4 h or approximately four days. Most of the eggs (65 %) hatched between 90 h ± 6 h and 102 h ± 6 h, whereby 35 % hatched after 90 h ± 6 h, and 30 % after 102 h ± 6 h. 3 % of the eggs hatched after 78 h ± 6 h and after 114 h ± 6 h (Fig. 83). Surviving rate of the total number of eggs was 66 % (n = 135).

2. *S. linguis*:

The eggs of *S. linguis* are ovoid in shape. Females lay their eggs on the substrate (ground of the *Sansevieria trifasciata* leaf) and arrange eggs into a tightly formed batch.

The chorion of the eggs is pale yellowish. In contrast to *F. occidentalis*, the outer surface of the chorion is sculptured with a basically hexagonal pattern reflecting the shapes of the follicle cells which secrete the chorion. There are ridges among these polygons which are made of porous grooves.

Two to three cells are visible at the posterior pole of the egg with a distinguishable structure. They are penta- and hexagonal structured as well, but smaller and they have an expanded cell border. Their surface appears to be enlarged. Probably, these cells represent aeropyles.

S. linguis eggs average in length 446.0 µm ± 4.8 and in width 163.3 µm ± 3.7. No striking changes of the length and width of eggs were observable during embryogenesis, as compared to *F. occidentalis* (Table 19).

Changes in length and width of the eggs were investigated in two different experiments.

In the first experiment eggs were collected every 12 h from single *Sansevieria trifasciata* leaves, transferred to leaf discs and kept in a climatic cabinet (see Chapter 2.2.1.). Length and width of the eggs were measured for all embryonic stages.

Table 19: Recorded lengths and widths of *S. linguis* eggs during embryogenesis. Eggs were collected every 12 h and measured after receiving all embryonic stages.

Age	Length		Width		Number
	Mean (µm)	Standard deviation	Mean (µm)	Standard deviation	
6 h ± 6 h	440.9	13.9	173.2	12.1	11
18 h ± 6 h	440.0	19.2	166.2	4.3	12
30 h ± 6 h	436.8	19.8	171.8	4.0	11
42 h ± 6 h	450.0	11.9	167.7	3.3	13
54 h ± 6 h	445.0	8.3	166.1	4.9	14
66 h ± 6 h	446.0	13.1	164.4	4.8	26
78 h ± 6 h	439.6	12.3	161.1	3.5	14
90 h ± 6 h	440.4	8.5	159.1	3.8	11
102 h ± 6 h	443.9	14.4	165.7	5.1	14
114 h ± 6 h	457.3	8.8	164.1	4.9	11
126 h ± 6 h	443.8	16.0	160.2	6.5	24
138 h ± 6 h	442.3	14.9	157.9	6.9	24
150 h ± 6 h	448.2	13.7	160.5	3.5	11
162 h ± 6 h	452.0	14.9	168.0	4.8	10
174 h ± 6 h	448.2	11.6	160.3	5.4	17
186 h ± 6 h	446.0	9.7	163.5	5.8	10
198 h ± 6 h	445.7	11.4	160.2	6.6	28
210 h ± 6 h	452.2	14.6	162.2	7.7	18
222 h ± 6 h	447.8	13.6	161.7	6.9	18
234 h ± 6 h	442.6	12.7	159.5	5.0	19
246 h ± 6 h	450.0	19.4	162.4	6.9	17
258 h ± 6 h	446.5	18.7	168.5	5.8	10
270 h ± 6 h	443.5	7.5	161.5	11.1	10
282 h ± 6 h	447.2	13.6	161.4	7.2	18
294 h ± 6 h	454.1	13.2	166.3	7.6	16

There was a large variation in length and width of single individuals and did not allow comparison. Length and width are presumed to vary only slightly. The second experiment was designed to measure egg changes over time.
Single eggs were positioned on microscope slides, numbered individually, and measured every day (Fig. 84, Table 20, see Chapter 2.2.1.).

Table 20: Documentation of length and width of eggs during embryogenesis of *S. linguis*. Eggs were collected at an age of 6 h ± 6 h (post oviposition) and measured every 12 h.

Age	Length		Width		Number
	Median (µm)	Standard deviation	Median (µm)	Standard deviation	
6 h ± 6 h	448.1	14.4	170.7	3.6	37
18 h ± 6 h	448.1	14.4	170.4	4.0	37
30 h ± 6 h	448.4	14.7	170.4	4.1	37
42 h ± 6 h	448.4	14.7	170.0	4.1	37
54 h ± 6 h	448.8	15.1	169.1	4.8	37
66 h ± 6 h	448.8	15.1	168.1	5.0	37
78 h ± 6 h	448.4	15.0	165.8	6.2	37
90 h ± 6 h	448.4	15.0	165.8	6.2	37
102 h ± 6 h	447.8	15.6	164.6	7.7	37
114 h ± 6 h	447.8	15.6	164.6	7.7	37
126 h ± 6 h	447.6	15.1	163.6	8.4	37
138 h ± 6 h	447.6	15.0	163.7	8.4	37
150 h ± 6 h	447.4	15.0	158.1	9.9	37
162 h ± 6 h	447.4	15.0	162.7	10.0	37
174 h ± 6 h	447.1	14.8	161.8	11.6	37
186 h ± 6 h	447.1	14.8	162.0	11.5	37
198 h ± 6 h	446.9	14.7	156.9	11.5	37
210 h ± 6 h	446.9	14.7	157.0	11.7	37
222 h ± 6 h	446.2	14.3	161.3	13.7	37
234 h ± 6 h	446.2	14.3	161.1	13.3	37
246 h ± 6 h	445.5	14.9	159.5	14.0	37
258 h ± 6 h	445.5	14.9	159.4	13.6	37
270 h ± 6 h	445.5	14.9	158.9	14.7	37
282 h ± 6 h	445.5	14.9	159.1	14.5	37
294 h ± 6 h	445.3	15.3	159.2	15.1	37

There was no striking change in egg length, length decreased slightly from 448.1 µm ± 14.4 at 6 h ± 6 h to 445.3 µm ± 15.3 at 294 h ± 6 h which corresponds to a decrease of 0.7 %.
The width decreased about 3.3 % from 170.7 µm ± 3.6 at 6 h ± 6 h to 159.2 µm ± 15.1 at 294 h ± 6 h. That is a reduction of 11.5 µm which is equivalent to 3.3 %.
Thus, *S. linguis* egg size is relatively stable during embryogenesis.

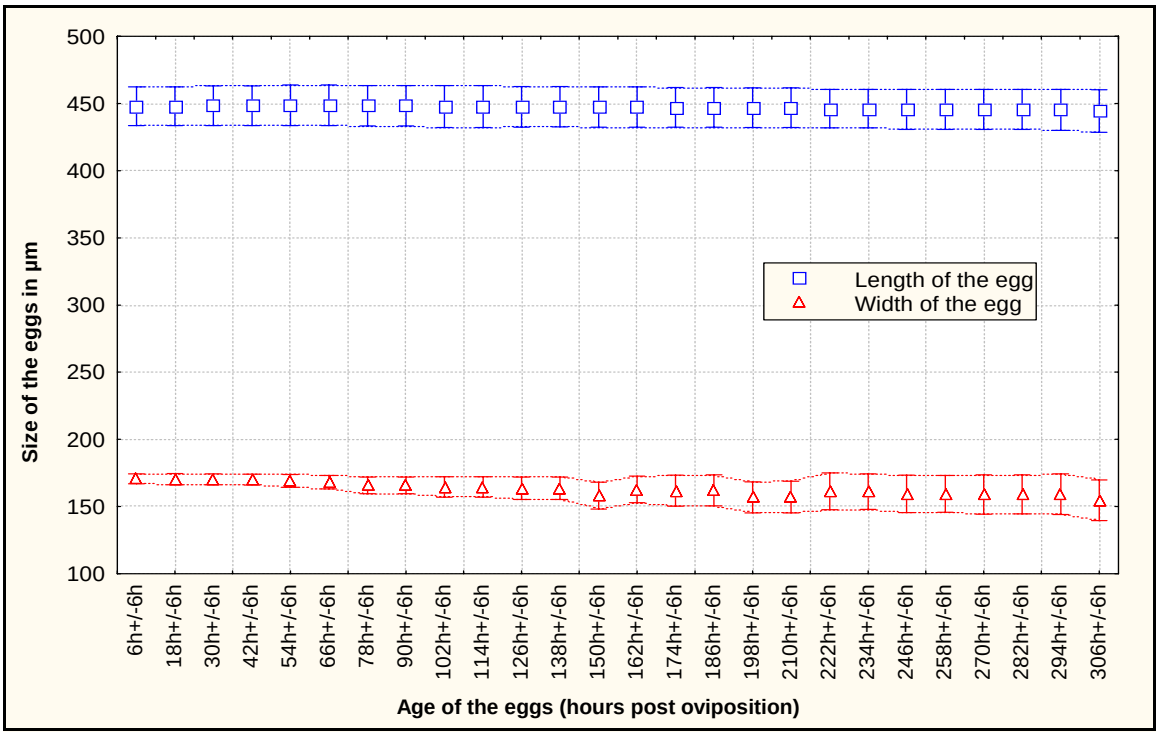


Fig. 84: Changes in the size of eggs during embryogenesis of *S. linguis* (n = 37).

The average developmental time of a *S. linguis* egg is 248.4 h or 10.4 d. A total of 88 % of the first instar larvae hatched between 222 h ± 6 h and 270 h ± 6 h. 67 % hatched after 264 h ± 6 h, 10 % of the eggs needed 222 h ± 6 h, and 11 % 270 h ± 6 h for their embryonic development. The last first instar larva hatched with 342 h ± 6 h (Fig. 85).
A total 91 % of all eggs hatched (n = 316). Compared with *F. occidentalis*, the mortality rate was very low (9 %).

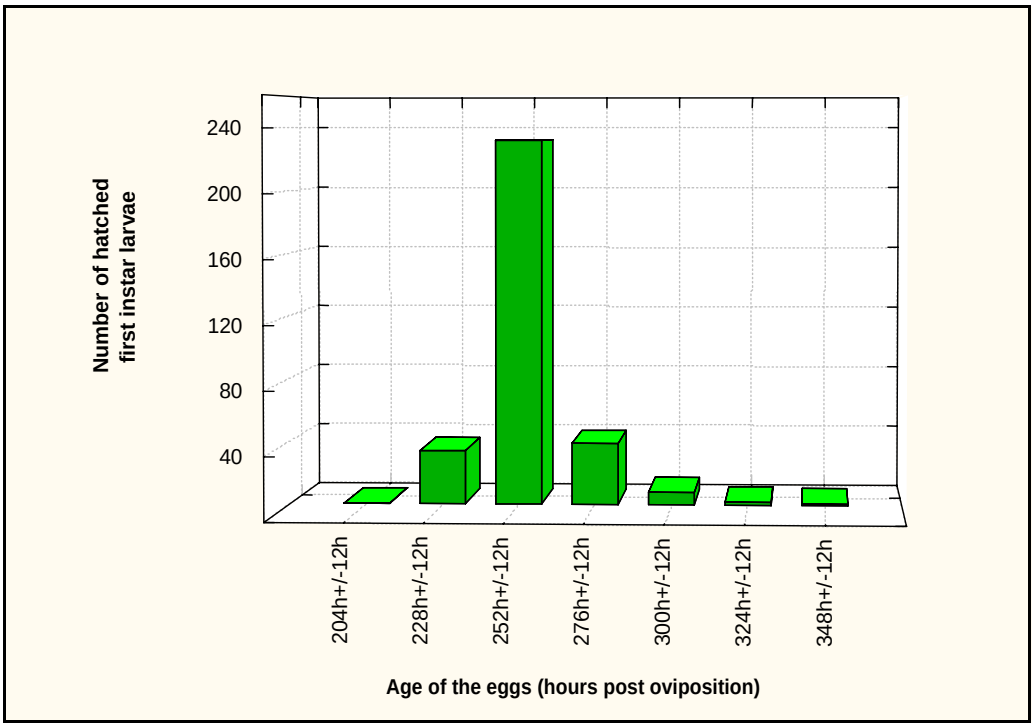


Fig. 85: Mean developmental time of eggs of *S. linguis* (n = 316).

3.3.2. Embryogenesis

1. *F. occidentalis*

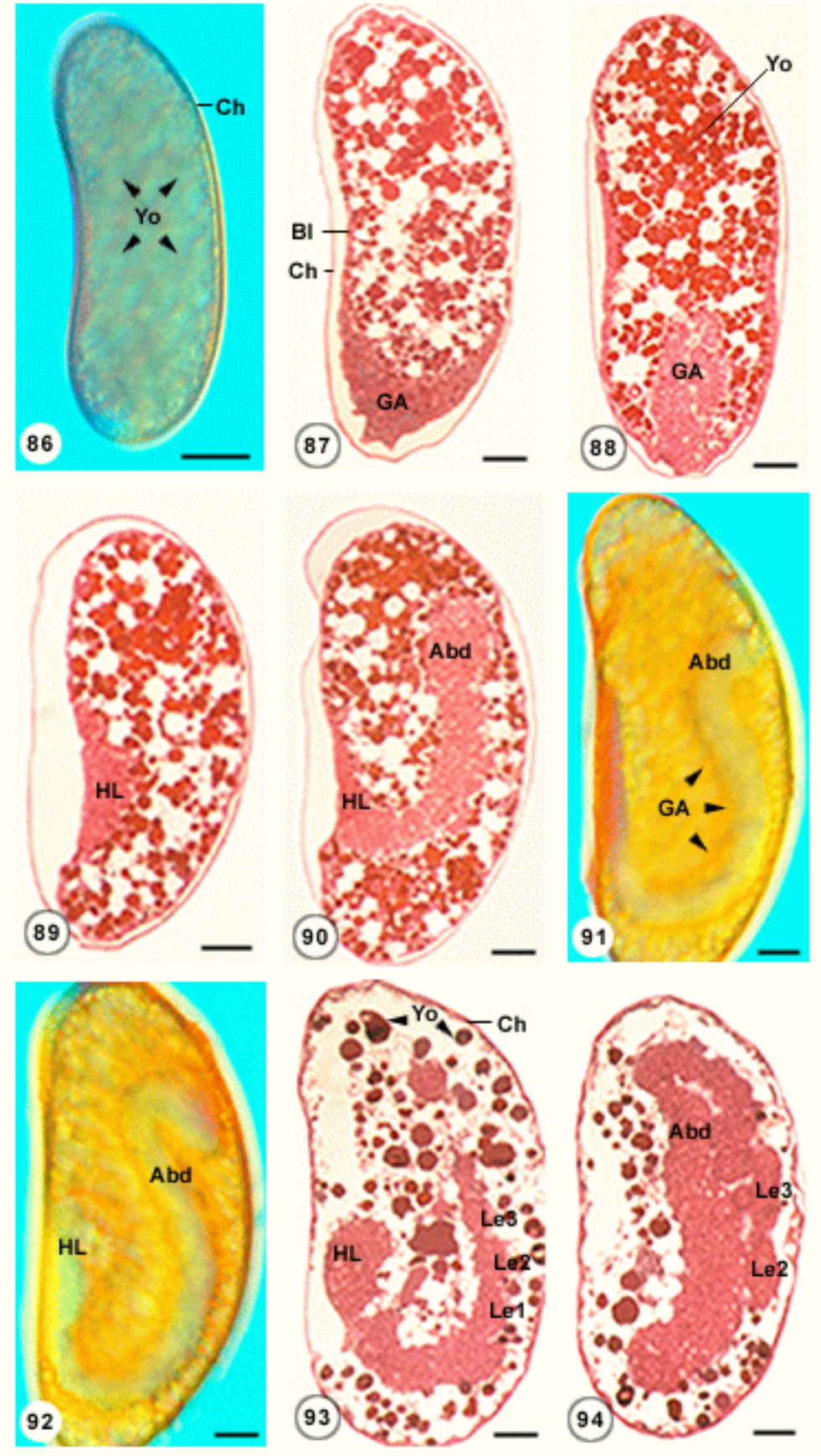
Early embryogenesis

Once the egg cell has been activated, the zygote nucleus subdivides by mitotic divisions to produce many daughter nuclei. These cleavage energids migrate to the periphery and create the plasmodial preblastoderm shortly after oviposition.

In *F. occidentalis*, eggs reach the blastodermal stage within the first couple hours after oviposition. Only a few energids remain within the cytoplasm forming the yolk cells or vitellophages which are assist in the breakdown of yolk.

Plate XIV: Fig. 86 - 94. Early embryogenesis of *F. occidentalis*, germ band formation, invagination, and anatrepsis. **Fig. 86.** *F. occidentalis*, egg, 6 h ± 6 h, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 87.** *F. occidentalis*, egg, 6 h ± 6 h, formation of the germ anlage at the posterior pole of the egg, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 88.** *F. occidentalis*, egg, 6 h ± 6 h, germ anlage, frontal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 89.** *F. occidentalis*, Egg, 18 h ± 6 h, head region of the developing embryo, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 90.** *F. occidentalis*, egg, 18 h ± 6 h, invagination of the germ anlage with prospective head region and abdomen, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 91.** *F. occidentalis*, egg, 18 h ± 6 h, invagination and elongation of the germ anlage, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 92.** *F. occidentalis*, egg, 18 h ± 6 h, germ anlage with head lobes and abdomen, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 93.** *F. occidentalis*, egg, 30 h ± 6 h, thoracal appendages, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 94.** *F. occidentalis*, egg, germ band at 30 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. Abd = abdomen, Bl = blastoderm, Ch = chorion, GA = germ anlage, HL = head lobe, Le1 = leg one, Le2 = leg two, Le3 = leg three, Yo = yolk.

Plate XIV


Ch
Yo
86
Bl
Ch
GA
87
Yo
GA
88
HL
89
Abd
HL
90
Abd
GA
91
Abd
HL
92
Yo
Ch
Le3
HL
Le2
Le1
93
Abd
Le3
Le2
94

Formation of the germ band, anatrepsis, and germ band elongation

Regional differentiation of the blastoderm leads to the formation of the germ anlage or embryonic primordium in the posteroventral region of the egg (Fig. 87, 88). Mitotic activity divides the blastoderm into the presumptive embryonic tissue (germ anlage) and extraembryonic cover (serosal layer).

Anatrepsis follows where the germ band is shifted inside the yolk and becomes elongated. The posterior end of the germ band is flexed upwards into the yolk so that the embryo is orientated with its head-end towards the posterior pole of the egg (Fig. 89, 90).

During this invagination, the germ band pulls a part of the extraembryonic cover in the yolk, which becomes the amnion, whereas the serosa remains at the surface.

There are two embryonic covers, the extraembryonic serosa which surrounds the germ band and yolk and the amnion which belongs to the germ anlage. The amnion covers the amniotic cavity which borders the germ band on the ventral side.

In *F. occidentalis*, the amniotic cavity remains connected with the serosa along the cranial part of the embryo during the elongation of the germ band.

Elongation of the germ anlage results from a growth zone. The germ anlage forms the presumptive head, while thorax and abdomen arise through the activity of the growth zone.

The result of the invagination is a total invaginated germ band. The head encompasses a large region and is situated at the convex side and posterior end of the egg (Fig. 95) while the caudal part of the embryo is bent creating an S-form and is positioned at the anterior egg pole (Fig. 91, 92). The germ band reaches its greatest extension between 30 h ± 6 h and 42 h ± 6 h and differentiates into the broad head region (protocephalon), a narrow tail (protocorm), and the midventral cells of the germ band which are the presumptive mesoderm and midgut. The presumptive stomodeum and proctodeum lie at either end of this.

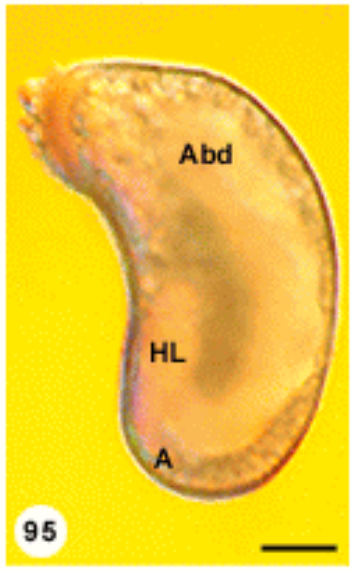
Mode of gastrulation is difficult to interpret, however, at the end of anatrepsis two germ layers developed due to the immigration of cell material. The outer layer is the ectoblastem and the inner layer is the hypoblastem.

Segmentation

Indication of segmentation on the embryonic head and thorax in the form of little swellings is visible after 30 h ± 6 h. First, the antennal buds (Fig. 95) grow posterolaterally on either side of the protocephalon. At approximately the same time the thoracic buds (Fig. 93, 94, 99, 100) emerge

Plate XV: Fig. 95 - 103. Differentiation of gnathal and thoracic appendages, embryo before katatrepsis. **Fig. 95.** *F. occidentalis*, egg, 30 h ± 6 h, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 96.** *F. occidentalis*, egg, 42 h ± 6 h, embryo with germ cells visible at the anterior region of the egg, sagittal section, HE-staining, BF, Bar = 25 µm. **Fig. 97.** *F. occidentalis*, egg, 30 h ± 6 h, germ anlage showing high mitotic activity (arrows indicating mitotic stages), sagittal section, Safranin-staining, BF, Bar = 15 µm. **Fig. 98 - 103.** Serial sections through an 42 h ± 6 h old egg, serosal cells at the anterior egg pole, embryo with gnathal and thoracic appendages (showing that both right and left mandible are differentiated before katatrepsis). **Fig. 98.** *F. occidentalis*, egg, 42 h ± 6 h, gnathal appendages, left mandible, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 99.** *F. occidentalis*, egg, 42 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 100.** *F. occidentalis*, egg, 42 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 101.** *F. occidentalis*, egg, 42 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 102.** *F. occidentalis*, egg, 42 h ± 6 h, right mandible, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 103.** *F. occidentalis*, egg, 42 h ± 6 h, gnathal appendages with right mandible, sagittal section, Safranin-staining, BF, Bar = 25 µm. A = antenna, Abd = abdomen, AbdS = abdominal segment, GC = germ cells, HL = head lobe, Le = leg, Le1 = leg one, Le2 = leg two, Le3 = leg three, Lb = labium, Md = mandible, Mx = maxilla, SerC = serosal cells.

Plate XV


Abd
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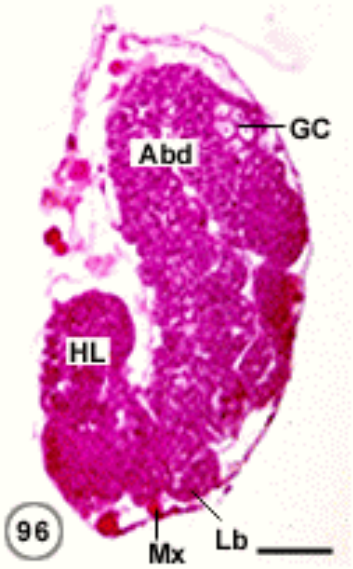
GC
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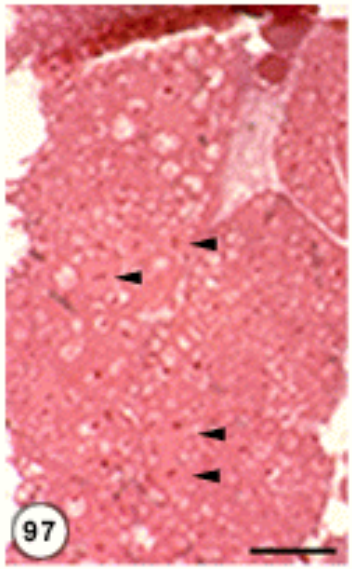
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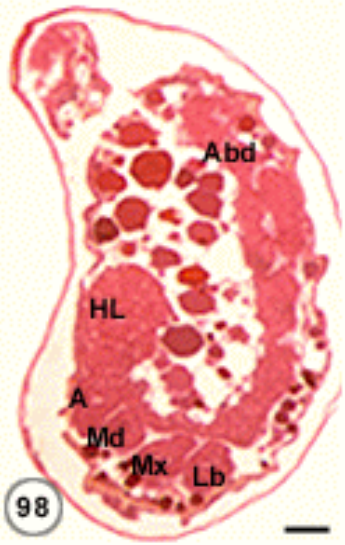
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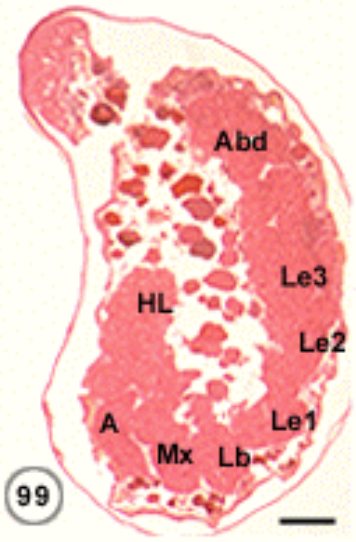
Abd
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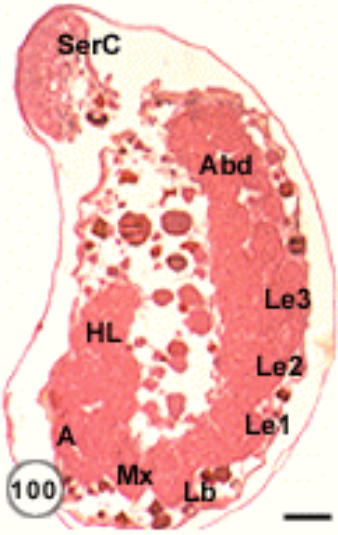
99


SerC
Abd
Le3
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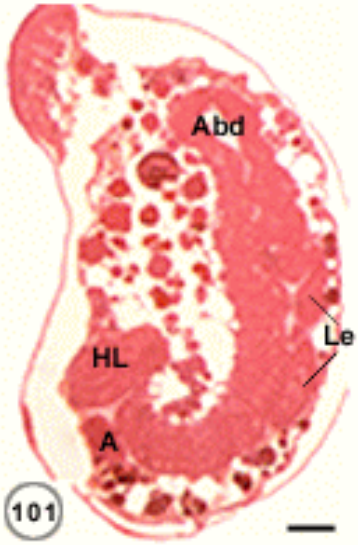
A
Le1
Mx
Lb
100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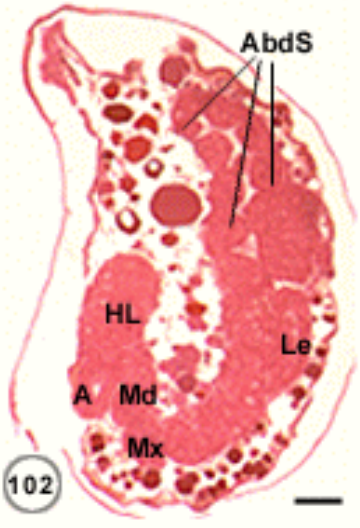
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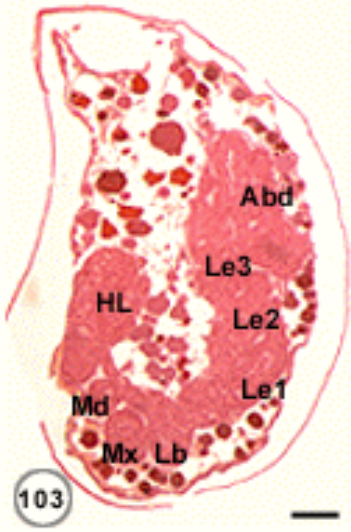
102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Le1
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Mx
Lb
103

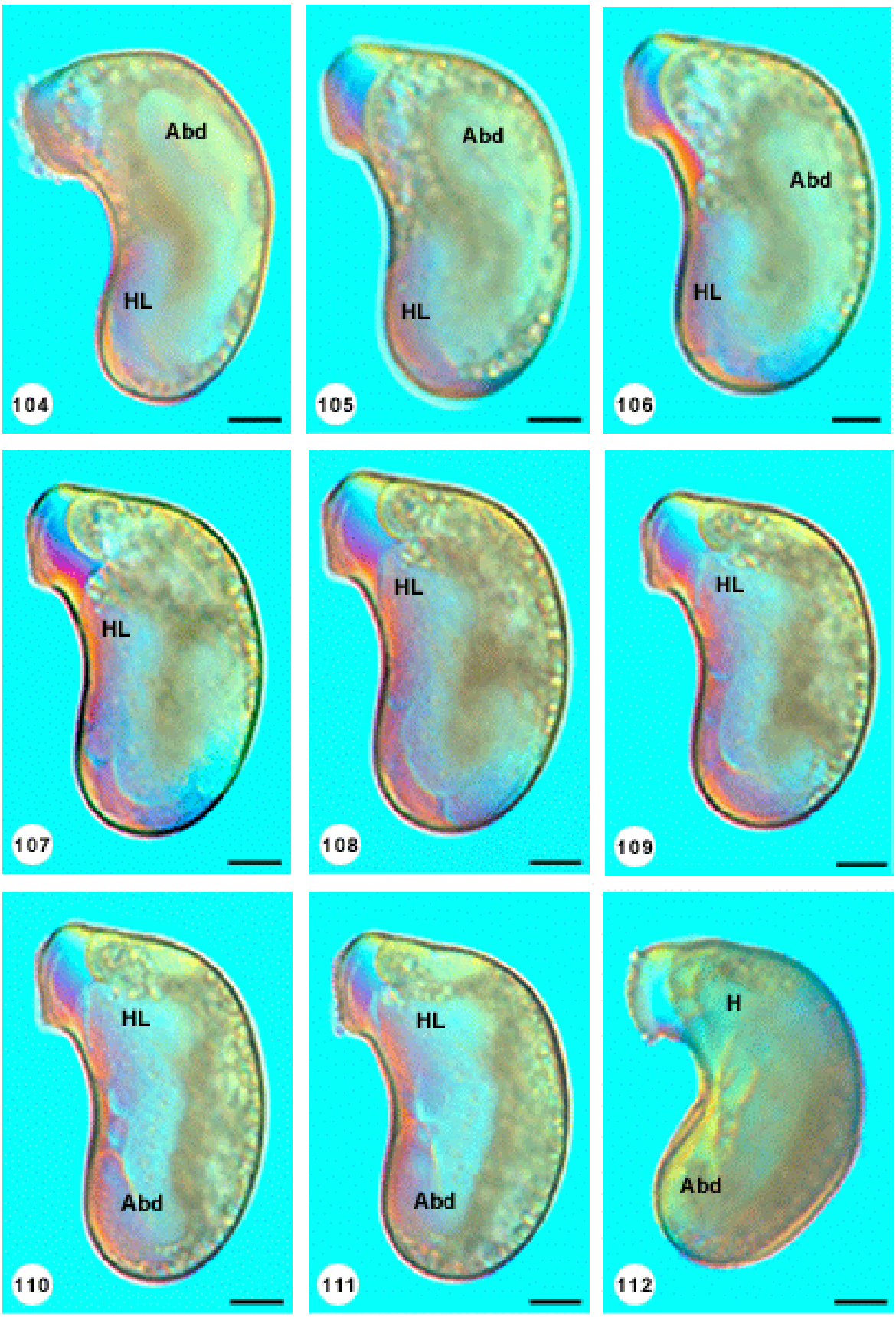
followed by the buds of the mouthparts (maxillae, labium, mandibles) situated immediately behind the protocephalon (Fig. 98-103). Fig. 98-103 show serial sections through a 42 h ± 6 h old embryo. Good recognizable are the anlagen of both right (Fig. 102, 103) and left (Fig. 98) mandible. There is a high mitotic activity during this process (Fig. 97).
All 11 abdominal segments are determinable before katatrepsis starts.
Shortly before katatrepsis, the degeneration of the right mandible takes place marked by necrotic cells and pycnotic nuclei, and pleuropodia appear as appendages of the first abdominal segment. Germ cells are visible enclosed at the flexed abdominal zone (Fig. 96).

