Reproductive strategies in *Latrodectus revivensis* (Araneae; Theridiidae): functional morphology and sexual cannibalism

I n a u g u r a l - D i s s e r t a t i o n

zur

Erlangung des Doktorgrades der

Mathematisch-Naturwissenschaftlichen Fakultät

der Heinrich-Heine-Universität Düsseldorf

vorgelegt von

Bettina Berendonck

aus: Duisburg

Düsseldorf 2003

Gedruckt mit der Genehmigung der
Mathematisch-Naturwissenschaftlichen Fakultät
der Heinrich-Heine-Universität Düsseldorf

Referent: Prof. Dr. Hartmut Greven

Korreferent: Prof. Dr. Klaus Lunau

Tag der mündlichen Prüfung: 05. Juni 2003

Contents

1. Introduction

Over the last decades, numerous empirical and experimental studies have shown that sexual conflict arising from divergent interests in reproduction by male and females is a decisive force in the evolution of male and female reproductive strategies (Trivers 1972; Dawkins 1976; Parker 1979; Andersson & Iwasa 1996; Stockley 1997; Chapman *et al*. 2003). Since Darwin (1871), it is generally believed that a male should try to increase his reproductive success by mating with numerous females to fertilise a maximum number of eggs (Bateman 1948; Trivers 1972). Thus, selection will favour traits that avoid sperm competition, e. g. by reducing the probability that their sperm will overlap spatially and/or temporally with those stored from previous males and by reducing the probability that the female(s) will remate with rival males (Simmons 2001). A female, in contrast, is expected to maximise mate 'quality' by choosing the best possible mate (Bateman 1948; Andersson 1994; Birkhead & Møller 1998). Female choice might be direct (discrimination between individual males) or indirect (restriction of an individual's set of potential copulation partners) (Wiley & Poston 1996). Additionally, direct and indirect choice can occur during the precopulatory, postcopulatory but prefertilisation and postfertilisation stages of reproduction (Cunningham & Birkhead 1998). The mating preferences of the female might be favoured indirectly (genetically by the Fisher process (sexy sons) (Fisher 1930) and/or the good genes process (handicap principle) (Zahavi 1975; but see Kokko *et al*. 2002) or directly (e.g. nuptial gifts, parental care, fewer parasites etc.) by sexual selection (Chapman *et al*. 2003). In the last decades additional benefits for female fitness from multiple matings with different males, beside receiving sufficient amounts of viable sperm, have been suggested (e.g. 'avoiding genetically incompatible sperm', Zeh & Zeh 1996, 1997; Jennions 1997; 'genetic diversity' and 'genetic benefits', see Yasui 1998 for references; 'bet-hedging strategy' Watson 1998; 'insurance against first male's infertility', Schneider & Elgar 1998; 'inbreeding avoidance', Tregenza & Wedell 2002; see reviews Keller & Reeve 1998; Jennions & Petrie 2000; Arnqvist & Nilsson 2000; Zeh & Zeh 2001). However, the intersexual conflict is reflected by the different strategies by which males or females try to maximise their reproductive success. These strategies involve the evolution of various morphological, physiological and behavioural characteristics (Thornhill & Alcock 1983; Smith 1984; Birkhead and Møller 1998).

Sexual cannibalism by the large females of their tiny mates in black widow spiders represents one of the best-known examples showing that the reproductive interests of females and males do not necessarily coincide. However, spiders in general provide a large potential for conflict over mating, since males are generally able to mate more than once and females can store sperm over long periods (Austad 1984; Elgar 1998; Schneider & Lubin 1998). Additionally, females frequently mate with more than one male (Jackson *et al*. 1981). For example, Watson (1998) was able to show that mate number and mate size were positively related to offspring growth rates and the size of the offspring in *Neriene litigiosa* (Linyphiidae).

In species where the female mates more than once, sperm priority patterns have important implications for the mating behaviour of both sexes. According to their gross reproductive anatomy araneomorphs can be roughly divided into two groups (Austad 1984; see details in Uhl 2002). In Haplogynae one duct, and in Entelegynae two ducts connect to each spermatheca. In Haplogynae, the spermatozoa have to pass through the same duct during insemination and oviposition. Since in most spiders spermatozoa are encapsulated by a protein coat and are thus immobile (Lopez 1987; see Foelix 1996 and citations therein) the last sperm to enter should be the first to leave. This 'cul-de-sac' condition would represent a 'last in-first out' system (Austad 1984), resulting in last male sperm priority. In Entelgynae the copulatory duct leads towards the spermatheca and a separate fertilisation duct connects to the uterus externus. In multiple-mated females with a typical 'conduit' type spermatheca, the first male's sperm would lie closest to the exit ('first in-first out') and a first male sperm priority would be expected (Austad 1984). As a consequence of Austad's hypothesis, haplogyne species ('last in-first out') are predicted to guard females after copulation and enetelegyne species ('first in - first out') before copulation. However, a study on correlation between spermathecal morphology and the mating system in several spiders only provided limited confirmation of these predictions (Eberhard *et al*. 1993). Examinations of female genital morphology (see summary in Uhl 2002) was able to show that the 'conduit' spermatheca of several entelegyne spiders may functionally be of the 'cul-de-sac' type instead. Consequently, the anatomy of the female reproductive tract needs to be examined in detail to reveal to what degree it follows a 'cul-de-sac' or a 'conduit' design (Uhl 2002) and, thus, has possible implications for the mating strategies.

However, a few authors studying sperm usage patterns, for example, have stressed the general importance of the pure number of spermathecae (e.g. Bukowski & Christenson 1997, 2000; Yoward & Oxford 1997; Bukowski *et al*. 2001). Males usually have to dismount and perform additional courtship sequences before possibly achieving a second bout with the same female. Often males are only allowed to inseminate one spermatheca, thus not fully utilising the (usually) two spermathecae available (Yoward & Oxford 1997). Rejecting males after the first copulation bout and letting a second, and maybe better, male fill the second spermatheca may represent a female strategy to gain additional control over fertilisation (e.g. as a bet-hedging strategy, Watson 1991; Yoward & Oxford 1997). In general, females might reject unwanted males through covert or evasive behaviour, for example by not assuming the mating posture or simply moving away (Bukowski *et al*. 2001).

Although seldom discussed in the context of mate rejection ('mate rejection hypothesis': female choice by precopulatory sexual cannibalism; Elgar & Nash 1988), sexual cannibalism may represent the most extreme form of female choice in spiders. Alternative explanations for the evolution of sexual cannibalism in favour of the female are the 'economic model' (precopulatory cannibalism as an adaptive foraging decision; Newman & Elgar 1992) and the 'feeding opportunism hypothesis' (pre- and postcopulatory cannibalism as an adaptive foraging decision; Andrade 1998). Other non-adaptive models that attempt to explain the evolution of cannibalism are the 'mistaken identity hypothesis' (the female mistakes the male for prey; see Robinson 1982; Gould 1984; Elgar 1992) and the 'aggressive-spillover hypothesis' (based on the assumption that sexual cannibalism has evolved as an indirect result of selection for high and non-discriminate aggression during previous ontogenetic stages; Arnqvist & Henriksson 1997; Johnson 2001; Schneider & Elgar 2002).

However, more cryptic mechanisms inside the female body after insemination may influence reproductive success in favour of certain males ('cryptic female choice' *sensu* Eberhardt 1996; Telford & Jennions 1998). For spiders it has been suggested that females might be able to bias paternity by selectively activating spermatozoa through secretions produced by specialised glands surrounding the sperm storage sites (spermathecae or uterus externus) (see summary in Uhl 2002). Another form of cryptic female choice through controlled movement of internal structures by specialised

muscles has only been suggested for insects thus far (Villavaso 1975). Physical resistance to further matings through hardening of the genital tract shortly after the first copulation in *Nephila clavipes* (Tetragnathidae; Higgins 1989) might represent another female adaptation functioning to reduce male-imposed limitations (Herberstein *et al*. 2002).

Similarly, male spiders have developed numerous adaptations to prevent male-male competition or override female choosiness. Males may fight off rival males in direct male-male combat (Austad 1983: Whitehouse 1991). The latter might also occur when males try to keep other males from copulating with the same female by pre-or postcopulatory mate guarding (Toft 1989; Prenter *et al*. 1994c). Watson (1986) was able to demonstrate that reduction of the female's web, and thereby the female pheromones on it, reduces the female's attractiveness to rival males. Sperm competition (*sensu* Parker 1970) is likely to occur over ejaculate size (see Bukowski *et al*. 2001) or by extruding rival males spermatozoa (Uhl 2002), for example. Males in some species are known to plug the entrance of the atrium or the copulatory ducts of the female by secretion or with broken-off parts of their pedipalps, thereby keeping other males from successfully transferring their own spermatozoa (see Tab. 5, chapter 4. 3. 4. 2.).

Other male strategies aim to manipulate the female's morphology, physiology and/or behaviour. Generally, the suppression of non-sexual responses is widely accepted as the major function of spider courtship (Barth 1982; Krafft 1982; Robinson 1982). Female physiology might be altered in such a way that she becomes completely cataleptic (Breene & Sweet 1985; Heeres 1991; Knoflach & van Harten 2002) either through vibrations and/or silk-borne pheromones produced by the male himself ('complementary pheromones', see Ross & Smith 1979; Lopez 1987). Other strategies to avoid a female attack might be the provision of a nuptial gift (Bristowe 1958; Austad & Thornhill 1986; Nitsche 1999) or 'opportunistic matings', i.e. the male only approaches the female after she has caught a prey item (Prenter *et al*. 1994b) or before her soft cuticle has hardened after her last moult (Robinson & Robinson 1980). Restricting the female's mobility by throwing strands of silk over her before copulation may prevent subsequent attacks ('bridal veil' Bristowe 1958; Breene & Sweet 1985). Furthermore, vibrations produced by the courting male may directly signal male quality and influence female choice (e.g. Parri *et al*. 1997). Eberhard (1985) assumed that the

genitalia of the male may function as 'internal courtship' devices that stimulate the female during copulation.

Furthermore, substances transferred with the seminal fluids (Gillot 1988) or the male hemolymph (see below) might reduce or even inhibit the female's receptivity of further males. Male redback spiders (*Latrodectus hasselti*), for example, are able to reduce the likelihood that the female will remate by sacrificing their own body (Andrade 1996). During copulation the male somersaults onto the female's mouth parts, and the female may puncture his abdomen and feed on him during copulation (Forster 1992, 1995). Buskirk *et al*. (1984) provided a model ('paternal investment model') suggesting that self-sacrifice might represent an adaptive male strategy as long as the male is expected to gain additional paternity benefits and his expected number of matings during his lifetime is low (see Parker 1979; Andrade 2003).

For the present study on male and female reproductive strategies in spiders, I chose the black widow spider *Latrodectus revivensis* (Theridiidae). Males and females can easily be located in the field, as well as maintained and manipulated in the laboratory. *L. revivensis* are expected to maintain a high level of sperm competition, because females store sperm over long periods and males and females are known to copulate with more than one partner, although a single copulation provides enough sperm for all of the egg-sacs of a single female. Additionally, males might be able to plug and monopolise the paired female sperm stores (spermathecae) by breaking off the embolus tip when withdrawing the intromitted part of the pedipalp (embolus) (Wiehle 1961; Bhatnagar & Rempel 1962; Abalos & Báez 1963, 1967; Kaston 1970). The loss of the embolus tips most probably restricts males and females to two successful copulation bouts, consequently increasing the intra- and intersexual conflict. Furthermore, the female's behaviour of frequently cannibalising her mating partner during or after copulation, possibly represents the most extreme example reflecting the conflict between males and females (Parker 1979).

Latrodectus revivensis Shulov, 1948 is an endemic species of southern Israel. It occurs in the central Negev desert and the Arava Valley, areas with an average annual rainfall of < 100 mm (Levy 1998). The spiders have an annual or subannual life cycle. Adults are present from March throughout the summer; first males mature earlier than females. A short time after their last moult, males leave their webs to search for

potential mates. Reproduction takes place from April to September. Egg sacs are produced throughout the summer and autumn (Levy & Amitai 1983) and may contain 60 to 1100 eggs (Shulov 1948). The time between copulation and oviposition takes from six days to eight weeks (personal observations). Emergence from the egg sac occurs within a week or two after oviposition and within 40 days after copulation (Levy & Amitai 1983). Some spiderlings emerge in mid- to late summer. Larger juveniles reach maturity and reproduce early in the summer, and their offspring may mature and produce a second generation in the same summer. Others overwinter as juveniles (Anava & Lubin 1993) or the eggs remain in the eggsac during the winter and hatch the following spring (Lubin *et al*. 1991). Dispersion of the spiderlings takes place by ballooning (Shulov 1948).

Females undergo seven or eight moults (in c. three months) before adulthood, whereas males only take five or six moults (in less than one month). Sexual size dimorphism is pronounced (2.6 to 5.3) with female total body length ranging from 9.0 to 18.5 mm and male total body length ranging from 3.5 to 7.5 mm (see data in Levy & Amitai 1983; Lubin *et al*. 1991; Levy 1998). In relation to body size, the legs of the male are relatively longer than those of the female (see data in Levy & Amitai 1983). The lifespan of adult males in the wild is usually only a few weeks, while the females live for several months.

L. revivensis mainly builds its webs in shrubs. The web of an adult female is constructed at a height of 30 - 60 cm (Szlep 1964). The whole web consists of the retreat, a bridge web, a catching web and the vertical threads (Szlep 1964) (Fig. 1a). The retreat is situated on the shrub and consists of a cone-like upper part and a broad and slightly curved funnel (Shulov & Weissman 1959). The upper part is opaque (Fig. 1b) and covered with material which may include plant material, small pebbles, snail shells, faeces and the carcasses of victims (Lubin *et al*. 1991) (Fig. 1c). The funnel represents a transparent network (Szlep 1964) (Fig. 1d). The bridge web connects the retreat to the catching web and sometimes to neighbouring shrubs (Szlep 1964). From the radially-arranged catching-platform vertical threads are stretched downwards. These so-called ‘gum-foots’ are covered over their last 2 - 5 cm with viscid droplets. Some additional vertical threads are situated beneath the bridge web (Fig. 1b). The food of *L. revivensis*

mainly consists of beetles, bugs and ants as well as isopods and small scorpions and other spiders (Shulov 1948; Shulov & Weissman 1959).

The present study aims to reveal morphological and behavioural characteristics involved in male and female reproductive strategies in *Latrodectus revivensis*, and to examine if common explanations for the evolution of postcopulatory cannibalism in spiders exist. Therefore,

1) I examined the secondary genitalia (pedipalps and epigynum) of virgin males, virgin and mated females, and female after their first oviposition, using light-, scanning- and transmission electron microscopy, to show in how far the shape of the female spermathecae ('the play ground') is able to determine sperm priority patterns, and to reveal further mechanism by which females ('cryptic female choice') and males ('sperm competition') are able to influence who's spermatozoa will actually be used for fertilisation.
2) I conducted a quantitative analysis of the courtship using video recordings (high speed shutter) to complement the hitherto anecdotal descriptions.
3) I conducted controlled matings in the laboratory to determine the frequency of cannibalism, and to check if the probability of being cannibalised (males) or to cannibalise (females) depends on male or female phenotype (size). Additionally, I checked the males for the loss of their embolus tip(s) at different times after the onset of courtship, in order to detect possible differences between cannibalised and non-cannibalised males in regard to the timing of their first mating and the number of copulation bouts achieved with a given female.
4) I collected females during different periods of their reproductive cycle, and counted and compared the number of male embolus tips in their epigyna to determine the remating probability of females in the field.
5) I surveyed the literature on the occurrence of different types of mating plugs in Araneae in order to reveal probable connections with the occurrence of sexual cannibalism.
6) I surveyed the available literature on cannibalism in spiders on a case-by-case basis in order to evaluate whether common explanations for the occurrence of sexual cannibalism in Araneae exist.

2. Material and Methods

2. 1. Animals

Spiders of different mating status were collected in the seasons of 1997, 1998 and 1999 in the vicinity of Sede Boquer (30°50´N:34°46´E) in the central Negev desert, Israel. Then the number of egg sacs in the webs of adult females was recorded. For video recordings of courtship additional subadult specimens were collected in spring 2000 and transported to Düsseldorf, Germany.

In the laboratory, males were kept individually in small plastic containers (height: 5 cm; diameter approx. 10 cm) and provided with water twice or three times a week. Most female were caged in glass aquaria (35 cm x 20 cm x 25 cm). Some females that were not used for mating experiments were kept in plastic containers (height: 15 cm; diameter approx. 12 cm). Females were fed tenebrionid beetles collected in the field, grasshoppers and meelworm beetles (*Tenebrio melitor*) and provided with water two to three times a week.

2. 2. Mating experiments in the laboratory

For mating experiments, only those males that were either taken from their own webs in the field or collected while in a premature state were used. To ensure virginity of the females, I used only those females that were collected as juveniles or subadults. Immature spiders were reared to adulthood. Females were used for mating trials not earlier than three days and not later than eight days after their final moult. Females were allowed to build complete webs in glass aquaria provided with wooden branches. They were fed three times a week and additionally a day before the mating trial. Preliminary experiments showed that the loss of an embolus tip by the male is a reliable indicator of the successful insemination of the female. In cases where the male had not lost an embolus tip after 24 h, the corresponding females were kept in plastic containers and checked for the production of a viable egg sac within the following weeks.

For trials, males were placed at the edge of the female web furthest away from the retreat. The time of onset of courtship was recorded. After 8 h, males were removed carefully from the web with a small paintbrush and checked for the loss of their embolus tips. Thereafter, most males were immediately reintroduced into the female

web and checked again after approx. 24 h after the onset of courtship (n = 40). Some males that had lost one embolus tip after 8 h (n = 10) or 24 h (n = 2) were introduced into another virgin female's web after a recovery period of 2 to 3 days. Cases of cannibalism (dead, wrapped males) and further mutilations of the male pedipalps (loss of adjacent embolus fragments, untangled embolus) were recorded.

Due to unexpected difficulties in the experimental design during the dry season of 1999, the number of specimens that could be used for the different analyses varies. After the mating experiments, males and females were used for further morphological experiments, and leg lengths (patella + tibia of right leg I) were measured when possible (see chapter 2.3.). Since the length of the long, coiled embolus of this species cannot be measured accurately, maximum cymbium width was used as a sexual character for further morphometrical analysis. Therefore, the pedipalps of the males were cut off and the emboli were removed. Afterwards the pedipalps were positioned on the frontal surface and the maximum cymbium width was measured to the nearest 10 µm using an ocular micrometer.

Observations of courtship and copulation were made directly and with the aid of a binocular microscope. Additionally, I observed and videotaped the courtship of three pairs in the laboratory in Düsseldorf for a more detailed analysis.

In this study 'courtship' comprises all actions by the male and the female that take place from as soon as the introduced male reacts to the female web until he tries to hook into the female epigynum to insert his embolus. Coupling attempts and successful coupling followed by intromission of the embolus are rated as parts of the actual 'copulation'. 'Postcopulatory events' are those behaviours recorded after the male has withdrawn his embolus from the female genitalia.

As there is a considerable divergence in the descriptive terminology of movements by males and females during courtship, in this text I have mainly adopted the terms and definitions used by Robinson and Robinson (1980) in their studies of tropical araneid spiders. Supplements and modifications have been made where necessary.

2. 3. Statistics

As the rigid cuticle of a spider leg does not change size after the final moult and its length is independent of the spider's condition, leg length (patella + tibia) of the right leg I of all specimens used for SEM, LM and TEM investigations were measured to the nearest 0.1 mm immediately after dissection. Because body length is closely correlated with leg length (tibia + patella) in *L. revivensis* (r^2 = 0.92, n = 211) (Lubin *et al*. 1991), leg length (tibia + patella) of the first right leg was used as an indicator of male and female body size in all statistical analyses.

Statistical analyses were performed using the programs Systat 9.0 and SigmaPlot 2001. I used the student t-test to compare the mean phenotype (leg lengths) of males or females. Fisher's exact test was used to assess whether number of copulation bouts (one-sided mated or two-sided mated) or time of first copulation (< or > 8 h) affected cannibalism (cannibalised or non-cannibalised) and whether double-mated males were cannibalised more often by the first or the second virgin female. A possible correlation between male and female leg length was checked by determining the Pearson correlation coefficient. A logistic regression and likelihood ratio-chi-square statistics for type 3 analysis were used to check the effect of male and female leg length on the likelihood of being cannibalised (males) and cannibalising (female) when male and female leg length were corrected against each other.

To test the variation in the proportions of genital and somatic characters in males and females, regression was performed of the size of one character on that of another. The log-transformation ensures that the data is scale-independent, i.e. that the analyses are unaffected by the unit of measurement (Smith 1980). Regression slopes (b = allometric value) indicating proportional changes in size and the coefficients of determination (r^2) are given. The coefficients of variation (CV = SD/mean x 100) and the relative amount of variation (comparing the variance of logarithms of measurements; Lewontin 1966) of the genital and somatic characters were determined.

2. 4. Light microscopy (LM)

The pedipalps and front legs of male spiders and the genitalia of females of different mating status were isolated and kept in 5 % KOH solution for several days until the tissue had dissolved. To increase the contrast of the cuticle some preparations were

stained with a 5 % Eosin red solution. Cleared specimens were finally transferred into glycerine and examined with a light microscope. The number and position of embolus tips and longer parts of the males' emboli inside the female spermathecae and connecting ducts were recorded. Where possible, length of embolus tips and the spermathecae were measured to the nearest 10 µm using an ocular micrometer. Male pedipalps, tarsi of the first legs and the female epigynal plates and genitalia were examined for different sensilla, such as tactile hairs, chemotactile hairs, trichobothria, slit sensilla and tarsal organs.

In order to view the spermatozoa inside, the spermathecae were dissected and transferred into a drop of an Orcein solution on a microscope slide (1 % Orcein in 45 % acetic acid). Then the spermathecae were cut longitudinally with a razor-blade and after 5 min of incubation the spermathecae-halves were carefully transferred into a drop of glycerine and observed under the light microscope.

Series of semi-thin sections (50 µm to 100 µm) of male and female organs fixed and embedded for transmission electron microscopy were cut with glass or diamond knives and stained with toluidine blue (1 %) borax (1 %) solution.

2. 5. Scanning electron microscopy (SEM)

The epigyna and isolated spermathecae of females of different mating status were cleaned with 5 % KOH and contact lens cleaner. The cleaned spermathecae of some females were transversally cut with a razor-blade in the region where the copulatory duct opens into the spermatheca.

Whole male pedipalps, first legs, female epigyna and isolated spermathecae of virgin and mated females were fixed and postfixed as for transmission electron microscopy (see chapter 2. 6.). After dehydration, some of these pedipalps, epigyna and spermathecae were cut in various planes with a razor blade. To reveal further aspects of the spermathecal cuticle, some spermathecae were carefully fractured with forceps.
All specimens were dehydrated in a graded series of ethanol, critical-point dried, sputter-coated, and examined with a Jeol JSM-5400 or a Leitz AMR 100 scanning electron microscope.

To prepare casts of the cuticle, cleaned spermathecae were embedded in a low-viscosity resin (Spurr 1969), fractured, and treated with NaOCl for two days to remove

the organic material (Boyde & Jones 1996). After treatment, the fractures that contained casts of the spermathecal cuticle were sputter-coated and examined under the SEM.

2. 6. Transmission electron microscopy (TEM)

Male teguli, female epigyna and the surrounding tissue were excised and fixed in ice-cold 2.5 % glutaraldehyde in 0.1 mol/l cacodylate buffer (pH 7.4) for 1 h. After carefully cutting off the most lateral edges of the copulatory ducts to allow complete infiltration of the resin, the specimens were washed in cacodylate buffer and postfixed for 1 h at 4°C in 1 % osmium tetroxide plus 0.5 % ferrocyanide (Karnovsky 1971). After washing the tissues in 0.1 mol/l cacodylate buffer they were dehydrated in a graded series of ethanol concentrations and embedded in a low-viscosity resin (Spurr 1969). Ultra-thin sections of female epigyna were cut with a diamond knife and stained with lead citrate (Reynolds 1963) and uranylacetate respectively and examined with a Seitz 109 transmission electron microscope.

2. 7. Photography and Videography

Photographs of live spiders and their webs were taken with a Pentax programA camera (Fuji Color 200 slide film). Further pictures were taken with an Olympus OM-2 camera mounted on an Olympus SZH binocular using Fuji Color 100/200 slide film.

Pictures of genitalia, cleared or stained specimens and semi-thin sections were photographed using an Olympus C-35AD-4 or an Olympus digital Camedia C3030 Zoom mounted on an Olympus AH-2 light microscope. Pictures taken with the digital camera were transferred to the computer using the program Olympus DP Soft.

I used Agfapan APX 25 b/w film for SEM micrographs, and Scientia EM film (23D56 P3 AH) for TEM studies.

Slides and negatives were scanned (Epson Perfection 1650) and edited using Adobe Photoshop 6.0 and Microsoft Powerpoint.

Courtship was videotaped using a digital CCD Camcorder Sony DCR-VX1000E (high-speed shutter 1/600 sec). Selected video sequences were transferred from DV-tapes (Panasonic Mini DV) to the computer with a digital video chart generating avi-files (Audio Video Interlaced). Single pictures (25 frames/sec) were extracted from the avi-files using the Main Actor program. To optimize the images (jpeg), half frames were generated using the Adobe Photoshop video filter (DE-interlace).

3. Results

3. 1. The female

The prosoma of an adult female *Latrodectus revivensis* is slightly longer than broad and very dark brown to almost black (Figs. 2a, b). The opisthosoma is relatively large, high and sub-globular or sub-spherical (Fig. 2a). Its colour shows considerable variation from dull grey, deep brown up to almost black (Shulov 1948). In dark specimens there is a light, more or less triangular marking behind the epigastric furrow (Fig. 2a). The surface of the opisthosoma is covered with strong, thick, slightly bent and tapering spines dispersed among appreciably smaller ones (see also species descriptions in Levy and Amitai 1983 and Levy 1998).

3. 1. 1. The epigynum

The epigynum is an arched and heavily sclerotised plate which is situated on the ventral side of the female's opisthosoma, immediately in front of the epigastric furrow (Figs. 2a, b). The epigynal plate is transverse, sub-oval and covered by a thick cuticle (approx. 30 µm) (Figs. 2d, c). Three layers (exo-, meso- and endocuticle) are apparent under light microscopy (Figs. 2c, 6b), each with a thickness of approx. 8 -11 µm. The hairs that partly overhang the nearly triangular opening of the atrium (Figs. 2d, e) are suspended in sockets in the cuticle (Figs. 2c, 6a, b). The epidermis underlying the fluid-filled extra-cellular space of the tactile hair contains large amounts of crystalline deposits. The adjacent cuboidal cells are filled with pigment granules (Figs. 2c, 6a, b). The posterior margin of the epigynal opening is curved slightly backwards, forming a carina that probably serves as a guide for the male pedipalp during copulation (Figs. 2d, e). The cave-like atrium is covered by smooth cuticle and, like all internal cuticular surfaces of the epigynum, is devoid of any neuroreceptive sensilla (Figs. 2e, 4a, b). At its anterior end, the ventral cuticle of the atrium bends upwards (Figs. 4b, c), forming a cone-shaped protuberance fitting into the pit created by the dorsal wall (Figs. 4c, 6d). The thickened cuticles of the ventral and dorsal walls fuse medially with each other and more dorsolaterally with the cuticle of the spermathecal walls (Fig. 4d). The two lumina created by the median separation represent the beginning of the paired copulatory ducts (synonymous with the 'bursae copulatrices' in Bhatnagar & Rempel 1962) (Fig. 4d). Each duct entwines the spermatheca on that side (Fig. 2f, not seen in Fig. 2g due to

preparation). After four coils in a posteriolateral direction, each duct makes a sharp turn back towards the spermatheca, completing another two coils. Thus, the spermathecae and the copulatory ducts originate from a single primary invagination (see discussion below), the copulatory ducts do not form a distinct, closed tube, but actually resemble the dilations of a complicated system of cuticle-lined folds (Figs. 4a-f, 5a-f). Consequently, as the series of semi-thin sections show, the lumina of the dilations remain connected with each other (Fig. 6c). In the wide parts of the copulatory ducts the underlying epithelium is thin. No specialised gland cells can be identified in semi-thin sections. The numerous pore canals of the adjacent cuticle give it a striated appearance (Fig. 6c).

Close to the entrance of the spermatheca, the copulatory duct of each side becomes very flat and one side forms a heavily sclerotised tube (Figs. 3f, g, 5b, 6g, h). This organisation is retained in the section where the cuticle of the copulatory duct fuses with the cuticle of the spermatheca. In transversely cut preparations, one can see that the lumen of this part of the spermatheca is reduced to a very narrow slit that continues into the spermathecal lumen medially (Figs. 5d, 42d, f). As in the copulatory duct, the slit is slightly widened laterally (not exceeding 17 µm), forming a tube that takes up the male embolus tip during copulation (Figs. 3d, e, 42a-f).

The paired spermathecae lie with their axes forming an angle of about 45° to each other (Fig. 2f) (for details see chapter 3. 1. 2.). The small fertilisation duct of each spermatheca penetrates the apical wall almost in the middle of the posterior lobe (Fig. 3f). The right and left small fertilisation ducts lead to a common cuticle-lined duct that connects the spermathecae to the uterus externus (Figs. 3h, 6f). To my knowledge, only separated fertilisation ducts leading from each spermatheca to the uterus have been described for entelegyne spiders thus far. Therefore, I have called the tube that connects the small fertilisation ducts with the uterus externus the ‘common fertilisation duct’. At the point where the lumina of the small fertilisation ducts lead into the common duct its dorsal walls are heavy sclerotised (Fig. 4f). These folded and obviously rigid structures form a valve that is pressed against the ventral epithelium which is covered by a thin cuticular lining only (Fig. 6e). Generally, the lumen of the common fertilisation duct is very narrow, laterally restricted by glandular cells that form cushion-like flaps (Figs. 5a,

6f). Anteriorly, the common fertilisation duct bends dorsally. Finally it fuses with the uterus externus (Figs. 5a, b, 27c).

Laterally the epigynal ducts and spermathecae are enclosed by the ventral and dorsal anterior dilators of the genital aperture (epigastric furrow) (Fig. 5f). Furthermore, some of the epigynal elements are connected by distinct muscular fibres. These fibres connect the common fertilisation duct and the narrow parts at the end of the copulatory ducts and the epigynal plate (Fig. 5b). The majority of fibres originate on the ventral side of the common duct, posteriorly from the rigid part where the lumina of the paired fertilisation ducts lead into the common duct (Figs. 4e, 6e), and extend to the anterior margin of the common duct (Fig. 5b). Some additional fibres originate at the tube-like part of the copulatory duct (Figs. 5b, 6h). All fibres run ventrally and, although originally paired, fuse into an apparently single muscle strand that inserts on the inside of the epigynal plate (Figs. 5b). Additional fibres connect the common fertilisation duct with the end of the copulatory ducts (Figs. 5b, 6g, h).

Dorsally the epigynal ducts and spermathecae are bounded by the ectodermal epigastric furrow (Fig. 4a) and uterus externus (Fig. 5d) and, at the anteriormost end, by the entodermal uterus internus (Fig. 5f).

3. 1. 2. The spermatheca

The spermathecae are dumb-bell-shaped and lined by a very thick and heavily sclerotised cuticle that is penetrated by numerous pores and pore canals. Each spermatheca consists of two rounded lobes (Figs. 4a, b, 5e) that are connected by a narrow middle region (Figs. 3a-f, 5a). The small fertilisation duct is formed by the spermathecal wall itself. It originates from the lateral apical wall almost in the middle of the posterior lobe (Fig. 4c). The lumen of the fertilisation duct is funnel-like (Fig. 3h). At the beginning it is relatively wide. Towards the end its bends medially and becomes narrow (Fig. 41f). The small fertilisation ducts of the right and left side lead to a common cuticle-lined duct that connects the spermathecae to the uterus externus (Figs. 3h, 6f).

3. 1. 2. 1. The cuticle

The spermathecal cuticle has a thickness of 30 - 45 µm. Its outer surface shows more or less regularly distributed protuberances (Figs. 7b, d). A laminated exo-, meso- and endocuticle, each 10 - 15 µm thick, can be distinguished by LM (Fig. 7a). In the TEM only two laminated layers and the epicuticle are seen (Figs. 7e, 8b). The epicuticle is 0.15 - 0.20 µm thick in all regions; a dense homogenous inner layer can be distinguished from a more electron-dense, outer layer (< 20 nm) (Figs. 8f, b). Exocuticle and endocuticle are composed of laminae ('lamellae' after Neville 1975) of varying thickness and electron-density running more or less parallel to the surface. The typical parabolic pattern of the laminae (Fig. 7f) is not resolvable in all sections (Fig. 7g). Casts of the cuticle reveal that the laminae of the exocuticle are more compact than that of the endocuticle due to the fact that the low-viscosity resin penetrated into the space most likely between the laminae (Fig. 7c).

Numerous twisted ribbon-shaped pore canals penetrate the cuticle terminating at the epicuticle (Figs. 7a, 8d). The inner epicuticle is penetrated by wax canals that do not open into the spermathecal lumen (Fig. 8f). Areas between the protuberances of the spermathecal surface, but also the protuberances are penetrated by a pore canal and the associated wax canals (Figs. 8a, b). Distally, close to the epicuticle the lumen of the pore canal becomes slightly widened (Fig. 8f). Throughout the rest of the exocuticle its diameter varies (Figs. 8c, g). In the endocuticle the pore canal becomes much wider having a diameter of up to 1.4 µm (Figs. 8h, e, 24a-c).

Each pore canal is filled with a finger-like projection of the intercalary cell clearly seen in the endocuticle. At its base the plasma membrane of the projection is in contact with the cell body (Figs. 8h, b, 24a-c). Most basally, the cell membrane lies closely attached to the surrounding cuticle, whereas more apically, the cell extension is separated from cuticle by a granular substance (Fig. 8i). Their cytoplasm is filled with numerous filaments which sometimes appear tubular (Fig. 24a). In the region of the exocuticle, however, the pore canal contains one, two or sometimes three more electron-dense tubes that are twisted along their longitudinal axis (Figs. 8c, e, g). In cross-section the tubes have an irregular or more or less rounded outline (Fig. 8j). The surrounding area is electron-lucent and contains only a few structures of different electron density (Figs. 8j, f, g). In fractures of KOH-treated cuticle, the tubes lying within the pore

canals are visible as single, double or triple slightly twisted strands (Fig. 8c). Apically, close to the epicuticle, the lumen of the tube becomes dilated (Fig. 8f).

3. 1. 2. 2. The epithelium

The epithelium that surrounds the spermatheca has a thickness of up to 60 µm (Figs. 9b, 41a, d, g, j). It is separated from the hemolymph by a prominent basement membrane (approx. 1 µm) (Figs. 14a, 28b, d). The cuticle overlying the epithelium of the anterior and posterior lobe is penetrated by numerous pores of varying size (Fig. 9a). Each pore contains one or several (up to ten) cuticular ductules (Figs. 9c, d), each of which can be assigned to a single glandular unit. The units are accompanied by ordinary epithelial cells (Fig. 9b). Around the middle portion of the spermatheca, no glandular units are present and only ordinary epithelial cells are found (Fig. 41g).

Two types of glandular units can be distinguished (type I and type II). Both are composed of a gland cell (G1/G2) and a secretory canal cell (C1/C2) and envelope cells (E) that surround the unit and the apical part of its ductule (Fig. 10a). Due to the size of the cells involved in the organisation of the glandular unit, parts of the apical neck of the gland cells were not able to be identified unequivocally (indicated by the red square in Fig. 10). Type I (G1/C1) might enter a pore by itself. More frequently, however, a cluster of units, either only of type I or of both types share a single pore (Figs. 16a, 19a, b). Apically, the glandular units separate. Eventually, each gland ends in its own small cuticular indentation (Fig. 9d). Intercalary cells (I) separate the glandular units or clusters of glandular units from one other (Figs. 10a, 12a).

The gland cell (G1): The gland cell that rests upon the basement membrane has some basal infoldings (Fig. 14a). The cell body only extends apically to one-half or two-thirds of the epithelium's depth (Figs. 11a, b). The lobed heterochromatic nucleus is basally located (Figs. 16a, 11b). Its nucleolus is positioned eccentrically (Fig. 14a). Rough endoplasmic reticulum is abundant and forms tightly-packed or sporadically-dilated cisterns around the nucleus (Figs. 12b, 14a, b, 15a). Elongated mitochondria lie between the cisterns (Figs. 15a, d). The supra-nuclear region contains dictyosomes, mitochondria and many membrane-bound vesicles of varying size and electron-density (Figs. 15a, c). Microvilli extend into an extra-cellular reservoir filled with moderately electron-dense or granular material (Figs. 14b, 15a, b). Large areas of the cytoplasm are filled with glycogen particles and ribosomes (Figs. 11b, 13a, b, 15a, c). The neck of the

gland cell is connected to the most basal end of the ductule of the secretory canal cell (C1) (Figs. 17a-e). Cross-sections reveal that the part of the ductule extending into the neck of G1 has an irregular outline (Figs. 11b, 17a, b). The wall of the ductule consists of a homogenous moderately electron-dense layer (approx. 0.1 µm) (Figs. 17a, b). Its lumen is filled with a homogenous electron-dense material (Figs. 17a-c). The ductule is surrounded by parallel-arranged microtubuli (Figs. 17b, e).

The secretory canal cell (C1): The secretory canal cell (C1) extends from the basement membrane almost to the apical end of the cuticular pore (Figs. 10a, 12b). In longitudinal (Figs. 12b, 16a, 11a, b) and especially the cross-sections (Figs. 13a, b) it becomes obvious that the secretory canal cell (C1) surrounds the gland cell (G1) separating individual gland cells from one other. The ovoid nucleus (nC1) lies apically (Figs. 11b, 13a). The nucleus does not contain as much heterochromatin as the nuclei of the other cell types (Fig. 13a). On one side, its inner membrane forms regularly-arranged microvilli-like projections (Figs. 13a, b, 18c). The large nucleolus lies more or less centrally (Figs. 11b, 13a, b). The secretory canal cell (C1) only contains a few cisterns of rough endplasmic reticulum, usually, in the basal part of the cell (Fig. 23a). Sometimes they are arranged along the plasma membrane that faces the gland cell (Fig. 12b). Conspicuous dictyosomes, numerous mitochondria, free ribosomes and vesicles of varying size and electron-density are present throughout the cytoplasm (Figs. 17a, d, e, 18d, 23b). In its centre, the secretory canal cell (C1) shows pronounced microvilli arranged around a central cuticular ductule (Figs. 16a, 19a). The ductule traverses up to two-thirds of the cell's length (Fig. 16a). At its most basal end the ductule is connected to the neck of the gland cell (G1) (Fig. 17). Externally, the microvilli are surrounded by an electron-dense material (Figs. 17a-e, 18a, b) that is continuous with the homogeneous cuticular ductule that remains intact after KOH treatment (Fig. 9c). The size of the inner diameter of the ductule varies from 0.4 to 0.5 µm. At the height of the spermathecal cuticle, the microvilli extending towards the ductule are shorter and less densely-packed than in the basal part (Figs. 19a, 18a). Apically, the lumen of the ductule contains electron-dense, granular material (Figs. 19b, 18b). Especially in the more apical regions of the secretory canal cell (C1), numerous microtubuli run along the cell periphery (Figs. 18a, 19b). The apical part of the ductule is surrounded by the envelope cell (Figs. 9e, f) (see below).