Katatrepsis

The blastokinetic process of katatrepsis begins at approximately 42 h ± 6 h and lasts about one hour. Duration of katatrepsis corresponds to 10.4 % of the duration of the whole embryonic development (Table 21). Changes which appear during katatrepsis concern the orientation of the embryo in the egg, the extraembryonic covers (amnion and serosa), and the yolk. One effect of katatrepsis is to reverse the relative positions of embryo and yolk. At first, the embryo lies on or in the yolk (Fig. 104), but when katatrepsis is completed, the yolk is contained within the embryo (Fig. 112).
First sign for the start of katatrepsis is liquefaction of the yolk starting at the anterior and posterior egg pole (Fig. 104, 105) and soon reaching the yolk surrounding the embryo (Fig. 106, 107). The posterior serosal cells and the craniodorsal amnion fuse and rupture at the point where the embryonic head is situated. Serosal cells at the anterior end contract and move to the thickened serosal cells at the posterior end.
This contraction seems to pull the embryo (first at the end of the head) along the surface of the yolk to the anterior end of the egg (Fig. 106-111). The amnion rolls back over the surface of the yolk replacing the serosa and covering the yolk mass within the midgut (primary dorsal closure).
The amnion performs the primary dorsal closure at first, later it is resorbed in the yolk and the provisional tissue is replaced by the embryonic ectoderm (definitive epithel).
The contracted serosal cells locating anterior to the embryonic head form a cap-like (hemispherical) secondary dorsal organ (Fig. 114) which remains for a while. The differentiating place of the dorsal organ is already marked before katatrepsis by thickened serosal cells at the anterior egg pole (Fig. 99-101).
Soon after blastokinesis, a second embryonic cuticle is formed which is thicker than the first cuticle.

Plate XVI: Fig. 104 - 112. Katatrepsis of *F. occidentalis* (**Fig. 105 - 111**, time serie of movements of the embryo). **Fig. 104 and 105.** Beginning of liquefaction of yolk at the anterior end of the egg. **Fig. 104.** *F. occidentalis*, egg, 42 h ± 6 h, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 105.** *F. occidentalis*, egg, 42 h ± 6 h, katatrepsis 0:00, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 106.** *F. occidentalis*, egg, 42 h ± 6 h, katatrepsis 0:10, head starts to move to the anterior pole of the egg, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 107.** *F. occidentalis*, egg, 42 h ± 6 h, katatrepsis 0:20, continuating movement, head and abdomen are situated in the first third of the egg, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 108.** *F. occidentalis*, egg, 42 h ± 6 h, katatrepsis 0:25, head moving more anteriorwards, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 109.** *F. occidentalis*, egg, 42 h ± 6 h, katatrepsis 0:35, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 110.** *F. occidentalis*, egg, 42 h ± 6 h, katatrepsis 0:45, shortly before katatrepsis is completed, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 111.** *F. occidentalis*, egg, 42 h ± 6 h, katatrepsis 1:10, end of katatrepsis, head situated at the anterior region of the egg and abdomen at the posterior region, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 112.** *F. occidentalis*, egg, 54 h ± 6 h, final position of the embryo, antenna and extremities visible, whole mounting (paraffin oil), DIC, Bar = 50 µm. Abd = abdomen, H = head, HL = head lobe.

Plate XVI


Abd
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H
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112

Organogenesis and early prolarva

The process of organogenesis extends from elongation of the germ band and gastrulation over the dorsal closure up to preimaginal stages.

Prior to katatrepsis, the primordiale anlagen of the prospective organ systems are visible in the developing embryo.

Nervous system: Prior to katatrepsis, the nervous system arises on the ventral side of the embryo and is a disc like neuroepithelial structure reaching from the head of the embryo up to the last abdominal segment. Neuroblasts divide and give rise to neurons and glial cells.

The protocephalic lobes begin to form during the invagination of the germ band. Three paired groups of neuroblasts, corresponding with the protocerebrum, deutocerebrum and tritocerebrum, develop in the protocephalon and form the cerebral ganglion. Post katatrepsis, these structures fuse to form a complex structure, the synganglion (Fig. 120). The protocerebrum performs a torsion of approximately 90 ° and is finally situated over the deutocerebrum.

Ventral nerve cord formation occurs shortly before katatrepsis at 42 h ± 6 h. A pair of ganglia forms within each abdominal segment. Ganglionic commissures and connectives are built, first in the gnathal region and later in the thoracic and abdominal regions. The ventral nerve cord formed first consists of 16 ganglia (three in the gnathal segments, three in the thorax and 11 in the abdomen).

The concentration of ganglia commences in the gnathal segments where ganglia are gathered through katatrepsis and finally fuse to form the suboesophageal ganglion (Fig. 116-120). The thoracic ganglia still remain separated.

Alimentary canal: The differentiation of the alimentary system starts after approximately 42 h ± 6 h. The foregut and hindgut arise as invaginations, the stomodeum and proctodeum. These invaginations carry the anterior and posterior anlagen of the midgut into the embryo. The anlagen then extend towards each other forming two longitudinal strands of tissue beneath the yolk (and above the visceral mesoderm). The strands eventually completely enclose the yolk by spreading midgut tissue out over the surface of the yolk (Fig. 117, 118).

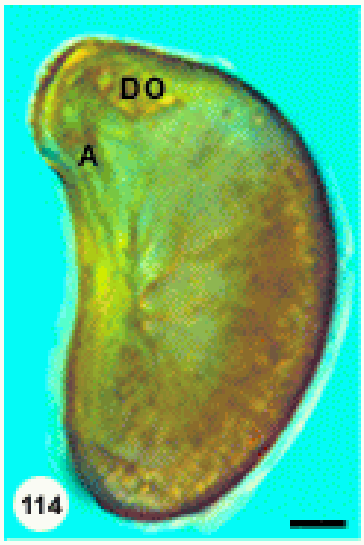
Cubical cells form pharynx and oesophagus. The rectum starts to differentiate and the valvula cardiaca becomes visible at the border of oesophagus and midgut.

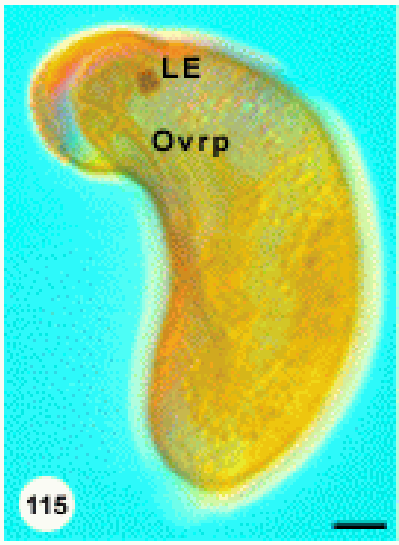
Anlagen of the rectal papillae become distinct in the proctodaeum. They develop prior to katatrepsis and undergo further differentiation later in embryogenesis.

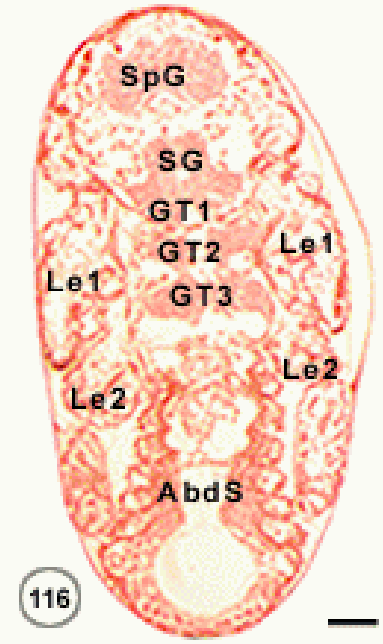
Plate XVII: Fig. 113 - 120. Early and late prolarva (respectively ready to hatch larva) of *F. occidentalis*. **Fig. 113.** *F. occidentalis*, egg, 54 h ± 6 h, embryo after katatrepsis, larval eye pigment visible (“red eye stage“), whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 114.** *F. occidentalis*, egg, 78 h ± 6 h, prolarval stage, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 115.** *F. occidentalis*, egg, 90 h ± 6 h, late prolarval stage, shortly before first instar larva hatches, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 116.** *F. occidentalis*, egg, 66 h ± 6 h, prolarval stage, frontal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 117 - 120.** Ready to hatch larva (organs show larval organization). **Fig. 117.** *F. occidentalis*, egg, 78 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 118.** *F. occidentalis*, egg, 78 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 119.** *F. occidentalis*, egg, 78 h ± 6 h, thoracic ganglia, sagittal section, Safranin-staining, BF, Bar = 15 µm. **Fig. 120.** *F. occidentalis*, egg, 78 h ± 6 h, supraoesophageal ganglion and suboesophageal ganglion, sagittal section, Safranin-staining, BF, Bar = 15 µm. A = antenna, AbdG = abdominal ganglion, AbdS = abdominal segment, Con = connective, DO = dorsal organ, GC = germ cells, GT1 = prothoracic ganglion, GT2 = mesothoracic ganglion, GT3 = metathoracic ganglion, Hg = hindgut, Le = leg, Le1 = leg one, Le2 = leg two, Le3 = leg three, LE = larval eye, Mg = midgut, Ovrp = oviruptor, SG = suboesophageal ganglion, SGl = salivary gland, SpG = supraoesophageal ganglion, Yo = yolk.

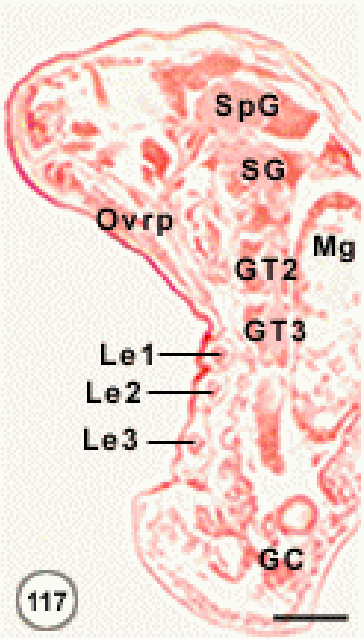
Plate XVII

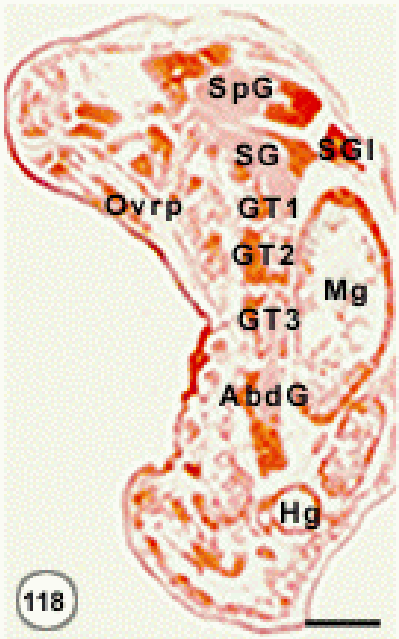

LE
Yo
113


DO
A
114


LE
Ovrp
115


SpG
SG
GT1
GT2
GT3
Le1
Le1
Le2
Le2
AbdS
116


SpG
SG
Ovrp
Mg
GT2
GT3
Le1
Le2
Le3
GC
117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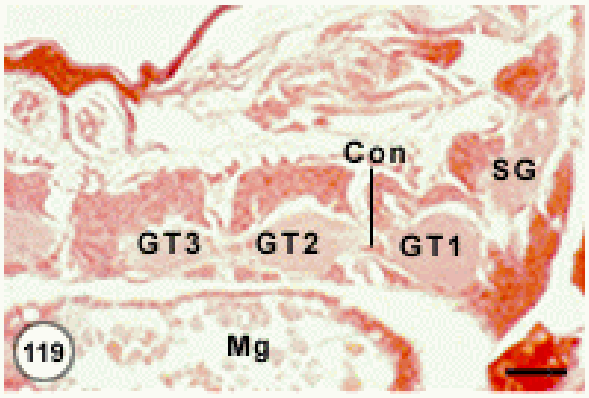
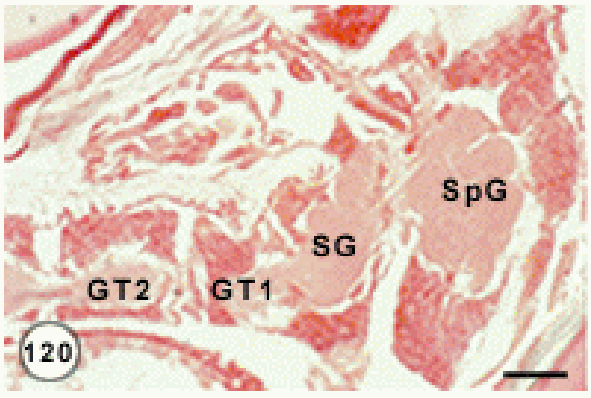
SG
SGl
Ovrp
GT1
GT2
Mg
GT3
AbdG
Hg
118


Con
SG
GT3
GT2
GT1
Mg
119


SpG
SG
GT2
GT1
120

The Malpighian tubules arise as evaginations (outgrowth) from the tip of the proctodeum. In the beginning of their development they reach caudad and later, their volume increases showing a distinct lumen.
Reproductive system: Germ cells become separated from the somatic cells relatively early during embryogenesis at the beginning of anatrepsis. Mesoderm encloses the germ cells and the germ cells increase in number before becoming separated into columns by ingrowth of the mesoderm. These columns form the germaria of the ovarioles or testis follicle.
Antennae are not completely defined in the early prolarva. The collective gnathal appendages of the embryo form the mouth cone. Reorganization of the mouth parts during katatrepsis produces an invagination of the basal parts of mandibles and maxillae as well as the medial fusion of the labrum. The right mandible degenerates totally.

Pleuropodia are formed after katatrepsis as a pair of glands in the region of the first abdominal ganglion. The secondary dorsal organ disappears.
End of the early prolarval stage is marked by pigmentation of the eye region (Fig. 113, 115) beginning at 54 h ± 6 h.

Ready-to-hatch larva

The ready-to-hatch prolarva is most like the first postembryonic stage. The abdomen is fused with the thorax and consists of ten fully developed segments shortly before the first instar larva hatches while the 11th segment is reduced.
Approximately 18 h before hatching, the peristalsis in the gut, especially the hindgut, appears and the prothoracic and cervical muscles start to contract serving as initiation for the upcoming hatching process.
Nervous system: The cerebral zone is moved caudad due to the formation of muscle groups in the gnathal region and the suboesophageal ganglion fuses with the prothoracic ganglion (Fig. 116, 118, 120). The abdominal ganglion cord consists of a fused ganglion complex (Fig. 118) and is situated between the first and fourth abdominal segment.
Differentiation of the cerebrum continues and lateral connectives of individual cerebral regions are recognizable which are the protocerebral-bridge, the protocerebral commisure, and the deutocerebral commisure. Prothoracic ganglion and suboesophageal ganglion are connected by short, thick connectives (Fig. 116, 120).
The prothoracic ganglion is lateral bulged. Meso- and metathoracic ganglion are paired ganglia knots (Fig. 116, 119). The metathoracic ganglion is also connected via short, thick connectives to the abdominal ganglion (Fig. 118). The fusion of the abdominal ganglion is still recognizable due to the visibility of numerous commisures and medial situated glial cells.
The larval eyes differentiate laterally on each side of the head and consist of four convex lenses formed by the corneagen cells. Beneath the corneagen cells, a crystal body is situated surrounded by pigment granulae.
Alimentary canal: The gut becomes totally differentiated shortly before the first instar larva hatches and is divided into fore-, mid-, and hindgut. The foregut reaches from the rima oris to the dorsal situated pharynx and oesophagus. Valvula cardiaca creates the connection from the foregut to the midgut. The midgut becomes elongated approximately two times during development from early prolarva to the ready-to-hatch larva. Therefore, the midgut forms a loop with turning points which lay cranial directly under the protocerebrum and caudal at the height of the fused abdominal ganglion complex. Four different regions are distinguishable in the hindgut, the ileum, the colon, the rectum, and the postrectal

region. The latter is marked by the rectal papillae.
Two different pairs of salivary glands develop already in the early prolarva. One pair is situated between the cranial loop of the gut and the protocerebrum and develops into a bag-like gland while the second pair is thinner and reaches the cranial abdominal region. There are no membranes between single cells and therefore the glands are syncytial.
Antennae have seven segments. The left mandibular stylet and a pair of the maxillary stylets are chitinized.

2. *S. linguis*

Early embryogenesis

Development of embryos within the ovary of females was not observed.
After oviposition, the cleavage energids enter the periplasm and form the plasmodial preblastoderm (Fig. 127-129), a thin nucleus-containing plasma cover. Eggs of *S. linguis* reach the blastodermal stage between 6 h ± 6 h and 18 h ± 6 h. Some of the energids do not move to the periphery of the egg, but stay in the yolk and become yolk cells (Fig. 129).

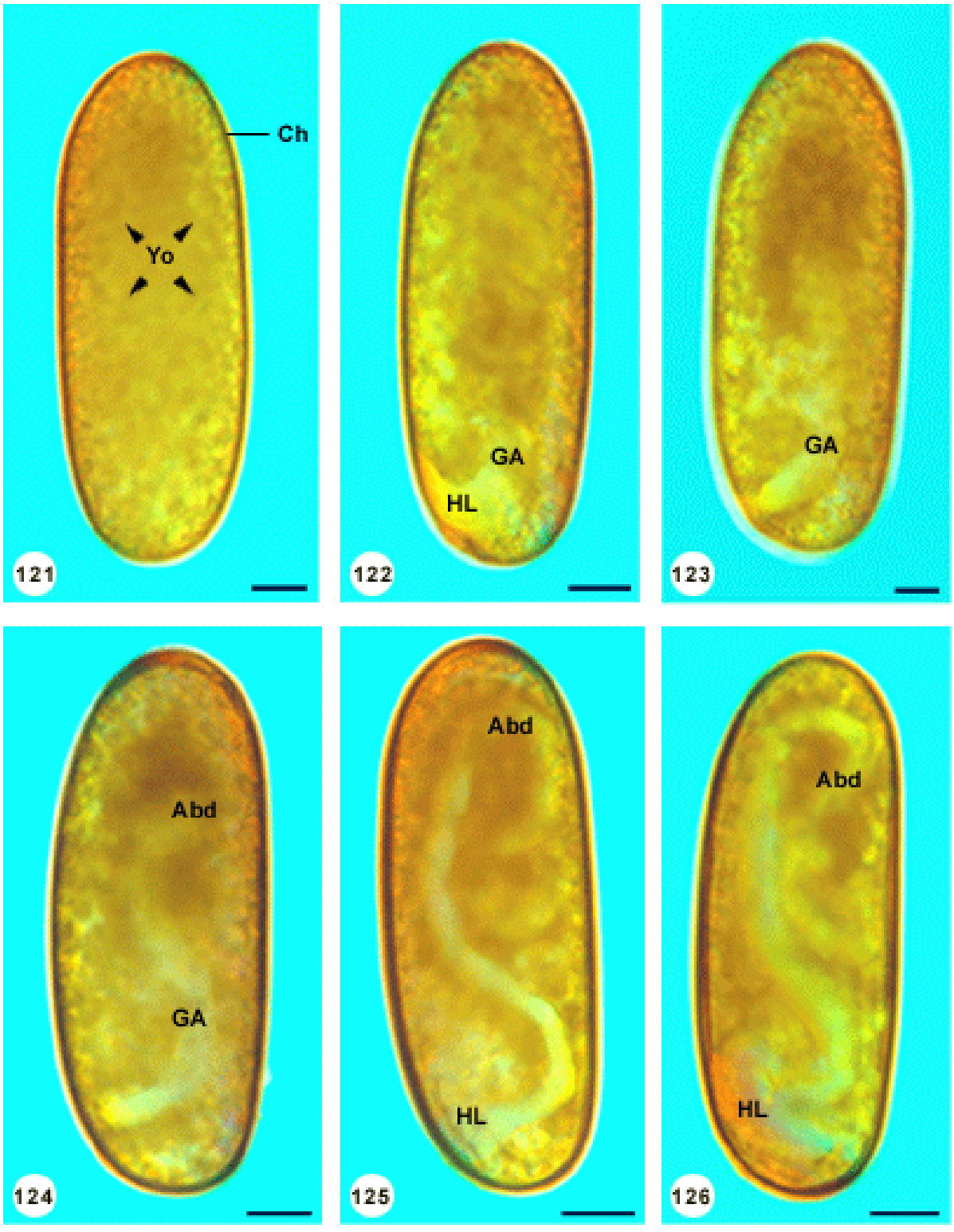
Formation of the germ band, anatrepsis, and germ band elongation

The initially uniform layer of the blastoderm becomes thicker in the posteroventral region of the egg due to the aggregation of cells (Fig. 130, 131). This thickening develops the germ anlage which is a one layered presumptive embryonic tissue. The remainder of the blastoderm becomes a thin membrane, the serosa or embryonic cover (extraembryonic tissue).
A transversal oriented V-shaped deflection of the serosa, the amniotic pore, appears at the posterior end of the germ anlage, the bottom of the V is orientated caudad (Fig. 132, 133). The germ anlage invaginates vertically in the yolk through this V-groove beginning with the caudal end (Fig. 133), then bends cephalad and starts to elongate (Fig. 122, 123). Serosal cells situated cephalad and laterad of the invagination are transported with the embryo in the yolk and form the amnion. Later the embryo separates from the serosa (between 42 h ± 6 h and 54 h ± 6 h) (Fig. 134, 135). The venter of the embryo faces the dorsal side of the egg and the posterior end of the embryo shows the anterior side of the egg (Fig. 125).

During anatrepsis and shortly afterwards, the germ band elongates (Fig. 123, 124, 136-138) and becomes thinner (Fig. 134, 139-143). The germ band grows along the longitudinal axis of the egg and reaches its maximal size at approximately 102 h ± 6 h. The caudal end of the latter abdomen bends ventrally (Fig. 125, 126, 143), resulting is an S-shaped germ band (Fig. 125, 126).

Plate XVIII: Fig. 121 - 126. Early embryogenesis of *S. linguis*, formation of germ band, invagination, and elongation. **Fig. 121.** *S. linguis*, egg, 18 h ± 6 h, egg shortly after oviposition, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 122.** *S. linguis*, egg, 42 h ± 6 h, germ anlage at the ventro-posterior region of the egg, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 123.** *S. linguis*, egg, 54 h ± 6 h, invagination of the germ anlage, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 124.** *S. linguis*, egg, 66 h ± 6 h, elongation of germ anlage, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 125.** *S. linguis*, egg, 90 h ± 6 h, germ band with head lobes situated at the posterior region of the egg and abdomen twisted in the first third of the anterior region of the egg, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 126.** *S. linguis*, egg, 102 h ± 6 h, whole mounting (paraffin oil), DIC, Bar = 50 µm. Abd = abdomen, Ch = chorion, GA = germ anlage, HL = head lobe, Yo = yolk.

Plate XVIII



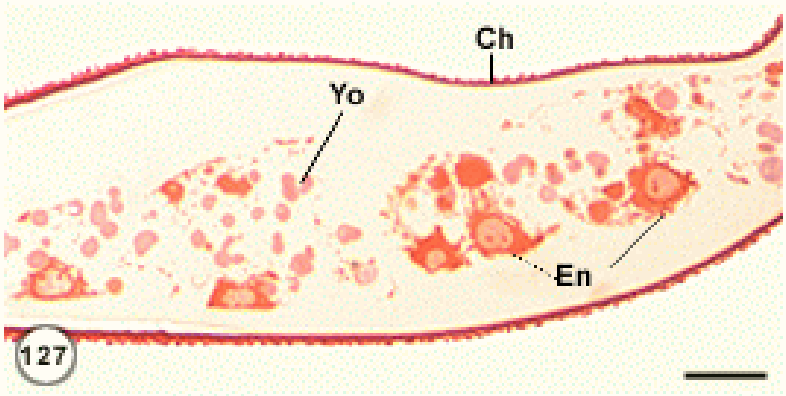
During invagination of the germ anlage, extraembryonic parts are pulled inside forming the amnion. The amniotic cavity loses the cranial connection relatively early during embryogenesis (during elongation process), while in embryos of *F. occidentalis* the amniotic cavity does not lose the contact with the embryonic head region during elongation.
As with *F. occidentalis*, *S. linguis* has a total invagination of the germ band (Fig. 126) resulting in the same developmental structure as described above for embryos of *F. occidentalis*.

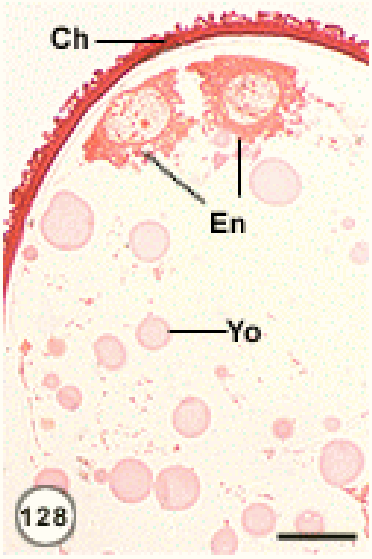
Segmentation
The elongated germ anlage becomes characterized by segmental organization after gastrulation (Fig. 139-143). The embryo progressively differentiates with the head, body segments, and appendages becoming increasingly well defined.
At approximately 90 h ± 6 h the protocephalic lobes are formed. Anlagen of the antennae (Fig. 139, 141, 144) and gnathal appendages (Fig. 140, 141, 145, 147) appear. While the germ band elongates, the thoracic appendages develop (Fig. 140, 141, 145) and the segmentation of the abdomen (Fig. 142, 143, 146) becomes distinct. Pleuropodia appear on the first abdominal segment (Fig. 145). Shortly before katatrepsis, the gnathal and thoracic appendages are developed (Fig. 162-167). The position of the labrum moves posteriorly, and that of the antennae move anteriorly. The length of the abdominal appendages increases and amnion and serosa lose their contact, whereby the total invaginated germ band comes into being.
Germ cells are situated at the end of the twisted abdominal region (Fig. 144, 146).

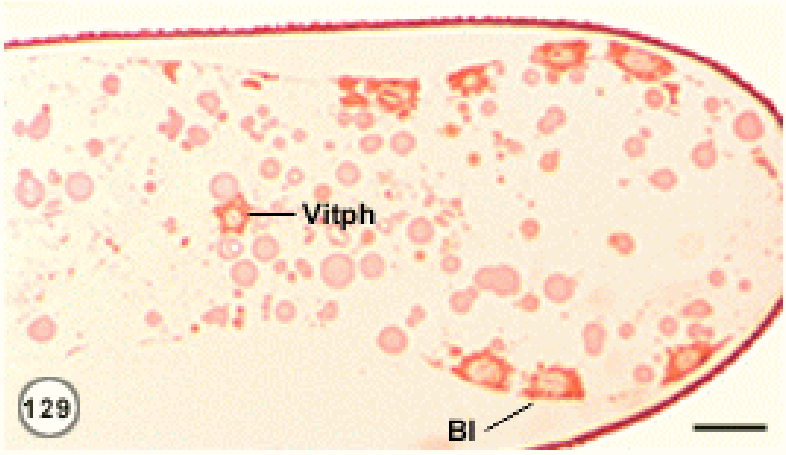
Katatrepis
In contrast to *F. occidentalis*, the head of *S. linguis* embryos lies at the posterior egg pole after anatrepsis (Table 21, Fig. 152, 162) and the ventral side of the embryo faces the ventral side of the egg. Comparing the positions of the embryo before and after katatrepsis, a rotation of 180° about the longitudinal axis of the embryo is necessary.
Katatrepsis takes about 48 h in *S. linguis* which corresponds to 19.3 % of the total duration of embryogenesis. Katatrepsis starts between 162 h ± 6 h and 174 h ± 6 h responding to (65 %) of the total duration of embryogenesis (Table 21).
Results of *S. linguis* katatrepsis are the same as described for *F. occidentalis*. The orientation of the embryo yolk system changes completely. Liquefaction starts at the posterior end of the egg where the presumptive head of the embryo is situated (Fig. 152-154) and extends anterior to the yolk which encompasses the embryo.

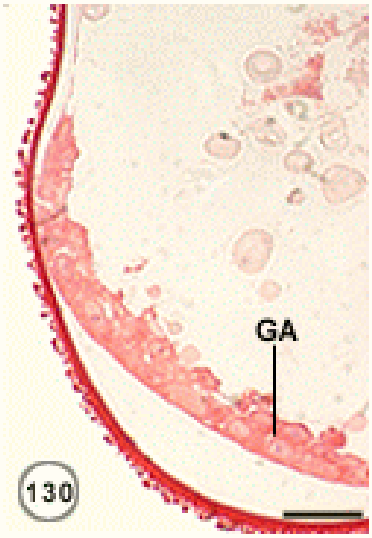
Plate XIX: Fig. 127 - 133. Blastoderm formation and differentiation of the germ anlage in *S. linguis*. **Fig. 127 - 129.** Energids at the periphery of the egg creating the plasmodial preblastoderm. **Fig. 127.** *S. linguis*, egg, 6 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 128.** *S. linguis*, egg, 6 h ± 6 h, energids containing a large nucleus and little cytoplasm, sagittal section, Safranin-staining, BF, Bar = 15 µm. **Fig. 129.** *S. linguis*, egg, 6 h ± 6 h, remaining energid in the yolk forming a vitellophage, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 130 and 131.** Formation of the germ anlage at the posterior pole of the egg (thickening of the blastoderm layer). **Fig. 130.** *S. linguis*, egg, 30 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 131.** *S. linguis*, egg, 30 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 15 µm. **Fig. 132 and 133.** Invagination of the germ anlage. **Fig. 132.** *S. linguis*, egg, 30 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 50 µm. **Fig. 133.** *S. linguis*, egg, 30 h ± 6 h, invaginating germ anlage with amniotic pore at the caudal end of the egg, sagittal section, Safranin-staining, BF, Bar = 25 µm. Am = amnion, AmPo = amniotic pore, Bl = blastoderm, Ch = chorion, En = energid, GA = germ anlage, Vitph = vitellophage, Yo = yolk.

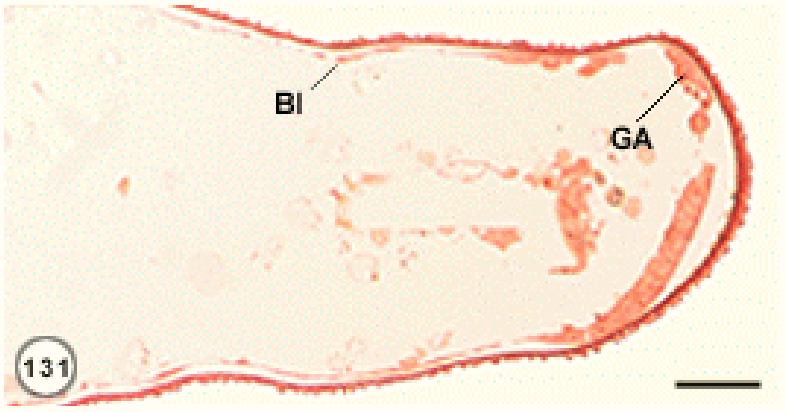
Plate XIX

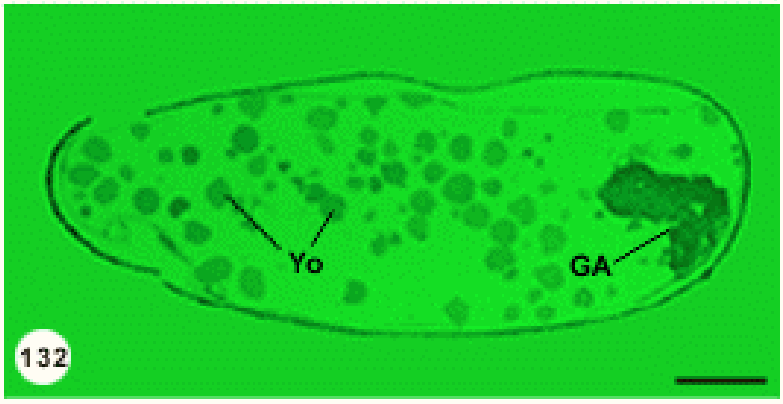

Ch
Yo
En
127

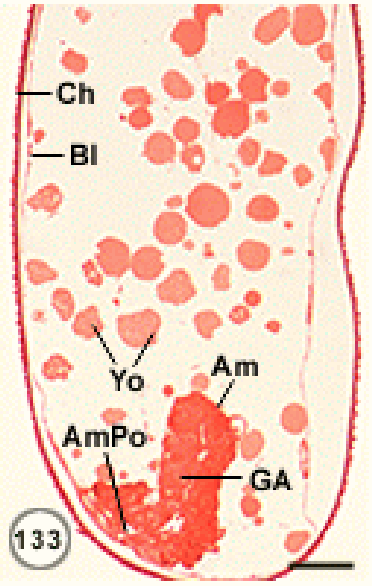

Ch
En
Yo
128


Vitph
Bl
129


GA
130


Bl
GA
131


Yo
GA
132


Ch
Bl
Yo
Am
AmPo
GA
133

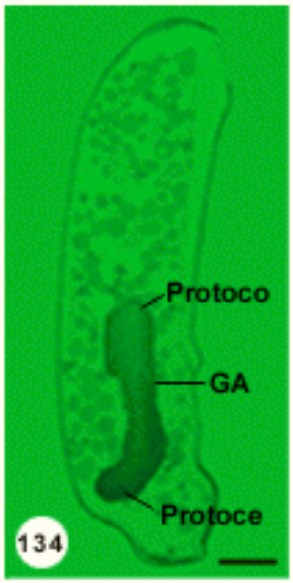
Embryonic envelopes break at the point of their fusion and serosal cells begin to contract towards the anterior pole. The embryo becomes shortened with a slight rotation and continues to rotate clockwise on its longitudinal axis to about 180°. Analysis of video records reveal that there is further rotation of the embryo, however, the position of the embryo after katatrepsis is the result of a 180° rotation.
During the rotation, the embryo moves out of the yolk and along the ventral surface of the egg towards the anterior pole (Fig. 155-157). At the end of katatrepsis the embryo comes to lie with its head on the anterior pole of the egg (Fig. 158, 159) and the ventral side of the embryo faces the dorsal side of the egg (Fig. 159, 160).
The contracted serosa remains temporarily as secondary dorsal organ (Fig. 170, 172-174) and is visible until 204 h ± 6 h, which corresponds to 82.1% of the total duration of embryogenesis in *S. linguis*. At the end of this stage, the provisional dorsal closure is completed (Fig. 171-173).
An embryonic cuticle consisting of an epicuticle and a chitinous endocuticle is formed after katatrepsis.

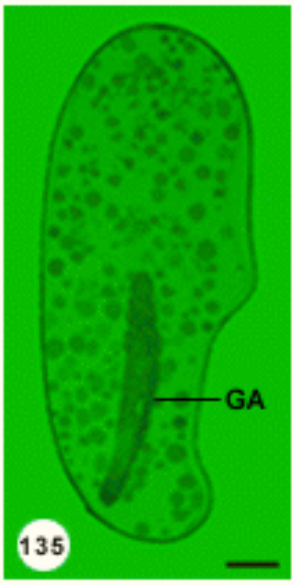
Table 21: Comparison of katatrepsis in *F. occidentalis* and *S. linguis*.

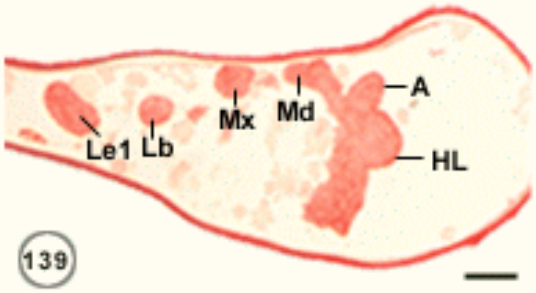
	F. occidentalis **(Terebrantia)**	***S. linguis*** **(Tubulifera)**
Start of katatrepsis	42 h ± 6 h	162 h ± 6 h
Duration of katatrepsis	1 h	48 h
Duration of katatrepsis (per cent of total embryogenesis duration)	10.4 %	19.3 %
Liquefaction of yolk starts	anterior and posterior end of the egg	anterior and posterior end of the egg
Position of the head before katatrepsis	ventral side of the egg	posterior egg pole
Position of the head after katatrepsis	anterior egg pole	anterior egg pole
Rotation about the longitudinal axis during katatrepsis	no	yes (180° or more)

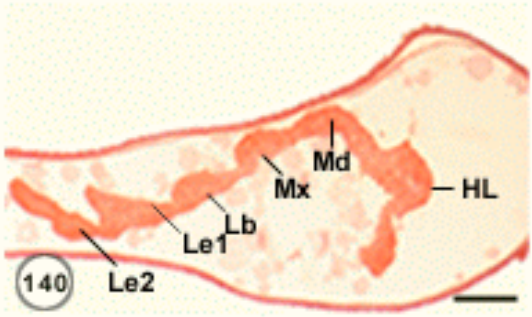
Plate XX: **Fig. 134 - 143.** Elongation of the germ band, first differentiation of thoracal and gnathal appendages in *S. linguis*. **Fig. 134 - 138.** Germ anlage growing anterior (elongation) with prospective head region (protocephalon) and abdomen (protocorm). **Fig. 134.** *S. linguis*, egg, 42 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 50 µm. **Fig. 135.** *S. linguis*, egg, 54 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 50 µm. **Fig. 136.** *S. linguis*, egg, 42 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 137.** *S. linguis*, egg, 42 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 138.** *S. linguis*, egg, 54 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 139 - 143.** Serial sections through an egg, anlagen of thoracal and gnathal appendages and abdominal segments. **Fig. 139.** *S. linguis*, egg, 90 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 140.** *S. linguis*, egg, 90 h ± 6 h, germ band, anlagen of gnathal appendages and extremities, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 141.** *S. linguis*, egg, 90 h ± 6 h, anlagen of extremities and antenna, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 142.** *S. linguis*, egg, 90 h ± 6 h, abdominal region of the developing embryo, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 143.** *S. linguis*, egg, 90 h ± 6 h, twisted abdominal region, sagittal section, Safranin-staining, BF, Bar = 25 µm. A = antenna, Abd = abdomen, AbdS = abdominal segment, GA = germ anlage, GC = germ cells, HL = head lobe, Lb = labium, Le1 = leg one, Le2 = leg two, Le3 = leg three, Md = mandible, Mx = maxilla, Protoce = protocephalon, Protoco = protocorm, Yo = yolk.

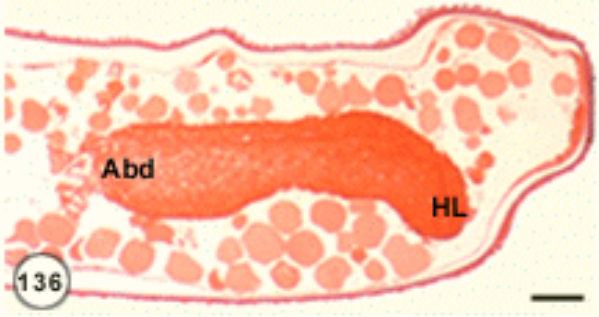
Plate XX

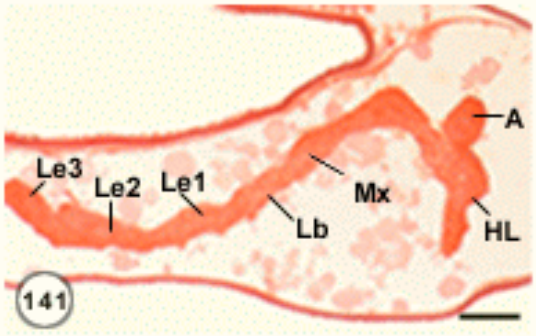

Protoco
GA
Protoce
134

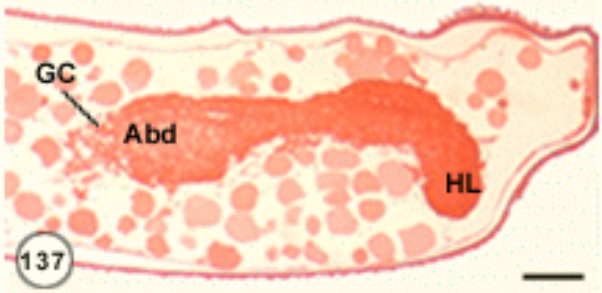

GA
135

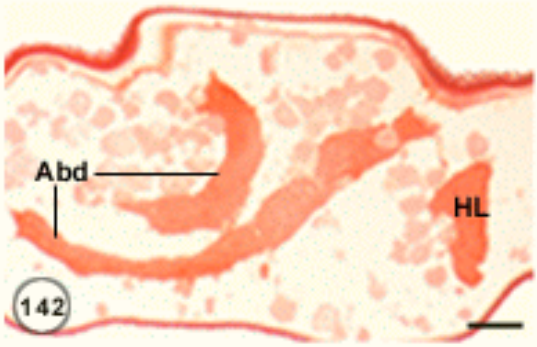

Le1
Lb
Mx
Md
A
HL
139

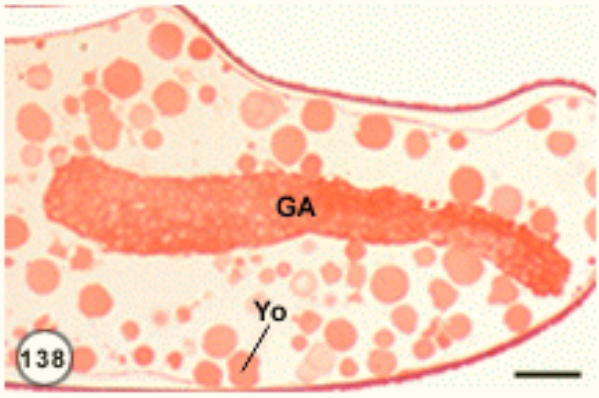

Md
Mx
HL
Lb
Le1
Le2
140

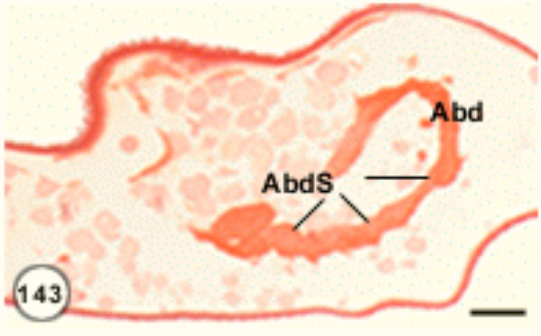

Abd
HL
136


A
Le3
Le2
Le1
Mx
Lb
HL
141


GC
Abd
HL
137


Abd
HL
142


GA
Yo
138


Abd
AbdS
143

Organogenesis and early prolarva

Most of the remaining organs originate from this stage and a lot of cells start to differentiate at the beginning of segmentation. As in *F. occidentalis*, the anlagen of the organ systems become apparent before katatrepsis begins.

Nervous system: Neuroblasts start to differentiate a short time before every segment becomes defined and immediately develop preganglionic cells.

During invagination of the germ band, the protocephalic lobes arise (Fig. 148, 149-151) and prior to katatrepsis, the three paired lobes of the cerebralganglion (protocerebrum, deutocerebrum, and tritocerebrum) become visible. The paired lobes fuse after katatrepsis and form the synganglion.

The ventral nerve cord differentiates before katatrepsis (Fig. 166, 167), while the gnathal ganglia fuse after katatrepsis and build the suboesophageal ganglion and the thoracic ganglia stay separated (Fig. 168, 169, 176-178, 182, 183, 185, 186).

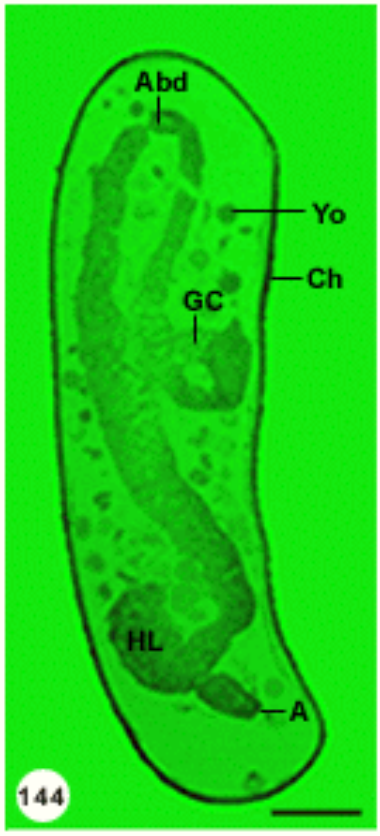
Alimentary canal: Stomodeum and proctodeum appear as first signs of the differentiating foregut and hindgut. Post katatrepsis, the midgut epithelium arise and enclose the yolk. Pharynx and oesophagus become visible at 198 h ± 6 h (Fig. 179, 181). Valvula cardiaca arises and builds the connection between oesophagus and gut.

Post katatrepsis, cells of the amnion (provisional dorsal closure) and embryonic epidermis start to secrete an embryonic cuticle and the dorsal closure commences.

Pleuropodia are visible as appendages of the first abdominal segment (Fig. 171) and later undergo reduction.

Plate XXI, XXII: Fig. 144 - 149. Further differentiation of thoracic and gnathal appendages in *S. linguis*. **Fig. 144.** *S. linguis*, egg, 102 h ± 6 h, embryo with head region and anlage of antenna, abdomen with germ cells, sagittal section, Safranin-staining, BF, Bar = 50 µm. **Fig. 145.** *S. linguis*, egg, 102 h ± 6 h, gnathal (mandible, maxilla, labium) and thoracic appendages (leg one to three), sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 146**. *S. linguis*, egg, 102 h ± 6 h, abdominal region of the embryo, germ cells situated at the twisted end of the abdomen, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 147.** *S. linguis*, egg, 102 h ± 6 h, differentiating extremities and mouthparts, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 148.** *S. linguis*, egg, 114 h ± 6 h, head lobes, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 149.** *S. linguis*, egg, 114 h ± 6 h, development of extremities, sagittal section, Safranin-staining, BF, Bar = 50 µm. **Fig. 150 - 161.** Embryo of *S. linguis* before katatrepsis, katatrepsis, embryo after completion of katatrepsis, and ready to hatch larva. **Fig. 150.** *S. linguis*, egg, 114 h ± 6 h, embryo with anlagen of gnathal appendages and antenna, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 151 and 152.** Egg shortly before katatrepsis. **Fig. 151.** *S. linguis*, egg, 138 h ± 6 h, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 152.** *S. linguis*, egg, 150 h ± 6 h, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 153.** *S. linguis*, egg, 162 h ± 6 h, liquefaction of yolk, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 154.** *S. linguis*, egg, 174 h ± 6 h, continuation of yolk liquefaction, embryonic head starts to move anteriorwards, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 155.** *S. linguis*, egg, 174 h ± 6 h, rotation of the embryo during katatrepsis, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 156.** *S. linguis*, egg, 174 h ± 6 h, further movement of the embryo, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig 157.** *S. linguis*, egg, 186 h ± 6 h, head reaches the anterior region of the egg, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 158.** *S. linguis*, egg, 198 h ± 6 h, embryo at the end of katatrepsis, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 159.** *S. linguis*, egg, 222 h ± 6 h, position of the embryo after katatrepsis, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 160.** *S. linguis*, egg, 234 h ± 6 h, embryo with segmented antenna, mouthparts, and extremities, whole mounting (paraffin oil), DIC, Bar = 50 µm. **Fig. 161.** *S. linguis*, egg, 270 h ± 6 h, ready to hatch larva, larval eye pigment visible, whole mounting (paraffin oil), DIC, Bar = 50 µm. A = antenna, Abd = abdomen, AbdS = abdominal segment, Ch = chorion, GC = germ cells, H = head, HL = head lobe, Lb = labium, Le = leg, LE = larval eye, Le1 = leg one, Le2 = leg two, Le3 = leg three, Md = mandible, Mx = maxilla, Yo = yolk.

Plate XXI


Abd
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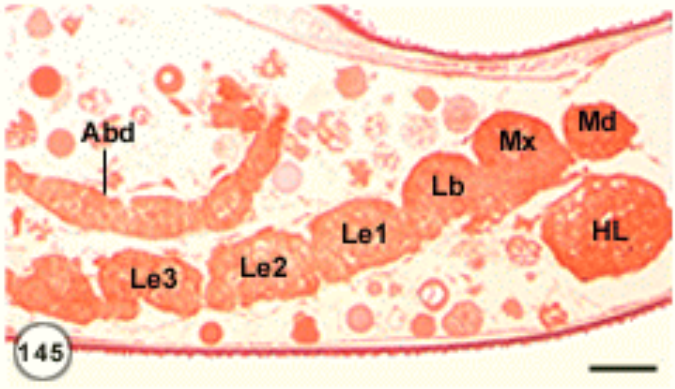
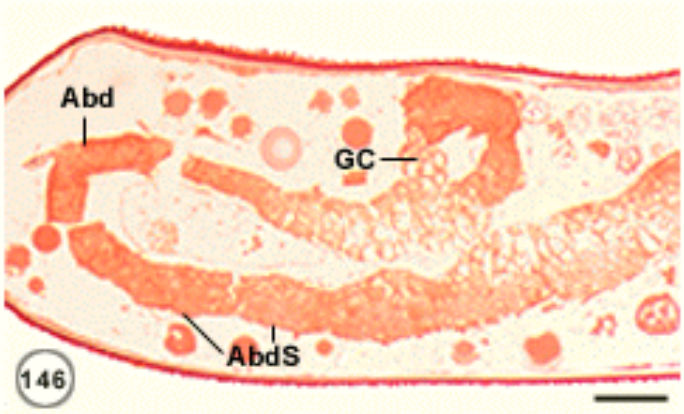
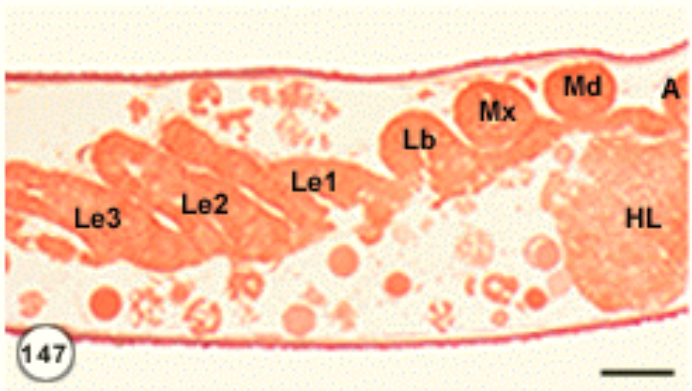
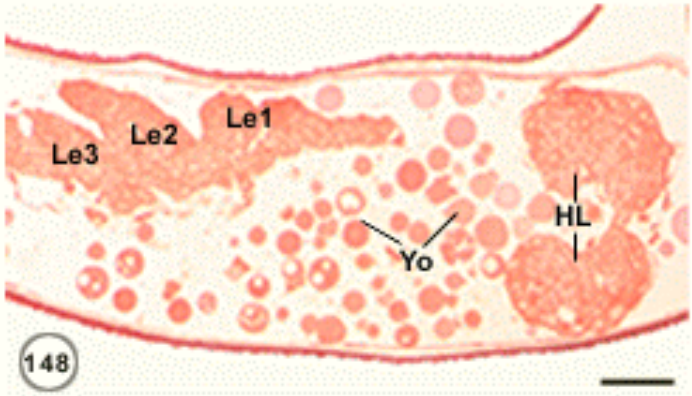
GC
HL
A
144


Abd
Md
Mx
Lb
Le1
HL
Le3
Le2
145


Abd
GC
AbdS
146


Md
A
Mx
Lb
Le1
Le2
Le3
HL
147


Le1
Le2
Le3
HL
Yo
148

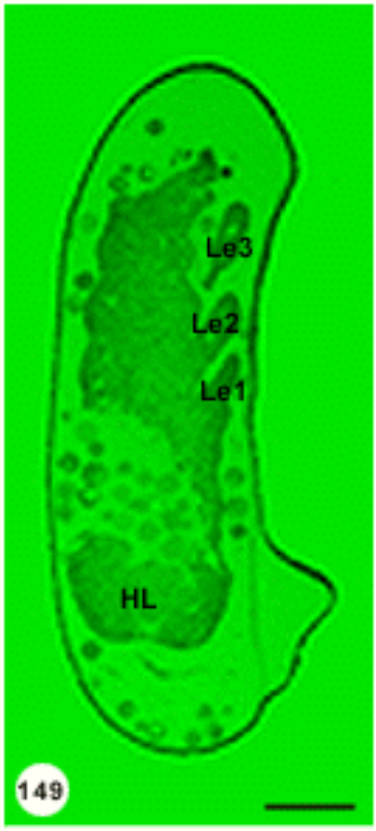
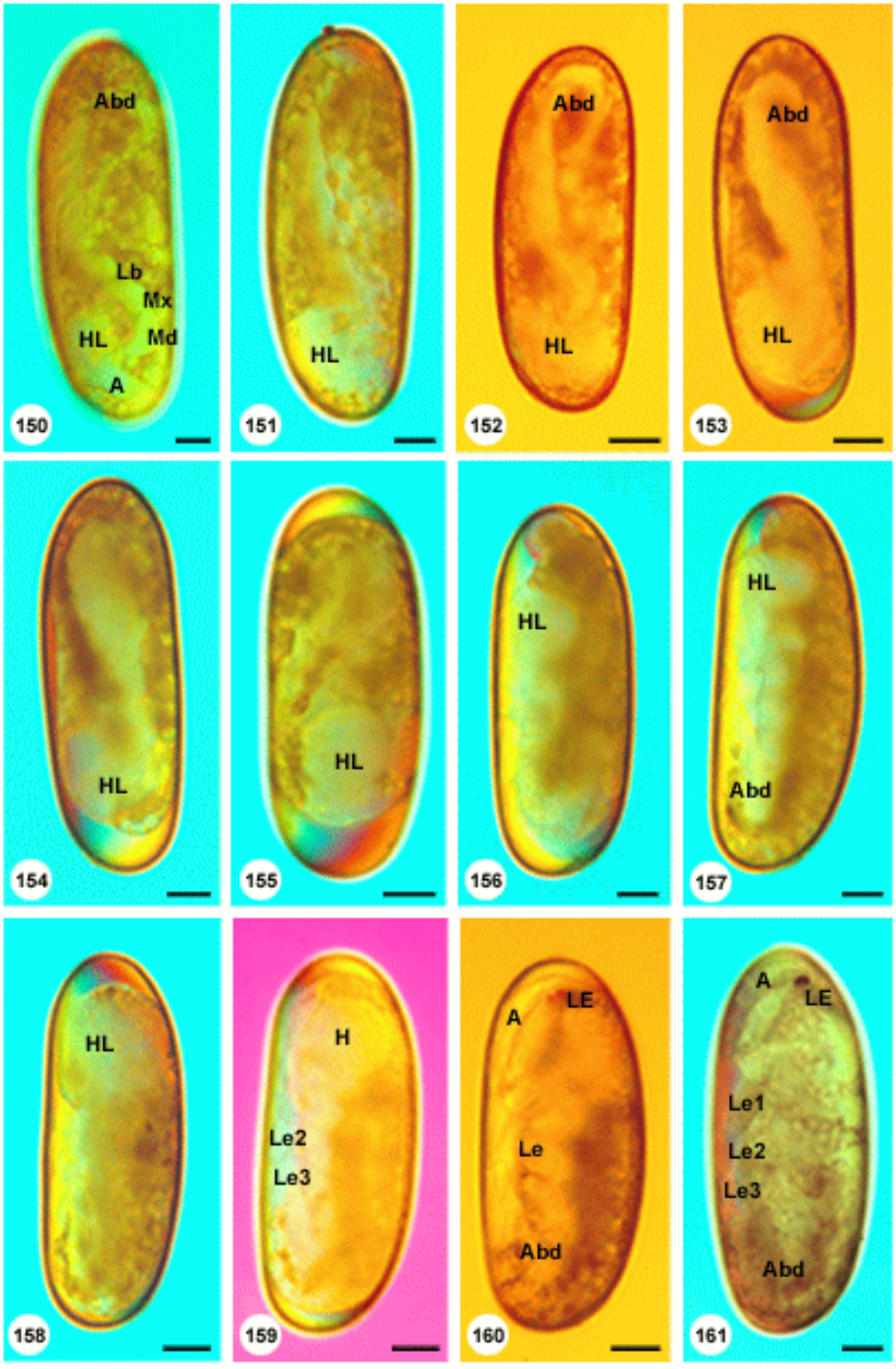

Le3
Le2
Le1
HL
149

Plate XXII


Abd
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Abd
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152
Abd
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156
HL
Abd
157
HL
158
H
Le2
Le3
159
A
LE
Le
Abd
160
A
LE
Le1
Le2
Le3
Abd
161

The dorsal organ disappears at the end of this stage. Compared with *F. occidentalis*, this takes place later in the embryonic development of *S. linguis*.
The differentiation of the larval eye (Fig. 161, 175, 180) continues and pigmentation is first recognizable at 210 h ± 6 h. The right mandible becomes decomposed and the formation of the typical mouthcone appears (Fig. 184).
Dorsal closure is completed during this stage. The stage is finished with the beginning of the segregation of the larval cuticle.

Ready-to-hatch larva

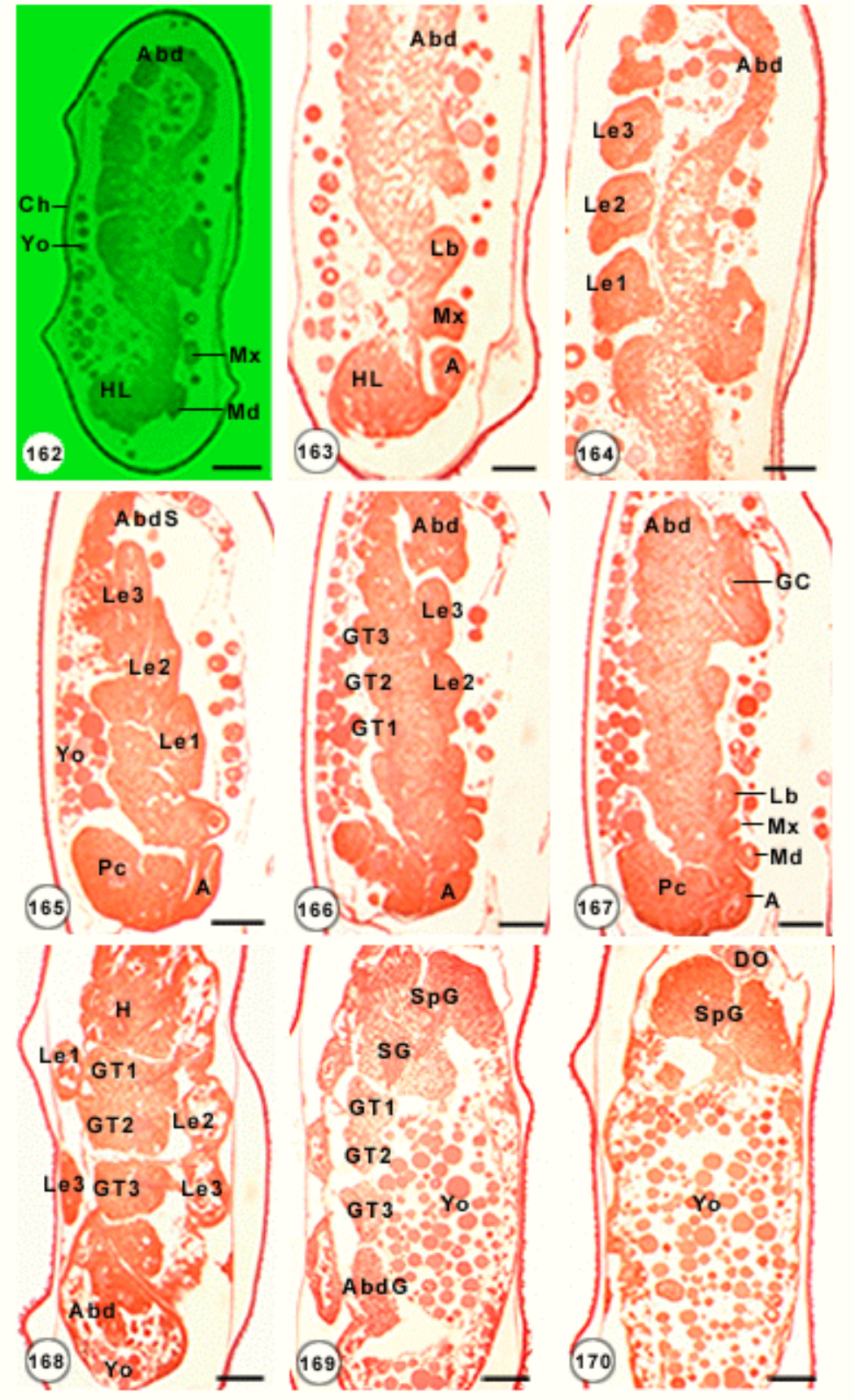
The embryo shows the same features as the first instar larva at the ready-to-hatch larval stage and organogenesis is completed during this stage. Almost no mitotic activity is visible and cells of the most organs finish their differentiation.