Gland cell (G2): The cytoplasm of the neck region of G2 that is connected to the basal end of the ductule of the secretory canal cell (C2) contains mitochondria, vesicles, electron-dense granules and microtubules (Fig. 21b). Numerous parallel-arranged microtubuli fill the part of the cell that reaches into the extra-cellular space of the secretory canal cell (C2) (Figs. 21a, b). In the more basal part of the epithelium, the cell membranes appear to have been destroyed by the fixation process. Within the cytoplasm, however, extra-cellular reservoirs, similar to that found in the gland cells (G1), are seen (Figs. 20a-c). In some of the reservoirs the central ductule is visible (Figs. 20a, c). None of the nuclei found in the basal epithelium can be assigned to G2 (Fig. 20a).

The secretory canal cell (C2): Together with the secretory canal cell (C1), a second type of secretory canal cell (C2) of the type II glandular unit sometimes enters the pores of the spermathecal cuticle (Figs. 19a, b, 20a). Basally, the outlines of the C2 cells cannot be clearly identified. In some areas cell membranes appear to have been destroyed by the fixation process. Similar to the secretory canal cell (C1), the cytoplasm contains numerous dictyosomes, mitochondria and vesicles of varying size and electron-density (Figs. 21a, b, 22b). Numerous microtubules run along the cell periphery (Figs. 21b, 22b). Long microvilli extend towards the ductule. They rarely contain vesicles or ribosomes, but are densely filled with parallel-arranged microtubules, predominantly in the apical region (Figs. 22a, b, 19b). The microvilli are less tightly-packed than in the secretory canal cell (C1), thus creating a large extra-cellular space (Figs. 20a, 21a, b, c) that is filled with granular material. The ductule that sometimes takes a curved course through the cytoplasm (Fig. 21a) is lined by a smooth cuticle (< 20 nm). The luminal side of its basal portion is conspicuously sculptured (Figs. 21a-c). The inner diameter varies between 0.5 - 0.6 µm. In the apical part, the tips of the microvilli are separated from the cuticular ductule by a moderate electron-dense fibrous mass (Figs. 21a, 22a, b). Here, the ductule has an inner diameter of approx. 0.5 µm and contains granular material (Fig. 22b). Like the ductule of C1, its apical part is surrounded by envelope cells (E) (Fig. 22a). At its most basal end the ductule of the secretory canal cell (C2) reaches into the neck of the gland cell (G2) (Figs. 19a, 21a-c).

The envelope cell (E): The envelope cell (E) stretches from the basement membrane to the most apical end of the pore where the cuticle of the ductule and the spermatheca fuse (Figs. 9e, f, 20a). The envelope cell closely wraps around the secretory canal cells (C1 and C2) (Figs. 16a, 22a, 23a, b). In clusters of glandular units, the envelope cells (one or two) surround each unit, forming a thin sheath that isolates the unit, or a whole cluster, from the surrounding intercalary cells (Fig. 12a). This arrangement is retained in the apical part where a single unit, or a cluster of units penetrates the spermathecal cuticle (Fig. 19b). Basally, the envelope cell forms infoldings of a similar appearance to the intercalary cell (I). Therefore assignment to a given cell type (E or I) is difficult in some sections (Fig. 12b). The irregularly-shaped, heterochromatic nucleus with an eccentric nucleolus can usually be found in a rather basal position (Figs. 23a, b). The cytoplasm is electron-lucent and contains sparse amounts of rough endoplasmic reticulum, few mitochondria, small vesicles and electron-dense particles (Figs. 23a, b). The most prominent feature of the envelope cells are the numerous microtubuli predominantly in the apical region (Figs. 19b, 22a, 23a, c). Apically, the envelope cells surround the distal portion of the ductule (Figs. 9f, i, 22a). Here the lumen of the ductule is slightly widened (Fig. 9e). Towards the surrounding cell membrane of the envelope cell (E) the cuticle bears numerous short protuberances (Figs. 9c, d, h, i). Two cuticular layers can be distinguished. The inner layer is 0.4 - 0.5 µm thick. The electron dense outer layer has a thickness of less than 20 nm. Most apically, the cuticle of the ductule fuses with the cuticle of the spermathecal wall (Figs. 9e, f, i) and, hence, the last part of the ductule resembles a simple pore that penetrates the spermathecal wall (Fig. 9i) and finally opens into the spermathecal lumen (Figs. 9e, g).

The intercalary cell (I): The intercalary cell extends from the basement membrane to the spermathecal cuticle (Fig. 11a). Basally, it forms infoldings similar to those of the envelope cells (Figs. 12b, 29d). The nucleus is irregularly shaped, with an eccentric nucleolus (Fig. 11a). The cytoplasm contains sparse amounts of rough and smooth endoplasmic reticulum, few dictyosomes and ribosomes. Aggregations of glycogen are present in the apical part (Figs. 12a, 24a) and, less densely packed, in the basal portion of the cell. The apical cell membrane forms numerous microvilli (Fig. 12a). The filaments of the cellular projections in the pore canals (see chapter 3. 1. 2. 1.)

reach far into the cytoplasm of the intercalary cell (Figs. 12a, 24b, c). Numerous mitochondria are arranged around the bundles of filaments and in the proximity of the microvilli (Figs. 24a, b). The plasma membranes of adjacent intercalary cells interdigitate apically (Figs. 24a, b).

The epithelial cells around the middle portion and the end of the copulatory duct: Where the cuticle of the copulatory ducts fuses with that of the spermatheca, the cuticle shows a striated appearance due to the high number of pore canals (Fig. 41g). The adjacent epithelial cells possess irregular-shaped, heterochromatic nuclei with an eccentric nucleolus (Fig. 25a). The cytoplasm is poor in organelles; only a few mitochondria, rough endoplasmic reticulum and vesicles are present. However, the cells are packed with numerous glycogen particles. In some areas the cells exhibit elongated, spindle-shaped light (LM, Fig. 41g) or electron-lucent (TEM) regions (Fig. 25a) not bound by cell membranes.

3. 1. 3. The uterus

The schematic drawing (Fig. 26a) of the longitudinally cut female genitalia of *L. revivensis* illustrates the complex organisation of the uterus.

The opening of the epigastric furrow (Fig. 2b) lies posterior to the atrium. In contrast to the dorsal wall close to the opening (see below), all other walls forming the epigastric furrow consist of a very thin cuboidal epithelium (approx. 3µm) covered by a cuticle with vertical extensions (Figs. 4e, 26c) that branch apically (Fig. 26b). Close to the opening of the epigastric furrow, the ventral wall is made up of a thin cuboidal epithelium with pigment granules (Fig. 26d). The adjacent cuticle is approx. 12 µm thick; the differentiation of the layers after toluidine blue is less pronounced than in the cuticle of the epigynal plate. Further forwards, the number of pigment granules of the ventral cuboidal epithelium decreases, whereas the degree of vacuolisation increases (Fig. 26e, 27a, b). The cuticle becomes thicker (approx. 15 - 25 µm) and, towards the junction with the common fertilisation duct, more and more folded (Figs. 27a, b).

The primary genital opening (gonopore) lies hidden inside the epigastric furrow (Fig. 26a). The most posterior part of the dorsal wall of the uterus externus forms a tongue-like protrusion (Fig. 4b). Its ventral epithelium consists of huge glands that are surrounded by prismatic epidermal cells that contain many vacuoles (or secretory granules) (Figs. 27a, b). A terminal gland cell reaches the basement membrane, but does

not seem to extend to the cuticle. The terminal gland cell has an invagination which seems to be in contact with a conducting canal of a more apical cell (Fig. 27b). The canal traverses the cuticle (approx. 1 - 2 µm) and opens into the lumen of the uterus externus. Here the secretion most probably produced by the glands mentioned, stains dark blue with toluidine blue (Figs. 27a, b). Following the uterus externus anteriorly, its lumen fuses with the lumen of the common fertilisation duct (Figs. 5a, 27c). Here only a few glandular units are visible among the more numerous, highly-vacuolised epidermal cells. The adjacent cuticle forms a very thin layer (less than 0.5 µm). The glandular pouches of the common fertilisation duct lie ventrally (Fig. 27c). Their surfaces are covered with a thick (approx. 10 µm) cuticle. The exocuticle is stained dark blue and sends troughs into the underlying cuticular layers (Fig. 27c). The general appearance of the cuticle of the pouches of the common fertilisation duct is similar to the cuticle that covers the more posterior, ventral wall (Fig. 27a). The opening of the common fertilisation duct, and partly the lumen of the uterus externus, is filled with light blue droplets imbedded in a homogenous, light pinkish secretion (Figs. 27c, d).

Anterior to the junction with the common fertilisation duct, the dorsal wall comprises a high columnar epithelium (Fig. 27e). Furthermore, the epithelium is characterised by pronounced basal infoldings and secretory granules (Fig. 27f). Its cuticle is less than 0.5 µm thick and partly covered by a homogenous secretion and a few light blue droplets. The light pinkish secretion is similar in colour to the cytoplasm of the columnar cells described above (Fig. 27f). Although less pronounced and covered by a thicker cuticle (approx. 2 µm), the ventral epithelium is similar to the dorsal one (Fig. 27e).

At the height of the anterior lobe of the spermathecae, the uterus externus fuses with the uterus internus (Fig. 5e). The uterus internus is formed by a secretory epithelium devoid of a cuticular lining (Fig. 27g). Its cells seem to have small bases and broad apices. Secretion is visible among the cells as light blue droplets of various sizes (Fig. 27h). Transversally-sectioned muscle fibres accompany the epithelium of the uterus internus (Fig. 27g).

3. 1. 4. Hemolymph and nervous supply

The hemolymph surrounding the spermathecae contains various cell types. Granular hemocytes that contain mitochondria and membrane-bound granules of varying electron-density are most abundant (Figs. 28a-c, 29a, b). Here rough endoplasmic reticulum around the nucleus and a few dictyosomes are present (Figs. 28c, 29a). In some granular hemocytes secondary lysosomes (e.g. residual bodies) are visible (Fig. 29a, b). Other hemolymph cells contain almost no cell organelles beside the nucleus with a prominent nucleolus (Fig. 29c).

Frequently, granular hemocytes are found in close contact with the basal infoldings of the spermathecal epithelium (Figs. 28b, c). Occasionally they seem to be completely surrounded by the basal infoldings (Fig. 28c). However, the presence of the basement membrane indicates that these hemocytes still lie outside the epithelium. In some cases hemocytes are found incorporated into the spermathecal epithelium (e.g. in the gland cell G in Fig. 28). In such case a basement membrane could not be identified. Sporadically, cells are seen within the epithelium, either basally or more apically, that contain myelin-like bodies (Figs 28d, e).

Few nerve fibres are seen in the hemolymph. The axons contain microtubuli, vesicles and granules. One or more axons are enclosed by glial cell extensions that contain glycogen and are surrounded by a basement membrane (Fig. 29d).

Small vessels with a diameter of 10 to 30 µm that presumably originate from the arteries supplying the opisthosoma (Foelix 1996), traverse the hemolymph. They may contain hemocytes (Fig. 28a).

3. 2. The male

Adult males *Latrodectus revivensis* have a sub-circular prosoma with the cephalic portion protracted into a protuberance. The opisthosoma is longer than broad. Its dorsal coloration consists of a deeply-scalloped black pattern with a median chain of sometimes discontinuous, large irregularly-shaped spots (Fig. 30a). Marked intra-specific variation of this pattern is often seen (see also Levy & Amitai 1983; Shulov 1948). The venter displays a large, light triangular blotch extending from the epigastric furrow to the spinnerets (Fig. 36h).

In spiders the spermatozoa are transferred indirectly to the female spermathecae *via* the modified male pedipalps. I examined the pedipalpal structures in order to identify possible mechanisms by which a male *L. revivensis* might be able to manipulate rival male's spermatozoa (e.g. mating plugs, sperm removal). Additionally, I checked the outer surfaces of the tarsi of leg I and the mouth region for sensory structure involved in mate localisation and courtship.

3. 2. 1. Pedipalp

The femur of the male pedipalp is relatively short. The tibia is bowl-shaped and forms a base for the cymbium. Typically it bears one dorsal and two retrolateral trichobothria, tactile hairs and few slit sensilla (Figs. 31a, c). The two distal segments of the pedipalp, the tarsus and pretarsus are modified and form the copulatory organ (Figs. 30b-f, 32a, b). The cymbium (tarsus) is asymmetrical and spoon-shaped (Figs. 30c-f). The deep cavity within the cymbium contains the palpal organ (Fig. 31b). The ventral part of the cymbium is lobed and beset with thick stout hairs (Figs. 30b, 31f). In the middle of the lobed surface lies the pit-like tarsal organ with a diameter of the opening of approx. 10 µm (Figs. 31f, j). The outer surface of the cymbium is covered with hairs of varying size (Figs. 30c-f, 31c) and numerous slit sensilla (Fig. 31d); chemoreceptive hair sensilla could not be observed. However, the cymbium bears previously undescribed structures of unknown function. The light-microscopical picture of cleared specimens shows approx. 15 of these structures lying unevenly distributed over the frontally-directed surface of the cymbium (Fig. 31e) on which, in an unexpanded pedipalp, the outer loop of the embolus comes to rest (Fig. 31c). The ampulla-shaped parts of these structures are approx. 40 µm long and 20 - 30 µm wide and directed towards the inside of the

cymbium (Figs. 31g, h). The club-shaped portion of approx. 20 - 30 µm in length protrudes from the cymbial surface (Figs. 31g-i).

The palpal organ (bulb *sensu* Comstock 1910) consists of outer hard, sclerotised parts (petioles, subtegulum, tegulum, median- and terminal apophysis, conductor, radix and embolus) and soft areas (basal and distal haematodocha). Sclerotised parts and haematodochae surround the internal parts of the spermophor (synonymous with the male 'receptaculum seminis' in Wagner 1887; for citation see Bhatgnagar & Rempel 1962). The spermophor consists of the fundus, the reservoir and the ejaculatory duct (Fig. 32b). The fundus and the reservoir form a sclerotised spiral coil, with one end overlapping the other. The transparent and slender ejaculatory duct originates from the reservoir. It has an outer diameter of approx. 5 µm and an inner diameter of about 4 µm (Figs. 32d, h). The embolus is the only external part of the genital bulb that is introduced into the copulatory duct and the spermatheca of the female during copulation (Fig. 42a). The base of the embolus is thickened and joined to the radix by a delicate cuticle (Fig. 31b). The embolus makes three coils on the retrolateral side of the embolus (Figs. 30b, c), then turns to the prolateral side and finally along the prolateral margin of the cymbium (Fig. 30b). In the unexpanded pedipalp the most apical portion comes to rest on the conductor and a short part projects from the apex of the conductor (Fig. 30b). The long, spirally coiled part of the embolus can be clearly divided into the dark brown and heavily sclerotised truncus and the *pars pendula* that runs along its inner concave side (Figs. 32d, e). In cross-sections prepared for SEM, it can be seen that the truncus forms a U-shaped channel closed by the *pars pendula* (Fig. 32h). Inside the channel lies the ejaculatory duct originating from the reservoir (Figs. 32d, h). Apically, the embolus possesses a solid S-shaped sclerite: the embolus tip (Figs. 32a, b, d, f). SEM pictures show that the transition between the embolus tip and the rest of the embolus is marked by a saddle-like thickening (Figs. 32f, g). The thickening is also visible in the embolus tips inside the female genital tract and indicates the site of fracture (Figs. 32b, e, 42a, b, c). The total length of the tip varies among individuals (approx. 300 - 400 µm; $n = 20$). The outer diameter of the tip is approx. 13 to 16 µm at the breaking point and 8 to 10 µm just beyond it (Figs. 32f, g). From here the diameter remains constant for the proximal third of the tip. Distally, the diameter decreases steadily towards the opening and tapers to the slightly flattened apex (Figs. 32c, f). A canal with a diameter of

approx. 4 µm runs through the tip (Figs. 32g, 42e). This canal is continuous with the ejaculatory duct that ends at the breaking point (Fig. 32h). The actual opening of the tip lies approx. 30 µm proximal from the apex. It is oval and has a diameter not exceeding 6 µm (Figs. 32c, f).

3. 2. 2. Tarsus of leg I

On the tarsus of *L. revivensis* three different types of bristles can be identified. Serrated bristles are situated on the ventral side, opposite the three moveable claws. They possess many small teeth on their ventral side (Figs. 33a, c). Tactile hairs, arranged in irregular rows, cover all the sides of the tarsus (Fig. 33a). The tactile hairs vary considerably in length. They point towards the proximal end of the tarsus, forming a steep angle to the leg axis (Figs. 33a). The surface of the hairs is ribbed longitudinally (Figs. 33a, b, d). Chemoreceptive hairs ('tip-pore hairs') are distributed in more or less longitudinal lines among the tactile hairs (Fig. 33a). On the ventral side they are more numerous. In contrast to tactile hairs, chemoreceptive hairs rise at a steep angle from the leg surface. The hair shaft is smooth and S-shaped. Its tip has a small opening to the outside (Fig. 33b). No trichobothria are present on the tarsus of *L. revivensis*.

Further sense organs of the tarsus are the tarsal organ and slit sensilla. Similar to that on the cymbium, the tarsal organ of the walking leg resembles a circular pit with a diameter of approx. 10 µm (Fig. 33d). Its relative position is 0.2 - 0.3 (given as a fraction of the tarsus) on the dorsal side of the segment.

Two single slit sensilla ('claw slits') are located on each ventrolateral side of the tarsus below the claws, bordering the serrated bristles (Fig. 33c).

A further sense organ, the metatarsal lyriform organ, consists of parallel slit sensilla and is situated behind a cuticular ridge at the distal end of the metatarsus. Its slits are oriented perpendicular to the long axis of the leg (Fig. 33e).

The set of sensilla found on the male tarsus (tactile hairs, chemoreceptive hairs, tarsal organ, claw slits), can be observed in similar positions on the female tarsus. However, as female legs are much longer (up to twice as long), their absolute number of hair sensilla is higher, but the relative number of chemoreceptive hairs seems to be lower in females (not expressly counted in this study).

3. 2. 3. Mouth region

The mouth opening is bordered in front by the rostrum, laterally by the maxillae and at the back by the labium (Fig. 33f). The anterior rim of each maxilla bears a serulla (Figs. 33f-h); the inner sides are provided with a dense cover of hairs (Figs. 33f, g). The chelicerae consist of a stout basal part and a moveable articulated fang. The sides of the cheliceral groove on the basal part are unarmed (Figs. 33f, g). The inner edge of the fang is finely serrated (Fig. 33h) and the opening of the poison gland is situated at the tip (Fig. 33g).

3. 3. Female and male interactions

3. 3. 1. Relation in size and variation in genital and somatic characters

Figures 43 and 44 show that the size relation between the genital character (male: cymbium width; female: spermatheca length) and the somatic character (leg length) is allometric in both sexes. The regression slopes reveal allometric values of $b = 0.401$ for females and $b = 0.396$ for males indicating similar negative allometric growth of genitalia compared to body size (as leg length). With a coefficient of determination of $r^2 = 0.267$, females showed much more scattered data points compared to males with a coefficient of determination of $r^2 = 0.670$.

The coefficient of variation (CV) is highest for the male somatic character (leg length) (CV = 11.6 %) and lowest for the male genital character (cymbium width) (CV = 5.6 %) (Tab. 1). In females the somatic character (leg length) shows a slightly higher coefficient of variation (CV = 8.3 %) than the genital character (spermatheca length) (CV = 6.6 %). The direct comparison of the variances in the log-transformed morphological measurements shows that the variance of somatic size and genital size is not significantly different in females ($p > 0.1$) or males ($0.1 > p > 0.05$), although a positive trend for the male somatic character is visible.

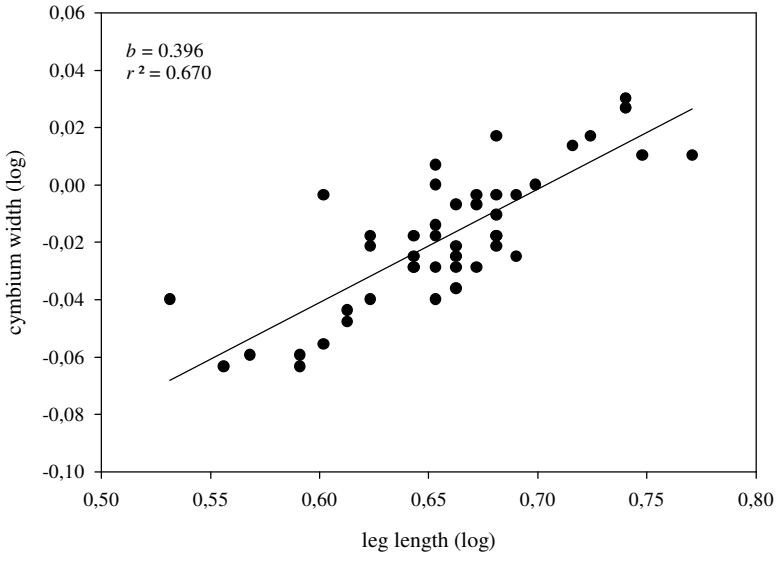


Fig. 43: Log-log regression of male genital character (cymbium width) on somatic character (leg length [patella + tibia]) ($n = 46$). Regression slope (b = allometric value) and coefficient of determination (r^2) are given.

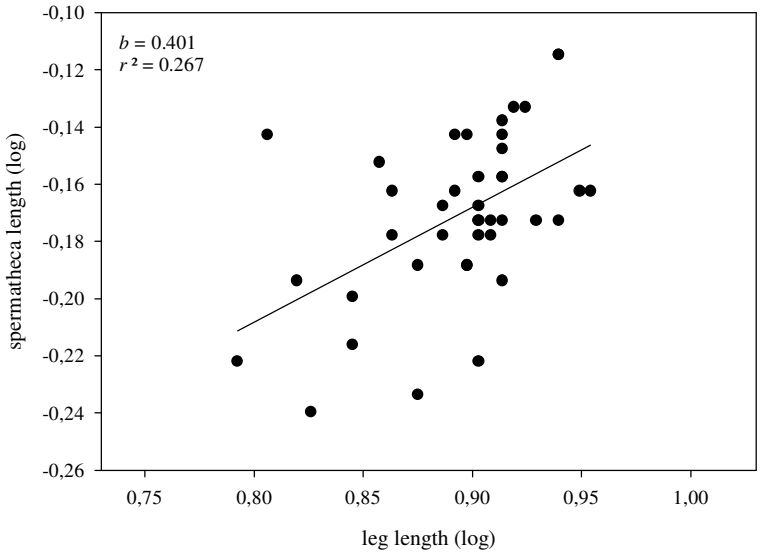


Fig. 44: Log-log regression of female genital character (spermatheca length) on somatic character (leg length [patella + tibia]) (n = 41). Regression slope (b = allometric value) and coefficient of determination (r^2) are given.

	mean (mm)	SD	min - max	coefficient of variation (%)	variance of log (x)
male leg length [tibia + patella] (n = 46)	4.59	0.53	3.4 - 5.9	11.6	0.003
male cymbium width (n = 46)	0.96	0.05	0.86 - 1.07	5.6	0.002
female leg length [tibia + patella] (n = 41)	7.86	0.65	6.20 - 9.00	8.3	0.001
female spermatheca length (n = 41)	0.68	0.04	0.58 - 0.77	6.6	0.001

Tab. 1: Male and female somatic characters (leg lengths [tibia + patella]) and genital characters (male: cymbium width; female: spermatheca length). Coefficients of variation (in %) and variance of log-transformed data (after Lewontin 1966) are given.

3. 3. 2. Courtship and copulation

3. 3. 2. 1. Behavioural elements

Before describing the courtship and copulation of *L. revivensis*, I will give a detailed description of the behavioural patterns used by the male. Terms for corresponding behavioural patterns used by other authors describing the courtship of *Latrodectus* species are given in parentheses.

Bouncing ('jerky movements of the legs' Kaston 1970)

Bouncing movements are those where the body of the male moves up and down on the web due to alternate flexions and relaxations of all the legs in contact with the line. Bouncing can be coupled with locomotion in a 'bouncing gait'.

Cutting

The male cuts the threads of the female web (Figs. 34a-f, 35a-d) with his chelicerae.

Spinning/ trailing silk ('swaddling' Shulov 1940)

With legs IV the male throws his own silk onto the female's web (Figs. 34g, 35e-h). Almost any other behaviour outside the retreat (cutting, bundling, twanging, tugging, but not jerking) is immediately followed by a short spinning sequence. Before spinning, the male usually makes a turn of approx. 180° on the same plane, facing away from the position of his latter activity (compare Figs. 35a-d 'cutting' followed by Figs. 35e-g 'spinning' and 'trailing'). Spinning is followed by the male walking around by trailing further silk (Fig. 35h). A special form of spinning and trailing silk takes place inside the female retreat, where either the retreat or the female is covered with male silken threads ('bridal veil'). Spinning in the retreat takes place by laying down silk with legs IV and spinneret-dabbing movements.

Bundling

After cutting, the loose silk threads are gathered up using the mouthparts and legs I-IV, finally compressed into bands and sheets (Fig. 34h) and covered with the male's own silk (Figs. 34c-g).

Jerking ('push-ups' Ross & Smith 1979)

'Jerking' is caused by a quick, oriented and vigorous flexion of the legs without releasing the lines of the web (Figs. 36a-d). Superficially, these jerks are similar to jerks spiders make in response to intruders.

Abdomen wagging (‘vibrating’ Ross & Smith 1979)

The male moves the abdomen up and down from the pedicel.

Strumming sequence

Frequently the male stops on a single thread, whether standing on it (Figs. 37a-d) or hanging from it (Fig. 36e). He takes a typical position as shown in Fig. 36e. The first pair of legs (legs I) is stretched out and grasps the main thread. The tarsi of legs II almost touch each other in front of the pedipalps forming a loop. The tarsi of legs III meet under the sternum of the prosoma. Legs IV are usually spread out grasping threads of the surrounding web; this keeps the spider in position on the single thread. Sometimes legs III grasp other threads to further stabilise the body, especially when the male is standing on top of the web in a rather wobbly position. During these stops the male performs several distinct movements, some of them simultaneously. Thus most of the movements are reminiscent of strumming the string of a harp and the whole sequence is termed a ‘strumming sequence’. The ‘strumming sequence’ comprises the following behavioural patterns (a-d):

a) Twanging

‘Twanging’ is used to refer to a movement on a thread during which the thread is rapidly tensed and then the tension is suddenly released (Figs. 36f-h).

b) Mouthpart tugging

‘Tugging’ is slow-motion twanging. The single thread runs along between the mouthparts (Fig. 36e). Which parts of the mouth or chelicerae are involved in tugging cannot be defined exactly due to the limited resolution of the video recordings (but see discussion).

c) Palp rubbing

The male moves one pedipalp in brief anterodorso-posteroventral movements (Figs. 37a-d). Anterior of his chelicerae the pedipalp is lifted from the silk, brought posteriorly and back downwards onto the thread just ventrally from the chelicerae. Finally, the pedipalp is moved frontally along the thread in a stroking manner. This ‘circling’ movement is repeated with the same pedipalp several times.

More frequently a simultaneous, though alternating movement of both pedipalps was observed. The pedipalps themselves do not touch each other, but the ventral lobes of the cymbium come into contact with the mating thread as described above (Fig. 36e).

Generally the antero-postero movements can be reduced resulting in a more or less up and down 'tugging' of the pedipalps.

d) Stroking

The tarsus is moved along the thread in a sliding contact with the silk, lifted off and brought back to a position close to the pedipalps. (Figs. 37e-h).

Tapping

The term 'tapping' describes a leg movement where the tarsus is lifted off the female's body and brought down again (Figs. 38g, h).

Scrabbling ('drumming' Shulov 1940; 'boxing' Kaston 1970)

'Scrabbling' describes alternating up and down movements of the pedipalps against the opisthosoma (Figs. 38e, f).

Cheliceral scrabbling/nibbling

With his mouthparts directly positioned over the female epigynal opening (Fig. 37d), the male chelicerae (and to some extent the corresponding pedipalps) alternatingly move up and down. Occasionally, a watery liquid can be observed glistening between the chelicerae.

3. 3. 2. 2. Phases of courtship

The courtship behaviour of *L. revivensis* can be divided into three phases: the 'chemical', 'vibratory' and 'tactile phase' followed by 'copulation' and eventually by 'postcopulatory events'.

Chemical phase: A few seconds up to several minutes after the male was introduced into the female's web, he started his courtship display. He either performed several initial jerks or directly started to walk around the web.

Vibratory phase: While exploring the female's web, the male walked beneath and upon it in a bouncing gait. Walking on the web sometimes appeared rather stilted or wobbly. Occasionally, he stopped to cut the web or to start a strumming sequence. Cutting the web was sometimes followed by bundling the loose strands. As courtship proceeded, portions of the female web were gathered up into concentrated sheets and bands (Fig. 34h) that were covered by the male's own silk. Cutting, bundling and the strumming sequences were always followed by the male turning 180° degrees on the same plane and throwing threads with legs IV. After a spinning sequence of a few seconds, the male started walking, usually trailing silk. For the strumming sequence the

male stopped on a single thread, standing on or hanging from it as described above. A strumming sequence usually lasted 1 to 3 min during which the male simultaneously performed mouthpart tugging, palpal rubbing and stroking movements with the tarsi of legs II. Legs III were repeatedly lifted off the silk and brought back down again. When standing on the thread the male's body sometimes tilted to one side resulting in a more or less hanging position. Twangs were not observed in all strumming sequences, but when shown they usually occurred in bursts of two to five at a time. Some of the twangs were so vigorous that the shaking of the female body could be observed with the naked eye. Comparison of the locations of subsequent strumming sequence showed that the male repeatedly returned to strategic points of the web, for example the supporting threads of the capture platform (Figs. 35a-d; 36e). Sometimes the strumming sequence ended in cutting, the single thread strummed upon. When the male cut a supporting thread the male bounced up and down over a distance of approx. 4 mm (Figs. 35a-d). The approach to the female was interspersed with one or more bouts of on-the-spot jerking. Usually, male jerks followed actions of the female, such as sudden movements of her legs and body (Figs. 35a-d). Her movements were reactions to the strong vibrations caused by vigorous twanging, cutting of supporting threads as well as too-rapid approach attempts of the male.

After a while (usually within the first hour) the male started to enter the female's retreat. The female sometimes initially rejected the male's attempts to approach. Rejection movements ranged from simple plucking or striking with the first pair of legs, a slight change in position, jerking, walking inside the retreat up to leaving the retreat and charging at the male. In the latter case he hastily retreated or dropped from the female's web. Amos immediately, the male returned to the web to continue the courtship display using an earlier stage (e.g. cutting, strumming).

Tactile phase: Having successfully entered the female retreat, the male achieved initial tactile contact by carefully caressing the female's front legs (Fig. 38a). Then the male started to walk over her and around the inner surface of the retreat. He climbed onto the female over her pedipalps and chelicerae and walked over her eyes. Silk was lain down during all these movements. It was attached to the surrounding web (retreat) and onto the legs and the body of the female (bridal veil). The female responded at any stage of contact courtship by grooming herself free of the male silk and attaching new

silk threads to her retreat. The male reacted with a sudden halt and a few jerks before resuming courtship activities.

From the ventral surface, the male circled around to the dorsal surface or back up into the retreat. Repeatedly, the male was found performing strumming sequences inside the retreat (Fig. 38b) very close or even touching the female's body with a leg. While he circled around the female, tapping with the tarsi of legs I (Figs, 38g, h) alternated with scrabbling the opisthosomal surface with his pedipalps (Figs. 38e, f). Periods of activity (circling, strumming, tapping, scrabbling, etc.) were interspersed with periods of rest. Generally, pauses became longer as the courtship proceeded.

Sooner or later the male moved onto the ventral side of the opisthosoma of the female. The partners then sat venter on venter, both facing in the same direction. He made close pedipalp contact with the surface as though feeling for the epigyne (Fig. 38d). With his mouthpart directly positioned over the female atrium (nibbling), the male chelicerae (and sometimes the corresponding pedipalps) alternately moved up and down (cheliceral scrabbling). Occasionally, a watery liquid could be observed glistening between the chelicerae. Several times it was observed that during a pause or a cheliceral scrabbling/nibbling sequence, the male positioned the tarsus of his first leg directly on the mouth region of the female (Fig. 38c). During any of the male's activities, but especially during the sequence of cheliceral scrabbling/ nibbling, the female reacted by slowly moving the tarsus of leg III towards the male. The slight leg flicking of the female was sufficient to send the male back to earlier courtship patterns such as circling around the female and the retreat. Sometimes the female started moving around the retreat attaching silk to the inner surface. However, any movement of the female was directly answered by a sudden stop from the male, followed by two or three small jerks (see above). The female of *L. revivensis* did not assume a distinct mating posture. The only obvious signs of acceptance were the lack of rejecting movements and the slight lowering of her body which allowed the male to reach her epigyne. This would otherwise be impossible since it is normally pressed against the silken walls of the retreat. Eventually, the female became more or less cataleptic and cheliceral scrabbling/nibbling was followed by coupling attempts.

3. 3. 2. 3. Copulation and postcopulatory events

During coupling attempts the male lifted his body up by stilting his legs (Fig. 39a). He moved his abdomen sideways so that his body axis formed an angle of approx. 45° relative to the body axis of the female. He moved his body to the right when trying to insert his right embolus and *vice versa* (Fig. 39a). When trying to insert his right embolus into the left copulatory duct of the female, the male lifted the left pedipalp. He then moved his right pedipalp even further to the left underneath the left pedipalp (Fig. 39b). With his whole body tilting and finally shifting to the right, he attempted to couple his pedipalp to the carina of the female epigynal opening (Fig. 39c). Usually, the first coupling attempts failed and the male moved a few millimetres backwards on the female opisthosoma and groomed his pedipalps by rubbing them against each other. Afterwards he rested for a few seconds up to several minutes (Fig. 39d). After an unsuccessful coupling attempt, the male resumed earlier courtship activities such as circling, spinning, tapping, scrabbling and finally cheliceral scrabbling/nibbling before starting another coupling attempt.

When the male successfully achieved genital coupling after shifting to the right, his body slowly tilted to the opposite, left side (Figs. 39e-g). The white, soft haematodochae inflated several times (Fig. 39g) until the male tried to withdraw his embolus.

The activities after successful couplings differed between the pairs. The few cases where coupling and post-copulatory events were observed are described here:
In one case I was able to observe that the haematodochae of the male inflated 7 times within 9 s. After the last inflation, the female suddenly became increasingly irritable. She started to move around while the male tried to remove his embolus from the female genitalia. Although it took the male about 40 s to free himself the female did not make any attempts to catch him. Afterwards both sexes started to groom themselves. The male cleaned his pedipalps and legs, and the female wiped the male silk off her body and attached new silk threads to her retreat. Eventually, male and female sat in close proximity (Fig. 39h). The female neither showed any signs of hostility towards the male, nor did the male show any signs of fear of the female. During the next two hours of observation, neither the male nor the female showed any further signs of activity and eventually, the male was removed from the web.

In other instances the female did not move at all until the male had slowly withdrawn the long, coiled embolus after approx. 1 min 30 sec. She even remained in deep catalepsy for some time. After several minutes the male resumed courtship activities outside the retreat. After a few alternating sequences of spinning and strumming he entered the retreat. He almost immediately moved onto the female ventral side and managed to insert the embolus of the second pedipalp at the first coupling attempt. He withdrew the embolus after approx. 2 min. The female still did not show any signs of activity. Within the next two hours the male did not take up any further courtship activities and was removed. The act of cannibalism itself could only be observed once. Here the female lowered her legs III onto the male back after he had inserted his embolus. She violently attacked him as soon as he tried to remove his pedipalp. Finally, he was wrapped up and consumed by the female.

3. 3. 3. Spermatozoa and secretion

To evaluate to what extent females may be able to manipulate spermatozoa (for example, by selective activation or sperm displacement), I examined the changes in spermatozoa and secretion (LM) occurring from the time they are stored inside the male spermophor until approx. 12 h after oviposition.

The spermophor of virgin males is filled with a mass of spermatozoa that lie loosely embedded in secretion (Fig. 40a). The secretion consists of a homogenous purplish, liquid matrix and small droplets. The droplets are regularly distributed among the spermatozoa (Figs. 40b, c) and stain bright blue with toluidine blue (Fig. 40b). The spermatozoa form small disks (Fig. 40b) that consist of the tightly-coiled sperm head and the flagellum, indistinguishable from the head in this stage (Figs. 40b, c). Each spermatozoa is surrounded by a capsule and the encapsulated sperm has a total diameter of approx. 4 µm.

The spermatheca of a virgin female is completely filled with a granular secretion (Fig. 3c, 40e) that stains pinkish with toluidine blue (Fig. 40d). At the periphery of the anterior and posterior lobes, the secretion appears rather homogenous. Here it is obviously expelled through the gland pores (Fig. 40d). Around this small region the secretion seems slightly diluted, but has the same granular appearance as in the centre of the spermathecal lumen.

In some females, approx. 24 h after copulation the anterior and posterior lumina were densely filled with encapsulated spermatozoa (Fig. 3d). The encapsulated spermatozoa differ strikingly from those in the male spermophor. The flagellum is clearly visible and coiled around the elongated sperm head (approx. 12 µm long) (Figs. 40i, j). The capsules appear dilated and more rounded with a diameter of approx. 6 µm (Fig. 40i). The capsules of neighbouring spermatozoa are in direct contact with each other, forming a compact mass with an overall structure that is reminiscent of a honeycomb (Figs. 40g, i). The majority of the female granular, pinkish secretion appears to be replaced by the sperm mass, forming a dense layer covering the cuticle of the spermatheca (Figs. 8i, 40f, g). Only some of the female secretion remains lying in islets of various sizes among the encapsulated sperm cells (Fig. 40f). A little purplish liquid secretion remains visible between the capsules. Further isolated islets are formed by blue droplets imbedded in the same purplish, liquid secretion, similar to those found in the male spermophor (Fig. 40h). In other recently-mated females, only the anterior lobe and, partly, the middle portion of the spermatheca contain sperm. The anterior lobe is densely packed with encapsulated spermatozoa, whereas in the middle portion spermatozoa are decapsulated. Decapsulated spermatozoa lack the protein capsule, but the heads are still curved and the tail is bent around it (Figs. 40e, f, h).