As in *F. occidentalis*, the abdomen consists of ten abdominal segments.
The nervous system shows larval construction (Fig. 185, 186). Due to the development of different muscle groups in the gnathal region, the cerebral areas are shifted caudad. The suboesophageal ganglion fuses with the prothoracic ganglion as in *F. occidentalis*. The abdominal ganglion complex consists of the fused ganglia of each abdominal segment.
Larval cuticle is deposited at the surface of the embryonic body. The gut finishes its differentiation and most of the yolk is consumed. Approximately one day before hatching, the peristalsis in the hindgut initiates muscle contraction. Larval cuticle and the top of the head start to expand and to contract. During hatching, the chorion breaks on its dorsal side immediately behind the aeropyle and the first instar larva hatches.

Table 22 shows a comparision of some features of embryogenesis in *F. occidentalis* and *S. linguis*.

Plate XXIII: **Fig. 162 - 170.** Embryo of *S. linguis* before katatrepsis and after katatrepsis. **Fig. 162 - 164.** Embryo increases in width, gnathal appendages and extremities. **Fig. 162.** *S. linguis*, egg, 126 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 50 µm. **Fig. 163.** *S. linguis*, egg, 126 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 164.** *S. linguis*, egg, 126 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 165 - 167.** Embryo shortly before katatrepsis starts, differentiation of ganglia, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 165.** *S. linguis*, egg, 156 h ± 12 h, head region and differentiating extremities, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 166.** *S. linguis*, egg, 156 h ± 12 h, thoracic ganglia and extremities, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 167.** *S. linguis*, egg, 156 h ± 12 h, gnathal appendages and abdomen with germ cells, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 168 - 170.** Embryo after katatrepsis, further differentiation of nervous system. **Fig. 168.** *S. linguis*, egg, 180 h ± 12 h, thoracic ganglia and extremities, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 169.** *S. linguis*, egg, 180 h ± 12 h, nervous system, differentiation of digestive system, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 170.** *S. linguis*, egg, 180 h ± 12 h, head region, dorsal organ, yolk enclosed by differentiating gut, sagittal section, Safranin-staining, BF, Bar = 25 µm. A = antenna, Abd = abdomen, AbdG = abdominal ganglion, AbdS = abdominal segment, Ch = chorion, DO = dorsal organ, GC = germ cells, GT1 = prothoracic ganglion, GT2 = mesothoracic ganglion, GT3 = metathoracic ganglion, H = head, HL = head lobe, Lb = labium, Le1 = leg one, Le2 = leg two, Le3 = leg three, Md = mandible, Mx = maxilla, Pc = protocerebrum, SG = suboesophageal ganglion, SpG = supraoesophageal ganglion, Yo = yolk.

Plate XXIII


Abd
Ch
Yo
Mx
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162
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Lb
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A
163
Abd
Le3
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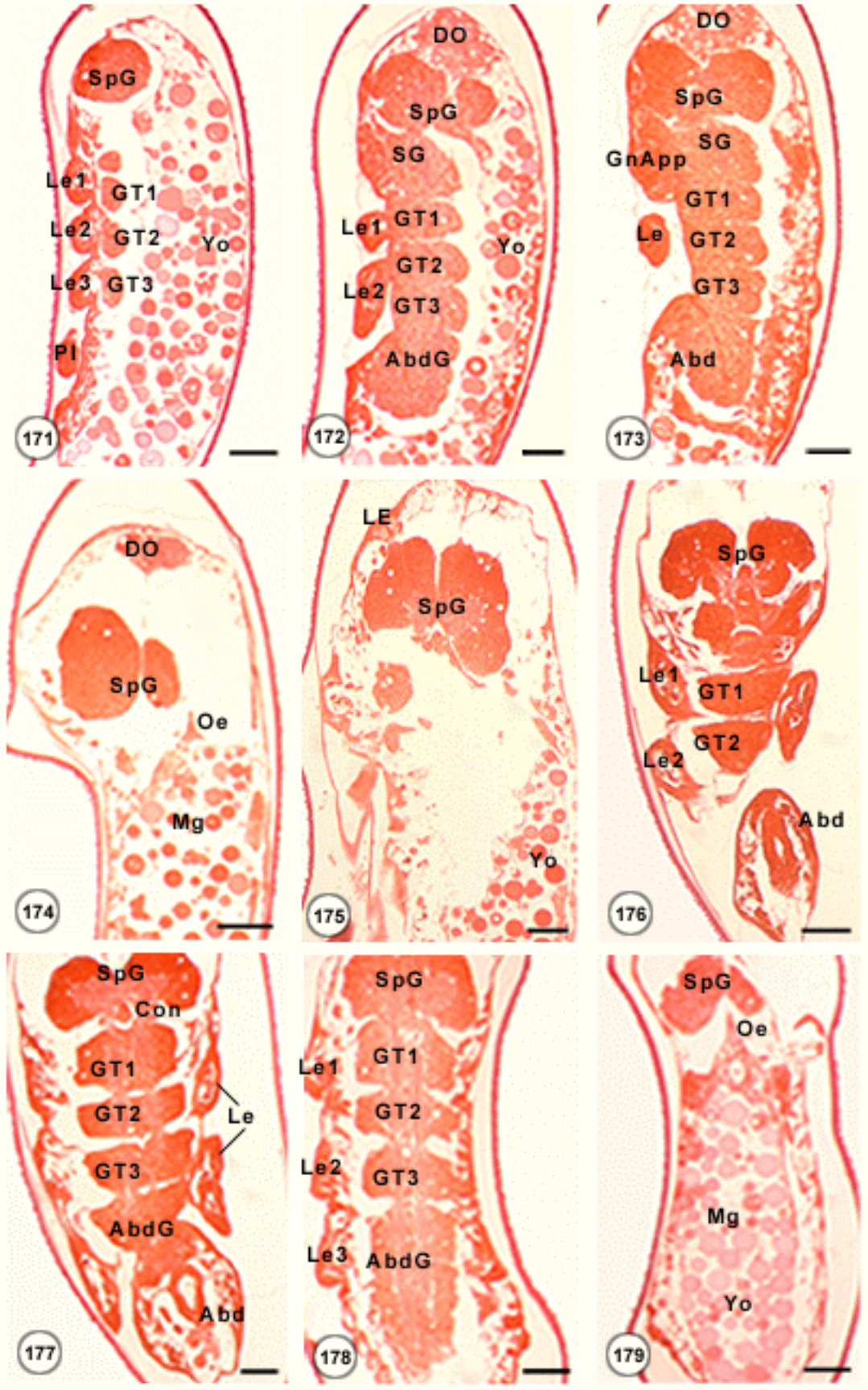
Le1
164
AbdS
Le3
Le2
Le1
Yo
Pc
A
165
Abd
Le3
GT3
GT2
Le2
GT1
A
166
Abd
GC
Lb
Mx
Md
Pc
A
167
H
Le1
GT1
GT2
Le2
Le3
GT3
Le3
Abd
Yo
168
SpG
SG
GT1
GT2
GT3
Yo
AbdG
169
DO
SpG
Yo
170

Table 22: Comparison of characteristics of the embryonic development in *F. occidentalis* and *S. linguis*.

	F. occidentalis **(Terebrantia)**	***S. linguis*** **(Tubulifera)**
Duration of embryogenesis	95.4 h (ca. 4 d)	248.4 h (10.4 d)
Size of eggs (length ± SD x width ± SD)	279.5 µm ± 6.9 x 128.9 µm ± 16.5	446.0 µm ± 4.8 x 163.3 µm ± 3.7
Mortality rate of the eggs	34 %	9 %
Formation of germ anlage	6 h ± 6 h	30 h ± 6 h
Position of germ anlage	posteroventral region of the egg	posteroventral region of the egg
Invagination of germ anlage	18 h ± 6 h	30 h ± 6 h
Start of segmentation	30 h ± 6 h	90 h ± 6 h
Start of organogenesis	18 h ± 6 h	66 h ± 6 h

Plate XXIV, XXV: Fig. 171 - 179. Embryo of *S. linguis* after completion of katatrepsis, dorsal closure. **Fig. 171.** *S. linguis*, egg, 186 h ± 6 h, embryo with thoracic extremities and pleuropodia, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 172 and 173.** Embryo with dorsal organ at the anterior region of the egg, nervous system. **Fig. 172.** *S. linguis*, egg, 186 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 173.** *S. linguis*, egg, 186 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 174.** *S. linguis*, egg, 204 h ± 6 h, dorsal organ, differentiation of oesophagus and gut (with yolk included), sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 175.** *S. linguis*, egg, 204 h ± 6 h, supraoesophageal ganglion with nervus opticus and differentiating larval eye, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 176.** *S. linguis*, egg, 210 h ± 6 h, supraoesophageal ganglion, frontal section, Safranin-staining, Bar = 25 µm. **Fig. 177 and 178.** Nervous system of the embryo. **Fig. 177.** *S. linguis*, egg, 210 h ± 6 h, frontal section, Safranin-staining, Bar = 25 µm. **Fig. 178.** *S. linguis*, egg, 210 h ± 6 h, frontal section, Safranin-staining, Bar = 25 µm. **Fig. 179.** *S. linguis*, egg, 210 h ± 6 h, oesophagus, valvula cardiaca and gut, frontal section, Safranin-staining, Bar = 25 µm. **Fig. 180 - 186.** Early and late prolarva (ready to hatch larva). **Fig. 180.** *S. linguis*, egg, 222 h ± 6 h, prothoracic and mesothoracic ganglion, salivary gland, nervus opticus and larval eye, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 181.** *S. linguis*, egg, 222 h ± 6 h, head region of the embryo with antenna, oesophagus and gut, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 182 and 183.** Nervous system at prolarval stage. **Fig. 182.** *S. linguis*, egg, 246 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 183.** *S. linguis*, egg, 246 h ± 6 h, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 184 - 186.** Late prolarval stage (ready-to-hatch-larva). **Fig. 184.** *S. linguis*, egg, 270 h ± 6 h, head and thoracic region, antenna (segmented), mouthcone, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 185.** *S. linguis*, egg, 270 h ± 6 h, thoracic ganglia and abdominal region, sagittal section, Safranin-staining, BF, Bar = 25 µm. **Fig. 186.** *S. linguis*, egg, 270 h ± 6 h, nervous system of ready-to-hatch larva, sagittal section, Safranin-staining, BF, Bar = 25 µm. A = antenna, AbdG = abdominal ganglion, AbdS = abdominal segment, Con = connective, DO = dorsal organ, GT1 = prothoracic ganglion, GT2 = mesothoracic ganglion, GT3 = metathoracic ganglion, Le = leg, LE = larval eye, Le1 = leg one, Le2 = leg two, Le3 = leg three, Mg = midgut, MthP = mouthparts, NOpt = nervus opticus, Oe = oesophagus, Pl = pleuropodium, SG = suboesophageal ganglion, SGl = salivary gland, SpG = supraoesophageal ganglion, Yo = yolk.

Plate XXIV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Yo
Le3
GT3
Pl
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DO
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SG
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Le2
GT3
AbdG
172
DO
SpG
SG
GnApp
GT1
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GT2
GT3
Abd
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DO
SpG
Oe
Mg
174
LE
SpG
Yo
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Abd
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AbdG
Abd
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178
SpG
Oe
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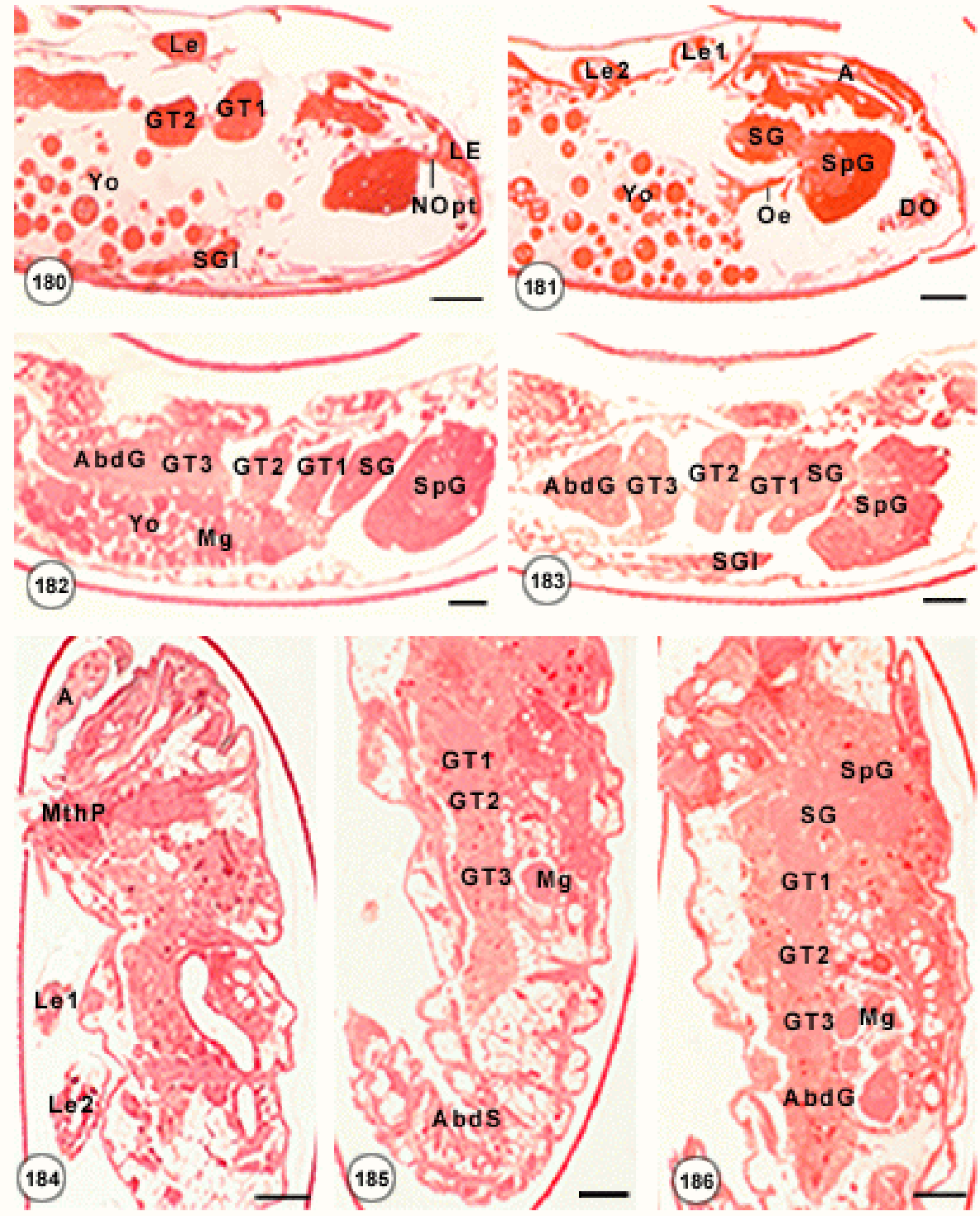
179

Plate XXV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GT3
GT2
GT1
SG
SpG
Yo
Mg
182
AbdG
GT3
GT2
GT1
SG
SpG
SGI
183
A
MthP
Le1
Le2
184
GT1
GT2
GT3
Mg
AbdS
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SpG
SG
GT1
GT2
GT3
Mg
AbdG
186

4. Discussion

4.1. Reproduction

4.1.1. Type of parthenogenesis, sex ratio

1. Parthenogenesis

Many insects reproduce through parthenogenesis, a common phenomenon found in most insect groups (SUOMALAINEN 1950). Three types of parthenogenesis can be distinguished (SUOMALAINEN 1950): (1) Arrhenotoky. Unfertilized eggs develop parthenogenetically into males, fertilized eggs develop into females. (2) Thelytoky. Unfertilized eggs develop into females. (3) Deuterotoky or amphitoky which means that unfertilized eggs develop into both sexes.

Thrips show all three types of parthenogenesis (LEWIS 1973; MORITZ 1997; GULLAN & CRANSTON 1994) and the mode of sex determination in thrips is thought to be haplodiploidy which means that female thrips are diploid and males are always haploid (WHITING 1945; RISLER & KEMPTER 1961; STANNARD 1968).

Haplodiploidy has been estimated to occur in at least 20 % of all named species of animals (CROZIER & PAMILO 1996) and can be caused by a number of different underlying genetic systems (CRUICKSHANK & THOMAS 1999). The most common of these is arrhenotoky which has evolved independently at least 17 times in Metazoa, 15 of these in arthropods (MABLE & OTTO 1998). In another system, pseudoarrhenotoky, males arise from fertilized eggs, but they eliminate the paternal genome at some point before spermatogenesis starts. The result is that the males do not pass this genome to their offspring. Pseudoarrhenotoky occurs in a number of taxa, including scale insects, mites, and scolytid beetles. Arrhenotoky can occur without haplodiploidy if a uniparentally male becomes diploid through fusion of the first two haploid cleavage nuclei. This phenomenon is referred to as diploid arrhenotoky and occurs in some scale insects (NUR 1972).

The exact status of male haploidy in the order Thysanoptera is still not understood. The parthenogenetic production of males is no proof of haplodiploidy. The demonstration of haploidy requires cytological evidence as well as genetic evidence. The evident demonstration of haploidy lies, among other things, in the investigation of the chromosome number of the somatic cells of male stages. Arrhenotoky was first demonstrated in *Haplothrips verbasci* (SHULL 1914). RAIZADA (1988) did chromosome preparations in *Microcephalothrips abdominalis* which showed that the somatic number in brain cells of females is diploid with 2n = 32, and in males haploid with n = 16. RAIZADA (1988) investigated only adult individuals and for this reason, an adjustment of the chromosome number during postembryonal stages cannot be excluded.

BOURNIER (1956a, b) tried to find out more about the chromosome cycle of the haplodiploid parthenogenesis in thrips. In females normal meiosis takes place and then the nucleus fuses with the second pole body. BOURNIER (1956a) was not able to determine the chromosome number in male spermatogonia or somatic mitosis. In spermatogenesis the first meiotic division is normal but the second rudimentary (BOURNIER 1956b). Furthermore, BOURNIER (1956b) supposed that a diploidization takes place in male cells due to measurements and comparison of nuclei diameters in both gonad and somatic cells. In contrast, RISLER & KEMPTER (1961) concluded that there is no diploidization in males and determined chromosome number in males and females of both somatic tissue and in gonads. Their results found males to be haploid (both in gonads and somatic tissue) with n = 15 and females diploid.

Merely cells of the fat body, midgut epithelium, Malpighian tubules, and oenocytes showed polyploidy in males and females (RISLER & KEMPTER 1961).

At this time, it is not possible to determine the exact number of chromosomes in examined thrips species.

The investigated species *Frankliniella occidentalis*, *Echinothrips americanus*, and *Suocerathrips linguis* exhibit an arrhenotokous mode of reproduction. In *F. occidentalis* and *E. americanus* it has been shown that unmated females produce male progeny and mated once produce both male and female progeny. *Parthenothrips dracaenae* is permanent thelytok producing only females. However, in larger numbers of individuals (at least 5000) males are found. The females of this species examined via light microscopy did not show spermathecae filled with sperm. Spermathecae were consistently small and always empty.

BOURNIER (1956a) regards the occasional appearance of males in thelytokous thrips as a cytological accident during the meiotic division of the oocyte. The thelytokous males are probably useless for reproduction. In *Hercinothrips femoralis*, another thrips species performing thelytoky, KOCH (1981) was able to observe one copulation of a rare male with a female of *H. femoralis*. MORITZ (1989d) did not find spermathecae filled with sperm in this species and supposed a reduction of this organ. In *H. femoralis* (thelytoky) the spermatheca measures 15 µm x 11 µm x 11 µm (MORITZ 1989d), in *Aeolothrips intermedius* (arrhenotoky) 100 µm x 100 µm x 100 µm (MORITZ 1982d), and in *H. verbasci* (arrhenotoky) 160 µm x 75 µm x 105 µm (TUZET & BOURNIER 1951, HEMING 1970b).

In Cynipidae (Hymenoptera) who have a thelytokous spring generation it has been demonstrated that occasional males do not mate (SUOMALAINEN 1950).

The mechanisms underlying thelytoky in thrips are not yet understood. Females develop from unfertilized eggs through automixis.

Two forms of thelytoky are recognized in Hymenoptera, revertible or microbe-associated thelytoky and non-revertible thelytoky (STOUTHAMER & KAZMER 1994). In microbe-associated thelytoky, bacteria of the genus *Wolbachia* cause parthenogenesis, and removal of these microbes by antibiotic or high-temperature treatments induces the production of males (STOUTHAMER *et al.* 1993). Microbes are absent in non-revertible parthenogenesis. Neither temperature nor antibiotic treatment causes them to revert to arrhenotoky (STOUTHAMER *et al.* 1990; STOUTHAMER & WERREN 1993). The sexual function of antibiotic-induced males ranges from possessing sperm although lacking the ability to transmit in *Encarsia formosa* (Hymenoptera) (ZCHORI-FEIN *et al.* 1992) to the successful production of female offspring in *Trichogramma* (Hymenoptera) (STOUTHAMER *et al.* 1990; STOUTHAMER & KAZMER 1994).

In two thelytokous thrips species, *Heliothrips haemorrhoidalis* and *H. femoralis*, *Wolbachia* was discovered in PCR and ftsZ gene primer analysis of these thrips (PINTUREAU *et al.* 1999). The *Wolbachia* discovery leads us to wonder if the thelytokous type of parthenogenesis in thrips is controlled by microorganisms. PINTUREAU *et al.* (1999) did not detect if *Wolbachia* was responsible for thelytoky in *H. haemorrhoidalis* and *H. femoralis*.

Investigations were made in this study to provide evidence of reversal of thelytoky in *P. dracaenae* using antibiotics. Unfortunately, it was not possible to ensure the uptake of antibiotics (thrips did not feed on sucrose-solution or honey mixed with antibiotics).

The maternally inherited *Wolbachia*-bacteria are responsible for various modifications in host reproduction, including cytoplasmic incompatibility (HOFFMANN 1988; BREEUWER & WERREN 1990; O'NEILL & KARR 1990; WERREN 1997), parthenogenesis (STOUTHAMER *et al.* 1993), feminization of genetic males (ROUSSET *et al.* 1992), and altered male fertility or female fecundity (WERREN 1997; BOURTZIS & O'NEILL 1998). The precise cellular mechanisms involved in these processes are still under investigation, but it is known that these bacteria alter early development and mitosis in their hosts.

Wolbachia are vertically transmitted via the ooplasm (HOFFMANN & TURELLI 1988; BINNINGTON & HOFFMANN 1989) but only occasionally, if at all, in sperm (HOFFMANN *et al.* 1990; BRESSAC & ROUSSET 1992).

2. Sex ratio

The study of sex ratio and their variation is important for understanding the causes and consequences in the differences of population structures, mating systems, and sociality (SHAW & MOHLER 1953; CHARNOV 1982; BULMER 1986; CROZIER & PAMILO 1996).

F. occidentalis, *E. americanus*, and *P. dracaenae* are major pests in a lot of crops (Bryan & Smith 1956; BRØDSGAARD 1989; OPIT *et al.* 1997; RAMAKERS *et al.* 2000; EPPO 2001) and an understanding of the mating processes and factors affecting sex allocation is essential for developing effective biocontrol strategies aimed at disrupting reproduction.

Little is known about the reproduction and sex ratio in *S. linguis*. Among the Phlaeothripidae, there are some species which display different levels of sociality and some eusociality in gall-inducing thrips (CRESPI 1986a, b, 1988b, 1990, 1992a, b). Knowledge acquired from various forms of social reproductive thrips species should reveal aspects of the evolution of sociality in thrips.

OLSEN (1984) discussed the difficulty in drawing conclusions based on sex ratios obtained from adult populations alone, due to differences in the biology, and in the longevity of the two sexes. The actual primary sex ratio of a population is defined as the number of males and females in the first progeny of the adults (MOUND 1992). Investigations undertaken in this study were aimed at looking at tendencies in the sex ratio of adult populations of thrips.

LIU & SMITH (2000) pointed out that species with a haplodiploid mode of reproduction often aside from being haplodiploid, show a female biased sex ratio (HAMILTON 1967), low heterozygosity (GRAUR 1985), more than one reproductive mode (PINTO *et al.* 1991), and some degrees of inbreeding (HARDY 1994). On the other hand, when the costs of producing sons and daughters are equal, a primary sex ratio of 1:1 could thus be expected (REINHOLD 1996). Thus the results in this study agree with the determined sex ratio of 1 : 0.9 (female : male) in *F. occidentalis* and 1 : 0.3 (female : male) in *E. americanus*.

Since HAMILTON'S (1967) influential idea that offspring sex ratio should be biased when brothers compete intensely for matings, the interest in sex allocation has grown. Under the condition of local mate competition, mothers benefit from producing more daughters as competition is less intense among offspring of this sex. Subsequent models of sex allocation have shown that evolutionary stable sex ratio should differ from unity whenever fitness returns to vary between daughters and sons (CHARNOV 1982).

HAMILTON (1967) demonstrated that when the offspring of one or a few mothers mate among themselves at their natal patch, before the daughters disperse, a female biased sex ratio is favoured. This has been termed local mate competition (WEST & HERRE 1998).

It would explain the fact that females of *E. americanus* mate before they disperse. There is a remarkable difference in the behaviour of *F. occidentalis* and *E. americanus*. Males and females of *F. occidentalis* move around more frequently than *E. americanus* which scarcely moves or disperses. Female biased sex ratio in *E. americanus* is probably due to local mate competition.

Local mate competition may also explain the female biased sex ratio in *S. linguis*. It is very likely that more than one generation lives on one *Sansevieria trifasciata* plant. Aggregations of adults of this species are observable at certain times at the top of the *Sansevieria trifasciata* plant and there are times where all individuals are gathered at the base of the plant. Dispersal to establish new colonies from *Sansevieria trifasciata* may be the reason for *S. linguis* movement to the top of the plant. Female biased sex ratio as determined for adults of *S. linguis* in this study are probably partly due to local mate

competition, where females mate in the place where they hatch.
A few tubuliferan species have both sexes living together in the same colony, therefore a mate maybe found in the colony and some males disperse to new and developing colonies to search for receptive females. In species where males are wingless, females are winged, and hosts are sparsely distributed, females may mate with their siblings before they disperse from the brood place. Female biased sex ratio is common in these cases and expected under local mate competition (HAMILTON 1967; CRESPI 1991, 1993). In *S. linguis* both males and females sometimes possess "cut-off" wings and this happens during the long copulations. This may be another strategy to keep the adults at sites where their progeny are to ensure that most of the progeny survive and dispersal is negated favouring a female biased sex ratio.
Female biased sex ratios have been commonly observed in many nonsocial taxonomic insect groups, and especially in Hymenoptera (WAAGE 1982; GRIFFITH & GODFRAY 1988; COOK *et al.* 1994; ODE *et al.* 1997). The alternative hypotheses for the evolutionary cause of the female biased sex ratios in Hymenoptera proposed are: (1) local mate competition (HAMILTON 1967); (2) the resource (or host) quality hypothesis (CHARNOV *et al.* 1981); (3) presence of partial bivoltinism (WERREN & CHARNOV 1978; SEGER 1983), and (4) the presence of constrained females (GODFRAY 1988, 1990).
In haplodiploid organisms, unmated or sperm depleted females are "constrained" to produce only male progeny (FAUVERGUE *et al.* 1998). When constrained females reproduce, the population sex ratio will shift towards males and unconstrained females will be selected to produce more females. In *Aphelinus asychis*, females mated later in life produced a more female biased sex ratio (around 60 %) after mating than females mated at emergence (40-50 % females) (FAUVERGUE *et al.* 1998). These results suggest that females facultatively adjust progeny sex ratio by manipulating the proportion of inseminated eggs they lay, and progeny sex ratio is a function of the time they spend virgin.
The extent to which members of a species can modulate their sex ratio in response to local conditions is strongly influenced by the type of sex determination the species possesses (VARNDELL & GODFRAY 1996). The system that allows perhaps the greatest flexibility is haplodiploidy. Females of haplodiploid groups can determine the sex of their offspring by controlling the access of sperm to the egg. There is now abundant evidence that many haplodiploid species have adaptive sex ratio strategies that are influenced by local conditions (CHARNOV 1982; WERREN 1987).
It is not known whether or not female thrips can control the fertilization of their eggs. Knowing how the sex of the progeny of arrhenotokous reproducing females is scattered through their lifetime could help in understanding whether males dominate in the beginning of the first progeny, whether sex ratio is dependent on the time the female mated, and whether some females produce exclusively male and female progeny (split sex ratios).
Split sex ratios are expected when there is: (1) variation among females in the cost ratio of producing daughters and sons; (2) a prevalence of virgin females in haplodiploid populations, as they can produce only sons (GRAFEN 1986); (3) worker biased sex allocation in eusocial haplodiploid colonies with polygyny or polygamy (BOOMSMA & GRAFEN 1991); or (4) partial sib mating (GREFF 1996). There have been numerous studies on Hymenoptera linking split sex ratio to relatedness or asymmetries (PAMILO & SEPPÄ 1994; CHAN *et al.* 1999) but few empirical studies have linked split sex ratios to virginity (HIGGINS & MYERS 1992; GUERTIN *et al.* 1996; ODE *et al.* 1997).
Split sex ratios have been identified in only two haplodiploid species with constrained females; the parasitoid wasp, *Bracon hebetor*, due to sperm depletion (GUERTIN *et al.* 1996; ODE *et al.* 1997) and western flower thrips, *F. occidentalis*, due to virginity (HIGGINS & MYERS 1992). For both of these species, the sex ratios of mated females were significantly female biased. KRANZ *et al.* (2000) presented data indicating that split sex ratios also occur in a gall-inducing thrips and the proportion of

virgin females range from zero to 2 %. However, in the greenhouse study with *F. occidentalis* virgin females comprised up to 24 % of ovipositing females (HIGGINS & MYERS 1992).
Thrips are unable to fully control their flight patterns and are effectively aerial plankton, except at very local scales (LEWIS 1964) and within about 0.2 m from the ground. Consequently, high levels of virginity in thrips are not unexpected due to the lack of mate contact after dispersal (KRANZ *et al.* 2000).
Eusociality in galling thrips and aphids is associated with extraordinarily high levels of intragroup relatedness. In eusocial aphids this is due to parthenogenesis (STERN & FOSTER 1996), and in thrips it is largely due to inbreeding (CHAPMAN & CRESPI 1998; CHAPMAN *et al.* 2000). In both cases the taxa are minute in body size, such that their flight control is limited, therefore, it is possible that parthenogenesis and inbreeding are evolutionary responses to the risks of not being able to find a mate after dispersal. It is likely that minute body size has had an influence in setting the stage for the evolution of eusociality in these taxa.