In the posterior lobe of the spermatheca of a female who had produced her first egg sac approx. 12 h after before dissection, only few decapsulated sperm cells lie in the centre of the lumen. The granular secretion appears less dense in the middle. However, at the periphery, in close proximity to the openings of the gland pores, the secretion looks similar to that in the posterior lobe of the spermatheca of a virgin female (Fig. 41a-c). Further anteriorly, decapsulated spermatozoa lie in the region where the small fertilisation ducts begins to form (Figs. 41d, e). The spermatozoa are surrounded by the pinkish granular secretion. The small fertilisation ducts are filled with coiled, but decapsulated spermatozoa (Fig. 41f). At the level of the entrance of the copulatory duct into the spermatheca the whole lumen is filled with decapsulated sperm and secretion products similar to those in the region described previously. Some blue droplets in a purplish, liquid secretion are visible (Fig. 41h). The TEM-picture shows a group of droplets in a liquid secretion, coiled, decapsulated spermatozoa and a granular secretion (Fig. 41i). The spermatozoa in the anterior lobe are still encapsulated. The LM-pictures

did not reveal any difference between the sperm mass inside the anterior lobe of the spermatheca of the female after the first oviposition (Figs. 41j-l) and a recently-mated female (see above).

3. 3. 4. Position of the inserted embolus and broken embolus tips

In most mated females one or more embolus tips and, in some cases, adjacent fragments of the embolus are found inside the female genital tract. By studying female epigyna in which longer embolus fragments are found, it becomes obvious that the male completely screws his coiled embolus into the similarly coiled copulatory duct of the female (Fig. 42a). The embolus tip is lodged deep inside the lateral part (tube) of the slit-like opening of the female spermatheca (Figs. 42d, f), where it finally snaps off at the breaking point. The space between the tip and the cuticle of the spermathecal opening is filled with a secretion (Fig. 42e). In most cases the tip breaks off and the rest of the embolus is withdrawn after copulation. Only the wider part close to the saddle-like thickening of the tip remains, lying inside the distal part of the copulatory duct (Figs. 3b, e, 42a). About 2/3 of the embolus tip's length extends into the anterior lumen of the spermatheca. The actual site where the seminal fluid is expelled is found at the most anterior wall of the spermatheca (Fig. 3e). Here the opening of the pointed end of the male embolus comes to rest during insemination. In the cleared epigyna of two females, two tips are seen in the opening, but neither of these tips is positioned deeply inside the opening as described above (Fig. 42b). Only between 1/3 to 1/2 of the tips' lengths reach the spermathecal lumen. In the semi-thin sections of one mated female, two tips are lying next to each other in the spermathecal opening (Fig. 41g). In some cleared specimens a second tip lies in the copulatory duct, behind a tip that has already been positioned in the spermathecal opening by another male (Fig. 42c). In some of the males that were used for the mating experiments in the laboratory, the whole embolus is completely uncoiled, but the embolus tip is still present (Fig. 42g).

3. 3. 5. Data from the field

To estimate the probability of remating of females under natural conditions, mated females collected in the field were divided into two groups. 1) 'Early females' which not yet produced an egg sac in the field, but produced a viable egg sac later in the laboratory; 2) 'late females' which had already produced one or more egg sacs in the field when collected. Females of *Latrodectus* species generally reject further males as time after the first mating proceeds and oviposition has taken place (Herms *et al*. 1935; Abalos & Báez 1966, 1967; Forster 1995; Andrade 1996; personal observations). In contrast to the 'late females' that are assumed to have completed their mating period, 'early females' might have accepted an additional male in the field.

The inspection of the cleared epigyna yielded the following results (Tab. 2).

	number of specimens	number of tips in the right - left sides				adjacent embolus fragments
		0 - 0	1 - 0 or 0 - 1	1 - 1	2 - 1 or 1 - 2	
'early females' (without egg sacs in the field)	35 (100%)	2 (5.7%)	15 **(42.9%)**	17 (48.6%)	1 **(2.9%)**	2 (5.7%)
'late females' (with one or more egg sacs in the field)	24 (100%)	1 (4.2%)	6 **(25.0%)**	11 (45.8%)	6 **(25.0%)**	3 (12.5%)
total ('early and late females')	59 (100%)	3 (5.1%)	21 (35.6%)	28 (47.5%)	7 (11.9%)	5 (8.5%)

Tab. 2: Number and percentages (in parentheses) of embolus tips and adjacent embolus fragments found in the right or left copulatory ducts and spermathecal openings of cleared epigyna of *L. revivensis* females collected in the field. 'Early females' had not yet produced an egg sac in the field, but produced viable offspring later in the lab. 'Late females' had already produced at least one egg sac in the field. **In bold type**: percentages of females that had a single tip in one side (clearly mated with only one male) and of females that had more than one tip in one side (clearly mated with more than one male).

A total of 5.1 % of the epigyna of 'early and late females' did not contain an embolus tip, although females produced viable egg sacs. 35.6 % of all females had one tip inside the spermathecal opening of one side, 47.5 % had one tip in each opening and 11.9 % had an additional tip in one side of the genital tract (Figs. 42b, c). In the latter cases only two female epigyna contained two tips inside the same spermathecal opening; both embolus tips reached the spermathecal lumen (Fig. 42b). In the other five cases one tip was lodged deep inside the spermathecal opening and another tip lay behind it in the

wider part of the copulatory duct (Fig. 42c). 8.5 % of all examined epigyna revealed an adjacent embolus fragment in addition to the corresponding tip (Fig. 42a).

To evaluate the remating probability for *L. revivensis* in more detail, I compared the change in the proportion of 'early' and 'late females' that unambiguously mated only once (1 - 0 or 0 - 1 tips) and those that obviously mated with at least two males (2 - 1 or 1 - 2). Whereas 42.9 % of the 'early females' (who might accept an additional male) accepted one copulation bout, only 25.0 % of the 'late females' (that are not expected to accept an additional male) had copulated only once. However, only 2.9 % of the 'early females' had clearly copulated with more than one male, whereas 25.0 % of the 'late females' had clearly copulated with at least two males.

3. 3. 6. Data from the laboratory matings

A total of 62 matings were observed. In 50 matings, virgin males were placed with virgin females. In 12 matings, males that had lost one embolus tip in a previous mating were placed with a second virgin female. Since ten of the latter males were removed 8 h after onset of courtship in their first mating, a total of 40 virgin males were allowed to stay with a virgin female over the whole 24 h period (Tab. 3).
All 62 virgin females accepted the courting male within 24 h.

	mated	no tip lost (but embolus untangled)	one tip lost	**one-sided mated** ($\sum$ no + one tip lost)	**two-sided mated** (two tips lost)	adjacent embolus fragment lost
cannibalised and non-cannibalised males	40 (100 %)	3 (7.5 %)	22 (55.0 %)	25 (62.5 %)	15 (37.5 %)	3 (7.5 %)
cannibalised males	12 (30.0 %)	3 (25.0 %)	8 (66.7 %)	11 (91.7 %)	1 (8.3 %)	0 (0 %)
non-cannibalised males	28 (70.0 %)	0 (0 %)	14 (50.0 %)	14 (50.0 %)	14 (50.0 %)	3 (10.7 %)

Tab. 3: Number and percentages (in parentheses) of mated, cannibalised and non-cannibalised males of *L. revivensis*, as well as the number of tips (and adjacent embolus fragments) lost during copulation. Males that did not lose a tip (but had one embolus untangled) and males that lost one embolus tip are summarised as **one-sided mated** males. Together with the males that lost both tips (**two-sided mated**) they represent the **mated** males. Some males lost an 'adjacent embolus fragment' in addition to the corresponding embolus tip.

Of the 40 virgin males kept with a virgin female over 24 h, three (7.5 %) males did not lose an embolus tip, but one embolus became completely untangled (Tab. 3). The disarrangement of the embolus (Fig. 42g) indicated that copulation with one pedipalp had taken place. The production of a viable egg sac by the relevant female showed that insemination had been successful. Twenty-two (55.0 %) males did lose one embolus tip. The 25 males (62.5 %) that either used one pedipalp (untangled) without losing the tip or lost one embolus tip were described through 'one-sided mated' males (Tab. 3). Fifteen males (37.5 %) lost both embolus tips ('two-sided mated'). Three males lost an adjacent embolus fragment. Two of them lost one embolus tip and the adjacent embolus fragment. The third male lost both tips and an adjacent embolus fragment.

Twelve (30.0 %) males were cannibalised by the female and 28 (70.0 %) survived copulation. The three males that did not lose an embolus tip (but had one embolus untangled) were cannibalised (25.0 %). Eight males (66.7 %) lost one tip. Consequently, 11 males (91.7 %) were 'one-sided mated' males. None of the cannibalised males lost an adjacent embolus fragment.

All of the non-cannibalised males lost one or both embolus tips. None of them had an untangled embolus. Fourteen males (50.0 %) lost one tip. Consequently, 14 non-cannibalised males (50.0 %) were 'one-sided mated'. Another 14 males (50.0 %) lost both tips. All of the three males that lost an adjacent embolus fragment in addition to the corresponding tip were found in the group of the non-cannibalised males (10.7 %).

Size and time of first copulation (< or > 8 h)

Comparing all males or females, the student t-test showed that there is no significant difference in leg length between males or females that mated before or after 8 h (male leg length: t_{25} = - 1.407, p > 0.171; female leg length: t_{25} = - 0985, p > 0.334).

Size and time of cannibalism (< or > 8 h)

Neither males that were cannibalised before or after 8 h (student t-test: t_5 = - 0.142, p > 0.892) nor females that cannibalised males before or after 8 h (t_5 = - 1.077, p > 0.331) differed in leg length.

Size and probability of cannibalism

Virgin males that were cannibalised by virgin females were significantly smaller (with leg length as an indicator of overall body size) than males that avoided being cannibalised (male leg length, $t_{25} = 4.028$, $p < 0.001$) (Fig. 45). Also the virgin females that cannibalised virgin males were significantly smaller than females that did not capture the male (female leg length, $t_{25} = 2.652$, $p < 0.014$) (Fig. 46). When corrected against each other, male leg length still had a significant negative effect, whereas female leg length did not (Likelihood ratio χ^2 statistics for type 3 analysis: male leg length $\chi^2 = 7.8974$, $p < 0.005$; female leg length $\chi^2 = 0.5568$, $p > 0.4556$). However, the sample size was rather small and the logistic regression showed that male and female leg length strongly correlated within pairs (Pearson correlation coefficient $b = 0.92$, $p < 0.030$). This might be responsible for the fact that female leg length had a significant effect on the probability of cannibalising a male when tested alone.

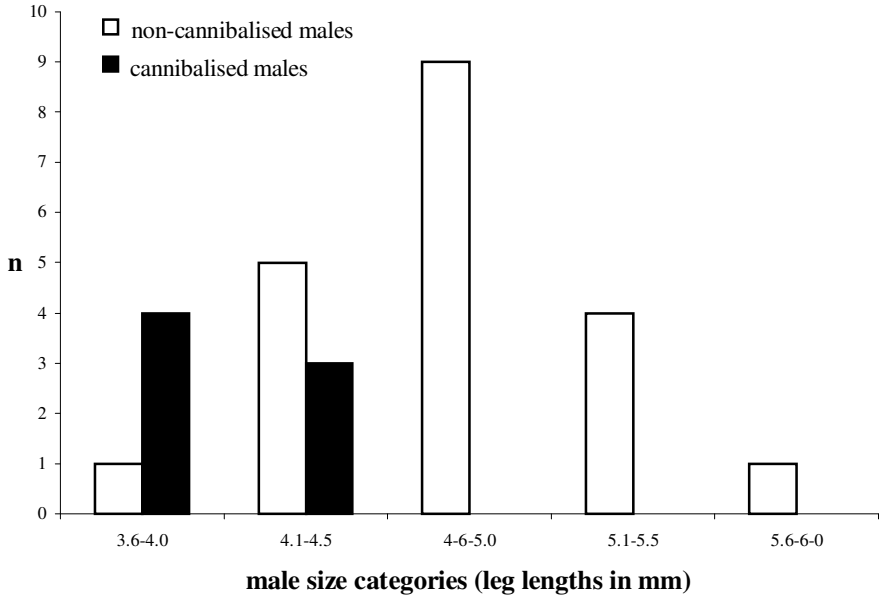


Fig. 45: Size categories (leg lengths in mm) of cannibalised and non-cannibalised males ($n = 27$).

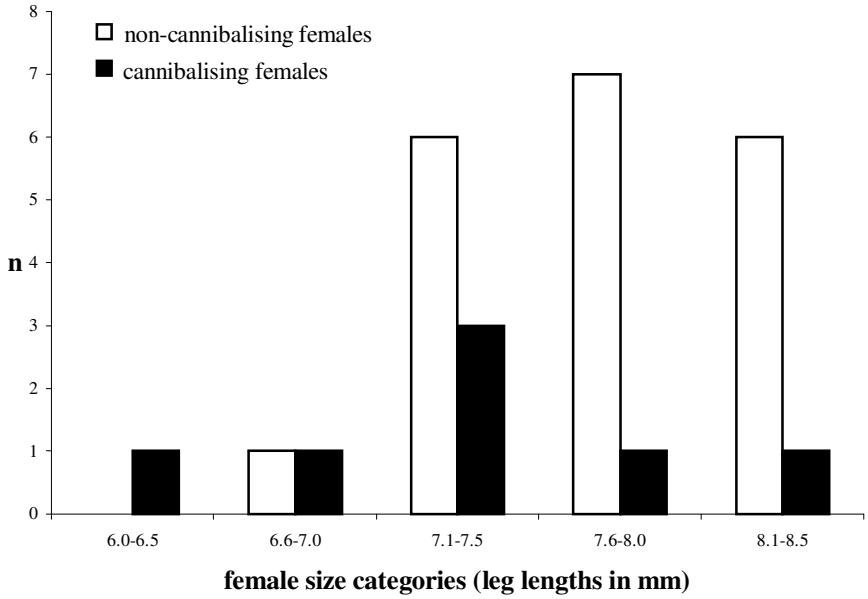


Fig. 46: Size categories (leg lengths in mm) of cannibalising and non-cannibalising females (n = 27).

Cannibalism and time of first copulation (< or > 8 h)

Males that achieved their first copulation bout earlier (< 8 h) were not cannibalised more often than males that had their first copulation bout later (> 8 h) (Fisher exact test $\chi^2 = 0.127$, $p > 0.735$).

Cannibalism and loss of embolus tips

The Fisher exact test showed that non-cannibalised males achieved a second copulation bout ('two-sided mated') more often than cannibalised males ($\chi^2 = 6.222$, $p < 0.015$) (Tab. 3).

Cannibalism and time of copulation of mated males with a second virgin female

Twelve males that had lost one embolus tip in the first mating were introduced into another virgin female's web. In their first mating 10 males copulated < 8h and 2 males > 8 h. In the matings with the second virgin female all males copulated in exactly the same time period as they had done with the first female. Mated males were not cannibalised more often by the second virgin female (Fisher exact test $\chi^2 = 0.05$, $p = 1.000$) than by the first one.

4. Discussion

4. 1. The female

The female epigynum and the uterus in *L. revivensis* represent a complex system partly surrounded by specialised glandular units.

4. 1. 1. The epigynum

In general, the female epigynal structures reveal many similarities to those of other *Latrodectus* species (e.g. Bhatnagar & Rempel 1962; Lauria de Cidre 1988). The general description of the epigynal plate of *L. revivensis* is in accordance with that given by Shulov (1948), Levi (1966) and Levy and Amitai (1983) for the same species. The plate is covered by a thick cuticle that, under the light microscope, shows an organisation into endo-, meso- and exocuticle of similar thickness. In contrast to the soft opisthosomal cuticle of *Cupiennius salei* for example (with its prominent endocuticle and an absence of exocuticle) (Barth 1969), the cuticular organisation of the epigynal plate of *L. revivensis* resembles instead the rigid prosomal cuticle of *L. hesperus* for example (Hadley 1981). None of the authors who have characterised the outer aspects of any *Latrodectus* species have mentioned the long and thin hairs that cover the epigynal plate and partly overhang the opening of the atrium (Shulov 1940, 1948; Levi 1959, 1983a; Bhatnagar & Rempel 1962; Abalos & Báez 1967; Mackay 1972; Levy & Amitai 1983). Semi-thin sections of the epigynal plate of *L. revivensis* show that these hairs represent mechanoreceptive sensilla characterised by their typical suspension in a socket and the fluid-filled extra-cellular space, although the enervating dendrite is not distinctly visible at the light-microscopical level (Foelix 1970, 1985, 1996). During courtship, a male touches the female's ventral abdomen with his legs, pedipalps and mouthparts. The tactile hairs that cover the entrance to her genitalia may enable the female to perceive stimuli provided by the male during courtship, especially during cheliceral scrabbling/nibbling. However, no tactile hairs, slit-sensilla or internal receptors were found in those regions inside the female genital tract that would be in direct contact with those parts of the male's pedipalp which are introduced into the epigynum during copulation. The mere presence of tactile hairs on the epigynal surface and the lack of sensilla inside the epigynum suggests that, during insertion, the female is able to detect the male's presence, but not to obtain information about male size, for

example embolus length or embolus tip diameter. Eberhard (1985) proposed that females might be able to discriminate between males on the basis of the stimulatory function of their genitalia and that female choice by stimulation might be a dominant force in the evolution of species specificity of spider genitalia. However, a copulatory courtship, as described by Eberhard (1994) for several insects and spiders does, not seem to play a role in *L. revivensis*.

Bhatnagar and Rempel (1962) described the ontogenetic development of the female genitalia in *L. curacaviensis*. In the fourth instar, the epidermal cells immediately in front of the uterus externus in the middle of the epigastric furrow become invaginated. A dorsal and ventral lobe are formed. The dorsal lobe establishes a new contact with the uterus externus via a narrow tube that finally forms the fertilisation duct. The opening of the ventral lobe gradually shifts ventrally, finally forming the genital aperture on the epigynal plate outside the epigastric furrow. As a result of the development of the epigynal structures from a single primary invagination, the copulatory ducts, the spermathecae and the fertilisation ducts remain connected, forming a complicated system.

In *L. curacaviensis* each spermatheca was said to have its own fertilisation duct that opens directly into the uterus externus (Bhatnagar & Rempel 1962). The same was suggested for *L. antheratus*, *L. mirabilis* and *L. corallinus* (de la Serna *et al*. 1987). According to the illustration of the female genitalia given by these authors I would rather suggest a similar organisation to that in *L. revivensis*, i.e. a small fertilisation duct leads from both spermatheca to a common fertilisation duct, which connects the spermathecae to the uterus externus.

Close to the spermatheca of *L. revivensis* the copulatory duct becomes flat; moreover, a distinct tube is formed in this region, whose wall is more sclerotised than the rest of the copulatory duct. This tube forms a guide for the male embolus during copulation. Additionally, it might act as a bottle-neck which the male embolus has to pass before the tip can enter the spermatheca to deposit spermatozoa.

Muscle fibres not previously described for *Latrodectus* species connect this end part of the copulatory duct to the ventral side of the common fertilisation ducts and the epigynal plate. The contraction of the fibres might result in pulling the tube-like section of the copulatory duct in a dorsomedial- as well as a ventromedial direction. As the

embolus tip usually reaches into the spermathecal lumen, a deterrence of the insertion of the male's embolus by the muscular movements by the female does not seem to take place in *L. revivensis*. A deterrence of the withdrawal of the embolus after insemination seems more probable. For *L. tredecimguttatus* (Shulov 1940) and *L. indistinctus* (Smithers 1944) it has been reported that males sometimes have problems freeing their embolus from the female epigynum after copulation. Frequently, males lose not only the embolus tip, but additional segments of the adjacent embolus (see Tabs. 2, 4 and see chapter 4. 3. 4. 1.). If the deterrence of the male withdrawal increases the chances of the female cannibalising her mate, this would provide a mechanism for her to exercise cryptic female choice (Eberhard 1996).

Surprisingly, the paired muscle reaching from the ventral side of the common fertilisation duct to the epigynal plate in *L. revivensis* has also not been mentioned in the otherwise very detailed description of the musculature of *L. mactans* given by Whitehead and Rempel (1959). However, muscle fibres that connect the common fertilisation duct with the epigynal plate were described in *L. antheratus* and *L. corallinus* (Lauria de Cidre 1988). When contracting, the muscles will most probably exert a downward-directed tension on the duct. The dorsal wall of the beginning of the common fertilisation duct forms a heavily sclerotised and rigid structure. The downward movement of the ventral portion of the duct lined by a thin cuticle will cause a dilation of the common duct. A similar mechanism was proposed by Lauria de Cidre (1988) for two other *Latrodectus* species. As a consequence, sperm may indiscriminately be sucked out of the small fertilisation ducts and the lumen of the spermathecae during oviposition. If the separate spermathecae are filled with the spermatozoa of two different males, their individual paternity may therefore depend on the amount of sperm deposited by each of them (Andrade 1996). For other spiders it has been proposed that the secretion produced by the spermathecal epithelium may mechanically force the sperm out of the spermathecae during oviposition (Cooke 1966; Lopez & Juberthie-Jupeau 1983). Similarly, Bhatnagar and Rempel (1962) suggested for *L. curacaviensis* that an increased glandular secretion into the spermatheca caused by an increase in hemolymph pressure in the genitalia may force the spermatozoa through the fertilisation tubes. But, since the comparison of the spermathecal contents in *L. revivensis* before and after ovipostion does not reveal an extensive production of

secretion or water during egg laying (see chapters 3. 3. 3. and 4. 3. 3.), the above-mentioned mechanisms are most likely not responsible for the displacement of spermatozoa in this species. Engelhardt (1910) described another possible mechanism for the theridiid spider *Theridium tepidariorum*. The sperm transport might be mediated by the pressure on the spermathecae that is produced when the eggs pass through the uterus externus into the vagina. Hence, the spermathecal walls of *Latrodectus* are rigid structures, the passage of the large eggs through the uterus externus would rather increase the low pressure in the common fertilisation duct, which would help to suck the sperm out of the spermathecal lumen.

4. 1. 2. The spermatheca

The paired spermathecae of *L. revivensis* are dumb-bell-shaped organs. Each spermatheca is divided into distinct compartments: the anterior lobe, the posterior lobe and the narrow middle portion. The copulatory duct is connected with the anterior lobe; the small fertilisation duct is part of the posterior lobe. Additionally, the small fertilisation duct runs from the middle of the posterior lobe in an anteriomedial direction, joining the common fertilisation duct almost at the height of the middle portion. The actual entrance and exit of the spermatheca lie clearly separated from each other. Judging from the illustrations of the genitalia of *L. curacaviensis* (see Bhatnagar and Rempel 1962), Uhl and Vollrath (1998b) assumed a conduit female spermatheca of the cul-de-sac type (entrance and exit lie close to each other) for *L. hasselti*. However, the present observations and the illustrations of female spermathecae of various *Latrodectus* species by other authors (Levi 1959, 1983a; Wiehle 1961, 1967a; Abalos & Báez 1963, 1967; Kaston 1970; Levy & Amitai 1983; Müller 1985; Knoflach & van Harten 2002) suggest a spatial separation of the entrance and exit for all *Latrodectus* species and, hence, a spermatheca that is functionally of the conduit type. If several males manage to transfer spermatozoa into the same spermatheca, a first male sperm priority would be expected due to the stratification resulting from this spermathecal design (‘first in-first out’).

4. 1. 2. 1 The cuticle

In general, the cuticle of the spermatheca corresponds to that of other arthropods. In the epicuticle two layers can be distinguished: the dense homogenous inner layer (inner epicuticle according to Neville 1975) and the outer, more electron-dense and thin layer (outer epicuticle) (for spiders see Barth 1969; Hadley 1981). Epicuticular components, such as lipids, might have been lost during TEM preparation.

Ornamentations (protuberances or ribs) on the outer surface of the cuticle (e.g. in *Cupiennius salei*; Barth 1969) may be composed solely of the epicuticle or, as in the spermatheca of *L. revivensis*, of the exocuticle covered by the thin epicuticular layers. Differences between the two species can also be seen in the distribution of pore and wax canals that only lie between the ribs in *C. salei*, but, additionally, penetrate each protuberance in *L. revivensis*.

Generally, the mesocuticle in arthropods differs from the endocuticle in the degree of impregnation with proteins and lipids (Neville 1975; Hackman 1984). As is usual for other spiders and insects (Neville 1975; Dalingwater 1987), the two layers cannot be distinguished under the TEM. Here the outer region of the endocuticle is equivalent to the mesocuticle described by light microscopy (Dalingwater 1987), that merely represents a transition zone between endo- and exocuticle. Generally, the exocuticle is highly sclerotised by phenolic tanning (Neville 1975; Hackman 1984). In *L. revivensis*, exocuticular laminae sometimes appear to be arranged less regularly than the endocuticular ones. This might be caused when the microfibrillar layers of the helicoidal cuticle are cut at slightly different planes exhibiting the changing orientation of the microfibres within each lamina. However, the different nature of endo- and exocuticle becomes indirectly evident in the SEM micrographs of KOH-treated spermathecae and low-viscosity resin casts. In the former, the laminae of the exocuticle appear more compact, in the latter, the resin penetrated into spaces of the endocuticle. In their studies on arthropod cuticles, Krishnakumaran (1960) and Dennell (1976, 1978) demonstrated the presence of lamina membranes between single laminae which persisted even after treatment with potash and acetic acid. The view that laminae are real structures contradicts the basic Bouligand model (Bouligand 1965; Neville *et al*. 1969; Barth 1970; Neville 1984), which states that the laminae are purely artificial structures caused by the changing orientation of the microfibres between successive

layers. The distance between the thin layers of the cast in *L. revivensis* suggest that the resin penetrated into the spaces between single laminae. Here organic material may have been washed out during treatment with KOH. Whether this material resembles or belongs to a real 'lamina membrane' must be investigated in further studies. During sclerotisation, the protein chains of the exocuticle become cross-linked (Hackman 1984). This probably prevents washing out of organic material from the exocuticle of *L. revivensis*.

Pore canals are interpreted as a device that transports impregnating material, for example, into the laminate cuticular layers (Neville 1975) or wax (Locke 1961; Locke & Huie 1980) and adhesive excretions (Gorb 1997) to the cuticular surface. The twisted ribbon shape of pore canals is determined by the helicoidal architecture of the chitin-protein complex of the surrounding cuticle (Barth 1970; Neville 1975). Studies of various arthropods indicate that shortly after the moult the pore canal is filled with cytoplasmic extensions of the underlying epithelial cell (Neville 1975) that may contain microtubuli (e.g. in *Rhodnius prolixus*; Lai-Fook 1968 cited in Neville 1975). In some cases the pore canal contains structures that appear to be chitin microfibres in a protein matrix, a single pore canal filament or a central lipid filament surrounded by chitin microfibres and imbedded in a protein matrix (Locke 1961; see citations in Neville 1975; Gorb 1997).

In *L. revivensis* the pore canal in the endocuticle contains finger-like extensions of the intercalary cell and their cytoplasm is densely filled with filaments. In the exocuticle the pore canal contains one to three hollow and apically-dilated tubes whose electron-dense border does not resemble a plasma membrane. A similar distinction between the apical and basal part of the pore canal has only been described for the walking leg of *Cupiennius salei* (Barth 1969). Here the contents of the endo- and mesocuticular pore canals has a stringy, loosened structure. In the exocuticle it appears solid and electron-dense. To my knowledge, such structures at the transition of the pore canal to the wax canals as in *L. revivensis* (dilated, hollow tube) have not been described thus far. However, wax canal filaments that arise from the wax canals and fuse to form the pore canal filament (Neville 1975) were not found in *L. revivensis*. Sewell (1951) demonstrated chitin (chitosan test) in the pore canals of the exocuticle in

Tegenaria atrica. The presence of the tubes in the KOH-treated cuticle of *L. revivensis* suggest that they might likewise contain cuticular material.

4. 1. 2. 2. The epithelium

The spermatheca of *L. revivensis* is surrounded by a complex epithelium which is similar to that of other araneomorph spiders (Suhm & Alberti 1993; Uhl 1994b, 2000). It comprises two types of glandular units and various ordinary epithelial cells. In type I, similar to the basal 'gland cells' or 'secretory cells' in other spiders and insects (Gillot 1988; Noiret & Quennedy 1974, 1991; Suhm & Alberti 1993; Uhl 1996, 2000), the gland cell (G1) is surrounded by the secretory canal cell (C1) that forms the cuticular ductule. Both cells and the most apical part of the ductule are ensheathed by envelope cells (E). The same almost certainly holds true for type II, although the cell body of the secretory gland cell G2 could not be unequivocally assigned. A single glandular unit (G1/C1), or clusters of glandular units (up to 10 G1/C1 or G2/C2), and their envelope cells are interspersed with intercalary cells.

The ultra-structural aspects of the gland cell (G1) are that of a cell producing glycoproteins. The cell possesses an extra-cellular reservoir with microvilli that might serve to collect synthesised material. From here the secretion becomes transported into the ductule that penetrates the neck portion of the cell. A similar organisation is suggested for the second glandular unit. Although no further cytoplasmic components can be unequivocally assigned to G2, the basal cells (considered as gland cells G2) contain extra-cellular reservoirs that contain a central ductule. Although not unequivocally demonstrated, this duct might be continuous with the ductule of the secretory canal cell (C2). Similar glandular units have been described in the genital accessory glands of *Pholcus phalangioides* (Uhl 1994b). Here the collecting system of the gland cell is a simple extra-cellular space bordered by microvilli without any specialised structures (e.g. an 'end apparatus' with a fenestrated cuticular wall covered by a thicker fibrillar or filamentous layer frequently found in insects) (Quennedy & Noiret 1974, 1991; Gillott 1988). Moreover, the gland cell possesses an apical elongated neck portion that connects to the ductule of the canal cell (Fig. 7b in Uhl 1994b).

In *L. revivensis* two different types of secretory canal cells can be distinguished (C1 and C2). Both contain only a few cisterns of the rough endoplasmic reticulum, but a considerable number of dictyosomes. They differ in the assembly of microvilli, the

surrounding, extra-cellular material and in the structure of the cuticular ductule. Microvilli of C1 are densely packed and surrounded by homogenous and electron-dense material similar to that in the basal part of the ductule. Microvilli of C2 are less densely packed and supported by abundant microtubuli. The large extra-cellular spaces are usually filled with granular material similar to the content of the ductule. In both secretory canal cells the ductule is lined by a very thin and electron-dense cuticular layer. In the most apical part it has an additional inner layer. The outer layer corresponds to the outer, the inner layer to the inner epicuticle as seen for instance in the cuticle of the spermatheca. Thus, the ductule consists entirely of epicuticular material as in insect class III cell units defined by Noiret and Quennnedy (1974) (see also below).

The envelope cells, intercalary cells and cells in the middle region each resemble ordinary epithelial cells. The epithelia cells of the middle portion of the spermatheca and the intercalary cells are associated with pore canals.

The large numbers of microtubuli in the cytoplasm of the envelope cells indicate their supportive role (Odhiambo 1969). Additionally, they are most probably involved in the production of the apical part of the glandular ductule.

The intercalary cells exhibit apical microvilli and numerous mitochondria and glycogen particles. This suggests a secretory or resorbtive function (see chapter 4. 3. 3.).

The spindle-shaped light, electron-lucent areas of the epithelial cell that surround the middle portion of the spermatheca and the end of the copulatory duct are not bound by a unit membrane. They are filled with few glycogen particles, if any. This indicates that material has been lost during fixation and embedding of the tissue. Comparable results, however, at the light microscopical level were reported for *Araneus diadematus* (Kovoor 1981). She identified vacuole rich epidermis cells around parts of the spermatheca and the copulatory ducts.

Detailed TEM studies of the epithelia associated with female sperm storage devices (spermathecae or uterus externus) in spiders are scarce. The spermathecae of various mygalomorphs (*Grammostola burzaquensis*, *G. pulchripes*, *G. vachoni*, *G. inermis*, *Acanthoscurria sternalis* (Theraphosidae) (De Carlo 1973) and *Telema tenella* (Telemidae) (Lopez & Juberthie-Jupeau 1983)) possess simple glands without a ductule (class I gland cell according to Quennedy & Noiret 1974, 1991). In the haplogyne spider *Pholcus phalangioides*, the uterus externus itself functions as a sperm store. The

glandular units of the epithelium consist of two joined secretory cells surrounded by an inner and an outer envelope cell. The latter two cells produce parts of the ductule that open onto a cuticular pore plate (Uhl 1994b). In the spermatheca of the haplogyne spider, *Dysdera erythrina* (Dysderidae), three gland cells discharge their secretory products into a common duct produced by three successive canal cells (Uhl 2000). In both species the glandular units are separated from each other by intercalary cells, similar to those of *L. revivensis*. To my knowledge, *Amaurobius fenestralis* is the only entelegyne spider (with distinct spermathecae) whose spermathecal epithelium has been investigated at the ultrastructural level thus far (Suhm & Alberti 1993). The authors detected two different types of pores and, accordingly, two different types of glandular units. They counted 20 small primary pores, each containing a cuticular ductule and (mostly) two ciliated, one secretory, one connecting, one canal and one sheath cell. The single large secondary pore comprises epithelial cells that contain microtubules, various vesicles and microvilli.

Both types of glandular units of *L. revivensis* open into a similar structured pore that penetrates the spermathecal wall. According to Bennet (1992), they can be classified as typical primary pores characterised as simple canals which convey gland ducts through the walls of the spermathecal lobes.

According to the classification of insect epidermal glands by Noiret and Quennedy (1974, 1991), the glandular units described for *L. revivensis* can be roughly assigned to the glandular units with class III gland cells. These units comprise a terminal gland cell and one or more associated epithelial (intercalary) canal cells that surround the ductule and might also be secretory. In insects the terminal gland cell usually has an expanded invagination lined with microvilli and containing the 'end apparatus'. Here the cuticle is fenestrated and its luminal surface is covered by a thicker fibrillar or filamentous layer (Noiret & Quennedy 1974, 1991, Gillott 1988). In *L. revivensis* no such elaborate structures could be detected. Moreover, in all spiders with class III gland cells investigated so far, 'end apparatuses' are lacking (Uhl 1996b, 2000; Suhm & Alberti 1993). The (intercalary) canal cells of insects resemble regular epithelia cells. However, they do not reach the basement membrane. They are involved in the formation of the ductule and the spermathecal cuticle. Also in *L. revivensis* canal cells

produce the cuticular ductule, whereas intercalary cells are involved in the formation of the spermathecal cuticle.

4. 1. 3. The uterus

The epigastric furrow is lined by a cuticle with vertical extensions similar to those described for the book lungs of spiders (Foelix 1996). However, as the cuticle in the epigastric furrow is relatively thick, the vertical extensions might serve to prevent the furrow from collapsing rather than act as a ventilatory organ.

The cuboidal epithelium of the ventral wall is similar to that of the body surface. The nature and origin of the increasing number of vacuoles and/or granules towards the anterior is as yet unknown. However, the overall resemblance can be explained by the ontogeny of the genital structures (see chapter 4. 1. 1.). The opening that finally comes to lie on the outside anterior to the epigastric furrow primarily develops inside the epigastric furrow immediately in front of the uterus externus. Its final position results from an increase in length of the wall between the opening of the uterus and the opening of the primary invagination (Bhatnagar & Rempel 1963).

At its posterior end the dorsal wall possesses huge glands. As far as can be seen in semi-thin sections, the glandular units represent typical class III glands according to Quennedy and Noirot (1974, 1991; also see chapter 4. 1. 2. 2.). It is most likely that the secretion that covers the cuticle of the posterior section is produced by these glands.

The high columnar epithelium of the uterus externus has basal infoldings typical for solute- and fluid-transporting epithelia.

The secretory products seen between the cells of the epithelium of the uterus internus of *L. revivensis* suggests that it has a secretory function.

Only few studies deal with the glandular equipment of the uterus in spiders. The findings in *L. revivensis* are in general accordance with the short light microscopical description of the genital system of *L. corallinus* and *L. antheratus* given by Lauria de Cidre (1988). Here the uterus externus contains gland cells with ovoid nuclei, basophil cytoplasm and apical ductules that traverse the cuticle lining. The uterus internus is said to produce proteins and is supposed to be involved in the formation of the egg envelope.

More reports are available on the structure and function of the epithelia of the lateral and common oviduct in insects (see summary in Gillot 1988). Similar to the columnar epithelium of the uterus externus of *L. revivensis*, the epithelial cells of the

insect oviduct are columnar, have apical microvilli as well as basal invaginations. Secretions are mainly proteinaceous in nature (Gillott 1988). They may act as lubricants when eggs are passing through the genital tract or may help in cementing the eggs to each other and to the substrate. The latter is also plausible for the secretory products of the uterus externus (and maybe uterus internus) of *L. revivensis*: For oviposition the female first produces a silken shallow cone with a basal plate. Standing under the canopy she extrudes the egg mass together with a fluid that not only sticks the eggs together, but also attaches the whole mass to the underside of the basal plate (Kaston 1970). Then the egg sac is closed at the bottom. As reported for spiders in general, the liquid that covers the eggs during oviposition eventually dries onto the chorion which then appears opaque and granular (Foelix 1996; Austin & Anderson 1978; personal observations). This might provide protection against pathogens, parasites and predators (Gillott 1988). Regarding the differences in the epithelia, the environment in the uterus externus probably differs from that inside the spermatheca. The change in pH or ionic composition, for example, might result in the final activation of the spermatozoa that have already been decapsulated inside the spermatheca. The extrusion of eggs during ovipostion in *L. revivensis* lasts only a few seconds. During this time the sperm mixes with the eggs and, probably, fertilisation takes place. This requires a fluid environment provided by the female secretion, e.g. produced by the uterus internus or externus.

Kovoor (1981) and Kovoor *et al*. (1981) described glands that open on the lips of the genital fold (epigastric furrow) in the mygalomorphs *Nemesia caementaria* (Ctenizidae), *Atypus piceus* (Atypidae) and a number of entelegyne spiders (*Uroctea durandi* (Oecobiidae); *Lycosa radiata* (Lycosidae); *Agelena labyrinthica*, *A. consociata* (Agelenidae); *Araeneus diadematus* (Araneidae); *Linyphia triangularis*, *Leptyphantes sanctivincentii* (Linyphiidae)). In *A. diadematus* the anterior and posterior walls of the genital fold (epigastric furrow) are supposed to bear glands that open into the fold through a cuticular canal. It has been suggested that these glands produce either a volatile or a contact pheromone, but the technique used (paraffin-imbedding) does not allow such a far-reaching speculation (see also Uhl 1990). In any case, in *L. revivensis* the production of sex pheromones which have to be transported to the surface from glands so deep inside the epigastric furrow is not very plausible. Glands associated with

the body surface and the spinnerets are more likely candidates for spreading pheromonal substances over the females' integument or depositing them onto the silk (Lopez 1987).

The glands at the posterior end of the gonopore in *L. revivensis* that correspond to type III glands of Noirot and Quennedy (1974, 1991), might best be called accessory sex glands, hence they most likely have a "secretory structure that directly assists in the reproductive process" (Gillott 1988, p. 320). Their secretion might serve or assist one of the functions proposed for the secretory cells of the uterus externus above (lubrication, cementing, activation, protection).

4. 1. 4. Hemolymph and nervous supply

The hemolymph that surrounds the spermatheca of *L. revivensis* contains various hemocytes. Some of them seem to be incorporated into the spermathecal epithelium. Additionally, nerve fibres and vessels traverse the mixocoel.

According to the scheme of the 'differentiation' and subsequent 'dedifferentiation' of the hemocytes of *Cupiennius salei* (Seitz 1972a, b), most granular hemocytes in *L. revivensis* resemble 'storing hemocytes', for example hemocytes that have stopped synthesis of proteins (e.g. for yolk synthesis, Seitz 1972b). In the course of 'dedifferentiation', the number of lysosomes (e.g. residual bodies) increases. The hemocyte devoid of most cell organelles shown in Fig. 29b resembles a hemocyte at the end of dedifferentiation (Seitz 1972b).

Granular hemocytes are involved in protein synthesis, as well as the storage and transport of reserve materials taken up from the surroundings by endocytosis (Sherman 1973, 1981). In *L. revivensis* granular hemocytes are closely associated with the basal infoldings of the spermathecal epithelium. Thus, transfer of material from the hemocyte into the spermathecal epithelium might take place across the cell membranes and the enclosed basement membrane. Interestingly, hemocytes appear to be incorporated into the glandular epithelium and cells within the epithelium seem to undergo remarkable changes as indicated by the myelin-like bodies. The significance of immigrating cells deserves further attention.

Nerve fibres have not been found to contact the spermathecal epithelium as is the case in the same tissue in the spider *Amaurobius fenestralis* (Amaurobidae) (Suhm & Alberti 1993). Therefore, the glands of the spermathecal epithelium of *L. revivensis*

appear not to be under direct nervous control. This lack of enervation is a common feature in insect epidermal glands (Noiret & Quennedy 1974).

4. 2. The male

Like other theridiids, *Latrodectus* species possess one of the most complex pedipalps known in spiders (Levi 1961). In general, the cymbium and palpal organ of *L. revivensis* are similar to those described in detail for *L. curacaviensis* (Bhatnagar & Rempel 1962) and other *Latrodectus* species (Knoflach & van Harten 2002). According to the classification of Comstock (1910), the embolus of *Latrodectus* species belongs to the free type and spiral subtype. Wiehle (1960) reclassified the emboli according to their function. He defined the embolus of *Latrodectus* as an 'Einführungsembolus' ('introducing embolus') of the subtype 'Querschleifen-Embolus mit besonderem Endstück' ('transversely coiled embolus with a special terminal piece') (Wiehle 1961, p. 480). In this type, the plane of the coil is positioned vertical to the longitudinal axis of the cymbium. The embolus is more sclerotised on the convex side and accompanied by a softer part on the inner, concave side. Towards the distal end, the embolus becomes very slender and the terminal piece (= embolus tip) can be clearly distinguished from the rest (Wiehle 1961). Bhatnagar and Rempel (1962) confirmed this organisation for *L. curacaviensis*. My observations and the figures of the emboli of *L. geometricus* (Abalos & Báez 1963) and *L. mactans* (Breene & Sweet 1985) suggest a largely uniform embolus structure within this genus. It perfectly combines rigidity and flexibility which enables the embolus to penetrate the variably-shaped copulatory duct of the female. The embolus tip of *L. revivensis* is rigid and has an internal canal. A translucent, circular tube inside the tip described for *L. geometricus*, *L. curacaviensis* and *L. mactans* by Abalos and Báez (1963) on the basis of light microscopical investigations could not be found in the present species. In *L. revivensis* the ejaculatory duct extends only up to the breaking point. The embolus tip of *L. revivensis* possesses a saddle-like thickening close to the breaking point which is similar to the backward-directed tooth of the tip of *L. curacaviensis* (Bhatnagar & Rempel 1962). These structure might act as a barb when the male tries to withdraw his embolus, thus facilitating the rupture of the tip. The embolus tip of *L. revivensis* is perfectly shaped to guide the male embolus through the female copulatory duct, especially its narrow tube-shape part. The ejaculatory duct and

the canal of the tip of *L. revivensis* are very narrow (approx. 4 µm in diameter) and each encapsulated sperm cell has to pass it one at a time during sperm transfer. The mechanisms for the uptake and release of sperm by the male is still a matter of speculation (Juberthie-Jupeau & Lopez 1981; Lopez & Juberthie-Jupeau 1985; Suhm *et al.* 1996).

The pedipalps, tarsi and the mouth region bear numerous sensilla involved in mate localisation and courtship. Tactile hairs cover all surfaces. Chemoreceptive hairs are found on the tarsus and characteristic trichobothria on the pedipalpal tibia. The tarsus and cymbium, as they are homologous structures, bear slit sensilla and a single tarsal organ. Further structures of unknown function are located on the cymbium.

Not much is known about the exact function of chemoreceptive 'tip-pore' sensilla on spider legs and pedipalps. Several studies have been able to show that male spiders react to substances on female silk (Tietjen & Rovner 1982; Pollard *et al*. 1987; Prenter *et al*. 1994a; Miyashita & Hayashi 1996) and it has even been possible to identify some of these female pheromones (Schulz & Toft 1993; Papke *et al*. 2000, 2001). However, only in a recent study (cited in Barth 2002) was it possible to reliably identify a pheromone receptor on the pedipalp of *Cupiennius salei* (Ctenidae). Although Ross and Smith (1979) mention chemoreceptive hairs on the ventral surface of the palpal organs (cymbium or other segments?) of *L. hesperus*, the present SEM study does not reveal any chemoreceptive tip-pore sensilla on the cymbium of *L. revivensis*. However, in contrast to *L. revivensis*, *Cupiennius salei* bears numerous chemoreceptive hairs on its pedipalpal tarsus (Barth 2002). The difference between the two species is most likely due to their different life-styles. As a hunting spider, *C. salei* walks on the substrate, such as leaves, during the initial phase of courtship, using its pedipalpal tarsi to examine female draglines. In *L. revivensis*, courtship is elicited as soon as the male touches the female web, on which courtship takes place. Here the substrate is the female's web itself, and the male's legs are in direct contact with the female's threads and the pheromones on the silk. The cymbium, however, is possibly used for vibratory communication with the female. The tarsus of *L. revivensis* seems to bear relatively fewer chemoreceptive tip-pore sensilla in females than in males. The pedipalps of the wolf spider *Lycosa punctulata* show a similar sexual dimorphism, with male pedipalps (which are used to follow the female dragline during courtship) bearing about three time

as many chemoreceptive hairs as female pedipalps (Tietjen & Rovner 1982). This suggests that chemoreception might play a more dominant role in males than in females. However, threads laid down by the male on the female web (and later inside the retreat and even on the female's body), most likely contain sex pheromones that influence the female's physiological state (e.g. inducing catalepsy) (Ross & Smith 1979). Legendre (1956) identified another olfactory organ in the mouth region at the articulation of the rostrum and pedipalps in spiders belonging to different labidognath families. Whether such an organ is present in *Latrodectus* is unknown.

Chemoreceptive tip-pore sensilla are commonly observed on the labium and maxillae of spiders (Foelix 1996) and, although not examined in the present study, are assumed to be present on the mouthparts of *L. revivensis*, too. Chemoreceptive sensilla in the mouth region might not only play an important role during feeding, but also during courtship, when the male either touches the female silk with his mouthparts or grooms or 'licks' his legs, tasting the silk-borne sex pheromones (Prenter *et al.* 1995a) during the vibratory and tactile phase (see chapter 3. 3. 2.).

Trichobothria are fine and light hair sensilla. Their flexible suspension in a very thin cuticular membrane makes them extremely sensitive to the slightest air currents (Foelix 1996; Barth 2002). According to their life-style (e. g. hunting or web-building), the number and topography of trichobothria differs among spiders (Barth 2002, Foelix 1996). As expected for a web spider (Peters & Pfreundt 1985), no trichobothria are present on the tarsi of the walking legs of *L. revivensis*. However, three characteristic trichobothria are situated on the tibia of the male pedipalps, one dorsal and two retrolateral ones, similar to the condition in, for example, *L. diaguita* (Gonzales 1984), *L. mirabilis*, *L. antheratus* and *L. corallinus* (Gonzales 1980). The longitudinal axis of the cymbium forms an angle of less than 90° with the femoral axis, thus the trichobothria of the bowl-shaped tibia project in a more or less frontodorsal direction. In combination with their raised position, these tibial trichobothria are most likely in the appropriate location to detect the air current produced by any object right in front of the male spider, such as prey or the female he is courting.

A pit-like tarsal organ is situated on the dorsal side of the tarsus. Homologous to this, a similar-shaped tarsal organ is situated on the dorsal edge of the cymbium. The capsulated form where the receptors are protected by a cuticular hood is typical for

entelegyne spiders (Forster 1980). Its round shape resembles the typical tarsal organ of theridiid spiders first classified by Blumenthal (1935). Although an olfactory function was proposed for the sensillum in previous years, in more recent investigations of *Cupiennius salei*, no pheromone receptor cells have been found. Instead, it has been possible to show that the tarsal organ functions as a hygro- and thermoreceptor (Barth 2002). Especially for spiders living in an arid or semi-arid environment, the ability to detect and adjust their behaviour in accordance with the ambient temperature and humidity is crucially important. For example *L. revivensis* is known to adjust its web-building behaviour to seasonal changes (Konigswald *et al*. 1990; Lubin *et al*. 1991).

The arrangement of two single slit organs immediately behind the claws has already been described for females of *Araneus diadematus* (Foelix 1970) and males and females of the hunting spider *Cupiennius salei* (Barth 2002). In the latter species, an adequate stimulus for the two 'claw slits' is the active movement of the tarsus, but they are also effectively stimulated by external vibrations.

Lyriform organs are known to be highly sensitive vibration receptors (Foelix 1996, Barth 2002). Although the number of lyriform organs on the leg is nearly the same in web-building- and hunting spiders, the lyriform organs of web-building spiders possess more slit sensilla. Thus, the higher the number of slits per lyriform organ, the higher its sensitivity (Peters & Pfreundt 1985). This indicates the importance of these mechanoreceptive sensilla for spiders receiving a majority of stimuli *via* web-borne vibrations. The metatarsal lyriform organ differs from all other lyriform organs and slit sensilla through its position in the middle of the dorsal surface and the orientation of its slits, which are perpendicular to the long axis of the leg. Both features contribute substantially to its high sensitivity (Barth 2002).

Structures of unknown function were observed on the frontally-directed side of the cymbium. The light- and scanning electron microscopical pictures imply a function as sense organs, but further electron microscopical investigations are required. If these structure turn out to have sensitive properties, their function might be comparable to those of the hair plates at the joint between the coxa and prosoma. These are composed of groups of short hairs that are stimulated when the pleural membrane 'rolls over' the hairs during leg movement (Barth 2002). On the cymbium of *L. revivensis* sensilla might inform the male about the position of his embolus. Additionally, he might receive

further information when touching the female's opisthosoma and epigynum during courtship.

4. 3. Female and male interactions

4. 3. 1. Relation in size and variation in genital and somatic characters

The regression shows that the size of somatic and genital characters are correlated in males and females. However, the coefficient of variance is lowest in male genital size and highest in male somatic size. Although not significant, variance of male genital size tends to be lower than that of somatic size supporting the results of other studies on spiders (Coyle 1985; Cohn 1990; Eberhard *et al*. 1998; Uhl & Vollrath 2000). The data suggests that different selective forces are working on genital and somatic characters leading to intermediate, standardised sizes of male genitalia. The allometric value for the male genital character is comparably low in *L. revivensis* as in other spiders (e.g. *Nephila edulis*, Uhl & Vollrath 2000; *Tetragnatha* sp., *Physocyclus globosus*, *Argiope trifasciata*, *Araneus expletus*, see references cited in Eberhardt *et al*. 1998). This indicates that genital characters are subject to stabilising selection and female *L. revivensis* are expected to use cues other than a male's genital size to evaluate overall body size (see detailed discussion in Eberhard *et al*. 1998).

Consistent with other studies (Coyle 1985; Cohn 1990; Eberhard *et al*. 1998; Uhl & Vollrath 2000), no differences in the variance of somatic and genital size and the coefficient of variance of both characters could be shown for females. However, the low allometric value of the genital character suggests that stabilising selection might work on female genitalia, similar to the situation in males. Standardisation in females might aid selection on male genitalia ("lock and key" in the sense of sexual selection), for example, through cryptic female choice (Eberhard 1985; Uhl & Vollrath 2000).

4. 3. 2. Courtship

After Robinson (1982) the term "courtship" is used to refer to the 'heterosexual reproductive communicatory system leading up to the consummatory sexual act'. However, 'sexual behaviour' itself starts as soon as the male charges his pedipalps and leaves his web to search for a potential mate and includes courtship and copulation (Platnick 1971). Platnick (1971) divided spider courtship into three categories based on the prime releasers of male display. Level 1 requires direct contact between male and female. Level 2 needs pheromones to stimulate the male's courtship behaviour and level 3 postulates a visual recognition of the female by the male. As stated by Foelix (1996 and see discussion below), the courtship of *L. revivensis* falls into the second level, with the prime releasers being distance chemoreception of pheromones and chemotactic perception of silk. According to the most important type of sensory stimulus (see Barth 2002), the courtship behaviour of *L. revivensis* can be roughly divided into three phases: the chemical, vibratory and tactile phase.

Preliminaries to courtship are sperm induction and locating the female (Robinson 1982). After maturation, a male *L. revivensis* charges his pedipalps and leaves his web to search for potential mates. Some parts of the sexual behaviour that take place (under natural conditions) before the male enters the female web and starts courtship have to be included in the chemical phase, such as the process of locating the female. Females' webs are widely dispersed in the habitat. Anava and Lubin (1993) previously suggested that the males would find their webs through pheromones emitted by the female rather than by random search. In the field, male *L. revivensis* were attracted by virgin females' webs from a distance of several metres (M. Ziv personal communication; see also Papke 2000). Once entering the female's web, courtship is elicited by a putative contact pheromone detected by chemoreceptive sensilla. That this response is due to the female's silk and not the female's presence itself was shown for *L. revivensis* by Anava and Lubin (1993) and for *L. hesperus* by Ross and Smith (1979). Although the studies on different *Latrodectus* species (*L. hesperus*, *L. mactans*, *L. geometricus*) showed that males are not necessarily able to distinguish between conspecific and non conspecific webs (Ross & Smith 1979; Martindale & Newlands 1982; Schmidt 1990; Schmidt 1991), males of *L. hesperus* responded differently to webs of juvenile (positive response), virgin (positive response) and non-virgin females

of different ages (positive response to fresh webs, positive and negative responses to older webs) (Ross & Smith 1979). Papke (2000) analysed silk extracts and volatile substances emitted by females of *L. revivensis*. However, the experiments in which males were tested for their reaction to some of the detected substances (that were synthesised in the laboratory) did not yield any clear results (Papke 2000).

The female pheromones that attract males from a distance or trigger the different behavioural patterns on the web might originate from the glands cells at the opening of the gonopore into the epigastric furrow in *L. revivensis* (chapter 3. 1. 3.). A similar function has been ascribed to the epigastric glands of female *Araneus diadematus* (Kovoor 1981). Other, more likely candidates for the secretion of pheromones are the glands located in the legs, in the ventral tegument of the prosoma, of the pedicel and the spinnerets (see summary in Lopez 1987). Also the cuticle itself might contain substances that function as pheromones (Hackman 1984).

As soon as the male *L. revivensis* enters the web, he performs the various movements that cause a wide range of vibratory signals. Under laboratory conditions, the female might react with irritation to the presence of an approaching male. However, these reactions differ significantly from those shown towards prey caught in the web (e.g. throwing sticky silk, see *L. katipo*: Court 1971) and the female obviously does not mistake the identity of an approaching male (Elgar 1992).

Throughout the whole vibratory phase outside and inside the female retreat, the male frequently performs twanging, tugging, rubbing and stroking movements ('strumming frequency') especially on an isolated supporting thread. These elements show a striking similarity to the courtship elements performed by some araneids on the mating thread, e.g. *Araneus pallidus* (Grasshoff 1964), *Cyrtophora cicatrosa* (Blanke 1975) and diverse Nephilinae and Argiopidae (Robinson and Robinson 1980). The latter authors argue that courtship on a mating thread has not only evolved to reduce the risk of predation by the female, but also as a device to concentrate and localise the input of vibratory signals. I suggest that the 'strumming sequence' in *L. revivensis* with its multiple, conspicuous elements is a highly-specialised courtship pattern. Its high frequency during the whole duration of courtship and the fact that it is even performed in close proximity to the female inside the retreat during the tactile phase emphasises its importance in vibratory communication.

One element of the strumming sequence is mouthpart tugging. Here the single thread runs along between the mouthparts. It was not possible to precisely define which parts of the mouth or chelicerae are involved in tugging, due to the limited resolution of the video recordings. The examination of the mouthparts showed that the anterior rim of the maxilla is serrated. The serrulae are generally assumed to function as saws for cutting into prey (Foelix 1996). The lack of cuticular teeth on the sides of the cheliceral groove and observations of prey-catching behaviour (e.g. in *L. katipo*: Court 1971) show that prey items are not destroyed or mashed, but sucked out through small bite holes. After leaving their own webs, adult males make no attempt to actively capture prey but will occasionally suck up a small amount of water or liquid food if available (Herms *et al*. 1935; Ross & Smith 1979). The serrulae of *L. revivensis* males might function differently in courtship, for example as a device to produce characteristic vibrations during mouthpart tugging.

Another conspicuous behavioural pattern during the vibratory phase is 'cutting'. By cutting threads of the female web and bundling them with his own silk, males sometimes drastically reduce the capture area (gum feet and capture platform) of the web (Anava & Lubin 1993). This behaviour is interpreted as a mechanism for physically minimising the risk to a male of being attacked by the female (Robinson & Lubin 1979), or as a means of cutting off the female's escape route from the male and restricting her mobility (Chamberlain & Ivie 1935; Platnick 1971; Ross & Smith 1979). Since a *L. revivensis* female usually does not leave her retreat to attack a male as courtship proceeds and definitely does not show any tendency to escape from the male, these explanations do not seem to hold true here. Breene and Sweet (1985) assumed that cutting behaviour could effectively 'blind' the female by spatially disorienting her. This may serve to enhance the male's success in evading an attack. Rovner (1968) suggested that web removal reduces the possibility of interference from other males. In fact, Watson (1986) was able to demonstrate that web reduction reduces the attractiveness to rival males in *Linyphia triangularis* (Linyphiidae). Isolation of the female from external signals (e.g. produced by prey) (Rovner 1968) that might interfere with mating and prevent attraction of rival males are the most plausible explanations of web reduction in *L. revivensis*. However, another important function of web cutting seems to have been overlooked thus far. As seen in the video recordings, a male causes remarkable

vibrations of the female web by cutting exposed threads (such as supporting threads) at the end of a 'strumming sequence' followed by distinct up and down bouncing of his body (Figs. 35a-d). The passive movements of the female in her retreat caused by the male's actions are clearly visible, even with the naked eye. The vibrations might provide the female with additional information about male quality or might help to put her into a sufficiently cataleptic state (see chapter 4. 4. 1.).

Once in a while the male shows typical rapid flexions of the legs without releasing the lines of the web. These jerks usually follow any movements of the female, e.g. of her legs and body. The movements of the female seem to be reactions to the strong vibrations caused by vigorous twanging, cutting of supporting threads as well as too-rapid approach attempts by the male. The jerks of the male are similar to jerks spiders make in response to conspecifics and, thus, might be 'derived' from a behavioural pattern usually used in agonistic encounters (Tinbergen 1954).

In addition to the 'trailing' of silk with legs IV, the male attaches his threads onto the retreat and the female's body and legs. Some authors refer to the silk that is laid down on the female legs and body by a courting male as the 'bridal veil'. A similar behaviour was observed in some crab spiders (*Xysticus*, Bristowe 1974), *Uloborus* (Gerhardt 1933), *Nephila* (Robinson & Robinson 1973, 1980), *L. revivensis* (Anava & Lubin 1993) and various other *Latrodectus* species (Gerhardt 1928; Herms *et al*. 1935; Smithers 1944; Kaston 1970; Ross & Smith 1979; Forster 1992; Knoflach & van Harten 2002). As the female does not seem to have any difficulty in freeing herself after copulation, the bridal veil is assumed to have only a 'symbolic' significance. However, here I agree with Breene and Sweet (1985), who suggest that even though the bridal veil may detain the female for a second or less, this time would be sufficient for the male to escape by immediately dropping out of range. According to Anava and Lubin (1993), the investment of laying down silk might provide potential cues of male quality. Silk-borne pheromones produced by the male himself ('complementary pheromones' see Ross & Smith 1979; Lopez 1987) might serve a more direct function by inhibiting female aggression and inducing female catalepsy.

Generally, the suppression of non-sexual responses is widely accepted as the major function of spider courtship (Barth 1982; Krafft 1982; Robinson 1982). In *L. revivensis* the most obvious effect of male courtship that indicates this suppression is

the induction of female catalepsy. This process can also be understood as a kind of physiological priming (Forster 1995). Catalepsy of the female (torpor, hypnosis, trance or 'Zustand der Erschlaffung und Willenlosigkeit' = 'state of becoming limp and being without will', Gerhardt 1928) has been described for other *Latrodectus* species (Rivera 1901; Gerhardt 1928; D'Amour *et al.* 1936; Shulov 1940; Abalos & Báez 1967; McCrone & Levi 1964; Breene & Sweet 1985; Heeres 1991; Knoflach & van Harten 2002). In *L. revivensis*, the intensity of catalepsy varies strongly between pairs. Some females hardly show any signs of it at all and remain relatively active throughout the whole time of courtship and copulation. Other females are completely motionless and do not show any signs of activity for some time, even though the male has successfully finished copulation. The ability of a male to induce catalepsy and keep the female in this state most likely reflects male quality (see chapter 4. 4. 2.).

Generally, the female of *L. revivensis* does not assume a distinct mating posture. However, the male has to attain the right mating position to achieve genital coupling. Unusually for theridiids (Knoflach & van Harten 2002), *L. revivensis* males (like males of all other *Latrodectus* species) take a venter to venter position, facing the same direction as the female. The long stout hairs on the cymbial edge might help the male to find the right position. He lowers his mouthparts over her epigynal opening and during the cheliceral scrabbling/nibbling, a watery liquid can be observed glistening between the chelicerae. This was also observed in *L. formidabilis* (Rivera 1901) and *L. hasselti* (Forster 1995). As the female does not possess any glands around the epigynal opening or inside the atrium, the liquid is most probably discharged by the male. Lubrication of the female copulatory ducts might facilitate the intromission of his long coiled embolus.

Coupling attempts include very distinct movements and can (with the help of video recordings or a binocular microscope) easily be distinguished from other movements of the male such as cheliceral scrabbling/nibbling during the end of courtship. A male sometimes performed multiple unsuccessful coupling attempts until he finally managed to connect his pedipalp to the female epigynal carina. The male's ability to achieve genital coupling as quickly as possible might play a crucial role with regard to an individual's copulatory success, as the female may awaken from catalepsy and attack the male before he is able to withdraw his embolus.

In cases where the male successfully achieves genital coupling, his body slowly tilts to the side, still facing in the same direction as the female. The copulatory posture of *L. revivensis* is typical for most *Latrodectus* species. The only exception known so far is the Australian redback spider, *L. hasselti*. After a successful coupling the male of that species raises himself to a handstand position. After 2 - 5 s, he slowly turns a complete somersault, bringing his abdomen into the proximity of the female's mouthpart which she may penetrate with her fangs (Forster 1992, 1995; Andrade 1998).

The number and duration of insertions varies among different *Latrodectus* species. Most authors report that each pedipalp is used only once and a complete copulation may consist of one or two bouts (D'Amour *et al*. 1936; Shulov 1940; Kaston 1970; Forster 1992; Andrade 1996; Knoflach & van Harten 2002). In a few species, the male may return after two insertions to complete another two bouts (Rivera 1901; Mc Crone & Levi 1964; Knoflach & van Harten 2002). However, some authors describe repeated copulation bouts by a single male (Shulov 1940; Softly & Freeth 1970; Anava & Lubin 1993). In the present study, the single bout lasted for approx. 40 s, but sometimes for up to 2 min. For other species it is said to last from approx. 1 min to 37 min. However, regarding the above-mentioned data, it should be kept in mind that cheliceral scrabbling/nibbling, or an unsuccessful coupling attempt followed by a pause during which the male sits with his mouthparts lowered over the female atrium, can easily be mistaken for an actual copulation bout. Only the observation of the repeated inflation of the whitish haematodocha or the withdrawal of the long, spirally-coiled embolus seem to be sufficient indicators of a successful copulation and older descriptions of repeated copulations or insertions (e.g. those of Shulov 1940; Softly & Freeth 1970; Anava & Lubin 1993) should particularly be treated with caution. In general it can be said that copulations in *Latrodectus* species usually involves one or two bouts, but a second bout of one or both pedipalps that have already been used cannot be ruled out in some species.

Elgar (1995) conducted a comparative analysis of the duration of copulation and other life-history variables in various spiders. He found that the duration within orb-weaving spiders is associated with the location of mating (shortest in type C species, courting on exposed mating threads) and the frequency of sexual cannibalism, suggesting that the length of copulation is limited by the risk of predation (by predator

or female). As copulation duration in the sexually-cannibalistic *Latrodectus* species is comparably short, as in sexually-cannibalistic orb weavers, the results support the pattern described by Elgar (1995).

When the female *L. revivensis* does not attack and cannibalise the male during or after copulation, he sits in close proximity to the female, who does not exhibit any signs of aggression. As this behaviour has also been reported for other *Latrodectus* species (Bonnet 1938; Ross & Smith 1979), it suggests that the female attack is closely linked to the time when the male tries to withdraw his embolus. When not attacked by the female he might even stay on the female web for several days or weeks until he dies untouched (Herms *et al*. 1935; D'Amour 1936; Kaston 1970; Heeres 1993).

In other cases the males do not survive copulation. These cases are discussed separately in chapter 4. 4. 1.

Anava and Lubin (1993) reported a courtship time of 2 - 80 min for *L. revivensis*. However, the mating experiments and video observations showed that the duration of courtship in *L. revivensis* can last between approx. 50 min up to more than eight hours (> 8 h in 50% of the laboratory matings). Generally it can be said that courtship duration in *Latrodectus* species is highly variable, ranging from 10 min to more than 8 h (Shulov 1948; McCrone & Levi 1964; Kaston 1970; Ross & Smith 1979; Forster 1992; Knoflach & van Harten 2002).

4. 3. 3. Spermatozoa and secretion

As with the secretion in the spermophor of *Leptoneta microphthalma* (Juberthie-Jupeau & Lopez 1981), *Pholcus phalangioides* (Rose 1990) and *Leucauge mariana* (Eberhard & Huber 1998), the secretion (seminal fluids) preserved in the histological sections of the male spermophor of *L. revivensis* appear as homogenous material with small droplets. As suggested for other spiders (Juberthie-Jupeau & Lopez 1981; Rose 1990; cited in Uhl 1994a), the secretion inside the spermophor after sperm uptake are most probably produced by the vas deferens and the associated epigastric glands. As far as can be concluded from the staining properties (toluidine blue) of the histological sections of male and female sperm stores, the secretion seen in the male spermophor of *L. revivensis* is transferred into the female spermatheca during copulation.

The nature and the actual function of the male secretion accompanying the spermatozoa in spiders are a matter of speculation. Rose (1990) speculated that the proteinaceous secretions of *Pholcus phalangioides* might serve as a kind of nuptial gift for female egg production. In *L. revivensis* a single egg sac might contain several hundred eggs. The diameter of each follicle inside the ovaries increases (within 6 - 8 d) from approx. 0.08 mm at the time of copulation up to approx. 1.20 mm shortly before oviposition. One day after oviposition the egg inside an egg sac has a diameter of 1.20 - 1.30 mm (personal observation). The lobes of the spermathecae, however, have a maximum diameter of approx. 0.17 mm (posterior) and 0.24 mm (anterior). If the relatively small amount of actual secretion in the male seminal products is compared to the amount of material that has to be produced by the female to generate the size increase in all of her eggs, a significant provision of energy by the male secretion is clearly unreasonable. Furthermore, seminal fluids might nourish spermatozoa or maintain them (Engelhardt 1910; De Carlo 1973; Lamoral 1973; Coyle *et al*. 1983; Lopez & Juberthie-Jupeau 1985). However, Uhl (1994) doubts that the stored spermatozoa require much energy since they are inactive and encapsulated. The energy to maintain the low spider sperm metabolism may be incorporated in the sperm capsules (Uhl 1996). Lamoral (1973) suggested that the seminal fluids bathe the encapsulated spermatozoa to keep them moist. It may also act as a lubricant, may prevent compression of the capsules during ejaculation and keep the sperm mass coherent and quiescent. Considering that in *L. revivensis* the spermatozoa have to be pushed out through the long ejaculatory duct (whose inner lumen has a similar diameter to a single, encapsulated spermatozoon) within a few seconds, the provision of a lubricant seems highly plausible. In addition, spider spermatozoa react very sensitively to changes in the surrounding milieu, e.g. changes in pH or ionic composition (Muma & Stone 1965). My own preliminary experiments showed that spermatozoa transferred into physiological saline or even distilled water become active within a few seconds.

More studies were performed on the diverse seminal fluids produced by the gonads and accessory glands of male insects (see summaries in Davey 1985; Gillott 1988; Simmons 2001). The proposed functions (see summary in Kura & Yoda 2001) range from a nutritional gift as a paternal investment, physical and chemical help for spermatozoa to move and survive in the female's reproductive tract and to fertilise the

egg (in contrast to spider spermatozoa, insect spermatozoa are activated as soon as they leave the male genital tract and have to be kept mobile until fertilisation takes place). Other functions are either directed against other males' interests or directly influence female physiology. In the latter cases substances (in general peptides and proteins) either promote overall egg production (fecundity-enhancing substances, FES) or induce the refractory period (receptivity-inhibiting substances, RIS) (see summary in Gillott 1988). Although the females of *Latrodectus* species might be willing to remate shortly after their first copulation, they generally reject further males as time passes after the first mating (Herms *et al*. 1935; Bonnet 1938; Abalos & Báez 1966, 1967; Forster 1995; Andrade 1996). Therefore, the neural stimuli provided by the male during courtship do not serve as a sufficient cue to induce egg laying or a refractory period (personal observations). Other, most probably chemical, stimuli must trigger the necessary physiological changes inside the female. The male *L. revivensis* directly deposits his spermatozoa and associated secretions into the spermathecal lumen so an uptake of substances by the female that might serve as a nutritional gift and/or are destined to affect her physiological state (e.g. RIS) would have to be transported across the thick cuticle into the intercalary cells (see chapter 4. 1. 2. 2.).

In conclusion, the most probable functions of the male seminal fluids in *L. revivensis* are 1) the provision of the suitable milieu for the spermatozoa to retain their 'peculiar coiling' (see below) inside the male spermophor, 2) lubrication during sperm transfer, and 3) the provision of certain cues (e.g. by RIS) that trigger or induce changes in female physiology.

The spermathecal lumen of virgin females of *L. revivensis* is densely filled with a secretion that obviously originates from the spermathecal pores. In recently-mated females, the anterior lobe is filled with encapsulated spermatozoa that differ from the spermatozoa inside the male spermophor. The spermatozoa that lie loosely in the female secretion in the middle portion and/or the posterior lobe are already decapsulated. Interestingly, the picture of the spermatheca of a female a few hours after the first oviposition does not differ considerably from the latter one. The main difference that can be detected in histological sections is that the granular secretion in the posterior lobe seems more loosely distributed within the lumen. This putative decrease in the amount of female secretion may suggest that the female does release substances into the

spermathecal lumen after the final moult, but not during ovipostion. However, the TEM study shows that cells probably involved in the production of secretions also appear active in females after their first oviposition. A release of secretion that promotes the lysis of encapsulated spermatozoa needed for the fertilisation of the eggs of subsequent egg sacs seems possible and should be investigated in further studies. Activated, flagellate spermatozoa are neither found in the spermathecal lumen, nor inside the small fertilisation ducts.

The ultrastructure of the spermathecal epithelium of *L. revivensis* reveals at least three different types of cells that may be involved in the production of the female secretion. The extremely well-developed grandular endoplasmatic reticulum in the gland cells (G) suggests a high rate of protein production. Numerous dictyosomes in the gland cells (G) and the secretory canal cells (C1 and C2) indicate massive glycolisation of proteins. The female secretion most probably contains glycoproteins.

De la Serna de Esteban (1987) identified AB and PAS-positive material in the spermathecal epithelium of three South American *Latrodectus* species indicating glycoproteins. Glycoproteins were also identified in the spermathecal secretion of *Dysdera crocata* (Dysderidae) and *Eresus niger* (Eresidae) (Kovoor 1981). The investigations of the secretory products of Theraphosidae (*Grammostola burzaquensis*, *G. pulchripes*, *G. vachoni*, *G. inermis*, *Acanthoscurria sternalis*) indicate 'mucopolysaccharides' (De Carlo 1973) and Coyle *et al*. (1983) found proteoglycans and glycogen in the spermathecal epithelium of *Hypochilus thorelli* (Hypochilidae). Apart from the fact that the histochemical tests applied allowed only a very rough characterisation of the secretion, the authors most probably used inseminated females. Thus, the possibility that some of the substances identified actually originate from the male cannot excluded. Only Uhl (1996) analysed secretions from virgin females of *Pholcus phalangioides* (Pholcidae) by gel-electrophoresis identifying proteinaceous substances and glyco- and lipoprotein components in the sperm stores.

Speculations on the function of the female spermathecal secretions are numerous, but it has not been possible to verify any of them thus far. They may act as a pheromone guiding the male pedipalp towards the spermatheca and as a lubricant for the embolus (Kovoor 1981), may provide nutrition for the spermatozoa until fertilisation (see discussion above) and may help the retention of spermatozoa inside the

sperm storage site in spiders without distinct spermathecae (Uhl 1994a; 1994b; 1996) and may provide protection against desiccation. They also may serve as a tool for providing a favourable milieu (pH, ion-balance) and protection against venereal disease (Uhl 1996). Moreover, the secretion may be involved in the changes that occur in the spermatozoa from the time of insemination until oviposition. Like most araneomorphs, *L. revivensis* shows cleistospermy (*sensu* Bertkau 1877), with each spermatozoon encapsulated in its individual proteinaceous capsule when reaching the distal vas deferens (Lopez 1987; see Foelix 1996 and citations therein). During spermiogenesis, spermatozoa change to a transport or storage form by a peculiar coiling process. The flagellum loses its membrane and is apparently reabsorbed by rolling itself tightly around the nucleus (Alberti & Weinman 1985; Alberti 1991). In labidognath spiders, the individual mature spermatozoa still inside the testis possess large amounts of membranes, vesicles, or peripheral foldings of the plasmalem that act as a membrane reserve which is incorporated into the plasmalem when the spermatozoa become functional. In the spermophor of male *L. revivensis*, the fully differentiated spermatozoon forms a typical small disk (Boissin 1973, cited in Foelix 1996). The flagellum is not distinguishable from the tightly-coiled sperm head. The process of elongation in *L. revivensis* takes place shortly after copulation. After approx. 24 h in the female spermatheca, the protein capsule appears dilated and more rounded. The flagellum is clearly visible and coiled around the elongated sperm head. The changes in the spermatozoon (capacitation) might be mediated by either the loss of the male fluids when transferred into the spermatheca, or contact with female secretions. In the subsequent step the proteinaceous capsule of the spermatozoon is dissolved. However, the head is still curved and the spermatozoon is obviously immobile. Decapsulated spermatozoa can already be found in females shortly (approx. 24 h) after sperm transfer. This implies that the lysis of the capsule is not a process directly linked to the time of ovipostion and may be mediated by the female secretion (e.g. specific enzymes therein) produced during the virgin state. The involvement of female secretions in lysis of the sperm capsule has been discussed by previous authors (de Carlo 1973; Brignoli 1976; Lopez & Juberthie-Jupeau 1983). Preliminary experiments with *L. revivensis* spermatozoa showed that in activated, mobile spermatozoa the sperm head is straight and elongated. The flagellum is no longer coiled around the head. Such activated

spermatozoa were neither observed in the spermathecal lumen nor the fertilisation ducts. This suggests that the final activation may take place in the uterus externus (see discussion on uterus). Consequently, females might not have the potential to bias the fertilisation success of rival males by selectively activating stored sperm (Uhl 2002).

Bhatnagar and Rempel (1962), Cooke (1966), Lopez and Juberthie-Jupeau (1983) and Lopez (1987) suggested that female secretions may help to flush the spermatozoa out of the sperm storage site. However, the LM pictures show that a massive production of a secretion around the time of oviposition does not occur in *L. revivensis*. In this species, it is most likely that the sperm is indiscriminately sucked out of the spermathecae by a low pressure created by the contraction of the muscle that connects the ventral side of the common fertilisation duct and the epigynal plate and by the passage of the large eggs through the uterus externus during oviposition. A selective 'cryptic female choice' (Eberhard 1996; Telford & Jennions 1998) of spermatozoa from different spermathecae (and maybe different males) appears unlikely.

In some spiders the females are also said to contribute to the formation of a mating plug after copulation (e.g. for other theridiids such as *Theridium varians* by Gerhardt 1923; and various *Theridium* species by Knoflach 1998; or the tetragnathid *Leucauge mariana* by Eberhard & Huber 1998). The study of the genitalia of *Leucauge mariana* suggests that the secretions involved might be produced by the spermathecal epithelium. In any case, no plug formation by either male or female secretion was observed in *L. revivensis* (see chapters 3. 3. 4. and 4. 3. 4. 1.).