Sex ratio of thrips is based on field collection data of adults. Such ratios are typical for local species and depend on environmental conditions (e.g. temperature, time) (BRØDSGAARD 1994a; GAUM *et al.* 1994; RIJN *et al.* 1995; TSAI *et al.* 1995; MURAI 2000). CRESPI (1988a) found in *Elaphrothrips tuberculatus* that the ratio varies from almost 1 : 1 to strongly females biased throughout the year dependent on seasonal variation.
There seem to be geographical differences in the occurrence of males in different populations of the same species. *Thrips tabaci* is cosmopolitan, but males are absent or rare throughout much of its geographical range. Large numbers of *T. tabaci* males have only been collected in the eastern Mediterranean where its primary host, *Allium*, is native (MOUND 1992). Although males of *Aptinothrips rufus* are sometimes common in Europe, they are rare throughout most of its distribution in the temperate parts of the world, for example, absent from Illinois (STANNARD 1968); three males and 682 females recorded from New Zealand (MOUND & WALKER 1982).
Data known about the sex ratio in thrips (LEWIS 1973) suggest that the sex ratio of thrips species is usually female biased. Most thrips species probably live as relatively isolated groups and presumably it is this small local population size which helps drive the sex ratio its female bias (CHARNOV 1982), particularly if females mate before dispersal.
CRESPI (1988a) found evidence for the adjustment of sex ratios by females in *E. tuberculatus*. In this species a female will lay male-producing eggs only if there is a high probability that the resulting progeny will have a large brood size. Unfavourable environmental conditions result in a small number of progeny, then females lay female-producing, i.e., fertilized eggs. In *E. tuberculatus* each batch of eggs consists of only one sex. The extent to which females control sex allocation in this species and in the order of Thysanoptera is not understood.
In several thrips species, the sex ratios are known to vary between localities (OLSEN 1984). Attempts have been made to correlate geographical differences in sex ratios of thrips species with the prevailing meteorological conditions. One example was recorded by LEWIS (1973) where males become scarce with increasing air temperature. This is supported by MORISON (1957) who found that males of *T. tabaci* have never been recorded in greenhouses, but have been found in outdoor populations with cooler temperatures. Nevertheless, in the warm climate of Iran, *T. tabaci* has the sex ratio 1 : 1, and much lower ratios have been recorded on other, often colder, parts of the world (OLSEN 1984).
The results in this study show that *F. occidentalis* sex ratio is regulated by temperature reacting with a more female biased ratio with increasing temperature.
CHARNOV (1982) stated that competition for resources or a mate is the key-factor for the observed sex ratios, but its effect on the sex ratio may be quite different depending on the life history of the species

and the degree of crowding.
Intraspecific variation in the reproductive strategies of aphids can encompass obligate parthenogenesis, parthenogenesis with male production, facultative parthenogenesis, or obligate sexuality with intervening parthenogenetic generations (SIMON *et al.* 1999). Changes in climate and effects of gene flow between aphids of different life cycles are the predominant factors mediating the balance between sex and parthenogenesis. Parthenogenesis will be favoured when freezing conditions are rare, but will be replaced by sexual aphids in colder climates.
In contrast to their Asian and European counterparts, *Sitobion miscanthi* and *S. near fragariae* aphids in Australia exhibit a complete absence of sexual reproduction. The absence of sexual reproduction may be explained by a combination of environmental conditions that permit the survival during the whole year of parthenogenetic lineages and selection against sexual reproduction in a relatively stable environment (WILSON *et al.* 1999).
The common yellow dung fly *Scatophaga stercoraria* has overlapping generations (GIBBONS 1987) and adult males have a greater mortality under high temperatures than do females (WARD & SIMMONS 1990). Therefore, the summer months may result in a temporary lack of males in the population. A previous study has shown some evidence for male biased sex ratios in this species associated with prolonged sperm storage in the females (STOCKLEY & SIMMONS 1998). Although sex in some dipterans is chromosomally determined (WERREN & BEUKEBOOM 1998), evidence suggests that there is a potential mechanism, at least in scale insects, by which females could skew their offspring sex ratio (SEAL 2000). The mechanisms underlying the more female biased sex ratio at increasing temperature proofed in *F. occidentalis* are not known yet.
In additional tests unmated *F. occidentalis* females produced mostly male progeny but a few females hatched from unfertilized eggs at different temperatures (15 °C, 23 °C, 30 °C). Ian Dadura‘s (University of Perth, Australia) investigations of *F. occidentalis* examined in Australia coincide with these results (personal communication, 1999). *E. americanus* did not produce any females from unfertilized eggs at any temperatures tested. Virgin females of *Apterothrips apteris* can produce both sexes (MOUND 1992). However, no data on the number of female individuals produced by virgin females was recorded. The cytological mechanisms involved in sex determination in thrips species are not yet understood. In addition, it is not known whether females produced in this manner can reproduce and if so, what sex the progeny possesses. BANDARA & WALTER (1993) examined *Spalangia endius* (Hymenoptera), a parasitoid of house fly puparia, which is usually arrhenotokous. They discovered that some virgin females also produce female offspring, however the limited evidence available suggests this ability is not transmitted to subsequent generations.
It is possible that there is an error taking place during the meiosis in females so that diploid females are produced and the cytological mechanism underlying this “accident“ is not known.

4.1.2. Copulation behaviour

The copulation in *F. occidentalis* is very short and takes only a few minutes. *S. linguis* has extreme long copulation times and has been observed to last several hours. Sperm transfer was not determined during these copulations.
Duration of copulation varies among species of Thysanoptera. Among Terebrantia, average copulation times range from 3 to 15 min (LEWIS 1973; KIRK 1985a). Some Thripidae copulate for a long time; more than 60 min has been observed in *A. apteris* with an average of 35 min (STRAUSS & KARBAN 1995).

F. occidentalis pairs were tested in the laboratory in the absence of other males or females. Successful copulations lasted from 114 to 595 s, with an average of 240 s (TERRY & SCHNEIDER 1993). Females that mated for less than 69 s produced only male offspring, suggesting that no insemination takes place during shorter copulation times.

Among Tubulifera, some very brief copulation times have been observed. *Hoplothrips pedicularius* matings last from 7 to 70 s with an average of 26.3 s, and those of *Hoplothrips karnyi* range from 8 to 42 s with 19.2 s average (CRESPI 1986a, 1988b). Some idolothripines copulate for 3 to 15 min (ANANTHAKRISHNAN 1984).

There are many reasons why natural selection on both sexes should favour brief matings (DALY 1978). Long copulations can be energetically expensive, and may increase the risk of predation and the likelihood of an interruption before the transfer of the sperm is finished. Despite the above described selective factors, copulation duration is very long in many damselflies, reaching five to six hours in some *Ischnura* species (Zygoptera) (ROBERTSON 1985; CORDERO 1990; SAWADA 1995). Very long copulation times were also observed in *S. linguis* taking up to several hours.

Long copulations might be suggest sexual selection favouring male adaptations, for instance, to avoid sperm competition (PARKER 1970). Prolonged copulations could reduce sperm competition with future ejaculates if the male's body acts as a mating plug that prevents the female from remating before oviposition (ALCOCK 1994). Long copulations could also reduce competition with previous ejaculates if males inseminate more sperm (CORDERO 1990) or spend longer removing the sperm of their rivals. These two mechanisms assume that copulation is at least partly under male control and is probably based on the benefits that males obtain by prolonged copulations.

However, females might also influence male copulatory behaviour. A recent hypothesis postulates that females show a form of postcopulatory sexual selection by favouring some males over others (cryptic female choice-hypothesis, EBERHARD 1996). Thus, long copulations could serve to influence cryptic female choice mechanisms (EBERHARD 1996). Distinguishing between sperm competition and cryptic female choice might be difficult in some cases.

DANIELSON (1998) pointed out that prolonged copulation (copulation that continues after completed insemination) functions more or less in the same way as mating plugs, i.e. to block the female tract. Also, mate guarding prevents the female from remating, but without maintaining genital contact. The male pays a high price for the extra time spent on prolonged copulation or mate guarding, in terms of reduced time for mate searching. Mating plugs, on the other hand, are expensive in terms of energy, but after the copulation the male is free to search for new partners. Post-insemination associations are expected to evolve when the fitness benefits for males remaining with their mate exceed the cost in terms of lost mating opportunities (PARKER 1970).

A female refractory period, i.e. non-receptive time after copulation, is often induced by sperm or seminal products inseminated by the male (EBERHARD 1996). Males may in this way manipulate the female to reduce the risk of sperm competition. Males can also make the female less attractive by reducing her output of pheromones or by applying antiaphrodisiac substances that reduce her attractiveness (KUKUK 1985; EBERHARD 1996).

Females of *F. occidentalis* mate with a male and then retract following copulation attempts by males. TERRY (1997) observed the same behaviour in *F. occidentalis*. The reasons leading to this kind of behaviour in *F. occidentalis* are not understood.

S. linguis represents a subsocial lifestyle (MORITZ *et al.* 1998; SCHÄFER 1998). Data on copulation and oviposition behaviour of this species are rarely known and determining whether females mate several times or reject repeated matings as in *F. occidentalis* would be interesting. This knowledge helps to evaluate the social lifestyle and the evolution of sociality in thrips.

Several studies about the mating behaviour of tubuliferan species exist, which have long-lived hosts and stable habitats (KIESTER & STRATES 1984; CRESPI 1986a,b, 1988a,b, 1990, 1993). The habitat stability relative to the generation time of Tubulifera (in some species more than one generation per host) promote a more colonial or subsocial lifestyle (EVANS 1977), which includes cooperation in caring for young, overlap of at least two generations to contribute to colony labour, and reproductive division of labour. Studies by KIESTER & STRATES (1984) and CRESPI (1990, 1992a) exhibit some of these traits in Tubulifera. The tubuliferan species *S. linguis*, examined in this study, also possesses a social lifestyle. Among the Tubulifera there is a great diversity of feeding preferences and habitats, morphology and degree of wing development, and mating behaviour. Their mating systems are complex, comprising alternative male mating tactics, male territoriality, maternal care, oviparity or viviparity depending upon the species, environment, and sometimes sexual mating (CRESPI 1986a, b, 1988a, b, 1993).

Some fungus-feeding species have communal oviposition sites (*H. karnyi*, *H. pedicularius*, and *Sporothrips amplus*; CRESPI 1986a, 1993) where many females of the colony lay their eggs. Males of these species have enlarged fore legs which they use to fight other males in defence of territories consisting of the oviposition sites.

There is a trade-off in wingedness and fore leg size and an association of morphology with alternative male tactics (CRESPI 1988c). Apterous males have large legs with which they defend oviposition sites; small legged, alate males disperse to new sites searching for other colonies either already established or those being found. Small males avoid fights and mate by sneak mating. Large dominant males perform most of the matings (about 80 %) (CRESPI 1986a, 1988b). Other species, such as *Anactinothrips gustaviae* (KIESTER & STRATES 1984), are colonial or parasocial and have communal oviposition sites and males with enlarged fore legs. The females of some species, such as *E. tuberculatus* (CRESPI 1986b, 1990), have individual oviposition sites and guard their clutch of eggs until hatching. Males of this species guard and fight over the individual egg-guarding females. Large, non-guarding males challenge the guarding males. Small non-guarding patrolling males copulate with females by sneak mating. In *S. linguis* no fighting individuals could be observed and no morphological difference in the fore legs was detected.

Aggregations are common in Thysanoptera (ANANTHAKRISHNAN 1984), including Terebrantia. Three British Thripidae, *Thrips fuscipennis* and *Taeniothrips major* and a few *Thrips atratus*, aggregate and mate on flowers of *Calytegia sepium*, and dispersal to and from these sites occurs throughout the day (KIRK 1985a). No aggressiveness among males or females was observed and most females did not mate a second time, disappearing within a few minutes. These thrips were primarily engaged in mating and there was no aggression or oviposition at these specific sites. This is similar to a lek-type mating behaviour (CRESPI 1993).

Similar aggregation behaviour has been observed in *F. occidentalis* (TERRY & GARDENER 1990; TERRY & DYRESON 1996). *F. occidentalis* male aggregations have been observed on coloured or white surfaces similar to flowers and also on many flowers (TERRY & GARDNER 1990; MATTESON & TERRY 1992; TERRY & DYRESON 1996). Males aggregate at these sites throughout the day and patrol the blossoms. Almost all females that enter the aggregations mate and disperse immediately after mating. Females generally mated with the first male they encountered within the aggregation and then refused most other males (TERRY & DYRESON 1996). Females generally reject males for many days after mating, therefore, there is a strong selection on *F. occidentalis* males to be the first to mate (TERRY & SCHNEIDER 1993).

Both tubuliferan and terebrantian males are promiscuous (LEWIS 1973; STRAUSS & KARBAM 1994a,b), but few studies have documented the mating frequencies and success of individuals. Adults of

Thysanoptera generally mate within two to three days of eclosion from the pupal stage (LEWIS 1973), some males mate within six hours of eclosion. Tubuliferan males, *H. pedicularius*, *E. tuberculatus*, and *H. karnyi*, all mate several times with ovipositing females, some preferentially with females that have not yet oviposited (CRESPI 1986a, 1988b). Male *F. occidentalis* can mate in the first 24 hours after eclosion and throughout their life (TERRY & SCHNEIDER 1993) with only a slight decline in activity with age. In *Thrips palmi*, the male precopulatory period lasts six hours after eclosion (WANG & CHU 1990). Females vary greatly in their mating frequency. Several sporophagous/mycophagous tubuliferan females, *H. pedicularius*, *E. tuberculatus*, and *H. karnyi*, mate up to four times with the same guarding male prior to ovipositing (CRESPI 1986a, 1988b). Females were never observed rejecting males (CRESPI 1988b). *F. occidentalis* females can successfully mate within 12 h of eclosion and refuse males for more than five days after the initial mating (TERRY & SCHNEIDER 1993). Because males mate frequently and females are receptive infrequently, there is strong selection for males to find and mate with virgin females (TERRY & SCHNEIDER 1993). WANG & CHU (1990) found that *T. palmi* females mated immediately after eclosion, but only produced male eggs on the first two days, and subsequently produced mixed sexes thereafter.

Mating experiments with *Ischnura senegalensis* (Zygoptera) revealed that the sperm precedence of the last male to mate was nearly 100 % two days after copulation, regardless of copulation duration (SAWADA 1998). The interval between copulations in a female was about 2.3 days suggesting that the last male to mate gains advantages in sperm precedence regardless of the copulation duration. Complete sperm mixing (the point when the sperm precedence of the last male to mate was 50 %) occurred six days after copulation.

Currently, it is not known if sperm from more than one male is stored in the spermatheca examined in this study. The female terebrantian species *F. occidentalis* and *E. americanus* show one spermatophore within the spermatheca and is presumed to be from one male. Spermathecae containing several spermatophores were not observed. Sperm in the spermatheca of *S. linguis* is loosely arranged and the sperm origin could not be traced to a single or many males.

4.1.3. Oviposition behaviour

Morphological ovipositor characteristics clearly distinguish the two suborders of Thysanoptera. Terebrantian females have a well-developed ovipositor composed of a basal apparatus and a shaft. The ovipositor is curved upwards in Aeolothripidae and downwards in most other Terebrantia (HEMING 1970a; BODE 1975; MORITZ 1982d, 1989d, 1997). The ovipositor of Terebrantia is used to pierce plant tissue and deposit the egg, whereas tubuliferan ovipositors are reduced to a U-shaped chute (HEMING 1995) and eggs are laid on the surface of the substrate (LEWIS 1973). Terebrantian lay eggs singly into plant tissue but Tubulifera may lay clusters of eggs at oviposition sites that in some species are guarded by males or females. In *S. linguis*, observed in this study, the females lay eggs on different places on the plant but then transport them by pushing the eggs with their legs to a single batch. Eggs are protected at the ground of the *Sansevieria trifasciata* plant and males and females of this species guard the eggs.

A few tubuliferan species are known to have fighting males and egg guarding. Males of *H. karnyi*, a colonial fungus-feeding thrips, fight each other in defence of communal egg mass sites, where they mate with females that come to oviposit (CRESPI 1988b). CRESPI (1988b) discovered that fighting males stab each other with their enlarged, armed forelegs and strike each other with their abdomens.

Escalated fights occur between the large males of similar size and fights are often lethal with large males tending to win fights and guard egg masses and securing about 80 % of last matings with females prior to oviposition.

A. gustaviae is an advanced parasocial thrips (Phlaeothripidae: Idolothripinae) from Panama which lives in colonies on smooth barked trees, reproduces communally, and forages (KIESTER & STRATES 1984). Although this species is presumably haplodiploid, the patchy food supply is probably the primary factor which has promoted the evolution of advanced social behaviours in this species as opposed to most other thrips (MOUND & PALMER 1983a; KIESTER & STRATES 1984).

S. linguis also feeds on fungi which is not detectable on *Sansevieria trifasciata* without the thrips. Adults or postembryonic stages kept singly on a plant or leaf died in all cases. Adults of a group size of seven individuals stayed together and larvae added to the group could survive (SCHÄFER 1998). Females started to lay eggs between 14 and 18 days remaining together as a group. The availability of food is probably also in this species the primary factor which supported the development of a subsocial lifestyle.

Adults of many species defend or provision their young (TALLAMY & WOOD 1986). Parental care occurs in a number of orders like the eusocial Hymenoptera, Isoptera, and in the Homoptera (WOOD & DOWELL 1985).

Parental care is generally considered an adaptation to harsh conditions which could substantially decrease the survivorship of offspring where unprotected (CRESPI 1990). However, the selective pressure responsible for the origin and maintenance of parental behaviour is not well understood. Detecting and measuring selection on parental behaviour traits is important for the study of the evolution of social behaviour and contribution of these behavioural traits form a basis for analysing social evolution (CRESPI 1990).

The genetic asymmetries of hymenopteran haplodiploidy are sometimes regarded as causal in the evolution of sociality, because female helpers are more closely related to full sisters than to their own offspring (HAMILTON 1972). However, the Hymenoptera also exhibit a constellation of ecological and behavioural traits that may favour a high prevalence of simple parental care, nesting in protected locations, ability to build and improve nests, and the spectacular opportunities for defending afforded by the sting (HAMILTON 1972; ANDERSON 1984).

The Thysanoptera are haplodiploid, exhibit a wide variety of life histories, and show a wide range of social interactions, thus, offering a unique opportunity to study the contributions of genetic asymmetries and other variables to social behaviour. Egg defence, generally by adult females, has been reported in thrips by MANI & RAO (1950), ANANTHAKRISHNAN (1984), and KIESTER & STRATES (1984). Moreover, CRESPI (1986a, 1988b) reported that in two species of *Hoplothrips* females oviposit communally, and KIESTER & STRATES (1984) described the behaviour of a species of *Anactinothrips* exhibiting coordinated group foraging behaviour. These data suggest that the order Thysanoptera comprises species with complex social organization, such that they may provide insights into the evolution of sociality.

In *Elaphrothrips* (CRESPI 1986b) females oviposit and guard their eggs in sheltered locations on the leaf clusters, such as in curled areas of leaf or between leaves juxtaposed closely. Guarding females stand over their egg masses and curl the end of their abdomens toward approaching threats. Certain threats, such as the tips of fine forceps, approaching within a few millimetres of a guarding female, induces the female to produce a drop of brown fluid from the end of her abdomen, which is held on the anal setae. This drop, which contains the toxic chemical juglone, is deposited on the approaching threat with a quick movement of the abdomen (CRESPI 1986b).

Terebrantia will oviposit into most plant tissues, although some species have preferred plant tissue sites. *Thrips calcaratus* push their ovipositor into the sides of the main veins on the underneath side of the leaf of American basswood (RAFFA *et al.* 1992). Others scatter their eggs on various floral and vegetative tissue, depending upon the plant species and phenological stage.
Terebrantian eggs are embedded into tissue with their long axis at a shallow angel to the surface or a steeper angle of 30 to 45 ° (LEWIS 1973). In many cases oviposition causes direct damage to the plant, usually a cosmetic blemish but nevertheless an economic loss to producers of many crops (CHILDERS & ACHOR 1995). Eggs of Terebrantia not completely covered could die because of low humidity and are subject to predation as found in *Megalurothrips sjostedti* (TAMO *et al.* 1993). The time required to oviposit completely usually takes a few minutes and females either feed or rest after laying each egg (LEWIS 1973).
Tubulifera lay eggs in a variety of places depending upon the species. Gall-inhabitants generally lay inside the gall wall, others glue the eggs to the walls (VARADARASAN & ANANTHAKRISHNAN 1981; SOTA 1988; CRESPI 1992a). Tubulifera that feed on fungi lay their eggs near the fungal hosts, under bark, in bark crevices, or on old leaves (TERRY 1997).

Numerous studies on life table parameters including adult longevity and reproductive parameters (e.g. egg number per day) exist mainly on terebrantian species, which are pests in a lot of crops (SRIVASTAVA *et al.* 1986; TRICHILO & LEIGH 1988; MALCHAU 1991; TEULON & PENMAN 1991; GAUM *et al.* 1994; TSAI *et al.* 1995; HODDLE *et al.* 2000).
The mean life expectancy of *F. occidentalis* females was found to be 9.8 ± 6.5 days. The oldest female became 32 days. LEWIS (1997) stated that adults of thrips survive for an average of 10 to 30 days. LUBLINKHOF & FORSTER (1977) reported adult longevity for *F. occidentalis* depended on different temperatures with the longevity of adults decreasing with increasing temperatures. Mean life for adults in the laboratory was 56.8 days at 20 °C. RIJN *et al.* (1995) reported a mean life span of the adult being 20.5 days.
F. occidentalis start to lay eggs approximately 24 h after they emerge as adults. Fecundity started with low values per time unit but rose rapidly to a peak, from where it gradually declined again. The same results were obtained by GAUM *et al.* (1994), RIJN *et al.* (1995), and TRICHILO & LEIGH (1988).
Adults of *S. linguis* appeared to live longer than the observed individuals of *F. occidentalis*. Unfortunately, the exact hatching date of adult S. linguis was not determined, but some individuals were observed to live longer than 40 days.
Females of *F. occidentalis* laid on average 75.6 eggs during their entire lifetime and approximately 4.9 eggs per day. The number of eggs a single female of *S. linguis* lays during her entire life could not be determined, however, it is known that when they are in an egg-laying period they probably lay three to four eggs per day. *S. linguis* adjust the time when they lay eggs within the first two to three weeks of a new group establishment, when none of the female oviposited. This was reported in all new groups. Thus, females of *S. linguis* must be able to adjust their oviposition behaviour to environmental or group conditions.
LEWIS (1997) pointed out that individual females of thrips lay between 30 and 300 eggs during their lifetime depending on the species and quality of food. LUBLINKHOF & FORSTER (1977) found that *F. occidentalis* lays 95.5 eggs on average at 20 °C. The number decreased to 24 laid at 15 °C and to 43.8 at 30 °C indicating that the optimal temperature for reaching high fecundity is about 20 °C. BRØDSGAARD (1994a) showed that the mean preoviposition period and fertility did not differ among different day lengths. Furthermore, this study showed that short day length at 25 °C reduced reproductive fitness of *F. occidentalis*, but did not induce reproductive diapause in this species.

4.1.4. Morphology of inner and outer genitalia of females and males

1. Morphology of outer female reproductive organs

The general structure of the ovipositor as observed in *F. occidentalis* and *E. americanus* is common throughout the suborder Terebrantia (HEMING 1970a; BODE 1975; MORITZ 1982d, 1989d, 1997), except in the family Merothripidae where the ovipositor is less well developed (HEMING 1970a; BODE 1975). The ovipositor of Terebrantia resembles that of the species Thysanura, Dermaptera, Zoraptera, Hemiptera, and Hymenoptera in having first and second but no third valvulae (HEMING 1970a) and is most similar to the auchenorrhynchous Homoptera (KUNZE 1959; HELMS 1968).

The small ovipositor of *S. linguis* and other Tubulifera (HEMING 1970a) appears to be unique, forming kind of a chute (or funnel) rather than presenting a piercing organ. Thus, the valvular ovipositor of terebrantian thrips is absent in the adult of *S. linguis* and other phlaeothripids but was possibly present in some phlaeothripid progenitor, since there are developmental vestiges of them in the preimaginal instars of this species (the proliferation of the ventral epidermis in segment IX in the propupal stage and the paired origins of the ovipositor on the eighth sternum during the first pupal stage) (HEMING 1970a). Most modern phlaeothripid species live under the bark of living or dead trees, in fungi, or in forest litter (MOUND 1997) and a piercing ovipositor would be of little advantage in these environments.

2. Morphology of inner female organs

The number of ovarioles in an ovary varies in relation to size and lifestyle of the insect as well as its taxonomic position. In general, larger species within a group have more ovarioles than small ones, thus small grasshoppers commonly have only four ovarioles in each ovary, while larger ones may have more than 100 (CHAPMAN 1998). Similarly, in Diptera, *Drosophila* has 10 to 30 ovarioles in each ovary, whereas Calliphora has about 100. Most Lepidoptera have four ovarioles on each side regardless of their body size. All examined thrips species possess four ovarioles in each ovary (e.g. HEMING 1970a; MORITZ 1989d, 1997) and this is believed to be a common feature of the Thysanoptera.

Two basic categories of insect ovarioles are traditionally recognized, panoistic and meroistic (BÜNING 1994, 1996). In the panoistic ovarioles, all oogonia are transformed into functional gametes (oocytes), whereas in the meroistic ones some germ cells differentiate into often polyploid nurse cells (trophocytes) that supply the oocytes with macromolecules (e.g. rRNA, mRNA) and organelles during the previtellogenic growth. The spatial organization of the ovarioles and relationship between the oocytes and nurse cells allow the subdivision of meroistic ovarioles into two groups: polytrophic and telotrophic. In the polytrophic ovarioles, each oocyte is accompanied by its own group of nurse cells. Such oocyte-nurse cell complexes are invested with somatic (follicular) cells and constitute the functional units, termed egg chambers (ovarian follicles). In the telotrophic ones, all trophocytes are retained in the apical part of the ovariole thereby forming a trophic chamber (tropharium). The contact of growing oocytes with the distant tropharium is ensured by elongated cytoplasmic extensions, referred to as trophic cords (WEBER 1954; GULLAN & CRANSTON 1994; CHAPMAN 1998).

Panoistic ovarioles, which have no specialized nurse cells, are found in the more primitive orders of insects, the Thysanura, Odonata, Plecoptera, Orthoptera, and Isoptera. Among the holometabolous insects, only Siphonaptera have ovarioles of this type (BILIŃSKI & BÜNING 1998).

Telotrophic ovarioles are found in Hemiptera, Coleoptera, Rhaphidioptera, and Megaloptera (GOTTANKA & BÜNING 1993).

Among the primitive insect orders, only the Dermaptera are known to have polytrophic meroistic ovaries (YAMAUCHI & YOSHITAKE 1982) whilst all others are believed to be panoistic (TELFER 1975). Besides,

Ephemeroptera (mayflies) have been found to possess telotrophic meroistic ovaries, albeit of a very primitive type. In all developmental stages investigated, they found germline cells connected to other germline cells by intercellular bridges (GOTTANKA & BÜNING 1993).
Polytrophic ovarioles occur in Dermaptera, Psocoptera, Phthiraptera and throughout the holometabolous orders, except for the most Coleoptera and the Siphonaptera (CHAPMAN 1998).
The distribution of ovary types among various insect groups suggest that: (1) polytrophic meroistic ovaries evolved twice from panoistic ones: once in Entognatha (BILIŃSKI 1983, 1993; BILIŃSKI & SZKLARZEWICZ 1992), once in the common ancestor of Dermaptera and Eumetabola (ŜTYS & BILIŃSKI 1990; BÜNING 1994, 1996); (2) telotrophic ovaries represent the most advanced and specialized category that evolved independently four times: in Hemiptera, Coleoptera (Polyphaga), Rhaphidioptera, and Megaloptera (Sialidae) from a polytrophic background and in Ephemeroptera directly from a panoistic one (BÜNING 1994, 1996); (3) in some advanced taxa secondary panoistic ovaries evolved (by the loss of nurse cells) from meroistic ones (ŜTYS & BILIŃSKI 1990; BÜNING 1994). To indicate the evolutionary distinctness of such reduced ovaries from the primary panoistic ones, ŜTYS & BILIŃSKI (1990) have proposed the term neopanoism.
Among the hexapods secondary panoistic (neopanoistic) ovarioles evolved independently five times: in proturans (BILIŃSKI 1993) and in four taxa of true ectognathous insects: Thysanoptera (PRITSCH & BÜNING 1989; TSUTSUMI *et al.* 1995), Megaloptera (Sialidae and Chauliodidae) (BÜNING 1996), Siphonoptera (BÜNING & SOHST 1988) and Mecoptera (Boreidae) (BÜNING 1994). The ontogenetic development of such reduced ovarioles has been traced to date only in Thysanoptera. According to PRITSCH & BÜNING (1989), germaria of terebrantian thrips, *P. dracaenae*, contain germ cell clusters similar to those characteristic of meroistic ovarioles. All cells of the cluster develop into oocytes, become individual and migrate to the vitellarium.

An ovariole consists of different zones (terminal filament, germarium and vitellarium) (WEBER 1954) and the number of oocytes within the ovarioles of different thrips species was determined in this study. *A. intermedius* (Aeolothripidae) contains 11.3 ± 0.7 oocytes per ovariole or vitellarium, respectively, whereas *F. occidentalis* (Thripidae) had 8.6 ± 0.8, *E. americanus* (Thripidae) 5.9 ± 0.2, and *S. linguis* (Phlaeothripidae) 4.5 ± 0.3 oocytes per ovariole. These findings indicate that the number of oocytes within the vitellarium varies between different thrips species.
S. linguis had the lowest number of oocytes and was the only thrips examined with a subsocial lifestyle. Adult individuals of *S. linguis* take care of their young reducing the mortality and may be the reason for reduced oocyte number. In contrast, *A. intermedius* and *F. occidentalis* possess relatively high numbers of oocytes within the vitellarium. *A. intermedius* (predator: PATRZICH & KLUMPP 1991; KHOSBAYA 1999) and *F. occidentalis* (pest species: BRYAN & SMITH 1956; YUDIN *et al.* 1986; MANTEL & VAN DE VRIE 1988; BRØDSGAARD 1994a; RIJN *et al.* 1995) produce as many progeny as possible. They do not invest in taking care of their progeny which suggests a higher mortality, although, metamorphic stages of *A. intermedius* produce a cocoon which is an energetically intensive process that probably ensures a better survival rate for *A. intermedius*.
Confirming the data from this study, MORITZ (1982d) also found a high number of oocytes (13-14) in *A. intermedius* (Aeolothripidae). The number of oocytes varies within the Thripidae ranging from two to four in *A. rufus* (SHARGA 1933) to four to five in *H. femoralis* (SHARGA 1933) and 5.9 ± 0.2 in *E. americanus* to 8.6 ± 0.8 in *F. occidentalis* determined in this study. In the Phlaeothripidae HAGA (1975) found 10-14 oocytes per ovariole in *Bactrothrips brevitubus*. *S. linguis* has, compared with this, a low number of oocytes (4.5 ± 0.3).
DHILEEPAN & ANANTHAKRISHNAN (1987) studied five species of sporophagous Tubulifera and found that

the number of oogonial cells and the previtellogenic oocytes does not differ among polymorphic ovaries. Interestingly, the number of vitellogenic oocytes in each ovary is higher (10-12/ovary) in oviparous forms, comparatively less (6-9/ovary) in ovoviviparous forms and are lacking in the viviparous ovaries. Mature ova are evident only in oviparous forms (3-4/ovary). The number of embryos undergoing development in each lateral oviduct is higher in viviparous ovaries (10-12/each lateral oviduct) than in ovoviviparous ovaries (6-10/each lateral oviduct).

This is further evidence that the number of oocytes per ovariole (vitellarium) depends on the reproduction ecology of the insect. Five different species from the same family (Phlaeothripidae) were examined and considerable differences in their number of oocytes was determined (DHILEEPAN & ANANTHAKRISHNAN 1987).

SZKLARZEWICZ (1998a) found different numbers of germ cells (oocytes plus trophocytes) within the coccoids (Coccinae, Hemiptera) in relation to the phylogeny of this group. The ovaries of coccoids consist of numerous short telotrophic-meroistic ovarioles. The ovarioles of all investigated species share common characters (e.g. the same mechanism of ovariole development, lack of terminal filaments, occurrence of single oocytes in the vitellaria) supporting the concept of monophyletic origin of this group. Despite these characteristics, the ovaries of archaeococcoids and neococcoids differ in the number of germ cells in a single ovariole. In primitive families (Ortheziidae, Margarodidae), this number is relatively large (15-58), whereas in advanced ones (Pseudococcidae, Kermesidae, Eriococcidae, Cryptococcidae, Coccidae, Diaspididae) it is small and usually does not exceed eight. Therefore, SZKLARZEWICZ (1998a) concluded that during the evolution of Coccinea a gradual reduction in the number of germ cells in ovarioles took place.

The high number of oocytes per cluster (ovariole) in representatives of primitive scale insects (ranging from 5 to 29) and the reduced number in advanced families (often reduced to one) (SZKLARZEWICZ & BILIŃSKI 1995; SZKLARZEWICZ 1997, 1998b, c) is associated with the dramatic increase in the number of ovarioles per ovary and in some species the latter number may exceed 200 or 300 (SZKLARZEWICZ 1998b, c). In contrast, the ovaries of aphids consist of only five or six ovarioles that comprise numerous oocytes (BÜNING 1985) and in the Thysanoptera, the number of ovarioles per ovary is constant throughout the order.

Spermatheca:

Within the insects the form, arrangement, and number of spermathecae is quite diverse (CHAPMAN 1998; LAY *et al.* 1999).

The spermathecae of insects are, depending on the species, differently shaped attachments of the female gonoduct. They serve for the uptake and storage of the spermatozoa, which are transferred during mating and released to fertilize the egg cells. The transfer of the sperm can either be achieved directly (e.g. as in *Drosophila*) with the aid of a sperm pump, or indirectly through a spermatophore, whose structure varies from the simple sperm packet to the complicated tubular-formed extension of the aedeagus, and both received by the spermatheca (CHAPMAN 1998).

Terebrantia (*F. occidentalis* and *E. americanus*) and Tubulifera (*S. linguis*), examined in this study, both possess a single spermatheca.

BOURNIER (1956a) was the first who established the hypothesis about the presence of a spermatophore in female terebrantian thrips. BODE (1975) tried to find electron microscopic evidence to confirm this theory but could not detect if the spermatophore is built in the male (true spermatophore) or in the female.

It seems to be quite impossible that a spermatophore with a diameter of 15 µm could pass the valve being just 1 µm thick (BODE 1975). Besides, spermatophore-like structures have never been discovered

in males (HEMING 1970a; BODE 1975). These are arguments against the presence of real spermatophores in terebrantian thrips species.
LISKIEWICZ (1960) provided evidence that the spermatophore is brought in the vagina. He found structures in *Chirothrips manicatus* males which, he thought, were spermatophores, however, differing from the typical spermatophore-shape found in the spermatheca of the female. These structures were pear-shaped having a filament on one side. Size and shape of the "spermatophore" let assume that they are brought in the vagina. There the gelatinous wall material becomes dissolved (totally or partially) and the sperm with the surrounding solution is taken up by the spermatheca. Some secret is already in the spermatheca and when it comes in contact with the sperm it forms a sheath around the sperm. If this would truly happen then the spermatophore in thrips is not a real spermatophore since it is formed in the body of the female. A similar process was described by KLIER (1956) for *Trogium pulsatorium* (Psocoptera).
In thrips species who do not construct or differentiate a spermatophore the sperm is transported directly to the spermatheca by the aedeagus of the male. DEL-BENE *et al.* (1998) determined the absence of a spermatheca in *H. haemorrhoidalis* (Thripidae) based on histological serial sections through the vagina. Thus, *H. haemorrhoidalis* is the first thrips species observed with no spermatheca.
Several spermatophores in the spermatheca of terebrantian species could indicate repeated matings. In *F. occidentalis* and *E. americanus* no females were found containing more than one spermatophore in their spermatheca in this study. BOURNIER (1956a) reports that in *Sericothrips staphylinus* (Thripidae) the spermatheca is much larger than in other Thripidae observed and contains many spermatophores, some are broken and empty of sperm. Thus, it is evident that the female in this species mates successfully several times. *F. occidentalis* and *E. americanus* copulation appears to occur only once due to the presence of only one spermatophore unless there is some mechanism present in the spermatheca which destroys the spermatophore after its contents have been exhausted.
Spermatophores are produced by the males of at least some species of Collembola, Diplura, Thysanura, Orthoptera, Dictyoptera, Hemiptera, Psocoptera, Mallophaga, Anoplura, Neuroptera, Trichoptera, Lepidoptera, Hymenoptera, and Coleoptera, but vary greatly in their structure, in the method of formation, in the position of the female genital system, and in the manner in which they release their spermatozoa. Only in the Anoplura (MURKERJI & SARMA 1951), Psocoptera (KLIER 1956) and Thysanoptera (*Frankliniella fusca*) (HEMING 1970b) is the spermatophore situated in the spermatheca of the female. This also occurs in *F. occidentalis* and *E. americanus* observed in this study. It is interesting to note here that the Anoplura, Psocoptera and Thysanoptera are within the hemipteroid group (STANNARD 1957).

Accessory gland:
The reproductive tract of female insects typically includes paired accessory glands, whose function varies (HOSKEN & WARD 1999). Accessory reproductive glands produce oviposition pheromone secretions which coat and fasten eggs to laying substrates and provide lubrication and/or egg protection. In *Musca domestica* (Diptera) accessory gland secretion are moved with spermatozoa to the fertilization chamber, where they aid micropyle cap removal allowing fertilization to take place (LEOPOLD & DEGRUGILLIER 1973; LEOPOLD *et al.* 1978). In addition, VILLAVASO (1975) demonstrated that the accessory reproductive glands contribute to the maintenance of sperm motility and DALLAI (1975) and HUEBNER (1980) provide evidence for the maintenance of special ionic milieu in association with the entire spermathecal epithelium. Sperm-attracting effects were demonstrated by VILLAVASO (1975) and a partial degradation of the spermatophore was detected in these secretions (HARTMANN 1978).
The fact that an accessory gland is present only in those thrips having a valvular ovipositor (HEMING

1970a), provides evidence that it functions during oviposition and may produce a secretion dissolving the plant cell walls, making it easier for the female to insert her eggs or provide a lubricant aiding in the passage of eggs between the ovipositor valves.
The fact that female Thripidae have a single accessory gland provides relatedness to Mallophaga, which also has a single female accessory gland (DALLAI *et al.* 1995).

3. Morphology of outer male reproductive organs
There is considerable variation in structure and terminology of the genitalia of males in different orders (CHAPMAN 1998) and the difficulties in homologizing the different structures are outlined by SCUDDER (1971). According to CHAPMAN (1998) the basic elements are derived from a pair of primary phallic lobes. These phallic lobes divide to form an inner pair of mesomeres and an outer parameres, collectively known as the phallomeres. The mesomeres unit to form the aedeagus, the intromittent organ. The parameres develop into claspers, which vary in form and may be attached to the aedeagus on a common base, the phallobase. In many insects these basic structures are accompanied by secondary structures on segments VIII, IX, or X.
No intromittent organ is present in Collembola or Diplura. Male Archaeognatha and Thysanura have terminal segments similar to those in females, but with a median phallus which is bilobed in Thysanura. Paired penises are present in Ephemeroptera and some Dermaptera, but in the majority of pterygote insects there is a single median aedeagus. This is protected from injury in various ways. In grasshoppers and fulgorids, the sternum of the last abdominal segment extends to form a subgenital plate. In many Endopterygota, protection is afforded by withdrawal of the genital segments within the preceding abdominal segments.
Male Odonata differ from all other insects in having the intromittent organs on abdominal segments II and III.
HEMING (1970b) described the outer morphology of male terebrantian and tubuliferan species. This is consistent with the examined species *F. occidentalis*, *E. americanus*, and *S. linguis* in this study.

4. Morphology of inner male reproductive organs
The male reproductive organs of the investigated thrips species (*F. occidentalis*, *E. americanus*, and *S. linguis*) in this study consist of paired testes, deferent ducts, seminal vesicles and accessory glands.
In insects, usually each testis consists of a series of testis tubes or follicles ranging in number from one in Coleoptera (Adephaga) to over 100 in grasshoppers (Acrididae). In Lepidoptera the follicles are incompletely separated from each other, and the testes of Diptera consist of simple, undivided sacs, which may be regarded as single follicles. A single follicled testes could be observed in *F. occidentalis* and *E. americanus* and seems to be a feature of the suborder Terebrantia (HEMING 1970b).
The adult morphology of the male reproductive system in *F. occidentalis*, *E. americanus*, and *S. linguis* differs little from that described in other species of Terebrantia and Tubulifera (HARTWIG 1952, HEMING 1970b).
In contrast to most other insects, testes of the examined adult terebrantian species, *F. occidentalis* and *E. americanus*, do not contain germ cells at different stages of spermatogenesis, but include only fully developed spermatozoa (single follicled testis). In Tubulifera (*H. verbasci*), HEMING (1970b) described the testes of adults containing fully differentiated sperm.
In this study, it was observed that *S. linguis* testes include germ cells at different stages of spermatogenesis while *B. brevitubus* testes contain only differentiated sperm. Therefore, it can be concluded that there might be differences between species within the suborder Tubulifera.
The sperm flagellum in most insects has nine accessory tubules, which are formed into the simple 9 + 2

axoneme during late spermatogenesis (DALLAI & AFZELIUS 1993). Neuroptera sperm have no acrosome and occasional species with no acrosome occur in other orders (CHAPMAN 1998), which is also true for terebrantian thrips.

The sperm of some insects have two axial filaments. This occurs in Psocoptera, Phthiraptera, Thysanoptera and many Hemiptera (CHAPMAN 1998).

Sperm of *F. occidentalis* and *E. americanus* have a cork-screw shape. Ultrastructure of terebrantian sperm has been described by BODE (1983, 1988, 1990) for *Thrips validus*, *A. intermedius*, and *P. dracaenae*. Nucleus, mitochondrial derivative, and the highly modified flagellar complex are situated more or less side by side, not one behind the other, and acrosomal vesicle is missing. The flagellum consists of 27 microtubular elements. There is a characteristic arrangement of 18 doublets (nine carry dynein arms and nine are doublets without dynein arms) and nine singlets. Like half the doublets, the singlet microtubules have dynein arms, so they must be residual A-tubules of a former doublet. BODE (1983, 1990) concluded that the basic pattern does not consist of 18, but of 27 doublets, without true singlets, which does not correspond with two, but instead with three cilia. This hypothetical mode of origin was confirmed by investigations of the structure of *T. validus* spermatids during various developmental stages (BODE 1983).

ATPase activity was detected in the region of the arms which supports the observed motility of the sperm cells (BODE 1988). The outer morphology of the sperm noted in *F. occidentalis* and *E. americanus* in this study matches the observations of BODE (1983, 1988, 1990) and DALLAI *et al.* (1991). Motility in a sperm flagellum that seems to possess a disordered system of doublets is not unique. The dipteran family Cecidomyiidae contains many species of gall-midges that have motile flagella with unusual patterns (DALLAI & MAZZINI 1983; DALLAI 1988). Several patterns with different numbers of microtubular doublets have been described in this family, sometimes there are up to 2000 doublets.

BACCETTI *et al.* (1969) were the first who examined sperm cell ultrastructure of a tubuliferan species, *Crytothrips nigripes*. As in Terebrantia the components (nucleus, acrosomal vesicle, mitochondrial derivative, and the flagellar complex) are arranged next to each other rather than one behind the other. The authors reported a chaotically arranged bundle of 18 doublet microtubules without dynein arms and four singlet microtubules. In contrast, BODE (1988) found 24 tubules in the axonemal complex of *Haplothrips aculeatus* which is likely to consist of 18 doublets and six singlets. That means an arrangement of 2 x (9 + 3). Thus, the starting point for this configuration of tubules should be two cilia with three central singlets instead of two. The corresponding 9 + 3 flagellum is vary rare among insects, although common among arachnids. Whether the occurrence of 18 + 4 and 18 + 6 sperm in Phlaeothripidae corresponds to the range of the subfamilies Idolothripinae and Phlaeothripinae, has yet to be tested. Living *H. aculeatus* sperm cells show a strange cork-screw shape and appear to be completely immotile as expected due to the disordered axonemal complex and the lack of dynein arms on the doublet microtubules.

It is a paradox that sperm of the Thripidae is motile even though the vagina is directly next to the spermatheca and in Phlaeothripidae the sperm is immotile and has to be transported to the spermatheca over a much longer distance (HEMING 1970b). In both families the sperm is transported passively in the female. BODE (1983) assumes that the movement of the sperm in thripids serve to create streaming in the surrounding medium for a better supply of nutrients and oxygen.

Accessory gland:

The number and arrangement of accessory glands varies considerably between different groups of insects. In Lepidoptera, there is a single pair of glands, in *Tenebrio* (Coleoptera), there are two pairs, *Schistocerca* and *Locusta* (Orthoptera) have 15 pairs of accessory glands, and *Gryllus* has over 600

(CHAPMAN 1998).
The glands associated with the male organs of insects usually secrete a mucous or viscid substance which either is discharged with the spermatozoa or solidifies around the spermatozoa to form a spermatophore (HEMING 1970b). There is no evidence that Thripidae possess a real spermatophore, therefore, the function of the accessory glands in thrips remains unclear.

Adult male Thripidae have glandular areas in some abdominal sternites. Shape, size, and position of the cuticular pore plates of these glands have been used as taxonomic characters. The absence of these organs in females and larvae leads to the conclusion that the glandular areas in males play a role in mating behaviour (BODE 1978). PELIKAN (1951) proposed that the abdominal gland secretion is a pheromone that acts as an attractant and as an aphrodisiac.
BODE (1978) examined the abdominal glands of the males of *T. validus* and concluded that these structures are involved in pheromone production.

4.1.5. Life tables

Life tables are important instruments in dealing with pest insects. They allow predictions about developmental stages in varying conditions providing better management of the pest.
F. occidentalis originally comes from North America (MOUND 1997) and was introduced to Europe in 1983 (MOUND 1997). Today it is a worldwide pest in many crops and little is known about differences in postembryonic developmental times between populations. The developmental times of all postembryonic stages were determined and compared in two different populations, one from Halle (Germany) and one from Perth (Australia) in this study.
No striking differences between the two populations could be found. Average developmental times over one year decreased from March to November in both populations of *F. occidentalis*. Conditions under which the thrips were reared in the laboratory (temperature: 23 °C, humidity: 75 %, light regime of LD = 16 : 8) remained the same throughout the year in all three tests. Interestingly, both populations having different origins showed the same period of decrease in developmental time.
The effect of photoperiod on the bionomics of *F. occidentalis* was investigated by BRØDSGAARD (1994a). The immature developmental time significantly increased with decreasing day length from 13.15 to 14.75 days at 16 : 8 and 4 : 20 (L : D) h photoperiod, respectively. The effect was expressed primarily in the second larval instars. The same can be reported from the experiments carried out with the different populations of *F. occidentalis* and described in Chapter 3.1.5. The results of the present study suggest that the second instar larvae is flexible adjusting and adapting to different environmental conditions better than other postembryonic stages.
Studies show that other insects, available throughout the year, peak in number or have different developmental rates, for example, in *Galerucella birmanica* (Coleoptera) the life cycle was prolonged to 44 days in December while in September it was completed in 15.5 days (YADAV & GARGAV 2000) and the developmental time of *Galleria mellonella* was shortest in midsummer (CHANG & HSIEH 1992). These experiments were conducted in the laboratories under constant conditions.
The influence of three different (constant) temperatures on the developmental time of the postembryonic stages of *F. occidentalis* was examined in this study and results concluded that the developmental time of all postembryonic stages increased with decreasing temperature. The second instar larva showed the greatest variability and taking the longest time for development, whereas the

shortest stage was the propupa.
GAUM *et al.* (1994) investigated the duration of each developmental stage of *F. occidentalis* at different temperatures. The minimum value for development was 9.4 °C. The longest duration of development was 49 days at 15 °C and the shortest at 30 °C 12.5 days. The optimum temperature for development among those tested was 30 °C. The authors found that the propupal stage was more sensitive to temperatures than the other instars and its rate of development accelerated at higher temperatures. Developmental times for *F. occidentalis* were much shorter in this study with the longest developmental time at 21.6 days (15 °C) (more than half the time as described by GAUM *et al.* (1994) for *F. occidentalis*) and the shortest duration at 7.2 days (32 °C).
KAWAI (1990) examined the effects of temperature on the population growth of *T. palmi* revealing the generation time decreased with higher temperature. The developmental period taken by *Thrips nigropilosus* to complete a life cycle decreased with increasing temperatures (ANYANGO 1992) and *Gynaikothrips ficorum* developed from egg to adult in 49 days at 15 °C and 16 days at 30 °C and failed to develop at 12 °C and 35 °C.

The life table data obtained in this study for *E. americanus* reared on bean leaves is approximately the same as observed by OPIT *et al.* (1997) for *E. americanus* reared on cucumber. However, the metamorphosis was longer (5.2 days) in OPIT *et al.* (1997) and took in the experiment of the present study 2.94 days. The authors found that the postembryonic development of *E. americanus* on pepper is approximately 20 % longer than on cucumber.

Mortality rate for *F. occidentalis* was 69.5 % (at 23 °C) and for *E. americanus* 10.4 % in this study. *F. occidentalis* had the lowest mortality rate at 15 °C (50.4 %) and the highest at 32 °C (81.9 %). *F. occidentalis* individuals (especially the larval stages) are very active and move around a lot, while individuals of *E. americanus* are not so agile. This movement may explain the difference in the high mortality rate for *F. occidentalis*. Rearing conditions confine the larvae and having no chance to escape, the mortality rate additionally increased.
RIJN *et al.* (1995) showed that the mortality observed between egg hatching and adulthood was 19 % for *T. tabaci* and 7 % for *F. occidentalis* (reared at 25 °C) which is low compared with the results of this study (69.5 %, reared at 23 °C).
Mortality rate depends on several abiotic factors including temperature and photoperiod. In *T. nigropilosus* the best survival rate for egg-adult was realized at 20 °C (ANYANGO 1992). *F. occidentalis* immature mortality increased with decreasing daylight from 67.3 % to 87.5 % at photoperiods of 16 : 8 and 4 : 20 (L : D) (BRØDSGAARD 1994a).

4.2. Progenesis

4.2.1. Development of the female genital organs

HEMING (1970a) explains that the postembryonic division into four ovarioles begins in the pharate propupa in *H. verbasci* (Phlaeothripidae) and is not complete until midway through the first pupal stage. In all other thrips, in which this process has been described, separation occurs completely during the pupal stage.
In this study the species of the Thysanoptera suborders were found to have ovarioles separating in all

cases during the propupal stage. The ovarioles are fully separated during middle to end pupal stage in *F. occidentalis* and *E. americanus* (Terebrantia).
This separation was described by WATANE & THAKARE (1987) for the postembryonic development of the ovary in *Elaphrothrips greeni* (Phlaeothripidae). In the first instar larva of this species, ovary anlagen consist of terminal filament, germarium, and young primary oocytes. In the second instar larva prefollicular nuclei, primary oocyte, and vitellarium begin to differentiate. In the propupa the ovary divides and leads to the organization of four individual ovarioles. In the first pupal stage the vitellarium is well-differentiated and oocytes are arranged in linear fashion and the follicular epithelium becomes distinct. In pupal stage II, four ovarioles of each ovary are well differentiated. The only difference in development of the terebrantian species is one pupal stage where the differentiation of ovarioles is complete.
The ovarioles of thrips take form later than do those of most other exopterygotes. In Heteroptera (WICK & BONHAG 1955), Homoptera (HELMS 1968), and Psocoptera (GOSS 1954) ovariolar separation occurs in the embryo, or in first or second instars. Although the ovarioles of thrips are panoistic like those of the majority of exopterygote insects, their delayed development is more similar to the endopterygote morphogenesis (HEMING 1970a).
The reproductive system of the first stage juveniles of most Exopterygota is poorly defined (HEMING 1970a). This is the same organization found in the reproductive system among many endopterygote larvae. The endopterygotes usually retain this organization for almost the whole of the larval period, then abruptly approach the adult condition during the pupal stage. The exopterygote anlagen differentiate continuously and approach the adult condition more gradually with the transition spread over several immature stages. The development of the female reproductive system in thrips lies somewhere between the endopterygote and exopterygote mode of differentiation (HEMING 1970a).
In addition, HEMING (1970a) reports some degradation of structures connected to the reproductive system which takes place during the metamorphosis of thrips. The histolysis during the propupal and pupal stage of the larval ventral longitudinal muscles of segment VIII in *F. fusca* and *H. verbasci* can be looked upon as a further holometabolous characteristic as can the de novo ontogeny of most of the reproductive musculature in thrips. Degradation processes of larval structures are a common feature of insects undergoing holometabolous development. Insects which undergo metamorphosis generally have two distinct, free-living stages: (1) the larval stage, specialized for growth and feeding, and (2) the adult stage, specialized for dispersal and reproduction (HODIN & RIDDIFORD 1998). During the intervening pupal period, there is a radical morphological reorganization of the animal, characterized by the differentiation of wings, genitalia, and gonads. These structures are specified during embryogenesis, proliferate during larval life, and differentiate at metamorphosis. In thrips, larval and adult stage look very similar and the investment to produce an adult stage is energetically expensive. This metamorphosis with little change from larva to adult seems excessive and costly in Thysanoptera.

The formation of the ovarioles in thrips occurs due to the division of each ovary by an inflexion of its epithelial walls and not through an outgrowth of the ovarioles from the larval ovary. This suggests that the length of the ovary anlagen during the separation of the ovarioles is not noticeable greater than the length at the beginning (HEMING 1970a). The results from this study support this theory.
Ovoviviparity (i.e., the presence of a developing embryo in an ovariole) is known from a couple of thrips species. Most of them belong to the Phlaeothripidae, for example, *H. verbasci* (HEMING 1970a) and *E. tuberculatus* (HEMING 1989). MORITZ (1989d, 1997) found evidence for ovoviviparity in a species belonging to the Terebrantia, *H. femoralis*. In these insects the eggs, either fertilized or not, remain in the expanded vagina or uterus while undergoing embryogenesis. In thrips in which embryogenesis

have been shown to begin in the ovariole, the embryo is a haploid male (or a diploid female in the thelytokous species) developing parthenogenetically (HEMING 1970a; MORITZ 1997).
Ovoviviparity was not found in thrips species examined in this study. However, it cannot be discounted, because species are known which are facultatively viviparous and ovoviviparity is rare and not all species must show it.

4.2.2. Development of the male genital organs

Spermatogenesis and development of the male reproductive organs has been described in *Taeniothrips simplex, Limothrips denticornis, S. staphylinus* (BOURNIER 1956a), *H. verbasci* (HEMING 1970b), and *F. fusca* (HEMING 1970b). The processes taking place in these species during the development of the male genital system are the same of those occurring in *F. occidentalis*, *E. americanus*, and *S. linguis*.
These species have an arrhenotokous mode of reproduction. The meiosis occurring in the testes of haploid males must be aberrant and more in the nature of a mitosis. Indications of this are provided by BOURNIER (1956a) and HEMING (1970b), however, they were not able to count the number of chromosomes which would provide further evidence for the haploidy of males in thrips. RISLER & KEMPTER (1961) provided evidence that males of *Haplothrips statices* are haploid.
Species of Terebrantia and Tubulifera differ in the development of testes. Each testis of *F. occidentalis* and *E. americanus* can be considered as a single cyst. All the germ cells within it, at any given time, are in approximately the same stage of differentiation (HEMING 1970b). In the only *P. dracaenae* male found, the testes seem to be divided into two chambers and the two chambers contain fully developed spermatozoa. Since males are very rare in *P. dracaenae*, an investigation of the spermatogenesis in this species was not possible. Revealing the cytological mechanisms underlying the differentiation of males in thelytokous or deuterotokous species, respectively would be interesting.
There are three types of cytological spermatogenesis in haploid males (SUOMALAINEN 1950). In most Hymenoptera and in *Micromalthus debilis* (Coleoptera), meiosis I is abortive with an anucleate polar body which is given off, while meiosis II is mitotic. In *Telenomus fariai* (Hymenoptera), the first division is mitotic and in the second division an anucleate polar body is eliminated. In all other species there is a single equational division, although some meiotic characteristics may still be evident (SUOMALAINEN 1950).
HEMING (1970b) describes the cytological mechanism of spermatogenesis in *H. verbasci* and *F. fusca*. He pointed out that the meiotic division occurring in male larvae of this species differ from all three types described above. The difference is in the absence of spindle forms in the second division and in the presence of nuclear material in the polar body (HEMING 1970b).
HEMING (1970b) also discovered a cap-cell terminating the anterior end of each sperm bundle in the tubuliferan species *H. verbasci*. The cap-cell seems to be a common feature of insect sperm bundles (CHAPMAN 1998). Neither TUZET & BOURNIER (1951) nor BOURNIER (1956b) talked about the presence of such a gap-cell in the sperm bundles of the examined tubuliferan species, *H. verbasci* and *Liothrips oleae* respectively. Evidence for this type of cell could not be found in *S. linguis* (Phlaeothripidae) in the present study.
In most other insects, each testis contains a series of tubular follicles which vary considerably in number and size in different groups (WEBER 1954; CHAPMAN 1998). Each of these follicles corresponds to an entire testis of *F. occidentalis* or *E. americanus*. Single-follicled testes have been found also in

Collembola, Ephemeroptera, Zoraptera, Psocoptera, Trichoptera, and Coleoptera-Adephaga (WEBER 1954; CHAPMAN 1998).
There seem to be differences within the family of Phlaeothripidae as well. Each follicle contains a succession of zones from I to V in which germ cells are at different stages of development. These zones are present in the testes of *H. verbasci* at separate times during their differentiation but never all at once (HEMING 1970b). Only zone I is found in the anlagen of first and early second instar larvae. Zones II, III, and IV develop during the second stage successively while zone I and zone II have disappeared by the time of molt into propupa. During the propupal stage, zone III disappears while zone V develops in the posterior region of the testis. Only zone IV and V are found in the two pupal stages and only zone V in the adult. This is contrary to the observed development in *S. linguis* in this study, where more than one differentiating zone was present in the testis at different developmental stages.

4.3. Embryogenesis

Insect eggs are typically large relative to the size of the females that produce them because they contain a great deal of yolk. In general, eggs of Endopterygota contain less yolk and are smaller than those of Exopterygota (ANDERSON 1972b).
The length of eggs examined in this study corresponds to 18.8 % of the female length in *F. occidentalis* and 23.7 % in *S. linguis*. The eggs of thrips are large compared to the size of the female and the size of eggs in this respect corresponds more to holometabolous embryogenesis (ANDERSON 1972a, b; MORITZ 1988a).
Egg size is affected by different factors other than belonging to the hemi- or holometabolous type of development. Lepidoptera from temperate regions which have species overwintering in the egg stage, have larger eggs than species overwintering in other stages. Species feeding on woody plants have larger eggs than those feeding on herbaceous plants (REAVEY 1992; GARCIA 2000).

4.3.1. Egg morphology

The most common type of insect egg is an elongated oval which often indicates the polarity of the embryo. Prior to embryo formation, there is a noticeable albeit slight difference of the two poles and in a curvature of one side of the egg (WEBER 1954). ANDERSON (1972a, b) provided evidence that the eggs are smaller in more specialized forms, thus, he concluded that eggs larger than 1 mm predominate among the Hemimetabola while those of Holometabola are less than 1 mm in length or diameter.
Eggs of *F. occidentalis* (Terebrantia) measure an average of 279.5 µm ± 6.9 x 128.9 µm ± 16.5 and eggs of *S. linguis* measure 446.0 µm ± 4.8 x 163.3 µm ± 3.7. Thus, the egg size of Thysanoptera range at lower limits of the mean values found for the eggs of Hemimetabola (MORITZ 1988a).
In all oviparous, hemimetabolous insects, the freshly oviposited egg is still undergoing maturation and completion of fertilization. As with *F. occidentalis* and *S. linguis* in the present study, almost the entire substance of the egg consists of yolk (ANDERSON 1972a).
Insect eggs are always enclosed within two membranes, an inner vitelline membrane and an outer chorion. The vitelline membrane is generally said to be secreted by the oocyte. The chorion is a persistent, complex membrane secreted entirely by the follicle cells (ANDERSON 1970b; CHAPMAN 1998).