In conclusion, in female *L. revivensis* the production of secretions may be restricted to the time shortly after the last moult. However, depending on the active state of the secretory cells of the spermathecal epithelium in females after their first oviposition, a further release of substances before the next oviposition is possible. Secretory products may be 1) involved in the maturation of the spermatozoa, but, more likely, they are 2) responsible for the lysis of the protein capsule and 3) provision of a favourable milieu (pH, ion-balance, protection) for the decapsulated, but still inactive spermatozoa.

4. 3. 4. Mating plugs

4. 3. 4. 1. Embolus and embolus tips in *Latrodectus revivensis*

Although there are several parts of the genital bulb involved in the coupling process between male and female genitalia, the male embolus is the only part that is actually introduced into the female. This was demonstrated in a female of *L. revivensis* that retained the main parts of the embolus (adjacent embolus fragment) in one of her copulatory ducts after mating (Fig. 42a). The loss of the spirally-coiled embolus fragment has been reported for several *Latrodectus* species (Dahl 1902; Wiehle 1961; Abalos & Báez 1963; Mackay 1972; Müller 1985; Knoflach & van Harten 2002). As early as 1959, Levi suggested that the tearing off of a longer embolus fragment might be caused when the male tries to escape a female attack. Interestingly, in the lab matings of *L. revivensis*, all of the males that lost an adjacent embolus fragment escaped being cannibalised (Tab. 3; chapter 3. 3. 6.). For males that are attacked during withdrawal of the long embolus, its rupture might provide an escape mechanism. It is assumed that the loss of an embolus fragment happens more often in species whose females possess more coils in their copulatory duct (Abalos & Báez 1963; Abalos 1968). It was not possible to confirm this pattern by the data from *L. revivensis*. Although having a long embolus with four outer loops (similar to *L. geometricus*), only a rather intermediate number of *L. revivensis* females collected in the field (8.5 %) and in the lab matings (7.5 %) had embolus fragments lying in their copulatory ducts (Tab. 4).

	number of coils of copulatory duct	adjacent embolus fragments	number of specimens
L. revivensis (lab matings)	**4**	**3 (7.5%)**	**40 (100%)**
L. revivensis (field)	**4**	**5 (8.5%)**	**59 (100%)**
L. geometricus	4	9 (18.0%)	50 (100%)
L. corallinus (No 2)	3	5 (10.0%)	50 (100%)
L. antheratus (No 1)	2	2 (4.0%)	50 (100%)

Tab. 4: Number and percentages (in parentheses) of adjacent embolus fragments found in the female copulatory ducts of different *Latrodectus* species (data for *L. revivensis* **in bold letters**). For data regarding *L. geometricus*, *L. antheratus*, *L. corallinus* see Abalos and Báez (1966, 1967, 1980).

The embolus tip, however, does break off frequently inside the female genital tract (Dahl 1902; Smithers 1944; Levi 1959; Wiehle 1961, 1967a; Bhatnagar & Rempel 1962; Abalos & Báez 1963, 1967; Kaston 1970; Breene & Sweet 1985; Andrade 1996; Andrade & Banta 2002; Knoflach & van Harten 2002) at a well-defined breaking point ('Sollbruchstelle' Wiehle 1961). In most cases documented for various *Latrodectus* species, only a single tip was found in a particular side of the genital tract of females collected in the field. Similar to *L. revivensis*, the tip appears to be lodged deep inside the spermathecal opening with its apical part reaching into the spermathecal lumen. The thickened part of the embolus tip remains lying inside the lumen of the terminal part of the copulatory duct (Wiehle 1961; De Biasi 1962; Abalos & Báez 1963, 1966, 1967; Abalos 1968; Kaston 1970; Knoflach & van Harten 2002).

As long as the embolus of a male is not mutilated (e.g. ripped off or untangled) after the first insertion, a male might be able to copulate with another female (see Breene & Sweet 1985; Andrade & Banta 2002), but for several reasons a successful second copulation using the same pedipalp appears rather doubtful. An embolus devoid of the tip is too short to reach the lumen of the spermatheca. Furthermore, the diameter of the broken embolus is too wide to fit into the narrow spermathecal opening. This can be seen for example in the female specimen of *L. revivensis* which had an entire embolus in the copulatory duct (Fig. 42a). Spermatozoa expelled out of an embolus (with or without the tip) which had only reached the copulatory duct will be lost for fertilisation. Through the pressure a male is able to create, the sperm mass will be pushed backwards into the wider parts of the copulatory duct instead of entering the spermathecal lumen. Abalos and Báez (1967) wrote that 'when the apical element is situated in the canals of the female, the seminal mass is found in the canal' (p. 200). The expected 'sterility' of mated males that have lost their tips could be shown by experiments conducted on *L. hasselti* by Andrade and Banta (2002). Furthermore, the recharging of the pedipalp is not possible without the solid tip, hence, in a broken embolus the ejaculatory duct lies loosely between the truncus and pars pendula (Fig 32h). None of the authors who examined the sexual behaviour of *Latrodectus* observed postcopulatory sperm induction.

By leaving the broken-off embolus tip(s) inside the spermathecal opening after copulation, the male is able to erect a physical barrier against subsequent males. The

morphological pictures (LM, SEM) (especially in cross-sections) demonstrate that the tip closes the female spermathecal opening very tightly. The idea that the tip can act as a mating plug is supported by the fact that in those cases where two tips were found inside the same side of the epigynum, the second tip was usually lying behind the first tip in such a way that it did not reach into the spermathecal lumen. Second male's sperm would thus be lost for fertilisation (see above). A similar situation was observed in other *Latrodectus* species (de Biasi 1962; Kaston 1970). In those cases, where two tips of *L. revivensis* reached into the spermathecal lumen, neither tip was lodged deep inside the opening, suggesting that the first male was not able to position his tip properly. Moreover, the removal of a previously established embolus tip or direct manipulation (removal) of a rival's spermatozoa with the embolus tip by a second male appears impossible due to the shape and smooth surface of the tip.

The male's ability to monopolise one or even both spermathecae of a given female with mating plugs enhances competition between males. An individual male's fertilisation success will not only depend on his ability to be the first to mate with a virgin (or one-sided mated) female, but also on the number of copulations he is able to achieve with a given female (one or both sides).

A similar situation may occur in the other orbicularid species in which the male frequently loses defined parts or even the whole pedipalp linked to the female epigynum (Tab. 5; and see discussion on sexual cannibalism chapter 4. 4. 1. and 4. 4. 2.).

4. 3. 4. 2. Mating plugs in Araneae

Mating plugs are known from several other spiders, all belonging to the Entelegynae that are characterised by a separate entrance and exit of the spermathecae.

In the following list, I have summarised literature which reports on males establishing mating plugs inside the female genital tract (e.g. in the epigynal opening, fertilisation duct, spermathecal opening) (Tab. 5).

family/species [1]	type of plug [2]	frequency [3]	reference
Theridiidae (cobweb weavers)			
Latrodectus revivensis	embolus tip*	frequently	Berendonck & Greven (2002); this study
Latrodectus hasselti	embolus tip*	frequently	Abalos & Báez (1963); Andrade (1996) Andrade & Banta (2002)
Latrodectus mactans	embolus tip*	frequently	Wiehle (1960, 1967a); Kaston (1970); Breene & Sweet 1985)
Latrodectus hesperus	embolus tip*	frequently	Kaston (1970)
Latrodectus variolus	embolus tip*	frequently	Kaston (1970)
Latrodectus geometricus	embolus tip*	frequently	de Biaso (1962); Abalos & Báez (1963, 1967); Müller (1985), Knoflach & van Harten (2002)
Latrodectus indistinctus	embolus tip*	frequently	Smithers (1944)
Latrodectus antheratus (No. 1)	embolus tip*	frequently	Abalos & Báez (1967)
Latrodectus corallinus (No. 2)	embolus tip*	frequently	Abalos & Báez (1967)
Latrodectus curacaviensis	embolus tip*	frequently	Bhatnagar & Rempel (1962); Abalos & Báez (1963)
Latrodectus dahli	embolus tip*	frequently	Knoflach & van Harten (2002)
Latrodectus hystrix	embolus tip*	frequently	Knoflach & van Harten (2002)
Latrodectus renivulvatus	embolus tip*	frequently	Knoflach & van Harten (2002)
Latrodectus sp.	embolus tip*	frequently	Levi (1959)
Tidarren argo	pedipalp	frequently	Knoflach & van Harten (2001)
Tidarren cuneolatum	whole male	frequently	Knoflach & van Harten (2000)
Echinotheridion gibberosum	pedipalp/whole male	frequently	Knoflach (2002)
Achaearanea tepidariorum	embolus tip ('apical element')	anecdotal	Abalos & Báez (1963)
Teutana triangulosa	secretion ('Begattungszeichen')	frequently	Braun (1956)
Theridion varians	secretion+	frequently	Gerhardt (1923); Knoflach (1998)
Theridion petraeum	secretion+	frequently	Knoflach (1998)
Theridion refugum	secretion+	frequently	Knoflach (1998)
Theridion pinastri	secretion+	frequently	Knoflach (1998)
Theridion pictum	secretion+	frequently	Knoflach (1998)
Theridion melostictum	secretion+	frequently	Knoflach (1998)
Steatoda castanea	secretion	anecdotal	Gerhardt (1926)
Araneidae (orbweavers)			
Araneus diadematus	embolus tip ('scale')*	frequently	Levi (1969, 1971a)
Araneus pallidus	embolus tip ('cap')*/ whole male	frequently	Grasshoff (1968)
Araneus quadratus	embolus tip ('cap')*	frequently	Grasshoff (1968); Levi (1971a)
Araneus marmoreus	embolus tip ('cap')*	frequently	Levi (1971a)
Araneus corticarius	embolus tip ('cap')*	frequently	Levi (1971a)
Araneus washingtoni	embolus tip ('cap')*	frequently	Levi (1971a)
Araneus trifolium	embolus tip ('cap')*	frequently	Levi (1971a)
Araneus cavaticus	embolus tip ('cap')*	frequently	Levi (1971a)
Araneus gemmoides	embolus tip ('cap')*	frequently	Levi (1971a)
Araneus gemma	embolus tip ('cap')*	frequently	Levi (1971a)
Araneus pima	embolus tip ('cap')*	frequently	Levi (1971a)
Araneus nordmanni	embolus tip ('cap')*	frequently	Levi (1969, 1971a)
Araneus iviei	embolus tip ('cap')*	frequently	Levi (1969, 1971a)
Araneus saevus	embolus tip ('cap')*	frequently	Levi (1969, 1971a)
Araneus illaudatus	embolus tip ('cap')*	frequently	Levi (1969, 1971a)
Araneus groenlandicola	embolus tip ('cap')*	frequently	Levi (1969, 1971a)
Araneus (further 13 species)	embolus tip ('cap')*	frequently	Levi (1991)
Araneus sp.	embolus tip ('cap')*	frequently	Levi (1975, 1978)
Araneus angulatus	embolus tip*	frequently	Wiehle (1967a)
Araneus sp. (*Metepeira* sp.)	embolus tip*	frequently	Abalos & Báez (1963)
Araneus uniformes (*Metepeira candida*)	embolus tip*	frequently	Abalos & Báez (1963)

Tab. 5: Mating plugs Araneae (continued)

family/species [1]	type of plug [2]	frequency [3]	reference
Argiope keyserlingi	embolus tip*	frequent	Levi (1983b)
Argiope lobata	embolus tip* /whole male	frequent	Levi (1983b)
Argiope argentata	embolus tip*/ whole male	frequent	Abalos & Báez (1963); Levi (1968)
Argiope aemula	embolus tip*/ whole male	frequent	Levi (1983b)
Argiope reinwardti	embolus tip* /whole male	frequent	Levi (1983b)
Argiope bruennichi	embolus tip*	frequent	Levi (1983b)
Argiope aetherea	embolus tip*	frequent	Levi (1983b)
Argiope picta	embolus tip*	frequent	Levi (1983b)
Argiope (further 42 species)	embolus tip*	frequent	Levi (1983b)
Argiope flavipalpis	embolus tip*	frequent	Edmunds (1982b)
Argiope aetheroides	embolus tip*	frequent	Changmin *et al*. (1989)
Argiope pulchella	embolus tip*	frequent	Changmin *et al*. (1989)
Argiope pulchelloides	embolus tip*	frequent	Changmin *et al*. (1989)
Argiope versicolor	embolus tip*	frequent	Changmin *et al*. (1989)
Cyrtophora doriae	embolus	anecdotal	Strand (1920)
Hypsosinga sp.	scale at base of embolus*	anecdotal	Levi (1971b); Locket & Millidge (1953)
Tetragnathidae (longjawed orbweavers)			
Nephila plumipes	conductor*	frequent	Schneider *et al*. (2001)
Nephila madagascariensis	embolus	frequent	Wiehle (1960, 1967a, b)
Nephila inaurata m.	embolus	frequent	Schult & Sellenschlo (1983)
Nephila brasiliensis	embolus	frequent	Göldi (1892)
Nephila clavipes	embolus	frequent	Wiehle (1967b)
Nephila maculata	embolus	frequent	Wiehle (1967b); Robinson & Robinson (1980)
Nephila pilipes	embolus	frequent	Bertkau (1894); Schult & Sellenschlo (1983)
Leucauge sp.	embolus	anecdotal	Wiehle (1967b)
Leucauge mariana	secretion+	frequent	Eberhardt & Huber (1998)
Linyphiidae (sheet-web weavers)			
Minyriolus pusillus	embolus	anecdotal	Wiehle (1967a)
Linyphia triangularis	secretion	frequent	Stumpf & Linsenmair (1996)
Uloboridae (hackled orbweavers)			
Uloborus ferokus	secretion	frequent	Patel & Bradoo (1983)
Amaurobiidae (funnel weavers)			
Amarobius ferox	secretion	frequent	Gerhardt (1923); Suhm *et al*. (1996)
Amaurobius fenestralis	secretion	frequent	Suhm & Alberti (1993); Suhm *et al*. (1996)
Agelenidae (funnel-web spiders)			
Agelena labyrinthica	secretion	frequent	Strand (1906); Engelhardt (1910)
Agelena limbata	secretion	frequent	Masumoto (1993)
Thomisidae (crab spiders)			
Misumenops celer	secretion	frequent	Muniappan & Chada (1970)
Oxyptila nigrita	pedipalp	anecdotal	Bertkau (1889)
Salticidae (jumping spiders)			
Phidippus johnsoni	secretion	frequent	Jackson (1980a)

Tab. 5: Mating plugs in Araneae (continued)

family/species [1]	type of plug [2]	frequency [3]	reference
Clubionidae (sac spiders)			
Cheiracanthium erraticum	long embolus	anecdotal	Wiehle (1967a, b)
Clubiona brevipes	pedipalp	anecdotal	Wiehle (1967a)
Apostenus fuscus	secretion	anecdotal	Grimm (1986)
Phrurolithus festivus	secretion	anecdotal	Grimm (1986)
Clubionidae (no species given)	secretion	anecdotal	Forster (1967)
Dictynidae (meshweavers)			
Lathys similis	embolus	anecdotal	Wiehle (1967a)
Argenna pallida	secretion	frequent	Bertkau (1889); Gerhardt (1923)
Argenna testacea	secretion	anecdotal	Bertkau (1889)
Oxyopidae (lynx spiders)			
Peucetia viridans	secretion with distal part of paracymbium	frequent	Brady (1964); Exline & Whitcomb (1965); Whitcomb & Eason (1965)
Peucetia longipalpis	secretion	frequent	Brady (1964)
Toxopidae (lace web spiders)			
Toxopidae (no species given)	secretion	anecdotal	Forster (1967)

Tab. 5: Mating plugs in Araneae: Spider species in which the male is known to establish a mating plug inside the female genital tract (e.g. in the epigynal opening, fertilisation duct, spermathecal opening).
[1] In brackets: Species names as originally cited by the author(s).
[2] In brackets: name for the plug originally given by the author(s).
* 'Sollbruchstelle' or defined part of the pedipalp
[+] Female is supposed to be involved in the formation of the mating plug.
[3] Frequent: mating plug (or 'Begattungszeichen') reported to be either found frequently in the female genitalia and/or to be frequently lost by the male; anecdotal: plug occasionally found in the female genitalia.

Types of plugs can be roughly divided into two groups:

1) After copulation the male transfers a secretion (e.g. produced by a bulbus gland as in *Amaurobius* species, Suhm & Alberti 1993; Suhm *et al*. 1996) into the epigynal opening after his last copulation bout and thereby plugs more or less the single atrial opening that leads to the copulatory ducts. Only in a few species has the effectiveness of the mating plug been studied (e.g. 30 % in *Phidippus johnsoni* (Salticidae): Jackson 1980a; 62 % in *Agelena limbata* (Agelenidae): Masumoto 1993). Males are sometimes able to remove the plugs of a previous male and establish their own plugs after copulation (*Steatoda castanea* (Theridiidae): Gerhardt 1926; *Phidippus johnsoni* (Salticidae): Jackson 1980a; *Agelena limbata* (Agelenidae): Masumoto 1993). In the tetragnathid *Leucauge mariana*, the female is said to be involved in the formation of the (although not very effective) plug (Eberhard & Huber 1998).

2) Other males lose parts or even the whole pedipalp linked to the female epigynum. The ripping-off of the pedipalp or parts of it appears to occur in several entelegyne families. Some reports of pedipalp or embolus loss are anecdotal. To my knowledge, however, the frequent occurrence of the breakage of well-defined parts of the male pedipalp during copulation has only been observed in the families of the Theridiidae,

Araneidae and Tetragnathidae (Tab. 5), all belonging to the group of the Orbiculariae (orb weavers; see Foelix 1996).

In all *Latrodectus* species examined so far, the males frequently lose the embolus tip(s) inside the paired female's spermathecal opening(s) (see above).

A similar situation occurs in the araneids of the genus *Araneus* and *Argiope*. Here a well-defined, and often species-specific, 'scale', 'cap' or 'embolus tip' breaks off from the male pedipalp during copulation and is found inside the openings of the paired copulatory ducts (see citations in Tab. 5).

Most male tetragnathids of the genus *Nephila* are known to lose the terminal part of their emboli inside the female genitalia. The effectiveness of the obstruction of the spermathecal entrance by the long slender embolus is unclear. However, in *N. plumipes* the conductor has a peculiarly curved ending and a triangular process near the terminal end. In contrast to the other species, the tip of the conductor frequently breaks during matings and remains inside the female genital tract (the openings of the copulatory ducts situated inside the epigastric furrow) (for copulatory mechanics in *Nephila*, see Schult & Sellenschlo 1983). Although the conductor tip does not always completely obstruct the entrance to the spermatheca, it significantly decreases the chances of a second male losing his tip in the same opening. As the loss of the tip is positively related to the paternity a second male is able to achieve (P2), the conductor tip clearly acts as a mating plug. Also in this species the intromitted part (conductor) sometimes does not break at its usual location, but the entire pedipalp remains stuck in the genital opening, keeping other males from copulating successfully (in approx. 8 % of the matings of virgin males with virgin females) (Schneider *et al*. 2001).

In other theridiid spiders, the male itself might act as a non-permanent mating plug. In the theridiids *Tidarren cuneolatum* (Knoflach & van Harten 2000), *Tidarren argo* (Knoflach & van Harten 2001) and *Echinotheridion gibberosum* (Knoflach 2002), the male dies in copula and has to be subsequently removed by the female. In the latter two species the torn-off pedipalp remains fastened to the epigynum for some hours.

The survey shows that numerous species have developed different kind of mating plugs to prevent further competition with rival male's spermatozoa. As plugs made of secretion cover the common entrance (atrium) to the copulatory ducts, the success of a single male in monopolising the spermathecae will depend on the durability

of the material. In those species that lose solid parts of their pedipalps, the plug only obstructs the opening of a single copulatory duct. Therefore, an individual male's success will depend on the number of copulation bouts he is able to achieve. Consequently, the conflict over multiple female mating is expected to be higher in species with solid mating plugs (see discussion on sexual cannibalism in chapters 4. 4. 1. and 4. 4. 2.).

4. 3. 5. Female remating probability in the field

As the male is able to plug the spermathecal openings, the female also is usually restricted to two successful copulations (right and left side). The mating experiments showed that most (91.7 %) cannibalised males only achieved a single copulation bout. If cannibalism represents a mechanism by the female to ensure a second copulation with another male, female remating should be expected.

The number of females of *L. revivensis* and other *Latrodectus* species which contain more than one tip in one side of the epigynum (Tab. 6) indicates that females generally do mate with more than one male.

	number of specimens	number of tips in the right - left sides				
		0 - 0	1 - 0 or 0 - 1	1 - 1	2 - 1(0) or (0)1 - 2	2 - 2 or more
L. revivensis	**59 (100%)**	**3 (5.1%)**	**21 (35.6%)**	**28 (47.5%)**	**7 (11.9%)**	**-**
L. hasselti	23 (100%)	0 (0%)	7 (30.4%)	12 (52.2%)	4 (17.4%)	-
L. geometricus	50 (100%)	0 (0%)	9 (18.0%)	34 (68.0%)	7 (14.0%)	-
L. antheratus (No 1)	50 (100%)	0 (0%)	9 (18.0%)	33 (66.0%)	3 (6.0%)	5 (10%)
L. corallinus (No 2)	50 (100%)	0 (0%)	18 (36.0%)	20 (40.0%)	7 (14.0%)	5 (10%)

Tab. 6: Number and percentages (in parentheses) of tips found in the right and left copulatory ducts and spermathecal openings of females collected in the field. For data regarding *L. hasselti* see Andrade (1996) and data regarding *L. geometricus*, *L. antheratus*, *L. corallinus* see Abalos and Báez (1966, 1967, 1980).

In *L. revivensis*, the decrease in the proportion of females that mated with one male and the increase of females that accepted at least two males, as time in the mating cycle proceeds ('early females' - 'late females'), additionally indicate that females do frequently remate in the field. Moreover, many of those females which have only received a single copulation bout (e.g. those that cannibalised the first male after the first bout) accepted an additional male.

4. 4. Sexual cannibalism

4. 4. 1. Sexual cannibalism in *Latrodectus revivensis*

In the laboratory experiments, all females accepted the courting male within 24 h. Although a female may charge at the male at the moment he enters the web, no precopulatory cannibalism occurred, clearly indicating that females do not mistake the identity of the approaching males (Elgar 1992). Thirty percent of all males got cannibalised during or after a successful copulation. All but one of the cannibalised males only achieved a single copulation bout. The untangling of an embolus without losing the tip only occurred in cannibalised males, whereas loss of an adjacent embolus fragment only occurred in non-cannibalised males.

Many authors have previously reported that cannibalism in *Latrodectus* spp. occurs during or shortly after copulation (Gerhardt 1928; Herms 1935; Shulov 1940; Softly & Freeth 1970; Kaston 1970), preferably after the first copulation bout (Smithers 1944; Abalos & Báez 1966, 1967; Breene & Sweet 1985). Furthermore, it was noted that the female is especially sensitive at the time the male tries to withdraw his embolus (Gerhardt 1928; Shulov 1940; Smithers 1944). Difficulties of the male in withdrawing the long, coiled embolus reported, for example for *L. tredecimguttatus* (Shulov 1940) and *L. indistinctus* (Smithers 1944), were also observed in *L. revivensis* (this study). The female might be able to deter withdrawal by moving the copulatory ducts wit the help of the connected muscle fibres. Since all of the males that lost an adjacent embolus fragment survived copulation, ripping off parts of the embolus might resemble a final escape mechanism for the male. However, the cannibalised males who had an untangled embolus might not have been able to free themselves in time. If the female really is able to prevent a male's escape and thereby to increase her chances of cannibalising her

mate, this would provide a mechanism for her to exercise cryptic female choice (Eberhard 1996). A similar mechanism might occur in the cannibalistic spider *Nephila plumipes*, which loses sometimes not only the tip of the conductor but the entire pedipalp (Schneider *et al*. 2001; Tab. 5).

After copulation a male *L. revivensis* actively tries to escape a rapacious female and does not show any signs of complicity in being cannibalised. Furthermore, males are not expected to gain any obvious paternity benefits (e.g. by nutrients transferred to eggs, see chapter 4. 3. 3.) by being consumed by the female that outweigh the lost future reproductive opportunities, for example (Buskirk *et al*. 1984). Instead they lose the chance of monopolising the second spermatheca and possibly half the share of paternity if the female copulates with a second male. Although the expected number of matings (with different females) during a male's lifetime is low (due to natural constraints during mate search), the lack of male complicity and expected male benefits suggests that cannibalism does not represent an advantageous male strategy in this species.

A mechanism of a male *Latrodectus revivensis* to circumvent cannibalism is to suppress the female's aggression. A male's ability to induce a sufficient catalepsy, for example, might be reflected by either quantity or quality of courtship. The laboratory experiments on *L. revivensis* showed that the time until first copulation did not significantly differ between cannibalised and non-cannibalised males. Additionally, the time until the first copulation or cannibalism did not depend on male size. In *L. hasselti* mating success was higher for long-courtship males than for short-courtship males, and long-courtship males were more likely to achieve repeated copulations with the same female (Andrade & Banta 2001). However, a positive effect of courtship duration on the probability of escaping cannibalism might have been missed in the recent study due to the low sample size, resulting in a low statistical power of the tests. An indication that courtship duration does nonetheless reflect an individual male's characteristic is that all of the ten males which were allowed to copulate with a second virgin female did so in exactly the same time period as with the first female.

Since the quality of courtship cannot be determined directly, male body size (here measured as leg length) might best be used as an indicator reflecting courtship quality (e.g. vigour of vibratory courtship or amount of costly pheromones and/or silk is higher in larger males) (Halliday 1983). Male size (leg length) had a strong effect on the

male's probability of being cannibalised by the female, with cannibalised males being significantly smaller than non-cannibalised ones.

That females judge male quality on size *per se* appears unlikely. Only the male's pedipalps are in direct contact with those female structures probably allowing a 'size measurement'. However, female *L. revivensis* do not possess any appropriate sensory structures in the contact zones to evaluate pedipalp size, and the relatively low coefficient of variation of the pedipalpal cymbium width suggests that the male sexual character provides only an insufficient cue for the female to evaluate overall body size (Eberhard *et al*. 1998; and see chapter 4. 3. 1.).

Size may also indicate a male's physical ability to escape a female attack (Elgar *et al*. 1990; Newman & Elgar 1991; Elgar 1992; Prenter *et al*. 1995b). The relatively long legs of the male (compared to overall body size, see data in Levy & Amitai 1983) might be especially helpful for breaking free from the female after copulation. The selection pressures for large size in male *L. revivensis* are counterbalanced by selection pressures that favour smaller size. The field data and morphological investigations of the present study showed that males are able to monopolise one or even both female spermathecae by plugging their entrance(s) with (an) embolus tip(s). Males are under strong pressure to locate virgin or one-sided mated females before rival males. Therefore, selection may favour early maturation leading to smaller males (Vollrath & Parker 1992; Andersson 1994; Elgar 1998; Schneider *et al*. 2000). The relatively high coefficient of variation of male leg length indicates increased phenotypic variance. This supports the assumption that several selection pressures work on male size from different directions and males may follow different reproductive strategies (Pomiankowski & Møller 1995; Eberhard *et al*. 1998).

Regarding the ability of constructing mating plugs, an individual male's copulation success with a virgin female strongly depends on the number of copulation bouts he is able to achieve with that female. This pressure on the male is increased by natural constraints, such as heat and predation, that minimise the probability of a male encountering a second (suitable) female (Andrade 2003). Additionally, the loss of the embolus tip and/or sperm depletion after copulation leaves the male functionally sterile (Andrade & Banta 2002). The laboratory experiments showed that all but one (91.7 %) of the cannibalised males only achieved a single copulation bout. Although successfully

inseminating the female, 25 % percent of the cannibalised males did not even manage to plug a single spermatheca. They were found to have an untangled embolus with an intact embolus tip. A single male was cannibalised after his second copulation bout. Males that avoided being cannibalised after the first copulation bout, achieved a second bout significantly more often . In the wild, monopolising both female spermatheca would give a male in competition with other males the chance of securing a 100 % paternity.

Similarly, females usually are restricted to two copulation bouts. The field data showed that some of the females which only experienced a single copulation bout in their first matings do remate with (at least) one more male. Thus, cannibalism in *L. revivensis* might represent a mechanism by the female of achieving multiple matings with different males. Accepting any male for the first copulation bout ensures that she receives enough sperm to fertilise the eggs of all her egg sacs. Cannibalising the male after the first bout would leave her the possibility of copulating with a second male. Remating might provide insurance against the possibility of the first male being infertile (Watson 1991; Masumoto 1993; Andrade & Banta 2002), increase genetic variation (Elgar 1998) or provide the opportunity of exercising sequential female choice for a female which has no opportunity of assessing a large sample of males before mating ('bet-hedging strategy' according to Watson 1991, 1998; see also Elgar 1998; Schneider & Elgar 1998).

As the probability of being cannibalised depends on male size, the question arises as to whether the female directly chooses a particular phenotype (or the courtship qualities it reflects), thereby expressing her preference for bigger males, for example to increase the size of her own offspring (Watson 1998). Alternatively, the females may initially attack any male, and the male's ability to suppress female aggression (e.g. by inducing catalepsy) or to escape her attack would decide the outcome of a mating. The difficulties of distinguishing between direct and indirect female choice has been emphasised by authors in the past (Halliday 1983; Parker 1983; Andersson 1994; Eberhard 1996; Wiley & Poston 1996) and further experiments are required to answer this question in the present case.

Further factors, for example female hunger level and/or feeding history in previous life-history stages might influence female choice (active or passive). As early

as 1970 Kaston noted that cannibalism in *Latrodectus* spp. depended on female hunger level and Andrade (1998) demonstrated that well-fed *L. hasselti* were less likely to consume their mates. However, no direct benefit (e.g. fecundity increase by nutrients transferred to eggs) for the female through the consumption of the relatively small male is expected in *L. revivensis* and it was not possible to show this in the experiments conducted on *L. hasselti* (Andrade 1996) either. Therefore, it is unlikely that cannibalism evolved through purely economic foraging decisions by the female (see 'feeding opportunism hypothesis' Andrade 1998, modified according to the 'economic model' by Newman & Elgar 1991). The 'aggressive-spillover hypothesis' is based on the assumption that sexual cannibalism has evolved as an indirect result of selection for high and non-discriminate aggression during previous ontogenetic stages (Arnqvist & Henriksson 1997). According to Johnson (2001), fecundity selection favouring juvenile voracity should result in larger fixed adult size. Schneider and Elgar (2002) reversed the causation so that cannibalistic females are characterised by a history of poor feeding and, thus, smaller fixed adult size. In *L. revivensis* cannibalising females are smaller than non-cannibalising females, supporting the latter hypothesis at first glance. However, sample size was rather low and male and female leg length strongly correlated. When corrected against male size (leg length), female size (leg length) no longer had an effect on the probability of the female cannibalising a male. Several arguments speak against a strong effect of female feeding history on cannibalism in *L. revivensis*. For *L. geometricus* it was shown that prey availability did affect the time until maturation, but weight (a good indicator for size in virgin females) did not differ between feeding treatments (Heeres & Clark 1997). Additionally, Segev (1998) showed that the average female size of *L. revivensis* did not decrease towards the end of the season, although prey availability drastically decreases after spring and throughout summer (personal observations). Therefore, adult female size might be genetically determined to a great extent, and less affected by prey availability and female voracity during earlier life history stages.

In conclusion, the main line of evidence suggest that postcopulatory sexual cannibalism in *L. revivensis* is a female counterstrategy to overcome male monopolisation by mating plugs. As all males are invariably allowed to inseminate one spermatheca, she is on the save side having enough sperm for all her egg-sacs. But all

males that either do not meat her choice criteria (most likely courtship quality) or are simply not able to override the female aggression (for example by inducing sufficient catalepsy) are cannibalised after the first copulation bout. This leaves her the possibility to choose a second and maybe better male to fill her second spermatheca or even replace some of the spermatozoa of the first male that did not manage to plug the spermathecal opening.

4. 4. 2. Sexual cannibalism in Araneae

In order to evaluate whether common explanations for the occurrence of sexual cannibalism in spiders including *L. revivensis* exist, I surveyed the available literature on cannibalism reported for a variety of species belonging to numerous families. Tab. 7 includes those cases in which receptive, adult females cannibalised adult, virgin males.

I excluded those cases where 1) adult females preyed on subadults or juveniles (*Lycosa stonei*, Lycosidae, Montgomery 1903; *Pardosa chelata*, Lycosidae, Hallander 1967, 1970; *Mallos trivittatus*, Dictynidae, Jackson 1979), 2) adult males cannibalised adult females (*Dysdera crocata*, Dysderidae, Jackson & Pollard 1982; *Sparassus verescens*, Sparassidae, Ausserer 1867; *Micrommata virescens*, Sparassidae, Bristowe 1926b; *Simaetha paetula*, *S. thoracica*, Salticidae, Jackson 1985; *Phidippus johnsoni*, Salticidae, Jackson 1980b; *Herpyllus blackwalli*, Gnaphosidae, Bristowe 1974; *Pisaura mirabilis*, Pisauridae, Austad & Thornhill 1986), 3) adult males cannibalised adult males in combat (*Frontinella pyramitela*, Linyphiidae, Austad 1983; *Phidippus johnsoni*, Salticidae, Jackson 1980b), 4) adult females cannibalised adult females (*Cyrtophora moluccensis*, Araneidae, Lubin 1974); *Pardosa chelata*, Lycosidae, Hallander 1970; Nitzsche 1999) and where 5) adult males cannibalised subadults (*Phidippus johnsoni*, Salticidae, Jackson 1980b).

The literature survey additionally showed that some cases rated as 'sexual cannibalism' by the authors occurred instead in a context other than copulation. In *Metellina segmentata* (Tetragnathidae), males that were attacked by the female were actually engaged in male-male contests on a female's web (Rubenstein 1987). No cannibalism has been reported for the same species by other authors (Osterloh 1922; Gerhardt 1926; Blanke 1974; Prenter *et al.* 1994a, b; Bristowe 1974). Similarly, cannibalism in *Micrathena gracilis* (Araneidae) was not mentioned in a previous paper (Bukowski & Christenson 1997), but occurred before and after copulation in the

presence of a second male (Bukowski & Christenson 2000). In *Phonognatha graffei* (Tetragnathidae, Fahey & Elgar 1997), *Pardosa chelata* (Lycosidae, Hallander 1967, 1970) and *Heteropoda venatoria* (Sparassidae, Ross *et al*. 1982), postcopulatory cannibalism occurred in the context of cohabitation. In *Pisaura mirabilis* (Pisauridae, Austad & Thornhill 1986) death occurred during struggle over prey and females were in as much danger of being eaten by the courting male as *vice versa*. Those cases where cannibalism did not obviously occur in the direct context of courtship or copulation have not been included in the following discussion.

As the various models (see Introduction: 'paternal investment model' Buskirk *et al*. 1984; 'mate rejection' Elgar & Nash 1988: 'mistaken identity' Robinson 1982, Elgar 1992; 'economic model' Newman & Elgar 1991; 'aggressive-spillover' Arnqvist & Henriksson 1997; 'feeding opportunism' Andrade 1998) failed to give a common explanation for the evolution of sexual cannibalism in spiders, it has been suggested that sexual cannibalism independently evolved multiple times (Elgar 1992). However, to reveal similarities between species, which were possibly missed in previous studies, I analysed the available literature on a case-by-case basis (Tab. 7).

family/species [1]	context of cannibalism by females on males[2] and number of observed matings[3]	sexual cannibalism by female on male[3]		postcopulatory cannibalism[3, 5]		male behaviour (attempts to escape capture, 'Schocktod', somersault after 1st/2nd copulation bout, etc.)	reference
		pre-copulatory[4]	post-copulatory	after 1st copulation bout	after 2nd copulation bout		
Theridiidae (cobweb weavers)							
Latrodectus revivensis	**L: copulation (*n* = 40)**	**0 %**	**30.0 %**	**91.7 %**	**8.3 %**	attempts to escape capture	this study
Latrodectus hasselti	L: copulation (*n* = 20)	0 %	75 %			somersault on female chelicerae	Cariaso (1967)
	L: copulation (*n* = 56)	**0 %**	**58 %[#]**	**33 %[#]**	**66 %[#]**	somersault on female mouthparts female may exude digestive juices and may puncture male abdomen with her fangs	Forster (1992, 1995)
	L: copulation (*n* = 24)	**0 %**	**45.8 % (58.4 %)[#]**	**27.3 % (28.6 %)[#]**	**72.7 % (71.4 %)[#]**	somersault on female mouthparts female may exude digestive juices and may puncture male abdomen with her fangs	Andrade (1998); Andrade & Banta 2002)
Latrodectus mactans	L: copulation		+			attempts to escape capture	Herms *et al*. (1935); Breene & Sweet (1985); Softly & Freeth (1970); Kaston (1970); Cooke (1973)
Latrodectus hesperus	L: copulation		+			attempts to escape capture	Kaston (1970)
Latrodectus variolus	L: copulation		+			attempts to escape capture	Kaston (1970)
Latrodectus geometricus	L: copulation		+			attempts to escape capture	Bonnet (1938)
Latrodectus indistinctus	**L: copulation**		**+**	**+**	**+**	attempts to escape capture	Smithers (1944)
Latrodectus antheratus	**L: copulation**		**+**	**+**		attempts to escape capture	Abalos & Báez (1967)
Latrodectus tredecimguttatus	**L: copulation**		**+**	**+**		attempts to escape capture	Shulov (1940)

Tab. 7: Cannibalism in Araneae (continued)

family/species [1]	context of cannibalism by females on males[2] and number of observed matings[3]	sexual cannibalism by female on male[3]		postcopulatory cannibalism[3, 5]		male behaviour (attempts to escape capture, 'Schocktod', somersault after 1st/2nd copulation bout, etc.)	reference
		pre-copulatory[4]	post-copulatory	after 1st copulation bout	after 2nd copulation bout		
Theridiidae (cobweb weavers)							
Tidarren argo	**L: copulation (*n* = 45)**	**0 %** *	**100 %**	**100 %**	**male has only one pedipalp**	amputates one pedipalp after pen-ultimate moult; male dies in copula (of fatigue); pedipalp remains on epigynum for several hours	Knoflach & van Harten (2001)
Tidarren cuneolatum	**L: copulation (*n* = 34)**	**0 %**	**100 %**	**100 %**	**male has only one pedipalp**	amputates one pedipalp after pen-ultimate moult; male dies in copula (of fatigue)	Knoflach & van Harten (2000)
Echinotheridion gibberosum	**L: copulation (*n* = 18)**	**0 %**	**100 %**	**100 %**	**male has only one pedipalp**	amputates one pedipalp after pen-ultimate moult; male dies in copula (of fatigue); pedipalp remains on epigynum for several hours	Knoflach (2002)
Theridium formosum	F: copulation (*n* = 1)	(*n* = 1)					Gerhardt (1923)
Tetana triangulosa	F: copulation (*n* = 1)	(*n* = 1)					Montgomery (1903)
Steatoda marmorata	F: copulation (*n* = 1)	(*n* = 1)					Montgomery (1903)

Tab. 7: Cannibalism in Araneae (continued)

family/species [1]	context of cannibalism by females on males[2] and number of observed matings[3]	sexual cannibalism by female on male[3]		postcopulatory cannibalism[3, 5]		male behaviour (attempts to escape capture, 'Schocktod', somersault after 1st/2nd copulation bout, etc.)	reference
		pre-copulatory[4]	post-copulatory	after 1st copulation bout	after 2nd copulation bout		
Araneidae (orbweavers)							
Araneus diadematus	**L: copulation (*n* = 52)**	**25.0 %**	**15.4 %**	**100 %**	**0 %**		Elgar & Nash (1988)
	F: copulation	+ *	+				Gerhardt (1911, 1924a, b)
Araneus pallidus	**F/L: copulation**	**-**	**+**	**+**		somersault on female chelicerae	Grasshoff (1964)
Argiope keyserlingi	**L: copulation (*n* = 70)** **F: copulation (*n* = 10)**	**0 %** **0 %**	**61.4 %** **70.0 %**	**100 %**	**not observed**		Elgar *et al*. (2000)
	L: copulation (*n* =23)	**0 %** *	**30.4 %**	**100 %**	**not observed**		Herberstein *et al*. (2002)
Argiope aemula	**F: copulation (*n* = 11)** **L: copulation (*n* = 52)**	**0 %** **0 %**	**81.8 %** **90.4 %**	**42.6 %**	**47.4 %**	attempts to escape capture in first bout, but 'Schocktod', i.e. male dies in 2nd bout	Sasaki & Iwahashi (1995)
Argiope lobata	L: copulation (*n* = 4)	-	*n* = 4	-	*n* = 4	attempts to escape capture in first bout, but 'Schocktod', i.e. male dies in 2nd bout	Gerhardt (1928, 1933)
	F: copulation	-	+	+	+	attempts to escape capture; 1 male dies in copula	Robinson & Robinson (1980)
Argiope picta	F: copulation	-	+	+	+	attempts to escape capture; male jumps off more readily in 1st than in 2nd bout	Robinson & Robinson (1980)
Argiope aurocincta	F: copulation	-	+	+	-	attempts to escape capture	Robinson & Robinson (1980)
Argiope cupsidata	F: copulation	-	+	+	-	attempts to escape capture	Robinson & Robinson (1980)
Argiope ocyaloides	F: copulation	-	+	+	-	attempts to escape capture	Robinson & Robinson (1980)

Tab. 7: Cannibalism in Araneae (continued)

family/species [1]	context of cannibalism by females on males[2] and number of observed matings[3]	sexual cannibalism by female on male[3]		postcopulatory cannibalism[3, 5]		male behaviour (attempts to escape capture, 'Schocktod', somersault after 1st/2nd copulation bout, etc.)	reference
		pre-copulatory[4]	post-copulatory	after 1st copulation bout	after 2nd copulation bout		
Araneidae (orbweavers)							
Cyrtophora citricola	**L: copulation (*n* = 4)**	**(*n* = 2)**	**(*n* = 2)**	**(*n* = 1)**	**(*n* = 1)**		Gerhardt (1928)
	F: copulation (*n* = 20)	0 %	100 %	10 %	90 %	attempts to escape capture in 1st bout; no attempt to escape in 2nd bout	Blanke (1972)
Cyrtophora cicatrosa	**L: copulation (*n* > 29)**	**0 %**	**100 %**	**+**		somersault in 1st bout, tilts onto female mouthparts and is seized by female with chelicerae, removed and eaten	Blanke (1975)
Cyrtophora moluccensis	F: copulation (*n* = 15)	0 %	33.3 %				Berry (1987)
Micrathena gracilis	**L: copulation (*n* = 48) 2 males present**	**4.2 %[x]**	**6.3 %[x]**	**66.6 %[x]**	**33.3 %[x]**		Bukowski & Christenson (2000)
Micrathena sexspinosa	F: copulation (*n* = 5)		(*n* = 1)	(*n* = 1)		male drops off web after copulation	Robinson & Robinson (1980)
Gasteracantha cancriformes	**F: (staged): copulation (*n* = 52)**	**11.5 %***	**7.7 %**	**75.0 %**	**25.0 %**		Bukowski *et al.* (2001)
Gasteracantha minax	L: copulation (*n* = 4)		(*n* = 1)				Mascord (1967)
	L: copulation (*n* = 30)	10 %					Elgar & Bathgate (1996)
Gea sp. Wau no.1 (eff?)	F: copulation (*n* = 5)		(*n* = 1)	(*n* = 1)			Robinson & Robinson (1980)

Tab. 7: Cannibalism in Araneae (continued)

family/species [1]	context of cannibalism by females on males[2] and number of observed matings[3]	sexual cannibalism by female on male[3]		postcopulatory cannibalism[3, 5]		male behaviour (attempts to escape capture, 'Schocktod', somersault after 1st/2nd copulation bout, etc.)	reference
		pre-copulatory[4]	post-copulatory	after 1st copulation bout	after 2nd copulation bout[5]		
Tetragnathidae (longjawed orb-weavers)							
Nephila plumipes	**L: copulation (*n* = 20, but only *n* = 9 males copulated within time frame)**	**10 % (2/20)**	**88.9 % (8/9)**	**100 %**	**0 %**		Elgar & Fahey (1996)
	L: copulation (*n* = 79)	**0 %**	**55.7 %**	**100 %**	**0 %**	male changes position by 180° in the same plane, ending with opisthosoma in direction of female chelicerae	Schneider & Elgar (2001); Schneider *et al*. (2001)
	L: copulation (*n* = 64)	**0 %**	**62.5 %**				Schneider & Elgar (2002)
Nephila edulis	L: copulation (*n* = 92)	0 %	5.4 %				Schneider *et al*. (2000)
	L: copulation (*n* = 43)	**2.3 %**	**16.3 %**				Uhl & Vollrath (1998a)
Nephila maculata	F: copulation	(*n* = 1)					Robinson & Robinson (1980)
Nephila clavipes	F/L: copulation	+ (not clear if pre- or post-copulatory)					Christenson & Goist (1979); Christenson (1990)
	F: copulation	(*n* = 1)					Robinson & Robinson (1980)
	F: copulation	+ (not clear if pre- or post-copulatory)					Vollrath (1980)
Nephila madagascarienis	L: copulation (*n* = 13)	(*n* = 2)					Bonnet (1930)
	F/L: copulation	+ (not clear if pre- or post-copulatory)					Charézieux (1961)
Metellina segmentata	F: male - male combat in the vicinity of the female	+				males are engaged in contest close to resident female	Rubenstein (1987)
Phonognatha graffei	L: cohabitation (*n* = 45)	26.7 % (not clear if all males had mated)					Fahey & Elgar (1997)

Tab. 7: Cannibalism in Araneae (continued)

family/species [1]	context of cannibalism by females on males[2] and number of observed matings[3]	sexual cannibalism by female on male[3]		postcopulatory cannibalism[3, 5]		male behaviour (attempts to escape capture, 'Schocktod', somersault after 1st/ 2nd copulation bout, etc.)	reference
		pre-copulatory[4]	post-copulatory	after 1st copulation bout	after 2nd copulation bout[5]		
Thomisidae (crab spiders)							
Misumenops celer	L: cohabitation		+				Muniappan & Chada (1970)
Salticidae (jumping spiders)							
Phidippus johnsoni	L: copulation (encounter) (*n* = 1749)		1.0 %				Jackson (1980b)
Phidippus morsitans	L: copulation	+					Peckham & Peckham (1889)
Phidippus rufus	L: copulation	+					Peckham & Peckham (1889)
Simaetha paetula	L: copulation	(*n* = 2)					Jackson (1985)
Portia shultzi	L: copulation	+					Jackson & Hallas (1986)
Portia labiata	L: copulation	+					Jackson & Hallas (1986)
Marpissa marina	L. copulation	+	+				Jackson *et al*. (1990)
Dictynidae (meshweavers)							
Dictyna calcarata	L: copulation	(*n* = 1)					Jackson (1979)

Tab. 7: Cannibalism in Araneae (continued)

family/species [1]	context of cannibalism by females on males[2] and number of observed matings[3]	sexual cannibalism by female on male		postcopulatory cannibalism[3, 5]		male behaviour (attempts to escape capture, 'Schocktod', somersault after 1st/2nd copulation bout, etc.)	reference
		pre-copulatory[4]	post-copulatory	after 1st copulation bout	after 2nd copulation bout[5]		
Lycosidae (wolf spider)							
Tarentula barbipes	L: copulation		(*n* = 1)			male did not perform courtship	Bristowe & Locket (1926)
Lycosa rabida	L: copulation (*n* = 12)		(*n* = 1)			male pinches female after copulation with chelicerae	Rovner (1972)
Lycosa stonei	L: copulation	(*n* = 1)					Montgomery (1903)
Lycosa scutulata	L: copulation	(*n* = 1)*	(*n* = 1)				Montgomery (1903)
Pardosa chelata	L. copulation, cohabitation		+				Hallander (1967, 1970)
Pisauridae (nursery web spiders)							
Dolomedes fimbriatus	L: copulation (*n* = 6)	(*n* = 1)	(*n* = 1)				Gerhardt (1926)
	L: copulation (*n* = 89)	5.6 %					Arnqvist (1992)
	L: copulation (*n* = 126), in 83 cases a 2nd male was present	13.6 %					Arnqvist & Henriksson (1997)
Dolomedes triton	L: copulation	+*					Spence *et al*. (1996)
	L: copulation (*n* = 52)	**21.2 %**	**35.2 %**	**100 %**	**0 %**		Johnson (2001)
Pisaura mirabilis	F: struggle over prey (*n* > 70)	(*n* = 2)				males offer nuptial gift	Austad & Thornhill (1986)
	L: copulation (*n* = 222)	1.4 %	0.5 %			males offer nuptial gift	Nitzsche (1999)

Tab. 7: Cannibalism in Araneae (continued)

family/species [1]	context of cannibalism by females on males[2] and number of observed matings[3]	sexual cannibalism by female on male[3]		postcopulatory cannibalism[3, 5]		male behaviour (attempts to escape capture, 'Schocktod', somersault after 1st/2nd copulation bout, etc.)	reference
		pre-copulatory[4]	post-copulatory	after 1st copulation bout	after 2nd copulation bout		
Gnaphosidae (stealthy ground spiders)							
Herpyllus blackwalli		+ (not clear if pre- or post-copulatory)					Bristowe (1974)
Dysderidae (woodlouse spiders)							
Dysdera crocata	L: copulation	(*n* = 1)					Jackson & Pollard (1982)
Sparassidae (giant crab spiders)							
Heteropoda venatoria	L: copulation or ev. cohabitation		+				Ross *et al*. 1982
Uloboridae (hackled orb-weavers)							
Uloborus walckenaerius	F: copulation (*n* = 10)	*	(*n* = 3)				Gerhardt (1933)
Oxyopidae (lynx spiders)							
Oxyopes heterophthalmus	F: copulation		(*n* = 1)				Gerhardt (1933)

Tab. 7: Cannibalism in Araneae: Cases of sexual cannibalism by females on the male before (precopu latory), during or after copulation observed in araneid families.
Cannibalism during and after copulation is summarised as 'postcopulatory'. Context and timing of cannibalism are given.
'Male behaviour' describes the various actions shown by the male during or after copulation (sometimes female actions are included).
[1] Species names as originally cited by the author(s).
[2] F: observations under field conditions; L: observations under laboratory conditions.
[3] Observations made nondoubtful on **virgin females** and **virgin males** in bold type.
[4] *Additionally, precopulatory cannibalism by mated (presumably non-receptive) females on males has been observed.
[5] When possible, postcopulatory cannibalism (taken as 100 %) is divided into percentages of cannibalism after the 1st or 2nd copulation bout.
+ indicates that cannibalism (pre-, post- etc.) has been observed. When known, frequency is given in numbers or (when reasonable) percentages.
- indicates that cannibalism (pre-, post- etc.) has not been observed.
[#] The percentages given represent the actual death risk (dead males) in *Latrodectus hasselti*. When known, percentages of males that have been punctured by the female (defined as 'cannibalism' by Andrade 1998) are given in brackets.
[x] Cannibalism in *Micrathena gracilis* only occurred when two males were presented to the female simultaneously.

The survey revealed that only in a few families does 'sexual cannibalism' frequently occur in the context of copulation *per se*, i.e. receptive adult females cannibalise courting (or approaching) adult males.

Aggression of mated, unreceptive females towards approaching males has been reported for a broad range of taxa (e.g. *Cyrtophora cicatrosa*, Araneidae, Blanke 1975 ; *Baryphyma pratense*, Linyphiidae, Blest 1987; *Gasteracantha minax*, Araneidae, Elgar & Bathgate 1996). Those encounters frequently result in the death of the male (e.g. *Argiope bruennichi*, Araneidae, Gerhardt 1924a ; *Nephila maculata*, Tetragnathidae, Robinson & Robinson 1976; *Supunna picta* Clubionidae, Jackson & Poulsen 1990). These fatal attacks by mated, unreceptive females occurred in a wide range of taxa including species that did not show sexual cannibalism in any other context, or species that otherwise only showed postcopulatory cannibalism (see asterisks in Tab. 7). However, within each species they represent rather rare events. The occurrence of precopulatory cannibalism by mated, unreceptive females might be explained to some extent by the 'economic model' (Newman & Elgar 1991). Although the model originally tried to demonstrate that precopulatory cannibalism may arise through purely economic considerations in virgin females, it also shows that mated females are generally more likely to perform precopulatory cannibalism than virgin females under any of the given conditions (number of males encountered during the season, mass gained from other prey items). On the other hand, females might simply try to get rid of harassing males that do not offer any further direct or indirect benefits, but incur further costs, for example by increasing the risk of predation or reducing the prey capture rate (Herberstein *et al*. 2002). However, since the motivation of mated, unreceptive females to attack approaching males differs from that of receptive females, these cases are not deemed to be 'sexual cannibalism in the context of copulation *per se*'.

'Sexual cannibalism in the context of copulation *per se*' has been observed in various spider families (Tab. 7). In some cases, the reproductive status of the females (virgin, mated, receptive or unreceptive) is not unambiguously clear from the cited investigation. For reasons of comparability I have only discussed copulations between virgin females and virgin males, as individuals may change their behaviour according to their partners' mating status (e.g. second males adjust (prolong) copula duration, thereby increasing the risk of being cannibalised; males may retreat more readily , or

they might be influenced by plugs constructed by earlier males). Those cases where virgin status can be guaranteed are highlighted in bold type (Tab. 7, columns 2-7). Where possible, all cases of cannibalism (100 %) have been divided into pre- or postcopulatory cannibalism. I have set postcopulatory cannibalism as 100 % and distinguished cannibalism according to the first and the second copulation.

However, reports of a frequent occurrence of sexual cannibalism (> 10 % of observed matings) have actually only been made for few species within the Theridiidae, Araneidae and Tetragnathidae, all belonging to the group of the Orbiculariae (orb weavers; see Foelix 1996) and within the Pisauridae (Tab. 7).

Pisauridae

In contrast to the Orbiculariae, Pisauridae (fishing spiders) are large, semi-aquatic 'sit-and-wait predators'. Females indiscriminately attack the courting, similarly-sized males from a distance, before (*Dolomedes fimbriatus, D. triton*) or after the first copulation bout (*D. triton*). As in *D. fimbriatus* cannibalism had shown to incur costs (females remained unmated) and females did not balance the male's economic value as a meal versus his value as a sperm donor in the adaptive manner predicted by the 'economic model' (Newman & Elgar 1991), Arnqvist and Henriksson (1991) developed a model that attempted to explain the evolution of precopulatory cannibalism based on genetic constraints ('aggressive-spillover', see above). For *D. triton*, Johnson (2001) concluded that neither of the two hypotheses ('spillover hypothesis'/'economic model') were mutually exclusive. However, the female's stereotypical and indiscriminately aggressive behaviour towards any male in these active hunters differs from the behaviour observed in cannibalistic orb weavers (see below).

Orbiculariae

Within the Orbiculariae (orb weavers), sexual cannibalism has been observed frequently (> 10 %) in the genera *Latrodectus*, *Tidarren*, *Echinotheridion* (Theridiidae), *Araneus*, *Argiope*, *Cyrtophora*, *Gasteracantha* (Araneidae) and *Nephila* (Tetragnathidae) (Tab. 7). The degree of female aggression might have even been underestimated in some cases, as only fatal attacks resulting in male death have been included in the table.

On the other hand, laboratory conditions might have artificially increased the number of fatal attacks.

Interestingly, postcopulatory sexual cannibalism occurred in all of these species, contradicting the repeated statement by Elgar and co-authors that sexual cannibalism in orb-weaving spiders commonly takes place before copulation (Elgar & Nash 1988; Elgar 1991). Actual cases of precopulatory cannibalism occurred only in *Araneus diadematus*, *Gasteracantha cancriformes*, *Nephila plumipes* and *N. edulis*. In all other species, only postcopulatory sexual cannibalism has been observed.

Precopulatory cannibalism

Araneus

Sexual size dimorphism in *Araneus diadematus* at a level of 1.4 is relatively low compared to > 2.6 in all other cannibalistic orbweavers (Hormiga *et al*. 2000), and consumption of the male positively affects female mass (Elgar & Nash 1988). Unfortunately, the effect of cannibalism on female reproductive output has not been determined. However, since body mass and fecundity are positively correlated in orb weaving spiders (Wise 1979) the increase by approx. 15 % of the initial female body mass implies that cannibalism positively affects fecundity in this species. Precopulatory cannibalism in *Araneus diadematus* might represent an adaptive female strategy as a result of purely nutritional considerations explained by the 'economic model' (Elgar & Nash 1992).

Gasteracantha

Precopulatory (and postcopulatory) cannibalism during staged matings in *Gasteracantha cancriformis* described by Bukowski *et al*. (2001) was not observed in the wild by previous authors (Muma 1971; Robinson & Robinson 1980). The conspicuous number of failures (51 % of the males did not copulate) during the laboratory experiment suggests that females might not have been sufficiently receptive. Therefore, the (frequent) occurrence of precopulatory (and postcopulatory) cannibalism in this species should be confirmed in further experiments.

Nephila

Precopulatory sexual cannibalism has only been observed twice in *Nephila plumipes* (Elgar & Fahey 1996) and once in *N. edulis* (Uhl & Vollrath 1998). In all other studies of the same species (*N. plumipes*: Schneider & Elgar 2001; Schneider *et al*. 2001; Schneider & Elgar 2002; *N. edulis*: Schneider *et al*. 2000) no precopulatory cannibalism has been noted and hence fatal attacks before copulation might be a rare event in this genus. A weak indication that precopulatory cannibalism might nevertheless represent a foraging decision by the female is the fact that the two males captured by *N. plumipes* were relatively large (Elgar & Fahey 1996) (larger than all of the males used in the other studies, see data in Schneider & Elgar 2001; Schneider *et al*. 2001; Schneider & Elgar 2002).

Postcopulatory cannibalism

Females of all of the cannibalistic Orbiculariae studied in more detail, frequently consume their mates after copulation. In most of these species, cannibalism never takes place before copulation (for exceptions, see above). Furthermore, males are preferably consumed (or at least attacked) during or after their first copulation bout with a virgin female (Tab. 7).

Species in which virgin females frequently cannibalise virgin males after copulation are: *Latrodectus revivensis*, *L. hasselti*, *Tidarren argo*, *T. cuneolatum*, *Echinotheridion gibberosum* (Theridiidae); *Araneus diadematus*, *A. pallidus*, *Argiope keyserlingi*, *A. aemula*, *Cyrtophora cicatrosa*, *C. citricola*. and *C. moluccensis* (both with an uncertain female mating status) (Araneidae); *Nephila plumipes*, *Nephila edulis* (Tetragnathidae). In all other cases, reports on postcopulatory cannibalism are rare (< 10 %, only *Gasteracantha cancriformes*) or anecdotal (for all citations see Tab. 7).

Only a few authors studying sperm usage patterns in spiders, for example, realised the importance of two pedipalps and (two) separate spermathecae in spiders (e.g. Bukowski & Christenson 1997, 2000; Yoward & Oxford 1997; Bukowski *et al*. 2001). Yoward and Oxford (1997) noted that males spiders which use only one of their pedipalps during copulation are not fully utilising the number of spermathecae available. These authors hypothesised that usage of a single pedipalp and, thus, the filling of only one spermatheca, might represent a female strategy. “By not allowing the

first male to fill both spermathecae, the female leaves room for insemination by further males, thus increasing the genetic diversity of her progeny" (Yoward & Oxford 1997, p. 9). That males often achieve only a single copulation bout with a given female appears to be a common pattern in non-cannibalistic species too (Yoward & Oxford 1997). However, the arising intersexual conflict over female remating is expected to be higher in species in which males are able to monopolise one or both female spermathecae by using mating plugs (see discussion above on *L. revivensis*). Interestingly, mating plugs have been observed in many of the orbicularid species in which postcopulatory sexual cannibalism is known to frequently occur.

Latrodectus

The present study showed that all but one of the cannibalised male *L. revivensis* only achieved a single copulation bout filling and (sometimes) plugging only one spermatheca. Males avoided being cannibalised and most likely did not gain any obvious benefits by being consumed. In the wild females do remate. Assuming that multiple mating is beneficial to the female, postcopulatory cannibalism after one copulation bout may represent an adaptive female strategy to obtain spermatozoa from different males. According to the observations on copulation, cannibalism and the number of embolus tips found in the epigyna of mated females of other *Latrodectus* species (Tabs. 5, 6, 7), a comparable pattern is expected throughout the genus. Cannibalism is usually characterised by the female actively capturing and wrapping the male in silk. However, a different behaviour occurs in the Australian red back spider, *L. hasselti*. Although typical attacks followed by wrapping the male have been observed (Forster 1992), cannibalism usually occurs after the male deliberately somersaults onto the female's chelicerae (Forster 1992, 1995). The female exudes digestive juices and may puncture the male abdomen with her fangs. Only 1/3 of the males cannibalised (punctured) die during or after the first bout. Some of the males surviving the first bout return to the female and 2/3 of the cannibalised (punctured) males do not die until having achieved a second copulation bout. In her quantitative analysis, Andrade (2003) demonstrated that the measured mortality rate during mate search in combination with paternity benefits (decreased likelihood that the female will remate, increased paternity by increased copula duration of cannibalised second males; Andrade 1996) is sufficient

to male self-sacrifice adaptive for males, which supports the model of Buskirk *et al*. (1994). However, males gain an additional benefit overlooked so far. Although a relatively high percentage of males are ultimately cannibalised in *L. hasselti* (approx. 50 - 75 %, compared, e.g. with only 30 % in *L. revivensis*), less than 20 % of them (only 12 % in Andrade 1998, for further explanations, see Tab. 7) actually die after the first copulation bout. All of the others achieve a second copulation bout, therefore filling and most probably monopolising both spermathecae. Considering the resulting paternity benefits, self-sacrifice may have evolved as a counterstrategy to suppress or circumvent the cannibalistic attacks otherwise initiated by the female (Forster 1992) and allow two copulation bouts.

Tidarren, Echinotheridion

The mating system in these theridiid species fundamentally differs from that of all other species showing postcopulatory sexual cannibalism. The tiny males of *Tidarren argo*, *T. cuneolatum* and *Echinotheridion gibberosum* amputate and suck out one of their pedipalps after the penultimate moult (Knoflach & van Harten 2000, 2001; Knoflach 2002). Males are always consumed after their first and only copulation bout. However, closer observations showed that females in these species rarely attack their mates (Knoflach, personal communication). Males usually die in copula without intervention by the females. They are eventually removed from the epigynum and sucked out by the female. In *E. gibberosum* and *T. argo* the pedipalp remains fastened to the epigynum, blocking the entrance for some hours (Knoflach & van Harten 2001; Knoflach 2002). Here cannibalism might represent an incidental consequence following male self-sacrifice. As males and/or pedipalps hinder subsequent males from copulating with the same female, death in copula (as a kind of postcopulatory mate guarding) appears to be an effective (and most probably adaptive) male strategy.

Araneus

As early as 1975, Levi noted the difference in behaviour between species originally placed within the genus *Araneus*. In those species in which the embolus bears a cap, the female is passive (cataleptic) or aggressive towards the male, whereas in species where females solicit and approach the male, the male embolus lacks a cap. Nowadays the

latter species are placed in completely different genera. However, the tip of the embolus ('cap' or 'scale') usually breaks off, blocking the opening of the female copulatory ducts in *Araneus* species (see Tab. 5). Studies on *A. diadematus* and *A. pallidus* have shown that postcopulatory sexual cannibalism frequently occurs after the first copulation bout. In *A. diadematus*, males do not sacrifice themselves and smaller males run a higher risk of being cannibalised (Elgar & Nash 1988). Similar to the situation in *L. revivensis*, size-dependent cannibalism initiated by the female after the first copulation bout, combined with a lack of male complicity and obvious male benefits, suggests that cannibalism evolved as an adaptive female strategy to allow a female which is restricted to two copulation bouts to obtain sperm from different males. *A. pallidus* males perform self-sacrifice by somersaulting onto the female chelicerae (Grasshoff 1964). Although it is not clear from this study if males achieve a second copulation bout or invariably die in the first bout and information on male benefits are lacking, male *A. pallidus* may follow a similar strategy to that of *L. hasselti* males (see above).

Argiope

In *Argiope* species, the embolus tip also regularly breaks off, blocking the female copulatory tracts (see Tab. 5). Similar to *L. revivensis* and *Araneus diadematus*, *Argiope keyserlingi* females cannibalise significantly smaller males after the first copulation bout (Elgar *et al*. 2000; Herberstein *et al*. 2002). Again, size-dependent cannibalism initiated by the female after the first copulation bout combined with a lack of male complicity and obvious male benefits suggests that cannibalism evolved as an adaptive female strategy. In *A. lobata* and *A. aemula*, males try to escape the rapacious female after the first bout, but always die in their second copula (Gerhardt 1928, 1933; Sasaki & Iwahashi 1995). In the first bout, male and female behaviour resembles that of *L. revivensis*, *Araneus diadematus* and *A. keyserlingi* and, although further data is lacking in this regard, cannibalism appears to be a female strategy as in the other species. By remaining attached to the female after the second bout, the males themselves function as non-permanent mating plugs, preventing other males from copulating. However, since more detailed data is missing assumptions regarding adaptive capacity of male death in copula are still speculative.

Cyrtophora

Mating plugs have been reported for only one species to date (*C. doriae*, Strand 1920; Tab. 5). Males of the three examined species are not known to lose parts of their pedipalps within the female tract. In *C. citricola*, females rarely attack males after the first bout. Blanke (1972) reports that after the second bout, the female treats the male as an "alien element" that she has to remove from her epigynum (p. 165), suggesting that males exhibit a similar behaviour to that of males of *Argiope aemula* and *A. lobata* (see above). In *C. cicatrosa*, no extensive female aggressive behaviour has been observed either (Blanke 1975), but here males sacrifice themselves by somersaulting onto the female chelicerae and are subsequently removed by the female. As cannibalism is usually not initiated by the female in either species, cannibalism following male death most likely resembles a male strategy instead, and may best be explained by Buskirk *et al.*'s 'paternal investment model' (1994).

Nephila

In *Nephila*, males frequently lose the terminal part of their emboli inside the female genitalia (see chapter 4. 3. 4. 2. and Tab. 5, same chapter). As mentioned above, the effectiveness of the obstruction of the spermathecal entrance by the long slender embolus is unclear. However, in contrast to other *Nephila* species, in *N. plumipes* the peculiarly curved ending of the conductor frequently breaks during matings and remains inside the female copulatory ducts (Schneider *et al.* 2001). Interestingly, postcopulatory cannibalism after the first copulation bout frequently occurs in this species. Postcopulatory cannibalism in the other species is either rare (*N. edulis*) or reports are anecdotal (Tab. 7). In the past, various authors have tried to explain the evolution of cannibalism in *N. plumipes* as a female foraging strategy (Schneider & Elgar 2001; 2002) and a male strategy to improve his fertilisation success (Schneider & Elgar 2001). The male paternity advantage of being cannibalised could only be shown for second males. Moreover, it can simply be explained by the occurrence of a mating plug in this species. Schneider *et al.* (2001) showed that second males that use the copulatory duct not containing a plug of the first male, are more likely to be cannibalised. As males that try to use a blocked copulatory duct are less likely to achieve a 'successful' copulation followed by a female attack, they are expected to be cannibalised less often.

Consequently, non-cannibalised second males would be expected to sire a lower percentage of the clutch than cannibalised males (a result actually demonstrated by Schneider & Elgar 2001). However, even cannibalised second males only achieved a mean paternity (P_2) of not more than 56 %. These findings, the lack of male complicity and (first) male's benefits suggest that precopulatory cannibalism is not an adaptive male strategy in *N. plumipes*.

Gerhardt (1933) showed that food availability in earlier life history stages did not affect adult male size. Consequently, female adult size in *Nephila* is expected to be genetically fixed to a great extent rather than as a result of prey availability in earlier life history stages (similar to the situation in *Latrodectus*, Heeres & Clark 1997). Additionally, male *N. plumipes* usually start to approach the female after she has caught a prey item (Elgar & Fahey 1996). Opportunistic mating is expected to reduce female predatory behaviour (Prenter *et al*. 1994b). Consumption of the relatively small male is also not expected to affect female weight or fecundity (Schneider & Elgar 2002). Consequently, neither 'feeding opportunism' nor 'aggressive-spillover' provide convincing evidence to explain the evolution of cannibalism in this species. However, the fact that males are able to establish effective mating plugs in this species, combined with the high percentage of postcopulatory cannibalism strictly after the first copulation bout, suggest that in *N. plumipes* cannibalism also represents a female strategy to overcome male-imposed restrictions on the number of mating partners. Hunger level and/or feeding history might simply shape the actual outcome of a given copulation.

In conclusion, the survey showed that among spiders only a few species show precopulatory sexual cannibalism by virgin females. Reports on its frequent occurrence are only available for two species among the sit-and-wait predators of the Pisauridae and the araneid *Araneus diadematus*. Since the adaptiveness (heritable benefits) of male consumption has yet to be unequivocally proven for any species, two not necessarily mutually exclusive hypotheses ('adaptive foraging' = 'economic model' and 'aggressive spill-over') which attempt to explain its evolution remain under debate.

Frequent postcopulatory sexual cannibalism only occurs within the Orbiculariae. It is most probable that this evolved through opposing selection pressures arising from intersexual conflict over the female mating multiple times with different males. In some

species it may represent a strategy predominantly in favour of 1) the female (*L. revivensis*, *Araneus diadematus*, *Argiope keyserlingi*, *Nephila plumipes*, *N. edulis* (?), 2) the male (as a consequence of self-sacrifice) (*Tidarren argo*, *T. cuneolatum*, *Echinotheridion gibberosum*, *Cyrtophora citricola*, *C. cicatrosa*), or 3) a combination of both (*Latrodectus hasselti*; *Araneus pallidus*, *Argiope aemula*).

1) Assuming that multiple matings with different males provide essential benefits for the female (genetic diversity of her progeny, etc.) the restriction to two copulation bouts due to the establishment of mating plugs might provide the decisive selective pressure for the evolution of a counterstrategy such as postcopulatory sexual cannibalism. In fact, mating plugs are known to occur in all species where the female initiates the fatal postcopulatory attack. Hunger level and/or feeding history of the female might shape the actual outcome of a given copulation.

For some species it could be demonstrated that postcopulatory sexual cannibalism depends on male phenotype (size), usually showing that small males face a higher risk. The occurrence of catalepsy induced by the male and the generally high number of attacks, not necessarily leading to the death, indicate that postcopulatory cannibalism initiated by the female represents a form of indirect choice. The variance in the outcome of matings (cannibalised versus non-cannibalised) between different-sized males may actually reflect the dynamic evolutionary process in which 'competitive' males are selected to override the tactics evolved by females (Parker 1979).

2) Male self-sacrifice eventually leading to postcopulatory sexual cannibalism occurs in two different forms. Either the male somersaults onto the female chelicerae, or he dies in copula ('Schocktod' or 'shockdeath' according to Gerhardt 1928). Prolonged second copulations increasing the risk of being cannibalised might represent another form of self-sacrifice, although less drastic. Self-sacrifice may have evolved through ecological factors (low remating probability) in combination with male paternity benefits (e.g. increased female reluctance to remate, decreased female remating probability through permanent and/or non-permanent mating plugs, achievement of a second copulation bout) (Buskirk *et al*. 1984, Andrade 2003). The selection pressures potentially involved in the evolution of self-sacrifice might also be responsible for the maximal investment in the first and only copulation bout by species that amputate the second pedipalp after the penultimate moult.

3) Interestingly, male self-sacrifice occurs in many species with mating plugs. The increased risk of being attacked and cannibalised by the female resulting from the possible monopolisation, decreases the probability of a male remating even with the same female. Here male self-sacrifice might be especially favoured as a male adaptive counterstrategy for overriding the female's attack and, thereby achieving a second copulation bout and most likely fathering the majority (or even all) of her offspring.

5. Summary

To reveal morphological and behavioural characteristics possibly involved in male and female reproductive strategies in *Latrodectus revivensis*, I investigated the functional morphology of male and female secondary genitalia (pedipalps and epigynum), using light-, scanning- and transmission electron microscopy. Additionally, I determined the female's remating probability in the field by counting and comparing the number of male embolus tips in the epigyna of females during different periods of their reproductive cycle. In laboratory matings, the frequency of cannibalism and related factors were recorded. Furthermore, courtship was analysed qualitatively. The experiments were complemented by literature surveys on the occurrence of mating plugs and cannibalism in Araneae.

- The embolus of the male pedipalp possesses a solid S-shaped embolus tip with a defined breaking point. A first male' embolus tip tightly fits into the female spermathecal opening. Due to the establishment of this mating plug, a subsequent male is rarely able to reach the spermathecal lumen in order to deposit his own, and replace rival's spermatozoa.
- The relatively low variance in pedipalpal cymbium size suggests that different selective forces are working on genital and somatic characters leading to intermediate, standardised sizes of male genitalia. The low allometric values (genital character on somatic character) indicate that the genital characters are subject to stabilising selection in males and females.
- Males show highly specialised courtship patterns (cutting, strumming sequence, bridal veil, etc.) and eventually render the female in a more or less cataleptic state.
- Apart from the tactile hairs overhanging the opening of the atrium, the contact zones of the female epigynum are devoid of any sensilla, indicating that the female does not discriminate in favour or against males due to their genital size or stimulation through copulatory courtship.
- The dumb-bell shape and the spatial separation of the entrance and exit suggest that the paired female spermathecae are functionally of the conduit type.

- Muscle fibres attached to the end part of the copulatory ducts probably enable the female to exercise 'cryptic female choice' by preventing the withdrawal of the male's embolus after copulation.
- The epithelium that surrounds the spermatheca comprises two types of glandular units and various ordinary epithelial cells. Similar to other araneomorphs, a glandular unit contains a gycoprotein-producing, basal gland cell, a secretory canal cell and ensheathing envelope cells.
- During oviposition, it is most likely that spermatozoa are indiscriminately sucked out of the spermathecal lumina by the low pressure produced by the contraction of the muscle extending from the epigynal plate to the common fertilisation duct. As no greater amounts of secretion are produced by the female during oviposition, and no activated sperm are present within the female genital tract, the secretion produced by the spermathecal epithelium does not serve in displacement or (selective) activation of spermatozoa.
- The decreasing number of once-mated females, and the increasing number of multiple-mated females as time in the mating cycle proceeds, indicate that females do frequently remate in the field. Moreover, females who experienced only a single copulation bout by the first male regularly accept an additional male.
- In the lab matings, all females accepted the courting males within 24 h. Thirty percent of all males became cannibalised during or after a successful copulation. Males that avoided being cannibalised were significantly larger than cannibalised males. All but one of the cannibalised males only achieved a single copulation bout, whereas non-cannibalised males had a significantly higher probability of achieving a second copulation, monopolising both female spermathecae. The main line of evidence suggest that postcopulatory sexual cannibalism in *L. revivensis* is a female counterstrategy to overcome male monopolisation. Larger males, on the other hand, might be able to override the female's aggressive tendencies by, for example sufficiently inducing catalepsy.

- Mating plugs are found throughout entelegyne spider species. However, only in some orbicularid species do the males frequently lose defined parts, or even the whole pedipalp, blocking the female copulatory duct(s).
- The literature survey on cannibalism revealed that only a few species show frequent precopulatory sexual cannibalism. Frequent postcopulatory sexual cannibalism has only been observed within the Orbiculariae. The case-by-case study suggests that postcopulatory sexual cannibalism evolved through opposing selection pressures arising from intersexual conflict over the female mating multiple times with different males. In some species postcopulatory sexual cannibalism appears to be a strategy predominantly in favour of 1) the female, 2) the male or 3) a combination of both. 1) Postcopulatory cannibalism initiated by the female (preferably after the first copulation bout) only occurs within species in which the males establish mating plugs. Assuming that multiple mating with different males provides essential benefits for the female, the restrictions of both mating partners to two copulation bouts due to the establishment of mating plugs may create the decisive selection pressure for the evolution of postcopulatory cannibalism as an adaptive female counterstrategy against male monopolisation. 2) Self-sacrifice (somersault, "shockdeath" in copula) and eventual consumption by the female appears to be an adaptive male strategy providing paternity benefits, for example by decreasing the female's remating probability. 3) In species with mating plugs and cannibalism initiated by the female, male self-sacrifice might represent a counterstrategy to override the female's attack, thereby achieving a second copulation bout.

6. References

ABALOS, J. W. 1968. La transferencia espermática en los arácnidos. - Revista de la Universidad Nacional de Córdoba 9: 251-278.

ABALOS, J. W. 1980. Las arañas de genero *Latrodectus* en la Argentina. - Obra del Centenario del Museo de La Plata 6: 29-51.

ABALOS, J. W.; BÁEZ, E. C. 1963. On spermatic transmission in spiders. - Psyche 70: 197-207.