There is a striking difference in the outer sculpture of the eggs related to the distinct oviposition behaviour of the two suborders Terebrantia and Tubulifera (MORITZ 1988a, 1997). This difference is confirmed in observations of eggs of *F. occidentalis* (Terebrantia) and *S. linguis* (Tubulifera) in this study. Terebrantian species have a smooth egg shell designed for laying eggs within plant tissue (LEWIS 1973; MORITZ 1988a, 1997). Tubulifera lay their eggs on the substrate and have a penta- or hexagonal sculptured egg shell and often glue their eggs to the plant (LEWIS 1973; HAGA 1985). Females of *S. linguis* do not fix their eggs on the plant with a sticky patch, they just lay them on the plant and move them together creating a batch of eggs.

Extensive airspaces are usually present in the chorion adjacent to the oocyte (CHAPMAN 1998) and in insect species that lay their eggs in moist environments. These airspaces may extend through the entire thickness of the chorion like in the grouse locust, *Tetrix* (Saltatoria) (HARTLEY 1962). In the eggs of most species, however, openings through the chorion are restricted, and this limits water loss. For example, in *Musca* (Diptera), the inner meshwork in the chorion, which provides a continuous layer of air all round the developing embryo, connects with an outer meshwork by pores (aeropyles) through an otherwise solid middle layer (HINTON 1960). In many other species, the connections are even more restricted. In *Calliphora* (Diptera), the outer meshwork and aeropyles connecting with the inner meshwork are absent over the greater part of the egg, and are present only between the hatching lines (HINTON 1960). Eggs of *Ocypus* (Coleoptera) have an equatorial band of aeropyles connecting the inner air spaces, *Rhodnius* (Hemiptera) eggs have a ring of aeropyles just below the cap, and those of *Carausius* (Phasmida), have a single small pore at which the reticular inner chorion is exposed at the egg surface (CHAPMAN 1998).

In eggs of *F. occidentalis* no aeropyles have been found. Eggs of *S. linguis*, however, possess aeropyles at the posterior region of the egg. The presence of micropyles could not be detected in this study.

HEMING (1970a, 1979) found a micropylar cap at the anterior pole and a V-shaped micropyle at the posteroventral side of *H. verbasci* (Phlaeothripidae) eggs.

Chorion is laid down in the ovary and micropyles are necessary to allow subsequent entry of sperm. Micropyles are funnel shaped pores passing right through the chorion, usually near the anterior pole of the egg. The pores are 1-2 µm in diameter, often with a wider funnel at the surface of the chorion (CHAPMAN 1998).

The number of micropyles in insects varies. Most dipteran eggs have only a single terminal micropyle, while Acrididae (grasshoppers) commonly have 30 or 40 arranged in a ring at the posterior end of the egg (ROONWAL 1954; WEBER 1954; CHAPMAN 1998).

The first stage larvae of many species escape from the egg by chewing through the chorion or by using special egg bursting devices. However, the chorion of some species has a line of weakness along which it splits when the larva exerts pressure from within. These hatching lines are usually visible from the outside, and sometimes define a cap or operculum (HINTON 1960; CHAPMAN 1998).

KIRK (1985b) was the first to report the presence of an operculum in the thysanopteran *T. tabaci* and *F. fusca*. MORITZ (1988a) found an operculum in *H. femoralis* and concluded that it is a common feature of all terebrantian species. An operculum is present in *F. occidentalis* and absent in *S. linguis* which supports MORITZ'S (1988a) hypothesis.

Similar structured opercula are found in the Heteroptera, Phthiraptera, and Embioptera (RICHARDS & DAVIES 1977).

Tubulifera possess larger eggs (*Bactrothrips buffai*: 590 µm x 230 µm, BOURNIER (1966); *H. verbasci*: 420 µm x 150 µm, HEMING (1979)) than Terebrantia (*Frankliniella tenuicornis*: 339-370 µm x 119-

133 µm, HOLTMANN (1962); *L. denticornis*: 375 µm x 112 µm, HOLTMANN (1962); *Microcephalothrips abdominalis*: 118-121 µm x 78-85 µm, JAGOTA (1961)). The average egg size of *F. occidentalis* (279.5 µm ± 6.9 x 128.9 µm ± 16.5) and *S. linguis* (446.0 µm ± 4.8 x 163.3 µm ± 3.7) found in this study agrees with the above data.

Changes occurring in the size of the eggs during embryogenesis is different depending on the insect. DORN (1976) has observed a decrease in the volume and weight of *Oncopeltus fasciatus* (Heteroptera) where most insect eggs increase their egg volume during development. In Lepidoptera several reports on the increase in egg volume exist (KOBAYASHI & ANDO 1981; KOBAYASHI 1996), where it was evident that the egg volume of *N. albiantennella* rapidly increased in a certain developmental period and then became constant over time. Increase in the egg volume in this species may be attributed to absorption of water into the eggs, and the presence of thickened serosal cells is assumed to be closely associated with this phenomenon (KOBAYASHI 1998). A thin and elastic chorion also seems to enable the eggs to become larger (FEHRENBACH 1995).
In the exoporioan and ditrysian species (Lepidoptera), the egg size is constant throughout the egg period suggesting that the constancy of egg volume in Exoporia is due to the acquisition of the thick vitelline membrane and in Ditrysia to that of the thick lamellar chorionic layer (FEHRENBACH 1995). GÖRG (1959) could not find any change in egg size in *Hierodula crassa* (Mantodea).
In *F. occidentalis* the size of the egg changes in the same manner as described by MORITZ (1988a) for *H. femoralis*, i.e. the length increases just slightly during embryogenesis, but the width of eggs becomes enlarged about 37 %. *S. linguis* eggs stay more or less the same during the whole embryonic development. This may be due to the different oviposition behaviour. Eggs of *F. occidentalis* are embedded in the plant tissue and are able to take up water from the plant cells, while eggs of *S. linguis* are oviposited on the plant surface, a relatively dry environment. Individual *S. linguis* eggs survive in the climatic cabinet for duration of embryogenesis, while individual eggs of *F. occidentalis* survive only after katatrepsis without plant tissue.

Remarkable differences can be observed in insect embryogenesis related to the duration of embryo development. Many insects show a very fast embryonic development like *Drosophila melanogaster* (Diptera) (average 22 h), while others can take 85 days to complete embryonic development (ANDERSON 1972a). Insects with a long germ band (most holometabolous insects) have shorter embryonic periods than those with short germ bands (Orthoptera and related orders) (CHAPMAN 1998). The thrips species examined thus far exhibit a relatively short embryonic developmental time (MORITZ 1988a).
In *F. occidentalis* the average developmental time of an egg is approximately four days, while in *S. linguis* developmental time is 10.4 days. Thus, embryonic developmental time in *F. occidentalis* reflects holometabolic and *S. linguis* exhibits a hemimetabolic tendency.

Oviposition represents a major investment for female insects. To optimise this investment, two strategies have evolved (GAUVIN *et al.* 2001). Females can produce few eggs but invest more in resources in each egg. The reproduction rate in this case is low but the mortality rate of the eggs is also low. The other solution is to oviposit more eggs containing fewer resources. The reproduction rate of these species is increased but at the cost of a high egg mortality (SMITH & FRETWELL 1974; MCGINLEY *et al.* 1987). These eggs often need to absorb nutrients and water from their environment to complete development and, by doing so, increase in size.
The mortality of eggs was significant higher in *F. occidentalis* (34 %) than in *S. linguis* (9 %) and is evidence that females of *S. linguis* invest in taking care of the eggs and producing fewer eggs at a

higher survival rate. On the other hand, *F. occidentalis*, a worldwide pest species, is probably producing as many eggs as possible with a higher embryonic mortality rate.

4.3.2. Embryogenesis

Insects are classified in three groups according to their segmentation process: short germ band, intermediate germ band, and long germ band (SANDER 1976). Short germ band insects are usually representatives of primitive orders, while long germ band species belong to recent derived orders. One exception was found in Coleoptera where all three germ band types are present creating difficulty in understanding the ancestral body plan (PATEL 1994).
In short germ development the single layered and as yet unsegmented embryonic anlage, the germ anlage, is short by comparison with both egg and the germ band. Fate maps established with modern methods are lacking for short germ insects, but the main part of the germ anlage is likely made up of cells that will form the embryo‘s anterior head regions (protocephalon). The segmented parts of the germ band will then be successively generated, segment by segment, in an anterior-to-posterior sequence, through some kind of intercalation between the protocephalon and a small terminal zone (SANDER 1976, 1997).
In long term development almost the full number of cells required for the future germ band have formed before any segments become visible. Therefore, the germ anlage from its beginning is nearly as long as the egg (SANDER 1997). Segmentation here follows the subdividing mode by which the full number of segments is carved from the germ anlage within a short time. Gastrulation begins after all segments have been delineated, while in short germ development gastrulation precedes and/or accompanies the progress of segmentation (PATEL 1994).
Many insect groups, among them damselflies, crickets and leafhoppers, tend to combine traits of both the short and long germ types: an anterior stretch of the germ anlage subdivides rapidly to yield anterior segments, whereas the remaining segments are added successively. This is the semi-long or intermediate type of patterning which, like the other types, exists in several variants.
Recent work with beetles and butterflies has been shown that the segmentation mode does not fit in the short-intermediate-long germ band classification (SANDER 1996; NAGY *et al.* 1994; CARVALHO *et al.* 1999) suggesting a possible wider diversity of segmentation processes adopted by insects.
Thrips embryos examined so far (BOURNIER 1966; ANDO & HAGA 1974; HEMING 1979, 1980; MORITZ 1988a), including *F. occidentalis* and *S. linguis*, show a short germ embryo. Molecular mechanism of the pattern formation in thrips does not exist yet, therefore, results are based on morphological data.

Early embryogenesis:
Cleavage patterns can be either holoblastic or meroblastic. Holoblastic cleavage, or total cleavage, is characteristic of more primitive insects as observed in Collembola. Meroblastic, or superficial cleavage, is characterized by nuclear division followed by a syncytium formation, which is found in the majority of other insects (ANDERSON 1973; WEBER 1954). Cleavage types lead to a cellular uniform blastoderm of cuboidal cells (Apterygota) or columnar cells (Diptera and Hymenoptera) (ANDERSON 1973). In many insects the transition from blastoderm stage to gastrulation occurs in one step. However, in some insects there is an additional phase, the blastoderm differentiation (ANDERSON 1972b). This phase is characterized by a differential concentration of cellular division in one of the egg‘s poles. In addition, there is a gradual aggregation of the majority of the cells in a small disc at the ventral-posterior region

to form a compact embryo primordia and the extraembryonic ectoderm. This intermediate step is observed in primitive insects as Odonata and Orthoptera that are classified as short germ band (SANDER 1976). In higher orders as in Diptera and Hymenoptera neither cell concentration nor blastoderm area reduction is described.

In Thysanoptera, the germ anlage which is unsegmented arises through the aggregation of cells at the posterior region of the egg (BOURNIER 1966; HEMING 1979; MORITZ 1988a). The invagination is quite different concerning the direction of growth of the embryo in the suborders Terebrantia and Tubulifera (MORITZ 1988a). The germ anlage is growing directly to the anterior pole of the egg in *S. linguis*, while in *F. occidentalis* at the beginning the germ anlage grows in the opposite direction.
Elongation of the germ band takes place more or less in the same manner throughout the Thysanoptera and ending in an S-shaped germ band with a twisted abdomen (BOURNIER 1966; HEMING 1979; MORITZ 1988a, 1997). The segmentation and differentiation of the appendages was consistent in thrips examined in this study.
Regulation of blastoderm production and subsequent development into the embryo is most fully understood in *Drosophila* (Diptera). The cascade of early pattern decisions in *Drosophila* is started by the maternal gene products, which are asymmetrically localized in the egg or become locally activated (ST JOHNSTON & NÜSSLEIN-VOLHARD 1992). TAUTZ & SOMMER (1995) argued, however, that early *Drosophila* development is a highly specialized form of development that cannot serve as paradigm for most other forms of embryogenesis.
Segmentation has been studied at the molecular level in only one insect that does not belong to the holometabolic lineage, that of the extreme short germ embryo of the grasshopper *Schistocerca*. In *Schistocerca*, the two pair rule segmentation genes that have been examined do not show the same patterned expression as in the flies and beetles (PATEL *et al.* 1992; DAWES *et al.* 1994), suggesting that these orthopteran insects may not make segments in the same manner as *Drosophila*.

Katatrepsis:
HEMING (1980) and MORITZ (1988a) found (in *H. verbasci* and *H. femoralis*) pycnotic nuclei appearing within the area of the right mandible shortly before katatrepsis. The right mandible becomes degenerated in all thrips during embryogenesis. It is likely that this process is due to programmed cell death or apoptosis (LOCKSHIN & BEAULATON 1974). Similar processes are observed during the embryogenesis of *Calliphora erythrocephala* (Diptera) in the reduction of certain neuroblasts (STARRE-VAN DER MOLEN & OTTEN 1974).
Following the period of elongation and development of the appendages, the amnion and serosa, which enclose the embryos, fuse and rupture close to the head (BOURNIER 1966; DORN 1976; HEMING 1979; MORITZ 1988a). The embryonic membranes now pull back from the embryo leaving it exposed on the surface of the yolk. In species in which the embryo is already on the ventral surface of the egg, the embryo remains ventral. However, species that develop on the dorsal side of the egg, head towards the posterior pole, move around to position head towards the anterior pole. This movement is known as katatrepsis.
In holometabolous insects, the embryo elongates and differentiates with its head towards the anterior pole of the egg, and the extensive movements which occur in many hemimetabolous groups do not take place in holometabolous insects (ANDERSON 1972a, b). In some Coleoptera, such as *Dytiscus* and *Tenebrio*, the embryonic membranes fuse and rupture, and the embryo shortens rapidly, without changing its position (CHAPMAN 1998). Shortening also occurs in embryos of other holometabolous insects but the fate of the embryonic membranes varies (CHAPMAN 1998).
Lepidoptera are unusual among holometabolous insects in making extensive movements during

embryogenesis. The movements are called blastokinesis though they differ entirely from the movements occurring during the blastokinesis period in hemimetabolous insects (ANDERSON 1972b).
Katatrepsis is a very diverse process and does not show the same patterns in all insects. COBBEN (1968) exposed the phylogenetic connections of different types of blastokinesis in Heteroptera and proposed that the ancestral form, a total invaginated germ band, undergoes a further rotation about 180 ° during katatrepsis. This additional rotation about the longitudinal axis is also known in several other orders, for example, Isoptera (GEIGY & STRIEBEL 1959) and Homoptera (SANDER 1959).
In Thripidae and Aeolothripidae a rotation is not exhibited in embryo katatrepsis (MORITZ 1988a, 1997), however Tubulifera undergo a rotation of at least 180 ° (HEMING 1980). In *S. linguis* the exact degree of rotation could not be determined and appears that the embryo undergoes a rotation of more than 180 °.
Only speculative proposals exist about the functional significance of katatrepsis. Katatrepsis may be induced by mechanical and spatial effects caused by the growth of the embryo within the limited space of the egg (SWAMINATHAN & SRIRAMULU 1975). In *Chrysocoris purpureus* (Hemiptera), katatrepsis appears to maximize contact between the yolk-absorbing area of the embryo and the yolk (SWAMINATHAN & SRIRAMULU 1975). KELLY & HUEBNER (1989) indicate that the yolk-absorbing area in the embryo of *Rhodnius prolixus* (Hemiptera) is always in contact with the yolk and that the developmental significance of katatrepsis must lie elsewhere in this species. In *R. prolixus* katatrepsis has two important consequences: (1) Katatrepsis internalizes the yolk which is required for subsequent embryonic and larval development, (2) Katatrepsis facilitates hatching by re-orienting the embryo with its head next to the cap and with its appendages swept back to permit emergence. Katatrepsis is still poorly understood, however, it does play an essential part in completing the complex process of embryogenesis.
At the end of katatrepsis, the dorsal enclosure of the yolk is formed by extra-embryonic membranes (provisional dorsal closure) (ANDERSON 1972a) and later the provisional tissue is replaced by embryonic ectoderm which grows upwards to form the definitive dorsal closure (SANDER 1976).
As the ectoderm extends, amnion and serosa shrink and become confined to an antero-dorsal region where the serosa finally invaginates into the yolk in the form of a tube. This is known as the dorsal organ (ANDERSON 1972a).
The differentiation of the dorsal organ starts before katatrepsis and is recognizable by the thickened serosal cells. BOURNIER (1960) concluded that the numerous vacuoles of the dorsal organ possessed the function of a gland involved in the finishing of katatrepsis and dorsal closure. DORN (1972) proposed the main task of the dorsal organ was processing lipids in the yolk in *Oncopeltus fasciatus* (Heteroptera).
The dorsal organs of the Endopterygota are different from those known from other Arthropoda, they are not homologous (ZILCH 1974). Thus, the dorsal organ of Endopterygota is also called secondary dorsal organ (WEBER 1954; HEMING 1979).
BARNI *et al.* (1997) discovered that the serosa and amnion cells in some species of Blattaria undergo considerable morpho-functional modifications during the retraction of the serosa-amnion envelope. These modifications first assuming the aspect of secretory cells and afterwards showing the degeneration of the cytoplasm and the nucleus.
In light microscope examinations this degeneration takes place in a relatively short period (about two days) between the 16th and 17th day of embryonic development. The morphological and biochemical findings indicate that during the embryogenesis of *Periplaneta americana* (Blattaria) the dorsal organ, derived from the serosa epithelium and probably from amniotic cells, forms a compressed cluster of round cells undergoing apoptotic degeneration (BARNI *et al.* 1997).

The genetic control of physiological cell death (apoptosis) plays an essential role in regulating the cell mass of different structures during embryogenesis, metamorphosis, and adult life in both vertebrates and invertebrates (WYLLIE *et al.* 1980; ROBERTSON & THOMSON 1982; COMPTON & CIDLOWSKI 1992; CAVALIERE *et al.* 1998; CHAO & NAGOSHI 1999).
Apoptosis was shown in different insect species in different organ systems, such as the nervous (GOODMAN & BATE 1981; ABRAMS *et al.* 1993) and the muscular (DI NARDO *et al.* 1985), and in organs, such as the brain (YOUNOSSI-HARTENSTEIN *et al.* 1993) and the compound eyes (WOLFF & READY 1991). In embryos of *Drosophila melanogaster* (Diptera) DI NARDO *et al.* (1985) found apoptosis during the development of the caudal region of the embryo.
The degeneration of the dorsal organ in thrips is not known. Programmed cell death is presumed to occur during the degradation of the right mandible (MORITZ 1988a), but neither ultrastructural nor biochemical evidence exist.

Abdominal appendages in insects subsequently disappear after katatrepsis. However, in some insects the appendages of segments VIII and IX contribute to the ovipositor and those on segment XI form the cerci (CHAPMAN 1998). In Orthoptera and some other orders, the appendages of the first abdominal segment also persist for a certain time and are known as the pleuropodia and have a distal area in which the cells become very large. The pleuropodia degenerate, becoming torn off when the insect hatches. In Orthoptera, the pleuropodia probably secret an enzyme which digests the serosal endocuticle before hatching and serve the same purpose in *Belostoma* (Heteroptera), where they sink into the body to project a bowl-shaped cavity and reaching their greatest development just before hatching. In the cockroach, *Diploptera*, the external and lateral membranes of the cells of the pleuropodia are associated with large numbers of mitochondria, resembling fluid-transporting tissues. These may regulate fluid or osmoregulation in the embryo and the fluid surrounding it (CHAPMAN 1998). The pleuropodia have a special function in *Hesperoctenes* (Heteroptera) where the egg has no yolk or chorion as it develops within the female parent. Pleuropodia grow and fuse together to form a membrane which completely covers the embryo and makes contact with the wall of the oviduct to function as a pseudoplacenta (WEBER 1954, CHAPMAN 1998).
In thrips, pleuropodia are visible during katatrepsis and a couple hours afterwards at appendages of the first abdominal segment (BOURNIER 1966; HEMING 1979). The pleuropodia in thrips are similar to the pleuropodia of Heteroptera (COBBEN 1968), however, their function remains unclear. DORN (1972) proposed that the pleuropodia in thrips play a role during the hatching of the embryo.
Differentiation of the mouthparts starts after katatrepsis and is described in *H. verbasci* by HEMING (1980).
The segmentation process is similar in Thysanoptera and *Oncopeltus*. Prior to katatrepsis all segments are formed and postkatatreptic reductions become visible (DORN & HOFFMANN 1983).
Ganglia are strongly connected to the segments up to katatrepsis in Thysanoptera (WEBER 1954; MORITZ 1988a). Post katatrepsis some complexes of ganglia become relocated due to fusions and torsions. Rotations of the deutocerebrum and protocerbrum around the tritocerebrum are described by RYAN (1963) for *Coeloides brunneri* (Hymenoptera) and by WADA (1965) for *Tachycines* (Saltatoria). The fusion of gnathal ganglia is observed in all insects and the Thysanoptera additionally possess a strong affiliated prothoracic ganglion (MORITZ 1988a). The concentration of the abdominal ganglia starts immediately after katatrepsis. In the propupal stage, the abdominal ganglion (synganglion) reaches up to abdominal segment III or IV. MORITZ (1984) proposed a species-specific fusion of the abdominal ganglia which takes place during the postembryonic stages.
In Thysanoptera the differentiation of the gonads corresponds to the direct type and is comparable with

the findings in Dermaptera, Psocoptera, Homoptera, Apterygota, Onychophora, Myriapoda, and some Holometabola (ANDERSON 1972a,b). The development of gonads is marked by the early separation of germ cells either before or after blastodermis and developed several times independently.

Proliferation of germ cells in eggs of *H. verbasci* is asynchronous and occurs between blastoderm formation and the separation of the embryo from the serosa on completion of anatrepsis. These divisions form a mean of 36 germ cells in male embryos and 31 in females (HEMING 1979). In embryos of *F. occidentalis* and *S. linguis* it could not be determined if there is a difference in the number of germ cells corresponding to the sex of the embryo. In this study no differences in the size of the germ cells between males and females (as HEMING (1979) reported for *H. verbasci*) were detected. The primitive indirect differentiation of gonad development in Embioptera, Mantodea, Orthoptera, some Phasmida, Trichoptera, Hymenoptera, Heteroptera, and some Apterygota show a late segregation of germ cells (ANDERSON 1972a, 1973; MIYAKAWA 1974).

5. Summary

This study represents results on different aspects of thrips biology including morphological and developmental investigations. The aim was to describe (with the help of different methods) the thrips species process of reproduction and to outline the underlying morphological and developmental mechanisms. Main topics were:

(1) **Reproduction** of thrips. Data on the sex ratio of different thrips species, copulation and oviposition behaviour, and morphology of the genital organs were collected from *Frankliniella occidentalis*, *Echinothrips americanus,* and *Suocerathrips linguis*. Life tables were determined for *F. occidentalis* and *E. americanus* and data on the tospovirus-transmitting thrips species *Frankliniella fusca* and *F. occidentalis* were also included.

(2) The **progenesis** of thrips describes the differentiation of the genital organs during the larval and metamorphic stages of *F. occidentalis*, *E. americanus*, and *S. linguis*.

(3) **Embryogenesis** data on egg morphology, duration of embryogenesis, and mortality rate of *F. occidentalis* and *S. linguis* were collected and histological techniques and video documentation were used to describe the embryogenesis of both species as representatives of the two suborders Terebrantia and Tubulifera.

The results of the present study can be summarized as follows:

(1) Reproduction

- Data collected on reproduction of *F. occidentalis* and *S. linguis* underline the different strategies of reproduction in thrips.
- Sex ratio of four thrips species was determined. Sex ratios (female : male) were 1 : 0.9 (n = 145) for *F. occidentalis* (Thripidae, Thripinae), 1 : 0.26 (n = 123) for *E. americanus* (Thripidae, Thripinae), and 1 : 0.5 (n = 197) for *S. linguis* (Phlaeothripidae, Phlaeothripinae). Males are very rare in *Parthenothrips dracaenae* (Thripidae, Panchaetothripinae), only one ♂ could be found (n = 175). The results correspond to the type of parthenogenesis occurring in these species (*F. occidentalis*, *E. americanus*, and *S. linguis* - arrhenotoky; *P. dracaenae* - thelytoky).
- The sex ratio of *F. occidentalis* was tested under the influence of three different constant temperatures (15 °C, 23 °C, 30 °C). With increasing temperature the ratio was more female biased, at 15 °C 1 : 1.2 (female : male), at 23 °C 1 : 0.9 (female : male), and at 30 °C 1 : 0.5 (female : male).
- The sex ratio of the progeny of unmated females of *F. occidentalis* (at three different constant temperatures) and *E. americanus* (at 23 °C) was determined. A few females (two ♀♀ at 15 °C, n = 360; one ♀♀ at 23 °C, n = 116; two ♀♀ at 30 °C, n = 540) hatched from unfertilized eggs in *F. occidentalis* (contrary to the arrhenotokous mode of reproduction, where actually all females arise from fertilized eggs and males from unfertilized ones). In *E. americanus* all progeny of unmated females were males.
- *F. occidentalis* has very short copulation times lasting only a few minutes (average: 3.5 min) compared with *S. linguis*. *S. linguis* copulations were observed over several hours. Females of *F. occidentalis*, once mated successfully, rejected copulations with other males.
- Populations of *S. linguis* contain both females and males with broken (“cut-off“) wings. It has been shown that this breakage occurs during copulation. Individuals with cut-off wings are no longer able to disperse. These individuals remain with the newly hatched larvae, raising their young provides a strategy to ensure the survival of the progeny at a high number.

- Females of *F. occidentalis* lay their eggs singly in the plant tissue and begin laying eggs almost immediately after they hatch (on average one day after their emergence). The average number of eggs laid by one female was 4.9 ± 2.4 eggs per day. During their entire lifetime females lay on average 75.6 ± 52.4 eggs. The mean life of females was found to be 9.8 ± 6.5 days (the oldest female reached 32 days).
- Females of *S. linguis* lay their eggs on leaves at the soil level of *Sansevieria trifasciata* plants. Eggs are laid singly by the female and are moved by adult individuals creating a batch of eggs.
  In these groups of adult individuals (each consisted of 10 females and 5 males) females start laying eggs finally between 14-18 days. Probably, they have to establish food first. This delay in egg laying leads to the assumption that females possess some kind of mechanism to control their oviposition, e.g., retaining eggs until food for the progeny is provisioned.
- In females of both *F. occidentalis* and *E. americanus* belonging to the suborder Terebrantia, the ovipositor is composed of the basal apparatus (which means valvifers and basalvalvulae) and the shaft. Abdominal tergites IX to X form a protective cavity for the ovipositor.
- The ovipositor in females of *S. linguis* (Tubulifera) has the structure of a simple tube and is situated at the VIII. abdominal segment.
- The histologically examined species, *F. occidentalis*, *E. americanus*, and *S. linguis*, possess one pair of panoistic ovaries each and each ovary contains four ovarioles. The ovaries connect to a pair of lateral oviducti. These join to form a median oviduct which opens posteriorly into the vagina. The vagina is connected to the spermatheca. The observed terebrantian species possess an accessory gland.
- In *F. occidentalis* and *E. americanus* five different zones are identifiable in one ovariole. The terminal filament (zone I), the germarium (zone II), and three different zones (IIIa, IIIb, IIIc) in the vitellarium. Zone IIIa contains small oocytes, in zone IIIb the oocytes are recognizable on the previtellogenic growth of oocytes and a basophil yolk. In zone IIIc the vitellogenic growth of the oocytes takes place and the yolk appears acidophil. In *S. linguis* only two zones were distinguishable in the vitellarium of the ovarioles.
- To test whether a connection between the number of oocytes per ovariole and the different lifestyle of thrips exists, numbers of oocytes in the ovarioles of four different species were determined. The average number of oocytes per ovariole is 8.6 ± 0.8 for *F. occidentalis*, 5.9 ± 0.2 for *E. americanus*, 11.3 ± 0.7 for *Aeolothrips intermedius*, and 4.5 ± 0.3 for *S. linguis*. Thus, a connection between different reproduction strategies in thrips and the number of oocytes per ovariole was hypothesized. The species with the relatively high numbers of oocytes (*F. occidentalis*, *A. intermedius*, and also *E. americanus*) seem to aim at producing as many progeny as possible in a relatively short time. On the other hand, *S. linguis* has a low number of oocytes and, therefore, produces only a few offspring. This species also exhibits a subsocial life style and invests more in rearing the progeny.
- In *F. occidentalis* and *E. americanus* the sperm is arranged in a spermatophore, whereas in *S. linguis* the sperm is more loosely distributed in the spermatheca.
- The males of the examined thrips species (*F. occidentalis*, *E. americanus*, and *S. linguis*) possess an extrusible phallus contained within a genital chamber at the IX. abdominal segment.
- Each testis of *F. occidentalis* and *E. americanus* consists of a single cyst of germ cells, whereas in *S. linguis* testes contain a various number of cysts encompassing different stages of spermatogenesis. The testes of another tubuliferan species (*Bactrothrips brevitubus*) contained only fully differentiated sperm arranged in bundles.
  Testes lead caudally into the vasa deferentia. Each vas deferens expands posteriorly into a seminal vesicle.

- While *F. occidentalis* and *E. americanus* males possess one pair of accessory glands, *S. linguis* males have two pairs.
- The developmental times of postembryonic stages of two different populations of *F. occidentalis* were tested at constant conditions (23 °C, 75 % relative humidity, light regime: LD = 16 : 8) at three intervals during one year. The mean developmental time decreased in both populations from March 1996 to November 1996 about 18.5 % (European population) respectively 10.8 % (Australian population). But no significant changes of the mean developmental time occurred comparing the two different populations at any time interval during the year.
- The influence of three different constant temperatures (15 °C, 23 °C, 32 °C) on the development of postembryonic stages of *F. occidentalis* was tested. Mean developmental times (± SD) were 518.3 h ± 46.0 (15 °C), 217.1 h ± 27.5 (23 °C), and 173.3 h ± 13.2 (32 °C). The mean developmental time at 15 °C was approximately three times longer than the developmental time at 32 °C. The time decreased about 58.1 % from 15 °C to 23 °C and 20.2 % from 23 ° to 32 °C. Larval development took longer at the three temperatures with the second instar larvae showing greatest variability.
- The development of life stages of *E. americanus* was monitored. The mean developmental time was 185.5 h ± 9.7. The longest developmental time was recorded in the first instar larva with 63.7 h ± 8.4 or 34.3 % total developmental time.
- *E. americanus* showed the lowest mortality rate with 10.4 % (over all stages, at 23 °C). Mortality rate for *F. occidentalis* was 69.5 % at 23 °C.
  The surviving rate of *F. occidentalis* at different temperatures was also documented. *F. occidentalis* had the lowest mortality at 15 °C (50.4 %), and 81.9 % mortality at 32 °C, where only 18.1 % of the specimens became adults.
- Ultrastructural investigations of tospovirus-infected and non-infected tissue of *F. fusca* did not reveal any cytological differences between infected and non-infected tissue.
- Immunogold-labeling of putative receptor sites for tospoviruses within the midgut of the thrips were observed at the microvilli and basal membrane as well as the muscle cells lining the midgut in larval and adult stages of *F. occidentalis*.

(2) Progenesis

- Ovaries in the larval stages appear in all three examined thrips species (*F. occidentalis*, *E. americanus*, and *S. linguis*) as a pair of sac-like structures and do not show a distinct differentiation into ovarioles. The ovaries of the first instar larvae only consist of the germarium, whereas in second instar larvae three different zones are distinguishable in the ovaries. The late second instars of *S. linguis* already show a slight arrangement of the forming ovarioles (columns). The actual differentiation of the ovarioles takes place during propupal and pupal stage in all three species. Each ovary becomes divided into four ovarioles, which is finished a short time before the adult hatches.
- Spermatogenesis of species examined shows several differences between the two suborders of Thysanoptera. Spermatogenesis starts in both suborders with the immature stages and is finalized before the adult emerges in Terebrantia (*F. occidentalis*, *E. americanus*), whereas in Tubulifera (*S. linguis*) sperm production is also found during the adult stage.
- The testes of *F. occidentalis* and *E. americanus* consist in all developmental stages as a pair of single cysted testes which means that all germ cells are at the same differentiation stage. In mid-development of the second instar larva the whole of each testis contains functional and pycnotic spermatids. The pycnotic bodies form clusters which move to the periphery where they disintegrate.

During propupal and pupal stage the completion of the differentiation of spermatids into spermatozoa takes place.

- In second instar larvae of *S. linguis*, several cysts are formed in the testis each cyst containing spermatogonia at the same developmental stage. The events taking place in each single cyst are equivalent to that occurring in the whole testis of *F. occidentalis* and *E. americanus*.

(3) Embryogenesis

- The eggs of both *F. occidentalis* and *S. linguis* are relatively large compared to the size of the females that produce them (in *F. occidentalis* the egg is approximately 18.8 % of the total length of the adult female and in *S. linguis* 23.7 %). *F. occidentalis* and *S. linguis* eggs belong to the polylecithale type and the distribution of the yolk is the centrolecithale type. Eggs are enclosed by the vitelline envelope and the chorion.
- Eggs of *F. occidentalis* are on average 279.5 µm ± 6.9 x 128.9 µm ± 16.5. In this species the length and more so the width of the eggs increased during embryogenesis. The length changes slightly, the width increases about 37 %.
- The eggs of *S. linguis* measure 446.0 µm ± 4.8 x 163.3 µm ± 3.7. Compared with *F. occidentalis*, no striking changes of length and width are observable during embryogenesis.
- The average developmental time of an egg in *F. occidentalis* is 95.4 h (approximately 4 d). Survival rate of the eggs was 66 %. In *S. linguis* embryogenesis takes on averages 248.4 h (or 10.4 d), 91 % of the eggs hatched. Compared with *F. occidentalis*, *S. linguis* mortality rate was only 9 %.
- After oviposition, the zygote nucleus subdivides by mitotic divisions. The cleavage energids migrate to the periphery and create the plasmodial preblastoderm.
- The germ anlage develops in the posteroventral region of the eggs due to regional mitotic activity which divides the blastoderm into presumptive embryonic tissue (germ anlage) and extraembryonic cover (serosal layer).
- At approximately 18 h ± 6 h in *F. occidentalis* and 42 h ± 6 h in *S. linguis*, the posterior embryonic cells invaginate into the yolk. The germ band is shifted inside the yolk during the following anatrepsis and becomes elongated. Result is a S-shaped germ band and the embryo separates totally from the serosa and lies with its head-end towards the posterior pole of the egg.
- At 30 h ± 6 h in *F. occidentalis* and 90 h ± 6 h in *S. linguis*, segmentation starts in the thoracic region and proceeds cephalad and caudad (first the antennal and thoracic buds grow followed by the buds of the mouthparts). Shortly before katatrepsis begins, the degeneration of the right mandible takes place.
- Katatrepsis takes approximately 1 h in *F. occidentalis* and 48 h in *S. linguis* encompassing 10.4 % of the total time of embryogenesis in *F. occidentalis* and 19.3 % in *S. linguis*. First sign of katatrepsis is the liquefaction of yolk starting at the anterior and posterior pole of the egg in both *F. occidentalis* and *S. linguis*. The extraembryonic membranes fuse and rupture at the place, where the head of the embryo is situated. The contracted serosal cells locating at the anterior egg pole form the secondary dorsal organ which remains temporarily. Provisional dorsal closure takes place as the amnion rolls back and replaces the serosa covering the yolk and the embryo. The embryo of *S. linguis* rotates at least about 180 ° during katatrepsis, no rotation was observed in *F. occidentalis*.
- The process of organogenesis ranges from the beginning of segmentation and is finished with the ready-to-hatch-larva. The cells of most organs nearly finish their differentiation after katatrepsis. The larval eye pigment becomes visible at approximately 54 h ± 6 h in *F. occidentalis* and 210 h ± 6 h in *S. linguis*.
- Approximately 18 h before hatching in *F. occidentalis* and 24 h in *S. linguis*, the peristalsis in the gut

appears and the prothoracic and cervical muscles start to contract. This serves as initiation for the upcoming hatching process.

The results of this study about reproduction, progenesis, and embryogenesis of thrips represent useful information to answer questions, which are connected with the development of thrips as pests, the growing progress of resistance of these species against insecticides, and the development of suitable pest management strategies. Knowledge about morphology and developmental processes as well as the resulting behaviour and adaptations help to clarify, why some species are highly adapted to their host plant and while others show a broad host plant spectrum, why only a few thrips species act as tospovirus-transmitters, and which are the basics of the development of different social life styles within the order Thysanoptera.

Further studies should focus on investigations of cytological mechanisms taking place during oogenesis and spermatogenesis and on the mechanisms underlying the different types of parthenogenesis in thrips and their control using molecular and biochemical methods.

6. Zusammenfassung

Die vorliegende Arbeit präsentiert Ergebnisse zu verschiedenen Aspekten der Biologie einschließlich Morphologie und Entwicklung von Thripsen. Ziel war es durch die Einbeziehung verschiedener Methoden, die unterschiedlichen Möglichkeiten und Fähigkeiten verschiedener Thripsarten hinsichtlich Reproduktion und Embryogenese und der zugrundeliegenden morphologischen und entwicklungsbiologischen Mechanismen darzustellen. Schwerpunktmäßig wurden folgende Themenbereiche bearbeitet:

(1) **Reproduktion** von Thripsen. Hierbei wurden Daten zum Geschlechterverhältnis verschiedener Thripsarten der beiden Unterordnungen der Thysanoptera (Terebrantia und Tubulifera) und dessen Beeinflussung durch unterschiedliche Parameter, zum Kopulations- und Ovipositionsverhalten und zur Morphologie der äußeren und inneren Geschlechtsorgane ermittelt. Außerdem wurden Lifetables der beiden Schaderregerarten *Frankliniella occidentalis* und *Echinothrips americanus* erstellt und Daten der tospo-virusübertragenden Thripsarten *Frankliniella fusca* und *F. occidentalis* ermittelt.

(2) Auf der Grundlage von histologischen Untersuchungen wurde im Kapitel **Progenese** die Entwicklung der Geschlechtsorgane von *F. occidentalis*, *E. americanus* und *Suocerathrips linguis* dargestellt.

(3) Zur Beschreibung der **Embryogenese** von *F. occidentalis* und *S. linguis* wurden Daten zur Eimorphologie, Entwicklungsdauer und Mortalitätsrate erfasst und die Embryogenese der beiden Vertreter der Terebrantia und Tubulifera mittels histologischer Untersuchungen und Videodokumentation vergleichend dargestellt.

Die Ergebnisse lassen sich wie folgt zusammenfassen:

(1) Reproduktion

- Die Daten, die zur Reproduktion verschiedener Thripsarten (vor allen von *F. occidentalis*, *E. americanus* und *S. linguis*) gewonnen wurden, verdeutlichen die Mannigfaltigkeit der unterschiedlichen Reproduktionsformen und Verhaltensweisen, die innerhalb der Ordnung der Thysanoptera existieren.
- Es wurde der Sexualindex von vier Thripsarten bestimmt, *F. occidentalis* (Thripidae, Thripinae), *E. americanus* (Thripidae, Thripinae), *Parthenothrips dracaenae* (Thripidae, Panchaetothripinae) und *S. linguis* (Phlaeothripidae, Phlaeothripinae). Das Geschlechterverhältnis (Weibchen : Männchen) belief sich auf 1 : 0,9 für *F. occidentalis* (n = 145), 1 : 0,26 für *E. americanus* (n = 123) und 1 : 0,5 für *S. linguis* (n = 197). Innerhalb der untersuchten Individuen von *P. dracaenae* wurde ein ♂ nachgewiesen (n = 175).
- Die ermittelten Werte unterstreichen die unterschiedlichen Reproduktionsstrategien, die Thripse verfolgen. Außerdem korrespondieren die Ergebnisse mit den unterschiedlichen Parthenogenese-typen der Arten.
- Des weiteren wurde der Sexualindex von *F. occidentalis* unter dem Einfluss von drei konstanten Temperaturen (15 °C, 23 °C, 30 °C) getestet. Die ermittelten Werte ergaben, dass sich mit steigender Temperatur das Geschlechterverhältnis zu einem mehr Weibchen-dominierenden Verhältnis verschob. Das Geschlechterverhältnis belief sich bei 15 °C auf 1 : 1,2 (Weibchen : Männchen), bei 23 °C auf 1 : 0,9 (Weibchen : Männchen) und bei 30 °C auf 1 : 0,5 (Weibchen : Männchen).

- In einem weiteren Experiment wurde die Anzahl weiblicher und männlicher Nachkommen bestimmt, die aus unbefruchteten Eiern von *F. occidentalis* (gehalten unter konstanten Bedingungen und drei verschiedenen Temperaturen: 15 °C, 23 °C, 30 °C) und *E. americanus* (gehalten unter konstanten Bedingungen und 23 °C) entstehen. Interessanterweise wurden bei den Versuchen mit *F. occidentalis* bei allen drei Temperaturen jeweils einige Weibchen nachgewiesen, die aus unbefruchteten Eiern entstanden (2 ♀♀ bei 15 °C, n = 360; ein ♀♀ bei 23 °C, n = 116; zwei ♀♀ bei 30 °C, n = 540) (trotz arrhenotoker Parthenogenese). Bei *E. americanus* bestand der gesamte getestete Nachwuchs unbefruchteter Weibchen ausschließlich aus Männchen.
- Verglichen mit *S. linguis* wurden bei *F. occidentalis* sehr kurze Kopulationszeiten von wenigen Minuten (durchschnittlich 3,5 min) beobachtet. Bei *S. linguis* dauerten Kopulationen bis zu mehreren Stunden. *F. occidentalis* Weibchen verweigern, nachdem sie erfolgreich mit einem Männchen kopuliert haben, weitere Kopulationen.
- In *S. linguis* Populationen gibt es sowohl Weibchen als auch Männchen mit verkürzten, „abgeschnittenen" Flügeln. Es wurde beobachtet, dass das „Abschneiden" während der Kopulation erfolgt. Da Individuen mit abgeschnittenen Flügeln nicht länger in der Lage sind, sich aktiv zu verbreiten, wird damit sichergestellt, dass die in der Kolonie erzeugten Nachkommen dort geboren und aufgezogen werden. Die so in der Kolonie verbleibenden Imagines stellen außerdem einen gewissen Schutz für die preimaginalen Stadien dar, wodurch ermöglicht wird, dass ein hoher Prozentsatz der Nachkommenschaft überlebt.
- *F. occidentalis* Weibchen legen ihre Eier mit Hilfe eines orthopteroiden Ovipositors einzeln in das Pflanzengewebe. Sie beginnen mit der Eiablage ungefähr einen Tag, nachdem sie geschlüpft sind. Die durchschnittliche Eianzahl, die von einem Weibchen pro Tag produziert wurde, betrug 4,9 ± 2,4 Eier. Während ihres gesamten Lebens legte ein Weibchen im Durchschnitt 75,6 ± 52,4 Eier. Die durchschnittliche Lebensdauer eines *F. occidentalis* Weibchens betrug 9,8 ± 6,5 Tage, das älteste Weibchen wurde 32 Tage alt.
- *S. linguis* Weibchen legen ihre Eier am Grund der Blätter von *Sansevieria trifasciata* ab. Die Eier werden von den Weibchen einzeln abgelegt. Nach der Oviposition werden die Eier von den Imagines (mit Hilfe der vorderen Extremitäten) zusammengebracht, so dass letztlich alle Eier auf einem Haufen liegen. In Gruppen von adulten *S. linguis* (bestehend aus zehn Weibchen und fünf Männchen), die für die Gewinnung von Embryonalstadien mit definiertem Alter gehalten wurden, begannen die Weibchen in allen beobachteten Gruppen (n = 26) erst nach 14-18 Tagen mit der Oviposition. Dies lässt den Schluss zu, dass die Weibchen die Möglichkeit haben, ihr Ovipositionsverhalten zu steuern, was die Möglichkeit eröffnet, erst unter geeigneten Bedingungen mit der Eiablage zu beginnen.
- Der Ovipositor ist bei den Weibchen von *F. occidentalis* und *E. americanus*, die beide zu der Unterordnung Terebrantia gehören, aus dem Basalapparat (Valvifers und Basalvalvulae) und dem Schaft zusammengesetzt. Die Abdominaltergite IX bis X bilden eine schützende Hülle für den Ovipositor.
- Im Gegensatz dazu besitzen *S. linguis* Weibchen einen weniger gut ausgebildeten Ovipositor. Die Morphologie der äußeren weiblichen Geschlechtsorgane korrespondiert mit dem Ovipositionsverhalten der untersuchten Arten. *F. occidentalis* und *E. americanus* bringen ihre Eier mit Hilfe des sägeförmigen Ovipositors in das Pflanzengewebe ein, während *S. linguis* Weibchen die Eier auf das Pflanzengewebe legen.
- Die histologisch untersuchten Thripsarten *F. occidentalis*, *E. americanus* und *S. linguis* besitzen jeweils ein Paar panoistischer Ovarien. Pro Ovar sind vier Ovariolen ausgebildet. Jedes Ovar setzt sich in einen Oviductus lateralis fort. Die Oviducti laterali verbinden sich zu einem gemeinsamen

Oviductus, der sich posterior in die Vagina öffnet. Die untersuchten Terebrantia-Arten besitzen eine Anhangsdrüse.

- Die Ovariolen von *F. occidentalis* und *E. americanus* sind in fünf Zonen unterteilbar. Zone I bildet das Terminalfilament, Zone II das Germarium und im Vitellarium sind drei verschiedene Zonen (Zone IIIa, IIIb, IIIc) differenzierbar. Die Oozyten in Zone IIIa sind relativ klein und messen in *F. occidentalis* zwischen (Minimum-Maximum) 15 µm - 37.5 µm x 12.5 µm - 20 µm. Zone IIIb ist erkennbar am previtellogenen Wachstum der Oozyten und basophilen Dotter. In Zone IIIa findet das vitellogene Wachstum der Oozyten statt und der Dotter erscheint azidophil. Bei *S. linguis* sind innerhalb des Vitellariums nur zwei verschiedene Zonen unterscheidbar.
- Die durchschnittliche Anzahl der Oozyten pro Ovariole wurde bestimmt, um herauszufinden, ob es zwischen der Anzahl der Oozyten pro Ovariole und der Lebensweise der Thripse einen Zusammenhang gibt. Für *F. occidentalis* ergab sich eine durchschnittliche Anzahl von 8,6 ± 0,8 Oozyten pro Ovariole, für *E. americanus* von 5,9 ± 0,2, für *A. intermedius* von 11,3 ± 0,7 und für *S. linguis* von 4,5 ± 0,3. Diese Ergebnisse lassen einen Bezug zwischen unterschiedlichen Reproduktionsstrategien und der Anzahl der Oozyten im Ovar erkennen und demnach auch der Fähigkeit des Weibchens, wieviel Eier gelegt bzw. wieviel Nachkommen erzeugt werden können. Sowohl *A. intermedius* (Predator) als auch *F. occidentalis* (Schaderreger vieler Kulturpflanzen) scheinen das Ziel zu verfolgen, in möglichst kurzer Zeit eine hohe Anzahl von Nachkommen hervorzubringen. Demgegenüber besitzen Weibchen von *S. linguis* nur eine relativ geringe Anzahl von Oozyten pro Ovariole. In der gleichen Zeit produziert ein einzelnes Weibchen von *S. linguis* dadurch weniger Nachkommen als *A. intermedius* oder *F. occidentalis*. *S. linguis* zeigt eine subsoziale Lebensweise. Die Imagines investieren mehr in die Aufzucht der Nachkommen, wodurch sichergestellt wird, dass trotz geringer Eizahl genügend Nachkommen überleben.
- In der Spermatheka der *F. occidentalis* und *E. americanus* Weibchen sind die Spermien spermatophorenartig angeordnet. Demgegenüber sind die Spermien in der Spermatheka von *S. linguis* loser verteilt und lassen keine spermatophorenartige Struktur erkennen. Vielmehr ließe die Anordnung vermuten, dass die Spermien während der Kopulation einzeln übertragen werden.
- Die Männchen der untersuchten Thripsarten (*F. occidentalis*, *E. americanus*, *S. linguis*) besitzen einen extrusiblen Phallus in einer Genitalkammer am neunten Abdominalsegment.
- Die paarigen Testes von *F. occidentalis* und *E. americanus* (Terebrantia) bestehen aus jeweils einer einzelnen Zyste oder Kammer, die Keimzellen des gleichen Entwicklungsstadiums enthalten. Im Gegensatz dazu bestehen die Hoden von *S. linguis* Männchen (Tubulifera) aus mehreren Zysten, die Keimzellen verschiedener Differenzierungsstadien enthalten. In den Testes einer anderen Tubulifera-Art, *Bactrothrips brevitubus*, wurden hingegen nur reife Spermien gefunden.
  Testes gehen caudal in die Vasa deferentia über. Der Vas deferens endet posterior in einem Seminalvesikel.
- Während *F. occidentalis* und *E. americanus* ein Paar Anhangsdrüsen besitzen, weisen die Männchen von *S. linguis* zwei Paare auf.
- Die Entwicklungszeiten der postembryonalen Stadien von zwei unterschiedlichen *F. occidentalis* Populationen (Halle und Perth) wurden unter konstanten Bedingungen (23 °C, 75 % relative Luftfeuchte, Lichtregime: LD = 16 : 8) während drei verschiedener Zeiten im Jahr bestimmt. Die durchschnittliche Entwicklungszeit verkürzte sich in beiden Populationen von März 1996 bis November 1996 um 18,5 % in der Population aus Halle bzw. um 10,8 % in der Population aus Perth. Vergleicht man die postembryonalen Entwicklungszeiten der einzelnen Stadien der beiden Populationen, so sind keine deutlichen Unterschiede (hinsichtlich der Dauer der Stadien) zwischen den Populationen zu erkennen.

- Der Einfluss von drei konstanten Temperaturen (15 °C, 23 °C, 32 °C) auf die Entwicklungszeiten der postembryonalen Stadien von *F. occidentalis* wurde bestimmt. Die durchschnittlichen Entwicklungszeiten (vom Schlupf der Erstlarve bis zum Schlupf der Imago) betrugen 518,3 h ± 46,0 (15 °C), 217,1 h ± 27,5 (23 °C) und 173,3 h ± 13,2 (32 °C). Damit war die durchschnittliche Entwicklungsdauer bei 15 °C ungefähr dreimal so lang wie die Entwicklungszeit bei 32 °C. Die Dauer verkürzte sich um 58,1 % von 15 °C auf 23 °C und um 20,2 % von 23 °C auf 32 °C. Die Entwicklungszeit des zweiten Larvalstadiums war bei allen drei getesteten Temperaturen am längsten. Außerdem zeigte das zweite Larvalstadium verglichen mit den anderen Ontogensestadien die größte Variabilität hinsichtlich der Entwicklungsdauer.
- Für *E. americanus* wurde ebenfalls ein Lifetable erstellt. Die durchschnittliche Entwicklungszeit betrug 185,5 h ± 9,7 (23 °C, 75 % relative Luftfeuchte, Lichtregime: LD = 16 : 8) und war verglichen mit *F. occidentalis* um 13 % verkürzt. Die Erstlarve war mit 63,7 h ± 8,4 oder 34,3 % der Gesamtdauer der postembryonalen Entwicklung das längste Stadium.
- Vergleicht man die Mortalitätsraten von *F. occidentalis* und *E. americanus* fällt auf, dass die Mortalitätsrate der postembryonalen Stadien von *E. americanus* mit 10,4 % sehr viel niedriger als diejenige von *F. occidentalis* mit 69,5 % ist (Haltungsbedingungen: 23 °C, 75 % relative Luftfeuchte, LD = 16 : 8). Außerdem war die Mortalitätsrate bei *F. occidentalis* von der Temperatur abhängig. *F. occidentalis* zeigte die niedrigste Mortalitätsrate von 50,4 % bei 15 °C und die höchste Rate mit 81,9 % bei 32 °C.
- Die ultrastrukturelle Untersuchung von tospovirus-infiziertem und nicht-infiziertem Gewebe von *F. fusca* ergab keine zytologischen Unterschiede zwischen infiziertem und nicht-infiziertem Gewebe. Labeling mit polyklonalem Antikörper gegen einen möglichen Rezeptor für den Virus wurde im Mitteldarm vorrangig an den Mikrovilli sowie der Basalmembran und den Muskelzellen larvaler und adulter Stadien von *F. occidentalis* gefunden.

(2) Progenese

- Die Ovarien erscheinen in den Larvalstadien bei allen drei untersuchten Arten (*F. occidentalis*, *E. americanus*, *S. linguis*) als paarige Strukturen, die keine sichtbare Differenzierung in Ovariolen aufweisen. Die Ovarien in der Erstlarve bestehen nur aus dem Germarium, wohingegen in der Zweitlarve drei verschiedene Zonen mit Oogonien auf jeweils unterschiedlichem Entwicklungsniveau unterscheidbar sind. Späte Zweitlarven von *S. linguis* (kurz bevor Propuppe schlüpft) zeigen bereits eine Anordnung der Oozyten, welche auf die sich später bildenden Ovariolen hindeutet. Die eigentliche Differenzierung der Ovariolen findet bei allen drei Arten während der Metamorphosestadien statt. Jedes Ovar wird in vier Ovariolen unterteilt. Kurz bevor der Imago schlüpft, ist die Differenzierung der Ovariolen abgeschlossen.
- Hinsichtlich der Spermatogenese zeigen die Vertreter der beiden Unterordnungen der Thysanoptera Terebrantia (*F. occidentalis* und *E. americanus*) und Tubulifera (*S. linguis*) mehrere Unterschiede. Spermatogenese beginnt in beiden Unterordnungen in den Larvalstadien und ist bei den Terebrantia kurz vor der Häutung zum Imago beendet, wohingegen in der untersuchten Tubulifera-Art, *S. linguis*, Spermienproduktion auch im adulten Stadium zu beobachten ist. Dies konnte für eine andere Tubulifera-Art, *B. brevitubus*, nicht bestätigt werden. Hier war die Spermatogenese im Adultstadium, wie bei *F. occidentalis* und *E. americanus,* abgeschlossen. Die Testes enthalten reife Spermienbündel, die auf eine Unterteilung in Zysten während der postembryonalen Stadien hindeuten.
- Bei *F. occidentalis* und *E. americanus* stellen die Testes in allen Entwicklungsstadien ein Paar einzelner Zysten dar, was bedeutet, dass die Keimzellen stets auf dem gleichen Entwicklungsstand

sind. Ungefähr in der Mitte des Zweitlarvenstadiums enthalten die Testes funktionelle und pyknotische Spermatidien. Die pyknotischen Körper bilden Cluster, wandern zur Peripherie und werden abgebaut. Während des Propuppen- und Puppenstadiums wird die Differenzierung der Spermatiden zu Spermatozoen abgeschlossen.

- In der Zweitlarve von *S. linguis* enthält jeder Testis mehrere Zysten, die jeweils Spermatogonien des gleichen Entwicklungsstadiums enthalten. Die Ereignisse, die in jeder einzelnen Zyste stattfinden, sind äquivalent zu den Ereignissen im gesamten Hoden von *F. occidentalis* und *E. americanus*.

(3) Embryogenese

- Die Eier von *F. occidentalis* und *S. linguis* sind verglichen mit der Größe der Weibchen, die sie produzieren, relativ groß. In *F. occidentalis* erreichen die Eier 18,8 % der durchschnittlichen Länge eines Weibchens und in *S. linguis* 23,7 %. Betrachtet man die Menge an Dotter, so gehören die Eier der untersuchten Thripsarten zum polylecithalen Typ. Hinsichtlich der Verteilung des Dotters sind sie zum centrolecithalen Typ zu rechnen. Die Eier sind von einer Vitellinmembran und dem Chorion umschlossen.
- Die durchschnittliche Größe der Eier von *F. occidentalis* beträgt 279,5 µm ± 6,9 x 128,9 µm ± 16,5. Länge und Breite der Eier nehmen während der Embryogenese zu. Während sich die Länge nur leicht ändert, vergrößert sich die Breite um 37 %.
  Die Eier von *S. linguis* messen 446,0 µm ± 4,8 x 163,3 µm ± 3,7. Es treten keine deutlichen Veränderungen in der Länge und Breite während der Embryonalentwicklung auf.
- Die durchschnittliche Dauer der Embryonalentwicklung beträgt bei *F. occidentalis* 95,4 h (ungefähr vier Tage). Die Überlebensrate der Eier betrug 66 %.
  S. linguis weist eine durchschnittliche Embryogenesedauer von 248,4 h (oder 10,4 d) auf. 91 % der Eier entwickelten sich zur Erstlarve. Die Mortalitätsrate war somit - verglichen mit der von *F. occidentalis* (34 %) - sehr gering.
- Nach der Oviposition teilt sich der Nukleus des Eies bei *F. occidentalis* und *S. linguis* mitotisch. Die Teilungsenergiden wandern zur Peripherie und bilden das plasmodiale Präblastoderm.
- Die Keimanlage entwickelt sich in der posteroventralen Region des Eies, wobei sich durch mitotische Aktivität das Blastoderm in presumptives embryonales Gewebe (Keimanlage) und die extraembryonale Hülle (Serosa) differenziert.
- Nach ungefähr 18 h ± 6 h in *F. occidentalis* und ca. 42 h ± 6 h in *S. linguis* invaginieren die posterioren embryonalen Zellen in den Dotter. Das Keimband wird während der folgenden Anatrepsis in den Dotter verlagert und verlängert sich. Das Ergebnis ist ein S-förmiges Keimband. Der Embryo separiert sich von der Serosa, der Kopf ist dem posterioren Pol des Eies zugewandt.
- Die Segmentierung beginnt mit ca. 30 h ± 6 h bei *F. occidentalis* und 90 h ± 6 h bei *S. linguis* in der thorakalen Region und setzt sich cephalad und caudad fort. Zuerst erscheinen die Knospen der Antennen und Extremitäten gefolgt von den Mundwerkzeugen. Kurz vor der Katatrepsis findet die Degeneration der rechten Mandibel statt.
- Die Katatrepsis dauert zwischen ungefähr 1 h bei *F. occidentalis* und ca. 48 h bei *S. linguis*, was 10,4 % der Gesamtembryogenesedauer bei *F. occidentalis* und 19,3 % bei *S. linguis* entspricht. Das erste Anzeichen für die Katatrepsis ist die Verflüssigung des Dotters, welche sowohl bei *F. occidentalis* als auch bei *S. linguis* am anterioren und posterioren Eipol beginnt. Die extraembryonalen Hüllen fusionieren und reißen an der Stelle, wo sich der Kopf des Embryos befindet, auf (posteriorer Pol). Die kontrahierten Serosazellen, die sich am anterioren Eipol befinden, bilden das sekundäre Dorsalorgan, welches bei beiden Arten für eine Weile erhalten

bleibt. Der provisionale Dorsalschluss erfolgt, indem sich das Amnion zurückrollt, die Serosa ersetzt und dabei den Dotter und den Embryo umschließt. Während der Embryo von *S. linguis* eine Drehung um wenigstens 180 ° erfährt, findet bei *F. occidentalis* keine Drehung des Embryos während der Katatrepsis statt.

- S Der Prozess der Organogenese umfasst die Zeitspanne vom Anfang der Segmentierung bis zur schlupfreifen Prolarve. Die Zellen der meisten Organe haben nach der Katatrepsis ihre Differenzierung fast abgeschlossen. Außerdem wird das larvale Augenpigment nach 54 h ± 6 h bei *F. occidentalis* und nach 210 h ± 6 h bei *S. linguis* sichtbar.
- S Ungefähr 18 h (*F. occidentalis*) bzw. 24 h (*S. linguis*) bevor die Erstlarve schlüpft, setzt die Peristaltik im Darm ein und die cervicalen Muskeln beginnen sich zu kontrahieren. Damit wird der Schlupfvorgang eingeleitet.

Die Ergebnisse der vorliegenden Arbeit zu Reproduktion, Progenese und Embryogenese von Thripsen liefern Bausteine für die Beantwortung von Fragen, die im Zusammenhang mit der Entwicklung von Thripsen als Schaderreger, der zunehmenden Entwicklung von Resistenzen gegenüber Insektiziden und damit auch der Entwicklung von geeigneten Bekämpfungsmethoden stehen.

Wissen zur Morphologie und Entwicklung und der daraus resultierenden Anpassungen und Verhaltensweisen hilft darüber hinaus bei der Klärung der Fragen, warum verschiedene Thripsarten so eng an ihre Wirtspflanzen angepaßt sind, andere ein breites Wirtsspektrum besitzen, wieso nur einige wenige Arten als Virusüberträger fungieren und welches die Grundlagen für die Entwicklung verschiedener sozialer Formen innerhalb der Ordnung Thysanoptera sind.

Im Mittelpunkt zukünftiger Untersuchungen sollte u.a. die Klärung zytologischer Zusammenhänge während der Oogenese und Spermatogenese stehen. Des weiteren sind Arbeiten zu den der Reproduktion zugrundeliegenden parthenogenetischen Mechanismen und deren Steuerung notwendig.

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