ABALOS, J. W.; BÁEZ, E. C. 1966. Las arañas del género *Latrodectus* en Santiago del Estero. - Revista de la Facultad de Ciencias Exactas, Físicas y Naturales : 27: 5-30.

ABALOS, J. W.; BÁEZ, E. C.1967. The spider genus *Latrodectus* in Santiago dell Estero, Argentina. In: Animal Toxins (eds. F. E. Russell & P. R. Saunders), pp. 59-74. Pergamon Press, Oxford.

ALBERTI, G. 1991. On sperm ultrastructure and systematics of arachnida with special emphasis on Araneae and Acari. In: Comparative Spermatology 20 Years after (ed B. Baccetti), pp. 929-936. Raven Press, New York.

ALBERTI, G.; WEINMANN, C. 1985. Fine structure of spermatozoa of some labidognath spiders (Filistatidae, Segestriidae, Dysderidae, Oonopidae, Scytotidae, Pholcidae; Araneae; Arachnida) with remarks on spermiogenesis. - Journal of Morphology 185: 1-35.

ANAVA, A.; LUBIN, Y. 1993. Presence of gender cues in the web of a widow spider, *Latrodectus revivensis*, and a description of courtship behavior. - Bulletin of the British Arachnological Society 9: 119-122.

ANDERSSON, M. 1994. Sexual selection. Princeton University Press, Princeton.

ANDERSSON, M.; IWASA,Y. 1996. Sexual selection. - Trends in Ecology and Evolution 11: 53-58.

ANDRADE, M. C. B. 1996. Sexual selection for male sacrifice in the Australian redback spider. - Science 271: 70-72.

ANDRADE, M. C. B. 1998. Female hunger can explain variation in cannibalistic behavior despite male sacrifice in redback spiders. - Behavioral Ecology 9: 33-42.

ANDRADE, M. C. B. 2003. Risky mate search and male self-sacrifice in redback spiders. - Behavioural Ecology, in press.

ANDRADE, M. C. B.; BANTA, E. M. 2001. Female preference for prolonged courtship in redback spiders. - Advances in Ethology 36: 115.

ANDRADE, M. C. B.; BANTA, E. M. 2002. Value of male remating and functional sterility in redback spiders. - Animal Behaviour 63: 857-870.

ARNQVIST, G. 1992. Courtship behavior and sexual cannibalism in the semi-aquatic fishing spider, *Dolomedes fimbriatus* (Clerck) (Araneae: Pisauridae). - Journal of Arachnology 20: 222-226.

ARNQVIST, G.; HENRIKSSON, S. 1997. Sexual cannibalism in the fishing spider and a model for the evolution of sexual cannibalism based on genetic constraints. - Evolutionary Ecology 11: 253-271.

ARNQVIST, G.; NILSSON, T. 2000. The evolution of polyandry: multiple mating and female fitness in insects. - Animal Behaviour 60: 145-164.

AUSSERER, A. 1867. Beobachtungen über Lebensweise, Fortpflanzung und Entwicklung der Spinnen. - Zeitschrift Ferdinandeum Tirol 3: 181-209.

AUSTAD, S. N. 1983. A game theoretical interpretation of male combat in the bowl and doily spider (*Frontinella pyramitela*) - Animal Behaviour 31:59-73.

AUSTAD, S. N. 1984. Evolution of sperm priority patterns in spiders. In: Sperm competition and the evolution of animal mating systems (ed. R. L. Smith), pp. 223-249. Academic Press, New York.

AUSTAD, S. N.; THORNHILL, R. 1986. Female reproductive variation in a nuptial-feeding spider *Pisaura mirabilis*. - Bulletin of the British Arachnological Society 7: 48-52.

AUSTIN, A. D.; ANDERSON, D. T. 1978. Reproduction and development of the spider *Nephila edulis* (Koch) (Araneidae: Araneae). - Australian Journal of Zoology 26: 501-518.

BARTH, F. G. 1969. Die Feinstruktur des Spinneninteguments. I. Die Cuticula des Laufbeins adulter häutungsferner Tiere (*Cupiennius salei* KEYS). - Zeitschrift für Zellforschung und mikroskopische Anatomie 97: 135-159.

BARTH, F. G. 1970. Die Feinstruktur des Spinneninteguments. II. Die räumliche Anordnung der Mikrofasern in der lamellierten Cuticula und ihre Beziehung zur Gestalt der Porenkanäle (*Cupiennius salei* Keys., adult, häutungsfern, Tarsus). - Zeitschrift für Zellforschung und mikroskopische Anatomie 104: 87-106.

BARTH, F. G. 1982. Spiders and vibratory signals: Sensory reception and behavioral significance. In: Spider communication. Mechanisms and ecological significance (eds. P. N. Witt & J. S. Rovner), pp. 67-122. Princeton University Press, Princeton.

BARTH, F. G. 2002. A spider's world: senses and behavior. Springer-Verlag, Berlin.

BATEMAN, A. J. 1948. Intra-sexual selection in *Drosophila*. - Heredity 2: 349-368.

BENNET, R. G. 1992. The spermathecal pores of spiders with special reference to dictynoids and amaurobioids (Araneae, Araneomorphae, Araneoclada). - Proceedings of the Entomological Society of Ontario 123: 1- 21.

BERENDONCK, B,; GREVEN, H. 2002. Morphology of female and male genitalia of *Latrodectus revivensis* Shulov, 1948 (Araneae, Theridiidae) with regard to sperm priority patterns. In: European Arachnology 2000 (eds. S. Toft & N. Scharff), pp. 157-167. Aarhus University Press, Aarhus.

BERRY, J. W. 1987. Notes on the life history and behavior of the communal spider *Cyrtophora moluccensis* (Doleschall) (Araneae, Araneidae) in Yap, Caroline Islands. - Journal of Arachnology 15: 309-319.

BERTKAU, P. 1877. Über die Übertragungsorgane und die Spermatozoen der Spinnen. - Verhandlungen des Naturhistorischen Vereins der Preußischen Rheinlande und Westfalens 34: 28-32.

BERTKAU, P. 1889. Über ein ‚Begattungszeichen' bei Spinnen. - Zoologischer Anzeiger 12: 450-454.

BERTKAU, P. 1894 : Über Begattungszeichen bei Spinnen. - Sitzungsberichte der Niederrheinischen Gesellschaft für Natur- und Heilkunde in Bonn: 7 -9.

BHATNAGAR, R. D. S.; REMPEL, J. G. 1962. Structure, function and postembryonic development of male and female copulatory organs of the black widow spider *Latrodectus curacaviensis* (Müller). - Canadian Journal of Zoology 40: 465-510.

BIRKHEAD, T. R.,; MØLLER, A. P. 1998. Sperm competiton and sexual selection. Academic Press, London.

BLANKE, R. 1972. Untersuchungen zur Ökophysiologie und Ökethologie von *Cyrtophora citricola* Forskål (Araneae, Araneidae) in Andalusien. - Forma et Functio 5: 125-206.

BLANKE, R. 1974. Rolle der Beute beim Kopulationsverhalten von *Meta segmentata* (Cl.) (Araneae, Araneidae). - Forma et Functio 7: 83-94

BLANKE, R. 1975. Untersuchungen zum Sexualverhalten von *Cyrtophora cicatrosa* (Stoliczka) (Araneae, Araneidae). - Zeitschrift für Tierpsychologie 37: 62-74.

BLEST, A. D. 1987. The copulation of a linyphiid spider, *Baryphyma pratense*: does a female recieve a blood-meal from her mate? - Journal of Zoology / B 213: 189-191.

BLUMENTHAL, H. 1935. Untersuchungen über das Tarsalorgan der Spinnen. - Zeitschrift für Morphologie und Ökologie der Tiere 29:667-719.

BOISSIN, L. 1973. Etude ultrastructurale de la spermiogénèse de *Meta bourneti* Simon (Arachnides, Aranéides, Metinae). In: 2e Réunion des Arachnologistes d'expression francaise Montpellier, France (ed. Legendre), p. 7.

BONNET, P. 1930. Les Araignées exotiques en Europe. II. Elevage a Toulouse de al grande Araignée fileuse de Madagascar et considérations sur l'aranéiculture (Deuxième Partie) - Bulletin de la Société Zoologique de France 55: 53-77.

BONNET, P. 1938. Élevage de *Latrodectus geometricus*. - Bulletin de la Société d'Histoire Naturelle de Toulouse 72: 171-178.

BOULIGAND, Y. 1965. Sur une architecture torsadée répandue dans de nombreuses cuticles d'arthropodes. - Comptes Rendus des Séances de l' Académie des Sciences / D 261: 3665-3668.

BOYDE, A.; JONES, S. J. 1996. Scanning electron microscopy of bone: Instrument, specimen and issues. - Microscopy Research and Technique 33: 92-120.

BRADY, A. R. 1964. The lynx spiders of North America, north of Mexico (Araneae: Oxyopidae). - Bulletin of the Museum of Comparative Zoology 131: 429-518.

BRAUN, R. 1956. Zur Biologie von *Teutana triangulosa* (Walck.) (Araneae; Theridiidae, Asagneae). - Zeitschrift für Wissenschaftliche Zoologie 159: 255-318.

BREENE, R. G.; SWEET, M. H. 1985. Evidence of insemination of multiple females by the male black widow spider *Latrodectus mactans* (Araneae, Theridiidae). - Journal of Arachnology 13: 331-335.

BRIGNOLI, P. M. 1976. Ragni d' italia XXIV. Note sulla morfologia dei genitali interni dei Segestriidae e cenni sulle specie italiane (Araneae). - Fragmenta Entomologica 12: 19-62.

BRISTOWE, W. S. 1958. The world of spiders. Collins, London.

BRISTOWE, W. S. 1974. The world of spiders. Collins, London.

BRISTOWE, W. S.; LOCKET, G. H. 1926. The courthsip of british lycosid spiders and its probable significance. - Proceedings of the Zoological Society 22: 317-347.

BROWN, S. G. 1985. Mating behavior of the golden-orb-weaving spider, *Nephila clavipes*: II. Sperm capacitation, sperm competition and fecundity. - Journal of Comparative Psychology 99: 167-175.

BUKOWSKI, T. C.; CHRISTENSON, T. E. 1997. Determinants of sperm release and storage in a spiny orbweaving spider. - Animal Behaviour 53: 381-395.

BUKOWSKI, T. C.; CHRISTENSON, T. E. 2000. Determinants of mating frequency in the spiny orbweaving spider, *Micranthena gracilis* (Araneae: Araneidae).- Journal of Insect Behavior 13: 331-352.

BUKOWSKI, T. C.; LINN, C. D.; CHRISTENSON, T. E. 2001. Copulation and sperm release in *Gasteracantha cancriformis* (Araneae : Araneidae): differential male behaviour based on female mating history. - Animal Behaviour 62: 887-895.

BUSKIRK, R. E.; FROHLICH, C.; ROSS, K. G. 1984. The natural selection of sexual cannibalism. - The American Naturalist 123: 612-625.

CARIASO, B. L. 1967. Biology of the black widow spider, *Latrodectus hasse*lti Thorell (Araneidae: Theridiidae). - Philippine Agriculturist 51: 171-180.

CHAMBERLIN, R. V.; IVIE, W. 1935. The black widow spider and its varieties in the United States. - Bulletin of the University of Utah 25: 1-29.

CHANGMIN, Y.; JIAFU, W.; YONGJING Z.; XIANJING, P.; XIAOEN, C. 1989. The study on the subfamily *Argiope* from China (Araneae, Araneidae). - Journal of Natural Science of Hunan Normal University 12: 60-69.

CHAPMAN, T.; ARNQVIST, G.; BANGHAM, J.; ROWE, L. 2003. Sexual conflict. - Trends in Ecology and Evolution 18: 41-47.

CHARÉZIEUX, B. 1961. Contribution a l'étude de comportement sexuel de l'argiopide *Nephila madagascariensis* observé dans son pays d'origine. - Bulletin de la Société Zoologique de France 86 :372-379.

CHRISTENSON, T. E. 1990. Natural selection and reproduction: A study of the golden orb-weaving spider. In: Contemporary Issues in Comparative Psychology (ed. D. A. Dewsbury), pp. 149-174. Sinauer, Sunderland & Massachusetts.

CHRISTENSON, T. E.; GOIST, K. C. 1979. Costs and benefits of male-male competition in the orb weaving spider, *Nephila clavipes*. - Behavioral Ecology and Sociobiology 5: 87-92.

CODDINGTON, J. A; LEVI, H. W. 1991. Systematics and evolution of spiders (Araneae). - Annual Review of Ecology and Systematics 22: 565-592.

COHN, J. 1990. Is it the size that counts? Palp morphology, sperm storage, and egg hatching frequency in *Nephila clavipes* (Araneae, Araneidae). - Journal of Arachnology 18: 59-71.

COMSTOCK, J. H 1910. The palpi of male spiders. - Annals of the Entomological Society of America 3: 161-185.

COOKE, J. A. L. 1966. Synopsis of the structure and function of the genitalia in *Dysdera crocata*. - Senckenbergiana 47: 35-43.

COOKE, J. A. L. 1973. Unvealing the black widow. - Natural History 82: 66-75.

COURT, D. J. 1971. The behaviour and web structure of the katipo *Latrodectus katipo*. - Tane 17: 149-157.

COYLE, F. A. 1985. Two-year life cycles and low palpal character variance in a great smoky mountain population of the lamp-shape spider (Araneae, Hypochilidae, *Hypochilus*). - Journal of Arachnology 13: 211-218.

COYLE, F. A. HARRISON, F. W.; McGIMSEY, W. C.; PALMER, J. M. 1983. Observations on the structure and function of spermathecae in haplogyne spiders. - Transactions of the American Microscopical Society 102: 272-280.

CUNNINGHAM, E. J. A.; BIRKHEAD, T. R. 1998. Sex roles and sexual selection. - Animal Behaviour 56: 1311-1321.

DAHL, F. 1902. Über abgebrochene Copulationsorgane männlicher Spinnen im Körper der Weibchen. - Sitzungsberichte der Gesellschaft naturforschender Freunde, Berlin: 36-45.

DALINGWATER, J. E. 1987. Chelicerate cuticle structure. In: Ecophysiology of spiders (ed. W. Nentwig), pp. 3-15. Springer-Verlag, Berlin.

D'AMOUR, F. E.; BECKER, F.E.; VAN RIPER, W. 1936. The black widow spider. - Quarterly Review of Biology 11: 123-160.

DARWIN, C. 1871. The Descent of Man and Selection in Relation to Sex. John Murray, London.

DAVEY, K. G. 1985. The male reproductive tract. In: Comprehensive insect physiolology, biochemistry and pharmacology (eds. G. A. Kerku & L. I. Gilbert), pp. 1-13. Pergamon Press, New York.

DAWKINS, R. 1976. The selfish gene. Oxford University Press, Oxford.

DE BIASO, P. 1962. Estrutura interna e presença de segmentos do êmbolo no epígino de *Latrodectus geometricus* (Araneida : Theridiidae). - Papéis avulsos do Departamento de Zoologia 15: 327-331.

DE CARLO, J. M. 1973. Anatomia microscopica de las espermatecas de los generos *Grammostola* y *Acanthoscurria*. - Physis / C 32: 343-350.

DE LA SERNA DE ESTEBAN, C. J. ; LAURIA, L. ; SPINELLI, M. 1987. Female genitalia of three species of the genus *Latrodectus* (Araneae : Theridiidae): *L. antheratus*, *L. mirabilis* and *L. corallinus*. - Physis / C 45:31-37.

DENNELL, R. 1976. The structure and lamination of some arthropod cuticles. - Zoological Journal of the Linnean Society 58 : 159-164.

DENNELL, R. 1978. The cuticle of the hoplocarid crustacean *Squilla desmaresti* Risso. - Zoological Journal of the Linnean Society 62: 309-316.

EBERHARD, W. G. 1985. Sexual selection and animal genitalia. Harvard University Press, Cambridge, Massachusetts.

EBERHARD, W. G. 1994. Evidence for widespread courtship during copulation in 131 species of insects and spiders, and implications for cryptic female choice. - Evolution 48: 711-733.

EBERHARD, W. G. 1996. Female control: sexual selection by cryptic female choice. Princeton University Press, Princeton.

EBERHARD, W. G.; GUZMÀN-GÒMEZ, S.;CATLEY, K. M. 1993. Correlation between spermathecal morphology and mating systems in spiders. - Biological Journal of the Linnean Society 50: 197-209.

EBERHARD, W. G.; HUBER, B. A. 1998. Courtship, copulation and sperm transfer in *Leucauge mariana* (Araneae, Tetragnathidae) with implications for higher classification. - Journal of Arachnology 26: 342-368.

EBERHARD, W. G.; HUBER, B. A.; RODRIGUEZ, R. L.; BRICEÑO, R. D.; SALAS, I.; RODRIGUEZ, V. 1998. One size fits all? Relationships between the size and degree of variation in genitalia and other body parts in twenty species of insects and spiders. - Evolution 52: 415-431.

EDMUNDS, J. 1982. The species of *Argiope* (Araneae: Araneidae) found in Ghana, West Africa, with a description of the male of *Argiope flavipalpis* (Lucas). - Bulletin of the British Arachnological Society 5: 285-293.

ELGAR, M. A. 1992. Sexual cannibalism in spiders and other invertebrates. In: Cannibalism: Ecology and evolution among diverse taxa (eds. M. A. Elgar & B. J. Crespi), pp.128-155, Oxford University Press, Oxford.

ELGAR, M. A. 1995. The duration of copulation in spiders: comparative patterns. - Records of the Western Australian Museum / Supplement 52:1-11.

ELGAR, M. A. 1998. Sperm competition and sexual selection in spiders and other arachnids. In: Sperm competition and sexual selection (eds. T. R. Birkhead & A. P. Møller), pp. 757-777. Academic Press, London.

ELGAR, M. A.; BATHGATE, R. 1996. Female receptivity and male mate-guarding in the jewel spider *Gasteracantha minax*, Thorell (Araneidae). - Journal of Insect Behavior 9: 729-738.

ELGAR, M. A.; FAHEY, B. F. 1996. Sexual cannibalism, competition and size dimorphism in the orb-weaving spider *Nephila plumipes* Latreille (Araneae: Araneoidea). - Behavioral Ecology 7: 195-198.

ELGAR, M. A.; GHAFFAR, N.; READ, A. F. 1990. Sexual dimorphism in leg length in orb-weaving spiders: a possible role for sexual cannibalism. - Journal of Zoology 222: 455-470.

ELGAR, M. A.; NASH, D. R. 1988. Sexual cannibalism in the garden spider *Araneaus diadematus*.- Animal Behaviour 36:1511-1517.

ELGAR, M. A., SCHNEIDER, J. M.; HERBERSTEIN, M. E. 2000. Female control of paternity in the sexual cannibalistic spider *Argiope keyserlingi*. - Proceedings of the Royal Society of London / B 267: 2439-2443.

ENGELHARDT, V. 1910. Beiträge zur Kenntnis der weiblichen Kopulationsorgane einiger Spinnen. - Zeitschrift für Wissenschaftliche Zoologie 96: 32-117.

EXLINE, H.; WHITCOMB, W. H. 1965. Clarification of the mating procedure of *Peucetia viridans* (Araneida: Oxyopidae) by a microscopic examination of the epigynal plug. - Florida Entomologist 48: 169-171.

FAHEY, B. F.; ELGAR, M.A. 1997. Sexual cohabitation as mate-guarding in the leaf-curling spider *Phonognatha graeffei* Keyserling (Araneoidea, Araneae). - Behavioural Ecology and Sociobiology 40: 127-133.

FISHER, R. A. 1930. The genetical theory of natural selection, Oxford Univesity Press, Oxford.

FOELIX, R. F. 1970. Structure and function of tarsal sensilla in the spider *Araneus diadematus*. - Journal of Experimental Zoology 175: 99-123.

FOELIX, R. F. 1985. Mechano- and chemoreceptive sensilla. In: Neurobiology of Arachnids (ed. F. G. Barth), pp.118-137. Springer-Verlag, Berlin.

FOELIX, R. F. 1996. Biology of spiders. Oxford University Press, New York.

FORSTER, L. M. 1992. The stereoptyped behavior of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae: Theridiidae), the Australian Redback spider. - Australian Journal of Zoology 40: 1-11.

FORSTER, L. M. 1995. The behavioural ecology in *Latrodectus hasselti* (Thorell), the Australian redback spider (Araneae: Theridiidae): a review. - Records of the Western Australian Museum, Supplement 52: 13

FORSTER, R. R. 1967. The spiders of New Zealand. Part I. - Otago Museum Bulletin 1: 1-124.

FORSTER, R. R. 1980. Evolution of the tarsal organ, the respiratory system and the female genitalia in spiders. In: Verhandlungen des 8. Internationalen Arachnologen Kongress, Wien 1980 (ed. J. Gruber), pp. 269-284. H. Engermann, Wien.

GERHARDT, U. 1911. Studien über die Copulation einheimischer Epeiriden. - Zoologische Jahrbücher / Abteilung für Systematik, Ökologie und Geographie der Tiere 31: 643-666.

GERHARDT, U. 1923. Weitere sexualbiologische Untersuchungen an Spinnen. - Archiv für Naturgeschichte 89: 1-225.

GERHARDT, U. 1924a. Neue Studien zur Sexualbiologie und zur Bedeutung des Größendimorphismus der Spinnen. - Zeitschrift für Morphologie und Ökologie der Tiere 1: 507-538.

GERHARDT, U. 1924b. Weitere Studien über die Biologie der Spinnen. - Archiv für Naturgeschichte 90: 85-192.

GERHARDT, U. 1926. Weitere Untersuchungen zur Biologie der Spinnen. - Zeitschrift für Morphologie und Ökologie der Tiere 6: 1-77.

GERHARDT, U. 1928. Biologische Studien an grieschichen, korsischen und deutschen Spinnen. - Zeitschrift für Morphologie und Ökologie der Tiere 10: 576-675.

GERHARDT, U. 1933. Neue Untersuchungen zur Sexualbiologie der Spinnen, insbesondere an Arten der Mittelmeerländer und der Tropen. - Zeitschrift für Morphologie und Ökologie der Tiere 27: 1-75.

GILLOT, C. 1988. Arthropoda - Insecta. In: Reproductive biology of invertebrates. Vol. III: Accessory sex glands. (eds. K. G. Adiyodi & R. G. A diyodi), pp. 319-471. John Wiley & Sons, Chichester.

GÖLDI, E. A. 1892. Zur Orientierung in der Spinnenfauna Brasiliens. - Mitteilungen aus dem Osterlande 5: 1-37.

GONZALES, A. 1980. Estudio de la evolucion de los organos mecanoreceptores a traves del desarrollo postembrionario de *Latrodectus mirabilis*, *Latrodectus antheratus* y *Latrodectus corallinus* (Araneae, Theridiidae). - Revue de la Sociedad Entomologica Argentina 39: 207-219.

GONZALES, A. 1984. Desarrollo postembrionario y evolucion de los organos mecanorreceptores de *Latrodectus diaguita* Carcavallo, y estudio de la tricobotriotaxia de *Latrodetcus quartus* Abalos (Araneae, Theridiidae). - Physis Sección C Buenos Aires 42: 1-5.

GORB, S. N. 1997. Porous channels in the cuticle of the head-arrester system in dragon/damselflies (Insecta: Odonata). - Microscopy Research and Technique 37: 583-591.

GOULD, S. J. 1984. Only his wings remained. - Natural History 9: 10-18.

GRASSHOFF, M. 1964. Die Kreuzspinne *Araneus pallidus* - ihr Netzbau und ihre Paarungsbiologie. - Natur und Museum 94: 305-314.

GRASSHOFF, M. 1968. Morphologische Kriterien als Ausdruck von Artgrenzen bei Radnetzspinnen der Subfamilie Araneinae (Arachnida: Araneae: Araneidae). - Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 516: 1-100.

GRIMM, U. 1986. Die Clubionidae Mitteleuropas: Corinninae und Liocraninae (Arachnida, Araneae). - Abhandlungen des Naturwissenschaftlichen Vereins in Hamburg 27: 1-91.

HACKMAN, R. H. 1984. Cuticle: Biochemistry. In: Biology of the integument. I Invertebrates. (eds. J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards), pp. 583-610. Springer-Verlag, Berlin.

HADLEY, N. F. 1981. Fine structure of the cuticle of the black widow spider with reference to surface lipids. - Tissue and Cell 13: 805-817.

HALLANDER, H. 1967. Courtship display and habitat selection in the wolf *Pardosa chelata* (O. F. Müller). - Oikos 18: 145-150.

HALLANDER, H. 1970. Prey, cannibalism and microhabitat selection in the wolf spiders *Pardosa chelata* O. F. Muller and *P. pullata* Clerck. - Oikos 21: 337-340.

HALLIDAY, T. R. 1983. The study of mate choice. In: Mate choice (ed. P. Bateson), pp. 3-32. Cambridge University Press, Cambridge.

HEERES, A. 1991. Natural history observations of the brown widow spider *Latrodectus geometricus* (Araneae: Theridiidae). - The Naturalist 35: 31-34.

HEERES, A. 1993. Life history of the busy brown widow. - African Wildlife 47: 14-16.

HEERES, A.; CLARK, T. E. 1997. Changes in growth rate, weight and longevity in relation to prey availability in *Latrodectus geometricus* Koch 1841 (Araneae: Theridiidae). - Durban Museum Novitates 22: 57-59.

HERBERSTEIN, M. E.; SCHNEIDER, J. M.; ELGAR, M. A. 2002. Costs of courtship and mating in a sexually cannibalisstic orb-web spider: female mating strategies and their consequences for males. - Behavioral Ecology and Sociobiology 51: 440-446.

HERMS, W. B.; BAILEY, S. F.; McIVOR, B. 1935. The black widow spider. - Bulletin 591: 1-30.

HIGGINS, L. E. 1989. Effect of insemination on the morphology of the internal female genitalia of the spider *Nephila clavipes* (Araneae: Araneidae). - Annals of the Entomological Society of America 82: 748-753.

HINGSTON, R. W. G. 1923. The giant wood spider (*Nephila maculata*). - Journal of the Bombay Natural History Society 29: 70-76.

HORMIGA, G.; SCHARFF, N. CODDINGTON, J. A. 2000. The phylogenetic basis of sexual size dimorphism in orb-weaving spiders (Araneae, Orbiculariae). - Systematic Biology 49: 435-462.

JACKSON, R. R. 1979. Comparative studies of *Dictyna* and *Mallos* (Araneae, Dictynidae) II. The relationship between courtship, mating, aggression and cannibalism in species with differing types of social organization. - Revue Arachnologique 2: 103-132.

JACKSON, R. R. 1980a. The mating strategy of *Phidippus johnsoni* (Araneae, Salticidae): II. Sperm competition and the function of copulation. - Journal of Arachnology 8: 217-240.

JACKSON, R. R. 1980b. Cannibalism as a factor in the mating strategy of the jumping spider *Phidippus johnsoni* (Araneae, Salticidae). - Bulletin of the British Arachnological Society 5:129-133.

JACKSON, R. R. 1985. The biology *of Simaetha paetula* and *S. thoracica*, web-builing jumping spiders (Araneae, Salticidae) from Queensland: co-habitation with social spiders, utilization of silk, predatory behaviour and intraspecific interactions. - Journal of Zoology / B 1: 175-210.

JACKSON, R. R.; HALLAS, S. E. A. 1986. Comparative biology of *Portia africana*, *P. albimana*, *P. fimriata*, *P. labiata*, *P. shultzi*, araneophagic, web-building jumping spiders (Araneae: Salticidae): utilisation of webs, predatory versatility, and intraspecific interactions. - New Zealand Journal of Zoology 13: 423-489.

JACKSON, R. R.; PHIBBS, P.; POLLARD, S. D.; HARDING, D. D. 1981. Spiders that mate more than once. - Newsletter of the British Arachnological Society 30: 6-7.

JACKSON, R. R. POLLARD, S. D. 1982. The biology of *Dysdera crocata* (Araneae, Dysderidae): Intraspecific interactions. - Journal of Zoology 198: 197-214.

JACKSON, R. R.; POLLARD, S. D.; MacNAB, A. M. ; COOPER, K. J. 1990. The complex communicatory behaviour of *Marpissa marina*, a New Zealand jumping spider (Araneae: Salticidae). - New Zealand Journal of Zoology 17: 25-38.

JACKSON, R. R.; POULSEN, B. A. 1990. Predatory versatility and intraspecific interactions of *Supunna picta* (Araneae: Clubionidae). - New Zealand Journal of Zoology 17: 169-184.

JENNIONS, M. D. 1997 Female promiscuity and genetic incompatibility. - Trends in Ecology and Evolution 12: 251-253.

JENNIONS, M. D.; PETRIE, M. 2000. Why do females mate multiply ? A review of genetic benefits. - Biological Reviews 75: 21-64.

JOHNSON, J. C. 2001. Sexual cannibaslism in fishing spiders (*Dolomedes triton*): an evaluation of two explanations for female aggression towards potential mates. - Animal Behaviour 61: 905-914.

JUBERTHIE-JUPEAU, L.; LOPEZ, A. 1981. Ultrastructure du tube séminifère chez *Leptoneta microphthalma* SIMON, 1872 (Araneae, Leptonetidae). - Revue Arachnologique 3: 65-73.

KARNOVSKY, M. J. 1971. Use of ferricyanide-reduced osmium tetroxide in electron microscopy. - Journal of Cell Biology 51: 28.

KASTON, B. J. 1970. Comparative biology of american black widow spiders. - Transactions of the San Diego Society of Natural History 16: 33-82.

KELLER, L.; REEVE, H. K. 1998. Why do females mate with multiple males? The sexually selected sperm hypothesis. - Advances in the Study of Behavior 24: 291-315.

KNOFLACH, B. 1998. Mating in *Theridion varians* Hahn and related species (Araneae: Theridiidae). - Journal of Natural History 32: 545-604.

KNOFLACH, B. 2002. Copulation and emasculation in *Echinotheridion gibberosum* (Kulczynski, 1899)(Araneae, Theridiidae). In: European Archnology 2000 (eds. S. Toft & N. Scharff), pp. 139-144. Aarhus University Press, Aarhus.

KNOFLACH, B.; VAN HARTEN, A. 2000. Palpal loss, single palp copulation and obligatory mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae). - Journal of Natural History 34: 1639-1659.

KNOFLACH, B.; VAN HARTEN, A. 2001. *Tidarren argo* sp. nov. (Araneae: Theridiidae) and its exceptional copulatory behaviour: emasculation, male palpal organ as a mating plug and sexual cannibalism. - Journal of Zoology 254: 449-459.

KNOFLACH, B.; VAN HARTEN A. 2002. The genus *Latrodectus* (Araneae: Theridiidae) from mainland Yemen, the Socotra Archipelago and adjacent countries. - Fauna of Arabia 19: 321-361.

KOKKO, H.; BROOKS, R., McNAMARA, J. M.; HOUSTON, A. I. 2002. The sexual selection continuum. - Proceedings of the Royal Society of London / B 269: 1331-1340.

KONIGSWALD, A.; LUBIN, Y.; WARD, D. 1990. The effectiveness of the nest of a desert widow spider, *Latrodectus revivensis*, in predator deterrence. - Psyche 97: 75-80.

KOVOOR, J. 1981. Une source probable de phéromone sexuelles: les glandes tégumentaires de la région genitale de femelles d' araignées. - Atti della Società Toscana di Scienze Naturali / Memorie / B / Supplement 88: 1-15.

KOVOOR, J.; LOPEZ, A.; EMERIT, M. 1981. Des glandes tégumentaires particuliéres aux famelles chez *Lepthyphantes sanctivincentii* et *Linyphia triangularis* (Araneae, Linyphiidae). - Atti della Società Toscana di Scienze Naturali / Memorie/ B / Supplement 88:53-60.

KRAFFT, B. 1982. The significance of communication in spiders. In: Spider communication. Mechanisms and ecological significance (eds. P. N. Witt & J. S. Rovner), pp. 13-66. Princeton University Press, Princeton.

KRISHNAKUMARAN, A. 1960. Observations on the cuticular lamellae in *Carcinoscorpius*. - Zoologischer Anzeiger 165: 412-417.

KURA, T.; YODA, K. 2001. Can voluntary nutritional gifts in seminal flow evolve? - Journal of Ethology 19: 9-15.

LAMORAL, B. H. 1973. On the morphology, anatomy, histology and function of the tarsal organ on the pedipalpi of *Palystes castaneus* (Sparassidae, Araneaidae). - Annals of the Natal Museum 21: 609-648.

LAURIA DE CIDRE, L. 1988. El sistema genital feminino en dos especies del genero *Latrodectus* (Araneae, Theridiidae). - Revista Brasileira Biologia 48: 771-776.

LEGENDRE, R. 1956. Localisation d'un organe olfactif non encore décrit chez les aranéides. - Comptes Rendus des Séances de l' Académie des Sciences 243: 1237-1240.

LEVI, H. W. 1959. The spider genus *Latrodectus* (Araneae, Theridiidae). - Transactions of the American Microscopical Society 78: 7-43.

LEVI, H. W. 1961. Evolutionary trends in the development of palpal sclerites in the spider family Theridiidae. - Journal of Morphology 108: 1-9.

LEVI, H. W. 1966. The three species of *Latrodectus* (Araneae), found in Israel. - Journal of Zoology 150: 427-432.

LEVI, H. W. 1968. The spider genera *Gea* and *Argiope* in America (Araneae: Araneidae). - Bulletin of the Museum of Comparative Zoology 136: 319-352.

LEVI, H. W. 1969. Problems in the reproductive physiology of the spider palpus. - Bulletin du Muséum National d'Histoire Naturelle / Supplement 1: 108-111.

LEVI, H. W. 1971a. The *diadematus* group of the orb-weavers genus *Araneus* north of Mexico (Araneae: Araneidae). - Bulletin of the Museum of Comparative Zoology 141: 131-179.

LEVI, H. W. 1971b. Observations on the reproductive physiology of the spiders *Singa* (Araneidae). Arachnologorum Congressus Internationalis V., Czechoslovakia 1971: 189-191.

LEVI, H. W. 1975. Mating behavior and presence of embolus cap in male araneidae. - Proceedings of the 6th International Arachnological Congress, Amsterdam 1974: 49-50.

LEVI, H. W. 1978. Orb-webs and phylogeny of orb-weavers. - Symposia of the Zoological Society of London 42: 1-15.

LEVI, H. W. 1983a. On the value of genitalic structures and coloration in separating species of widow spiders (*Latrodectus* sp.) (Arachnida: Araneae: Theridiidae). - Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg 26: 195-200.

LEVI, H. W. 1983b. The orb-weaver genera *Argiope*, *Gea* and *Neogea* from the Western Pacific region (Araneae: Araneidae, Argiopinae). - Bulletin of the Museum of Comparative Zoology 150: 247-338.

LEVI, H. W. 1991. The neotropical and mexican species of the orb-weaver genera *Araneus*, *Dubiepeira*, and *Aculepeira* (Araneae: Araneidae). - Bulletin of the Museum of Comparative Zoology 152: 167-315.

LEVY, G. 1998. Fauna Palaestina. Arachnida III. Araneae: Theridiidae. The Israel Academy of Sciences and Humanities, Jerusalem.

LEVY, G.; AMITAI, P. 1983. Revision of the black widow-spider genus *Latrodectus* (Araneae: Theridiidae) in Israel. - Zoological Journal of the Linnean Society 77: 39-63.

LEWONTIN, R. C. 1966. On the measurement of relative variability. - Systematic Zoology 15: 141-142.

LOCKE, M. 1961. Pore canals and related structures in insect cuticle. - The Journal of Biophysical and Biochemical Cytology 10: 589-618.

LOCKE, M.; HUIE, F. 1980. Ultrastructure methods in cuticle research. In: cuticle techniques in arthropods (ed. T. A. Miller), pp. 91-144. Springer-Verlag, Berlin.

LOCKET, G. H.; MILLIDGE, A. F. 1953. British spiders, Vol. 2. Ray Society, London.

LOEHLE, C. 1997. The pathogen transmission avoidance theory of sexual selection. - Ecological Modelling 103: 231-250.

LOPEZ, A. 1987. Glandular aspects of sexual biology. In: Ecophysiology of spiders (ed. W. Nentwig), pp. 121-132. Springer-Verlag, Berlin.

LOPEZ, A.; JUBERTHIE-JUPEAU, L. 1983. Structure et ultrastructure de la spermathèque chez *Telema tenella* Simon (Araneae, Telemidae). - Mémoires de Biospéologie 10: 413-418.

LOPEZ, A.; JUBERTHIE-JUPEAU, L. 1985. Utrastructure comparée du tube séminifère chez les mâles d' araignées. Mémoires de Biospéologie 12: 97-109.

LUBIN, Y. D. 1974. Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). - Zoological Journal of the Linnean Society 54: 321-339.

LUBIN, Y.; KOTZMAN, M.; ELLNER, S. 1991. Ontogenetic and seasonal changes in webs and websites of a desert widow spider. - Journal of Arachnology 19: 40-48.

MACKAY, I. R. 1972. A new species of widow spider (Genus *Latrodectus*) from Southern Africa (Araneae: Theridiidae). - Psyche 79: 236-242.

MARTINDALE, C. B.; NEWLANDS. G 1982. The widow spiders: A complex of species. - South African Journal of Science 78: 78-79.

MASCORD, R. E. 1967. The mating behavior of *Gasteracantha minax* Thorell, 1859 (Araneidae: Argiopidae). - Journal of the Entomological Society of Australia 3: 44-47.

MASUMOTO, T. 1993. The effect of the copulatory plug in the funnel-web spider *Agelena limbata* (Araneae: Agelenidae). - Journal of Arachnology 21: 55-59.

McCRONE, J. D.; LEVI, H.W. 1964. North american widow spiders of the *Latrodectus curacaviensis* group (Araneae:Theridiidae). - Psyche 71: 12-27.

McKEOWN, K. C. 1952. Australian spiders, their lives and habits. Angus and Robertson, Sidney & London.

MIYASHITA, T.; HAYASHI, H. 1996. Volatile chemical cue elicits mating behavior of cohabiting males of *Nephila clavata* (Araneae, Tetragnathidae). - Journal of Arachnology 24: 9-15.

MONTGOMERY, T. H. 1903. Studies on the habits of spiders, particularly those of the mating period. - Proceedings of the Academy of Natural Sciences of Philadelphia 55: 59-149.

MÜLLER, G. H. 1985. Abgebrochene Emboli in der Vulva der 'Schwarzen Witwe' *Latrodectus geometricus* C. L. Koch 1841 (Arachnida: Araneae: Theridiidae). - Entomologische Zeitschrift 95: 27-30.

MUMA, M. H. 1971. Biological and behavioral notes on *Gasteracantha cancriformes* (Arachnida: Araneidae) - Florida Entomologist 54: 345-351.

MUMA; M. H.; STONE, K. J. 1965. Activation of spider spermatozoa. - Entomological News 76: 177-178.

MUNIAPPAN, R.; CHADA, H. L. 1970. Biology of the crab spider, *Misumenops celer*. - Annals of the Entomological Society of America 63: 1718-1722.

NEWMAN, J. A.; ELGAR, M. A. 1991. Sexual cannibalism in orb-weaving spiders: an economic model. - American Naturalist 138: 372-1395.

NEVILLE, A. C. 1975. Biology of the arthropod cuticle. Springer-Verlag, Berlin.

NEVILLE, A. C. 1984. Cuticle : Organization. In: Biology of the integument. I Invertebrates. (eds. J. Bereiter-Hahn, A. G. Matoltsy & K. S. Richards), pp. 611-625. Springer-Verlag, Berlin.

NEVILLE, A. C.; THOMAS, M. G.; ZELAZNY, B. 1969. Pore canal shape related to molecular architecture of arthropod cuticle. - Tissue and Cell 1: 183-200.

NITZSCHE, R. 1999. Das Brautgeschenk der Spinne. *Pisaura mirabilis* (Clerck, 1757) (Pisauridae). Nitzsche, Kaiserslautern.

NOIROT, C.; QUENNEDEY, A. 1974. Fine structure of insect epidermal glands. - Annual Review of Entomology 19: 61-80.

NOIROT, C.; QUENNEDEY, A. 1991. Glands, gland cells, glandular units: Some comments on terminology and classification. - Annales de la Société Entomologique de France 27: 123-128.

ODHIAMBO, T. R. 1969. The architecture of the accessory reproductive glands of the male desert locust 2: Microtubular structures. - Tissue and Cell 1: 325-340.

OSTERLOH, A. 1922. Beitraege zur Kenntnis des Kopulationsapparates einiger Spinnen. - Zeitschrift für Wissenschaftliche Zoologie. 119: 326-421.

PATEL, B. H.; BRADOO,B. L 1983. Observations on sperm induction, courtship and mating behavior of *Uloborus ferokus* Bradoo (Araneae: Uloboridae). In: Proceedings of the 9th International Congress of Arachnology, Panama 1983 (eds. Eberhard. W. G., Lubin, Y. D. & Robinson, B.C.), pp. 181-191. Smithsonian Institution Press, Washington & London.

PAPKE, M. D. 2000. Isolierung, Identifizierung und Synthese von Signalstoffen aus Spinnen. Dissertation, Universität Hamburg. http://www.chemie.uni-hamburg.de/bibliothek/diss2000.html

PAPKE, M. D.; RIECHERT, S. E.; SCHULZ, S. 2001. An airborne pheromone associated with male attraction and courtship in a desert spider. - Animal Behaviour 61: 877-886.

PAPKE, M.; SCHULZ, S.; TICHY, H.; GINGL, E.; EHN, R. 2000. Identification of a new sex pheromone from the silk dragline of the tropical wandering spider *Cupiennius salei*. - Angewandte Chemie 39: 4339-4341.

PARRI, S.; ALATALO, R. V.; KOTIAHO,J.; MAPPES, J. 1997. Female choice for male drumming in the wolf spider *Hygrolycosa rubrofasciata*. - Animal Behaviour 53: 305-312.

PARKER, G. A. 1970. Sperm competition and its evolutionary consequences in the insects. - Biological Reviews 45: 525-567.

PARKER, G. A. 1979. Sexual selection and sexual conflict. In: Sexual selection and reproductive competition in insects (eds. M. S. Blum & N. A. Blum), pp. 123-166. Academic Press, New York.

PARKER, G. A. 1983. Mate quality and mating decisions. In: Mate choice (ed. P. Bateson), pp. 141-166. Cambridge University Press, Cambridge.

PECKHAM, G. W. ; PECKHAM, E. G. 1889. Observations on sexual selection in spiders of the family Attidae. - Occasional Papers of the Natural History Society of Wisconsin 1: 1-60.

PETERS, W.; PFREUNDT, C. 1985. Die Verteilung von Trichobothrien und lyraförmigen Organen an den Laufbeinen von Spinnen mit unterschiedlicher Lebensweise. - Zoologische Beiträge 29: 209-225.

PLATNICK, N. 1971. The evolution of courtship behaviour in spiders. - Bulletin of the British Arachnological Society 2: 40-47.

POMIANKOWSKI, A.; MØLLER, A. P. 1995. A resolution of the lek paradox. - Proceedings of the Royal Society of London / B 260: 21-29.

PRENTER, J.; ELWOOD, R. W.; COLGAN, S. 1994a. The influence of prey size and female reproductive state on the courtship of the autumn spider, *Metellina segmentata*: a field experiment. - Animal Behaviour 47: 449-456.

PRENTER, J.; ELWOOD, R. W.; MONTGOMERY, W. I. 1994b. Male exploitation of female predatory behaviour reduces sexual cannibalism in male autumn spiders, *Metellina segmentata*. - Animal Behaviour 47: 235-236.

PRENTER, J.; ELWOOD, R. W.; MONTGOMERY, W. I. 1994c. Assessement and decisions making in *Metellina segmentata* (Araneae: Metidae): evidence of a pheromone involved in mate guarding. - Behavioral Ecology and Sociobiology 35: 39-43.

PRENTER, J.; MONTGOMERY, W. I.; ELWOOD, R. W. 1995a. 'Leg licking' and grooming during assessment behviour in *Metellina segmentata* (Clerck, 1757). - Newsletter of the British Arachnological Society 71: 6.

PRENTER, J.; MONTGOMERY, W, I.; ELWOOD, R. W. 1995b. Multivariate morphometrics and sexual dimorphism in the orb-web spider *Metellina segmentata* (Clerck, 1757) (Araneae, Metidae). - Biological Journal of the Linnean Society 55: 345-354.

POLLARD, S. D.; MACNAB, A. M., JACKSON, R. R. 1987. Communication with chemicals: Pheromones and spiders. In: Ecophysiology of spiders (ed. W. Nentwig), pp. 133-141. Springer-Verlag, Berlin.

REYNOLDS, E. 1963. The use of lead citrate at high pH as an electron-opaque stain in electron microscopy. - Journal of Cell Biology 17: 208-212.

RIVERA, M. J. 1901. Apareamiento del *Latrodects formidabilis*. - Actes de la Société Scientifique du Chili 11: 1-19.

ROBINSON, M. H. 1982. Courtship and mating behavior in spiders. - Annual Review of Entomology 27: 1-20.

ROBINSON, M. H.; LUBIN, Y. D. 1979. Specialists and generalists: The ecology and behavior of some web-building spiders from Papua New Guinea. II *Psechrus arge*ntatus and *Fecenia* sp. (Araneae: Psechridae). - Pacifics Insects Monographs 21: 133-164.

ROBINSON, M. H.; ROBINSON, B. 1973. Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. - Smithsonian Contributions of Zoology 149 : 1-76.

ROBINSON, M. H.; ROBINSON, B. 1976. The ecology and behavior of *Nephila maculata*: A supplement. - Smithsonian Contributions of Zoology 218 : 1 -22.

ROBINSON, M. H.; ROBINSON, B. 1978a. The evolution of courtship systems in tropical araneid spiders. - Symposia of the Zoological Society of London 42: 17-29.

ROBINSON, M. H.; ROBINSON, B. 1980. Comparative studies of the courtship and mating behavior of tropical araneid spiders. - Pacific Insects Monographs 36:1-218.

ROSE, H. W. 1990. Struktur und Funtionsmorphologie des männlichen Pedipalpus von *Pholcus phalangioides* (Archnida: Araneae: Pholcidae). Diplomarbeit, Universität Tübingen.

ROSS, K.; SMITH, R. L. 1979. Aspects of the courtship behavior of the black widow spider, *Latrodectus hesperus* (Araneae: Theridiidae), with evidence for the existence of a contact sex pheromone. - Journal of Arachnology 7: 69-77.

ROSS, J.; RICHMAN, D. B.; MANSOUR, F.; TRAMBARULO, A.; WHITCOMB, W. H. 1982. The life cycle of *Heteropoda venatoria* (Linnaeus) (Araneae: Heteropididae). - Psyche 89: 297-306.

ROVNER, J. S. 1968. Territoriality in the sheetweb spider, *Linyphia triangularis* (Clerck) (Araneidae, Linyphiidae). Zeitschrift für Tierpsychologie 7: 69-77.

ROVNER, J. S. 1972. Copulation in the lycosid spider (*Lycosa rabida* Walckenaer): A quantitative study. - Animal Behaviour 20: 133-138.

RUBENSTEIN, D. I. 1987. Alternative reproductive tactics in the spider *Meta segmentata*. - Behavioral Ecology and Sociobiology 20: 229-237.

SASAKI, T.; IWAHASHI, O. 1995. Sexual cannibalism in an orb-weaving spider *Argiope aemula*. - Animal Behaviour 49: 1119-1121.

SCHMIDT, G. 1990. Courtship behaviour, copulation and crossing experiments in *Latrodectus* species (Araneida: Theridiidae). - Acta zoologia Fennica 190: 351-355.

SCHMIDT, G. 1991. Further crossing experiments in *Latrodectus* species (Araneida: Theridiidae). - Bulletin Sociéte Neuchâteloise des Sciences Naturelles 116: 215-222.

SCHNEIDER, J. M.; ELGAR, M. A. 1998. Spiders hedge genetic bets. - Trends in Ecology and Evolution 13: 218-219.

SCHNEIDER, J. M.; ELGAR, M. A. 2001. Sexual cannibalism and sperm competition in the golden orb-web spider *Nephila plumipes* (Araneoidea. female and male perspectives. - Behavioral Ecology 12: 547-552.

SCHNEIDER, J. M.; ELGAR, M. A. 2002. Sexual cannibalism in *Nephila plumipes* as a consequence of female life history strategies. - Journal of Evolutionary Biology 15: 84-91.

SCHNEIDER, J. M.; HERBERSTEIN, M. E.; DE CRESPIGNY, F. C.; RAMAMURTHY, S. 2000. Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. - Journal of Evolutionary Biology 13: 939-946.

SCHNEIDER, J. M.; LUBIN,Y. 1998. Intersexual conflict in spiders. – Oikos 83: 496-505.

SCHNEIDER, J. M.; THOMAS, M. L.; ELGAR, M. A. 2001. Ectomised conductors in the golden orb-web spider, *Nephila plumipes* (Araneoidea): a male adaption to sexual conflict. - Behavioral Ecology and Sociobiology 49: 410-415.

SCHULT, J.; SELLENSCHLO, U. 1983. Morphologie und Funtion der Genitalstrukturen bei *Nephila* (Arach., Aran., Araneidae). - Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut 80: 221-230.

SCHULZ, S.; TOFT, S. 1993. Identification of a sex pheromone from a spider. - Science 260: 1635-1637.

SEGEV, O. 1998. Sperm competition and male mating strategies in the widow spider, *Latrodectus revivensis*. Poster abstract. XIV International Congress of Arachnology 1998, Chicago. http://www.arachnology.org/ISA/meetings/1998ISAabs.htm

SEITZ, K. A. 1972a. Zur Histologie und Feinstruktur des Herzens und der Hämocyten von *Cupiennius salei* Keys. (Araneae, Ctenidae). I. Herzwandung. Bildung und Differenzierung der Hämocyten. - Zoologische Jahrbücher / Abteilung für Anatomie und Ontogenie der Tiere 89: 351-384.

SEITZ, K. A. 1972b. Zur Histologie und Feinstruktur des Herzens und der Hämocyten von *Cupiennius salei* Keys. (Araneae, Ctenidae). II. Zur Funktionsmorphologie der Phagocyten. - Zoologische Jahrbücher / Abteilung für Anatomie und Ontogenie der Tiere 89: 385-397.

SEWELL, M. T. 1951. Pore canals in a spider cuticle. - Nature 167: 857-858.

SHERMAN, R. G. 1973. Ultrastructurally different hemocytes in a spider. - Canadian Journal of Zoology 51: 1155-1159.

SHERMAN, R. G. 1981. Chelicerates. In: Invertebrate blood cells. Volume II (eds. N. A. Ratcliffe & A. F. Rowley), pp. 355-384. Academic Press, London.

SHULOV, A. 1940. On the biology of two *Latrodectus* spiders in Palestine. - Proceedings of the Linnean Society of London 152: 309-328.

SHULOV, A. 1948. *Latrodectus revivensis* sp. nov. from Palestine. - Ecology 29: 209-215.

SHULOV, A.; WEISSMAN, A. 1959. Notes on the life habits and potency of the venom of three *Latrodectus* spider species of Israel. - Ecology 40: 515-518.

SIMMONS, L. W. 2001. Sperm competition and its evolutionary consequences in the insects. Princeton University Press, Princeton.

SMITH, R. J. 1980. Rethinking allometry. - Journal of Theoretical Biology 87: 97-111.

SMITH, R. L. 1984. Sperm competition and the evolution of animal mating systems. Academic Press, New York.

SMITHERS, R. H. N. 1944. Contributions to our knowledge of the genus *Latrodectus* (Aranaeae) in South Africa. - Annals of the South African Museum 36: 263-312.

SOFTLY, A.; FREETH, G. E. 1970. The laboratory maintenance of *Latrodectus mactans*. - Journal of the Institute of Animal Technicians 21: 117-126.

SPENCE, J. R.; ZIMMERMANN, M.; WOJCICKI, J. P. 1996. Effects of foof limitation and sexual cannibalism on reproductive output of the nursery web spider *Dolomedes triton* (Araneae: Pisauridae). - Oikos 75:373-382.

SPURR, A. R. 1969. A low-viscosity epoxy resin embedding medium for electron microscopy. - Journal of Ultarstructure Research 26: 31-43.

STOCKLEY, P. 1997. Sexual conflict resulting from adaptations to sperm competition. - Trends in Ecology and Evolution 12: 154-159.

STRAND, E. 1906. Studien über den Bau und die Entwicklung der Spinnen. I. Über die Geschlechtsorgane von *Agelena labyrinthica* (L.). - Zeitschrift für Wissenschaftliche Zoologie 80: 515-543.

STRAND, E. (1920). Indoaustralische, papuanische und polynesische Spinnen des Senckenbergischen Museums. - Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 36: 179-274.

STUMPF, H.; LINSENMAIR, K. E. 1996. Observations on the mating systems of two spiders, *Linyphia hortensis* Sund. and *L. triangularis* (Cl.) (Linyphiidae: Araneae). - Revue Suisse de Zoologie hors série: 627-634.

SUHM, M.; ALBERTI, G. 1993. The fine structure of the spermatheca of *Amaurobius fenestralis* (Stroem, 1768) (Amaurobiidae, Araneae). - Bolletino dell' Academia Gioenia di Scienze Naturali 26: 343-353.

SUHM, M., THALER, K.; ALBERTI, G. 1996. Glands in the male palpal organ and the origin of the mating plug in *Amaurobius* species (Araneae: Amaurobiidae). Zoologischer Anzeiger 234: 191-199.

SZLEP, R. 1964. The web-spinning process and web-structure of *Latrodectus tredecimguttatus*, *L. pallidus* and *L. revivensis*. - Proceedings of the Zoological Society of London 145: 75-89.

TELFORD, S. R.; JENNIONS, M. D. 1998. Establishing cryptic female choice in animals. – Trends in Ecology and Evolution 13: 216-218.

TIETJEN, W. J.; ROVNER, J. S. 1982. Chemical communication in Lycosids and other spiders. In: Spider communication. Mechanisms and ecological significance (eds. P. N. Witt & J. S. Rovner), pp. 249-280. Princeton University Press, Princeton.

TINBERGEN, N. 1954. The origin and evolution of courtship and threat display. In: Evolution as a process (eds. Huxley J., Hardy A. C. & Ford E. B.), pp 233-250. Allen and Unwin, London.

THORNHILL, R.; ALCOCK, J. 1983. The evolution of insect mating systems. Harvard University Press, Cambridge.

TOFT, S. 1989. Mate guarding in two *Linyphia* species (Araneae: Linyphiidae). - Bulletin of the British Arachnological Society 8: 33-37.

TREGENZA, T.; WEDELL, N. 2002. Polyandrous females avoid costs of inbreeding. - Nature 415: 71-73.

TRIVERS, R. L. 1972. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man, 1871-1971 (ed. B. Campbell), pp. 136-172. Aldine-Atherton, Chicago.

UHL, G. 1990. Spermienspeicherung bei weiblichen Zitterspinnen (*Pholcus phalangioides* Fuesslin: Araneae). Diplomarbeit, Universität Freiburg.

UHL, G. 1994a. Genital morphology and sperm storage in *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae; Araneae). - Acta Zoologica 75: 1-12.

UHL, G. 1994b. Ultrastructure of the accessory glands in female genitalia of *Pholcus phalangioides* (Fuesslin, 1775) (Pholcidae; Araneae). - Acta Zoologica 75: 13-25.

UHL, G. 1996. Sperm storage secretion of female cellar spiders (*Pholcus phalangioides*; Araneae): a gel-electrophoretic analysis. - Journal of Zoology 240: 153-161.

UHL, G. 2000. Two distinctly sperm storage organs in female *Dysdera erythrina* (Araneae: Dysderidae). - Arthropod Structure & Development 29: 163-169.

UHL, G. 2002. Female genital morphology and sperm priority patterns in spiders (Araneae). In: European Arachnology 2000 (eds. S. Toft & N. Scharff), pp. 145-156. Aarhus University Press, Aarhus.

UHL, G.; VOLLRATH, F.1998a. Little evidence for size-selective sexual cannibalism in two species of *Nephila* (Araneae). - Zoology 101: 101-106.

UHL, G.; VOLLRATH, F.1998b. Genital morphology of *Nephila edulis*: implications for sperm competition in spiders. - Canadian Journal of Zoology 76: 39-47.

UHL, G.; VOLLRATH, F. 2000. Extreme body size variability in the golden silk spider (*Nephila edulis*) does not extend to genitalia. - Journal of Zoology 251: 7-14.

VILLAVASO, E. 1975. Functions of the spermathecal muscle of the boll weevil, *Athonomus grandis*. - Journal of Insect Physiology 21: 1275-1278.

VOLLRATH, F. 1980. Why are some males small? A discussion including observations on *Nephila clavipes*. In: Verhandlungen des 8. Internationalen Arachnologen Congress, Wien 1980 (ed. J. Gruber), pp. 165-169. H. Engermann, Wien.

VOLLRATH, F.; PARKER, G. A. 1992. Sexual dimorphism and distorted sex ratio in spiders. - Nature 360: 156-158.

WATSON, P. J. 1986. Transmission of females sex pheromones thwarted by males in the spider *Linyphia litigiosa* (Linyphiidae). - Science 233: 219-221.

WATSON, P. J. 1991. Multiple paternity as genetic bet-hedging in female sierra dome spiders, *Linyphia litigiosa* (Linyphiidae). - Animal Behaviour 41: 343-360.

WATSON, P. J. 1998. Multi-male mating and female choice increase offspring growth in the spider *Neriene litigiosa* (Linyphiidae). - Animal Behaviour 55: 387-403.

WHITCOMB, W. H., EASON, R. 1965. The mating behavior of *Peucetia viridans* (Araneida: Oxyopidae). - Florida Entomologist 48: 163-167.

WHITEHEAD, W. F.; REMPEL, J. G. 1959. A study of the musculature of the black widow spider, *Latrodectus mactans* (Fabr.). - Canadian Journal of Zoology 37: 831-870.

WHITEHOUSE, M. E. A. 1991. To mate or fight? Male-male competition and alternative mating strategies in *Argyrodes antipodiana* (Theridiidae, Araneae). - Behavioral Processes 23: 163-172.

WIEHLE, H. 1961. Der Embolus des männlichen Spinnentasters. - Zoologischer Anzeiger / Supplement 24: 457-480.

WIEHLE, H. 1967a. Steckengebliebene Emboli in den Vulven von Spinnen (Arach., Araneae). - Senckenbergiana 48: 197-202.

WIEHLE, H. 1967b. *Meta*, - eine semientelegyne Gattung der Araneae. - Senckenbergiana 48: 183-196.

WILEY, R. H.; POSTON, J. 1996. Indirect mate choice, competition for mates, and coevolution of the sexes. - Evolution 50: 1271-1381.

WISE, D. H. 1979. Effects of an experimental increase in prey abundance upon the reproductive rates of two orb-weaving spider species (Araneae: Araneidae). - Oecologia 41: 289-300.

YASUI, Y. 1998. The 'genetic benefits' of female multiple mating reconsidered. - Trends in Ecology and Evolution 13: 246-250.

YOWARD, P.; OXFORD, G. 1997. Single palp usage during copulation in spiders. - Newsletter of the British arachnological Society 77: 8-9.

ZAHAVI, A. 1975. Mate selection - a selection for a handicap. - Journal of Theoretical Biology 53: 205-214.

ZEH, J. A.; ZEH, D. W. 1996. The evolution of polyandry I: intragenomic conflict and genetic incompatibility. - Proceedings of the Royal Society of London / B 263: 1711-1717.

ZEH, J. A.; ZEH, D. W. 1997. The evolution of polyandry II: post-copulatory defenses against genetic incompatibility. - Proceedings of the Royal Society of London / B 264: 69-75.

ZEH, J. A.; ZEH, D. W. 2001. Review: Reproductive mode and the genetic benefits of polyandry. - Animal Behaviour 61: 1051-1063.

7. Figures

7. 1. Abbreviations

al	anterior lobe
at	atrium
ax	axon
bi	basal infoldings
bm	basement membrane
bw	bridge web
c	cuticle
C1	secretory canal cell 1
C2	secretory canal cell 2
cd	copulatory duct
cf	common fertilisation duct
ch	chemoreceptive hair
cl	chelicera
co	cone
cw	catching web
cy	cymbium
d	dictyosome
du	ductule
dd	dorsal anterior dilator
E	envelope cell
ed	endothel
ef	epigastric furrow
ej	ejaculatory duct
em	embolus
en	endocuticle
ep	epigynal plate
ex	exocuticle
f	fundus
fa	fang
fi	filaments
fu	funnel
G1	gland cell 1
gl	glia cell
go	gonopore
he	hemolymph
I	intercalary cell
I/E	intercalary or envelope cell
la	labium
ly	lysosom
m	mitochondrium
me	mesocuticle
mu	muscle fibres
mp	middle portion
mt	microtubuli
mv	microvilli
mx	maxilla
n	nucleus
nC1	nucleus of secretory canal cell 1
nE	nucleus of envelope cell
nG1	nucleus of gland cell 1
nI	nucleus of intercalary cell
nI/E	nucleus of intercalary or envelope cell
no	nucleolus
pc	pore canal
pl	posterior lobe
pp	*pars pendula*
r	reservoir
rer	rough endoplasmic reticulum
s	spermatozoon/a
sb	serrated bristle
se	secretion
sf	small fertilisation duct
sl	slit sense organ
sp	spermatheca
spe	spermathecal epithelium
spl	spermathecal lumen
t	embolus tip
ta	tarsal organ
tc	tacticle hair
ti	tibia
tr	trichobothrium
tu	truncus
vd	ventral anterior dilator
ue	uterus externus
ui	uterus internus
v	vesicle
ve	vessel
vt	vertical threads

7. 2. Figures

Fig. 1a Schematic drawing of the web of *Latrodectus revivensis* (modified after Konigswald *et al*. 1990). The retreat is situated on the shrub and consists of a cone-like upper part and the slightly curved funnel. The bridge web connects the retreat to the catching web. At their last 2 - 5 cm the vertical capture threads are covered with viscid droplets.

Fig. 1b Web of female *L. revivensis* built in a glass aquarium provided with wooden branches.

Fig. 1c The cone-like part of the retreat is covered with plant material, snail shells and carcasses of victims. The female inside the retreat guards an egg sac.

Fig. 1d The funnel represents a transparent network.

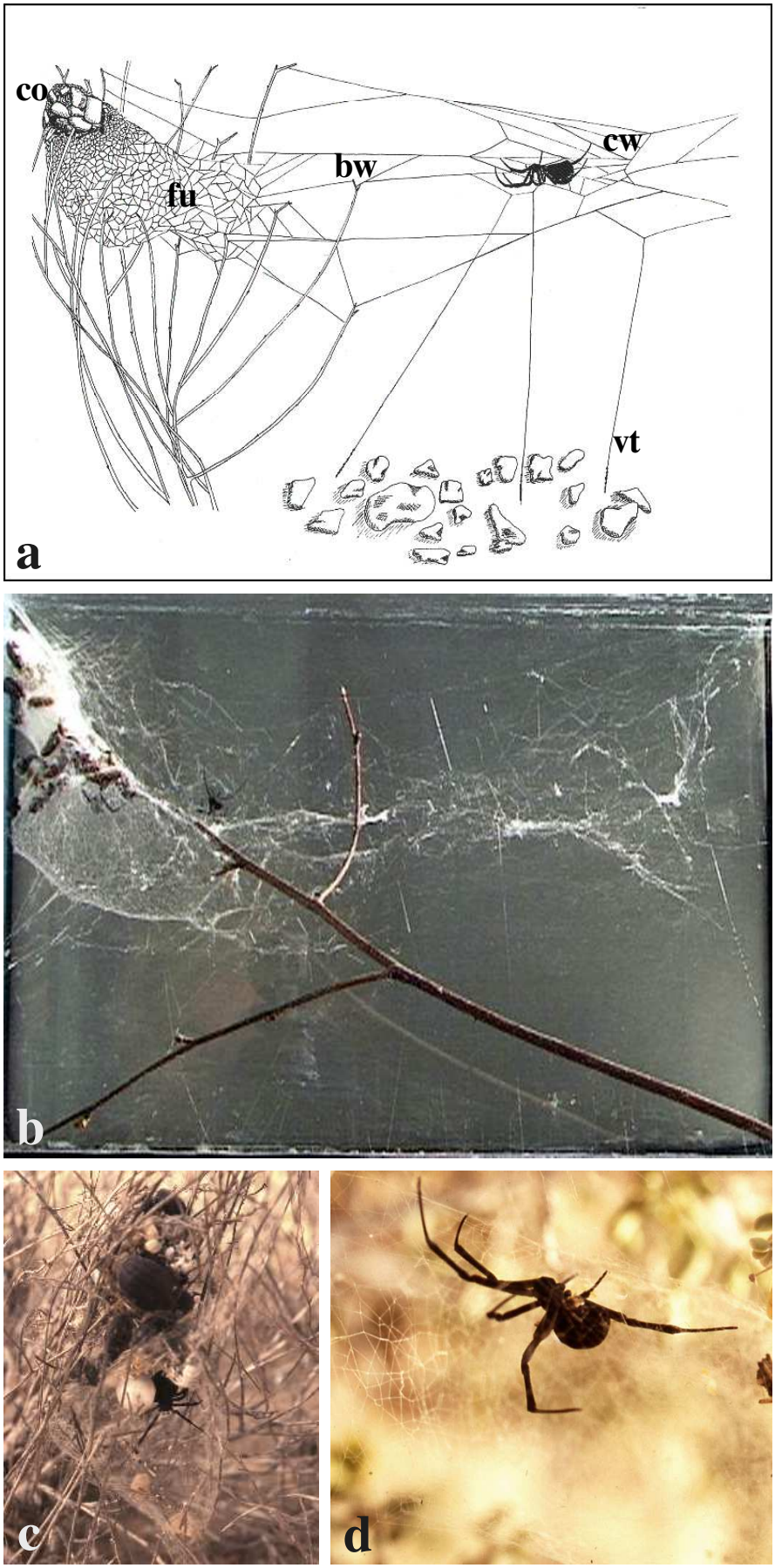

co
fu
bw
cw
vt
a
b
c
d

Fig. 2a Adult female *Latrodectus revivensis* (ventral view). The large, sub-spherical opisthosoma has a light, more or less triangular marking behind the epigastric furrow. Scale bar: 5 mm.

Fig. 2b The epigynum (lateral view) is an arched and heavily sclerotised plate located in front of the epigastric furrow (arrow). Scale bar: 500 µm.

Fig. 2c Tactile hairs (arrows) are suspended in sockets in the relatively thick cuticle of the epigynal plate. The epidermis underlying the fluid-filled extra-cellular space of the tactile hair contains large amounts of crystalline deposits (black asterisk). The adjacent cuboidal cells are filled with pigment granules (white asterisk). Scale bar: 20 µm.

Fig. 2d Epigynal plate (ventral view). The posterior margin of the nearly triangular opening of the atrium is curved slightly backwards forming a carina (arrow heads). Scale bar: 200 µm.

Fig. 2e Epigynal plate cut medially (ventral view). The posterior margin of the atrial opening is curved slightly backwards, forming a carina (arrow head). Tactile hairs (tc) overhang the opening of the atrium. Scale bar: 50 µm.

Fig. 2f Female epigynum (dorsal view). The paired spermathecae lie with their axes forming an angle of about 45° to each other. Each copulatory ducts entwines the spermatheca. After four coils (1 - 4) in a posteriolateral direction, each duct makes a sharp turn back towards the spermatheca. Scale bar: 200 µm.

Fig. 2g Cleared epigynum (dorsal view) with slightly sclerotised copulatory ducts. Scale bar: 200 µm.

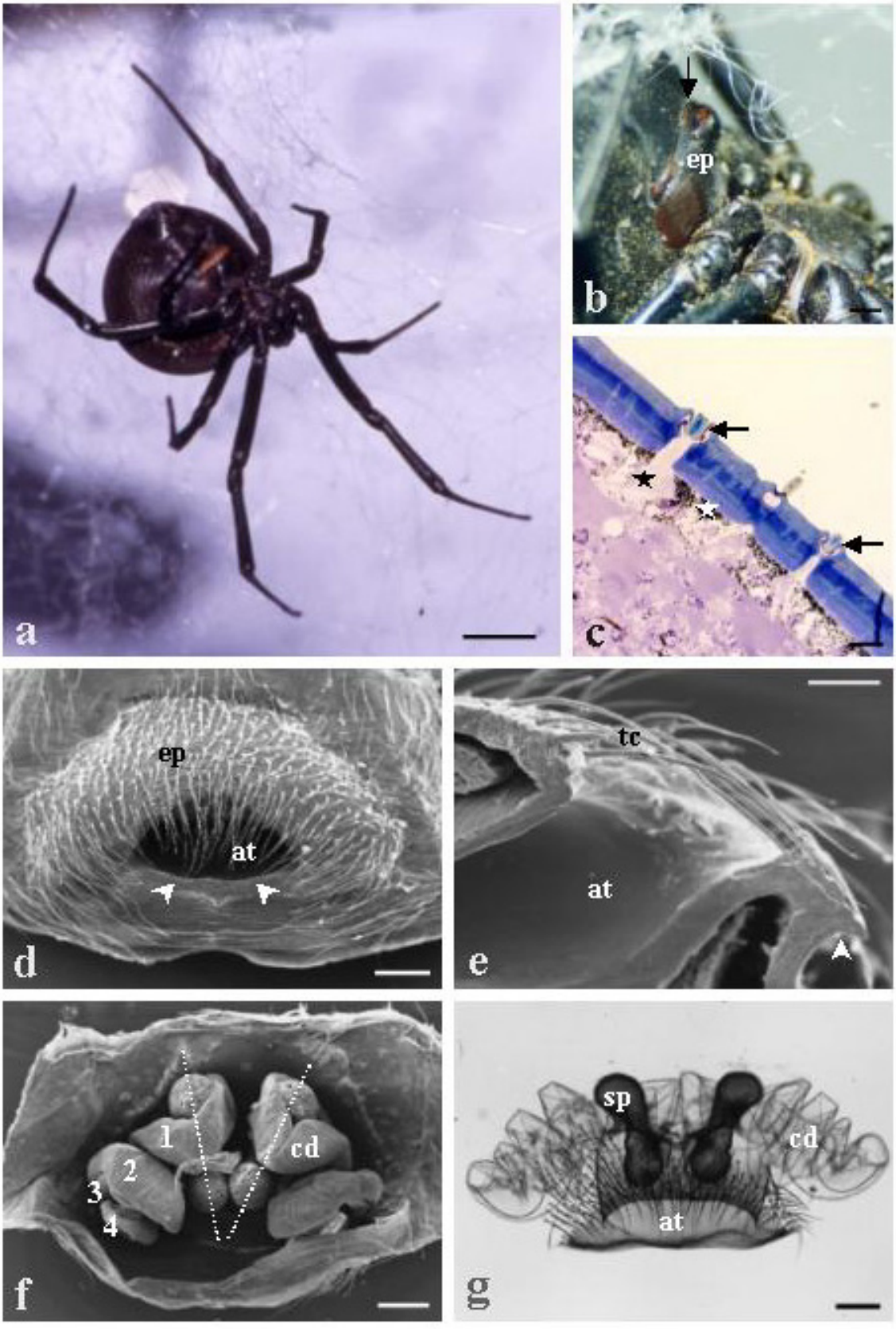

a
b
ep
c
d
ep
at
e
tc
at
f
1
2
3
4
cd
g
sp
cd
at

Fig. 3a Right spermatheca (medial view). The dumb-bell-shaped spermatheca comprises an anterior lobe (al), a middle portion (mp) and a posterior lobe (pl). Scale bar: 100 µm.

Fig. 3b Left spermatheca (medial view). A male embolus tip (t) is lodged inside the opening. Scale bar: 100 µm.

Fig. 3c The virgin female's spermatheca (cut medially) is completely filled with secretion (asterisk). Scale bar: 100 µm.

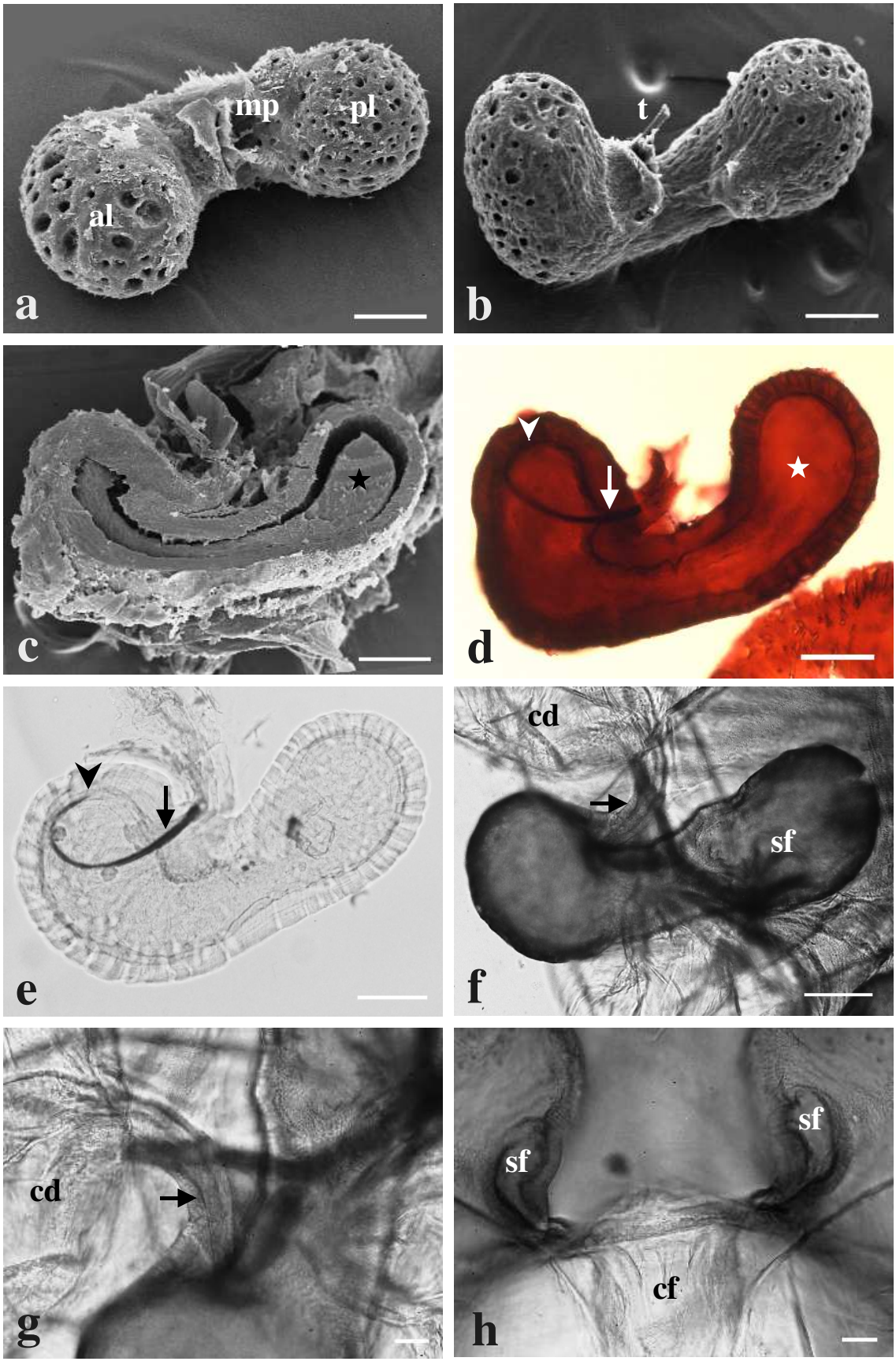
Fig. 3d The mated female's spermatheca (cut medially) is completely filled with spermatozoa stained red with Orcein (asterisk). The opening of the embolus tip that is lodged in the narrow spermathecal opening (arrow) rests at the most anterior wall of the spermatheca (arrow head). Scale bar: 100 µm.

Fig. 3e Cleared spermatheca (medial view) with a male embolus tip in the narrow opening (arrow). The opening of the pointed end of the embolus tip rests at the most anterior wall of the spermatheca (arrow head). Scale bar: 100 µm.

Fig. 3f Cleared spermatheca (medial view). Close to the spermatheca the flat copulatory duct forms a heavily-sclerotised tube (arrow). Scale bar: 100 µm.

Fig. 3g Cleared spermatheca. A narrow tube is formed by the end part of the copulatory duct (arrow). Scale bar: 50 µm.

Fig. 3h Cleared spermatheca. The funnel-shaped small fertilisation ducts originate from the apical, lateral wall of the posterior lobe. They slightly bend anterior finally fusing with the common fertilisation duct. Scale bar: 50 µm.


mp
pl
al
a
t
b
c
d
e
cd
sf
f
cd
g
sf
sf
cf
h

Figs. 4a-f Serial sections (LM) of a virgin female epigynum starting from the posterior. The squares refer to the corresponding figures showing details.

Fig. 4a The cave-like atrium (at) is covered by a smooth cuticle. Scale bar: 100 µm.

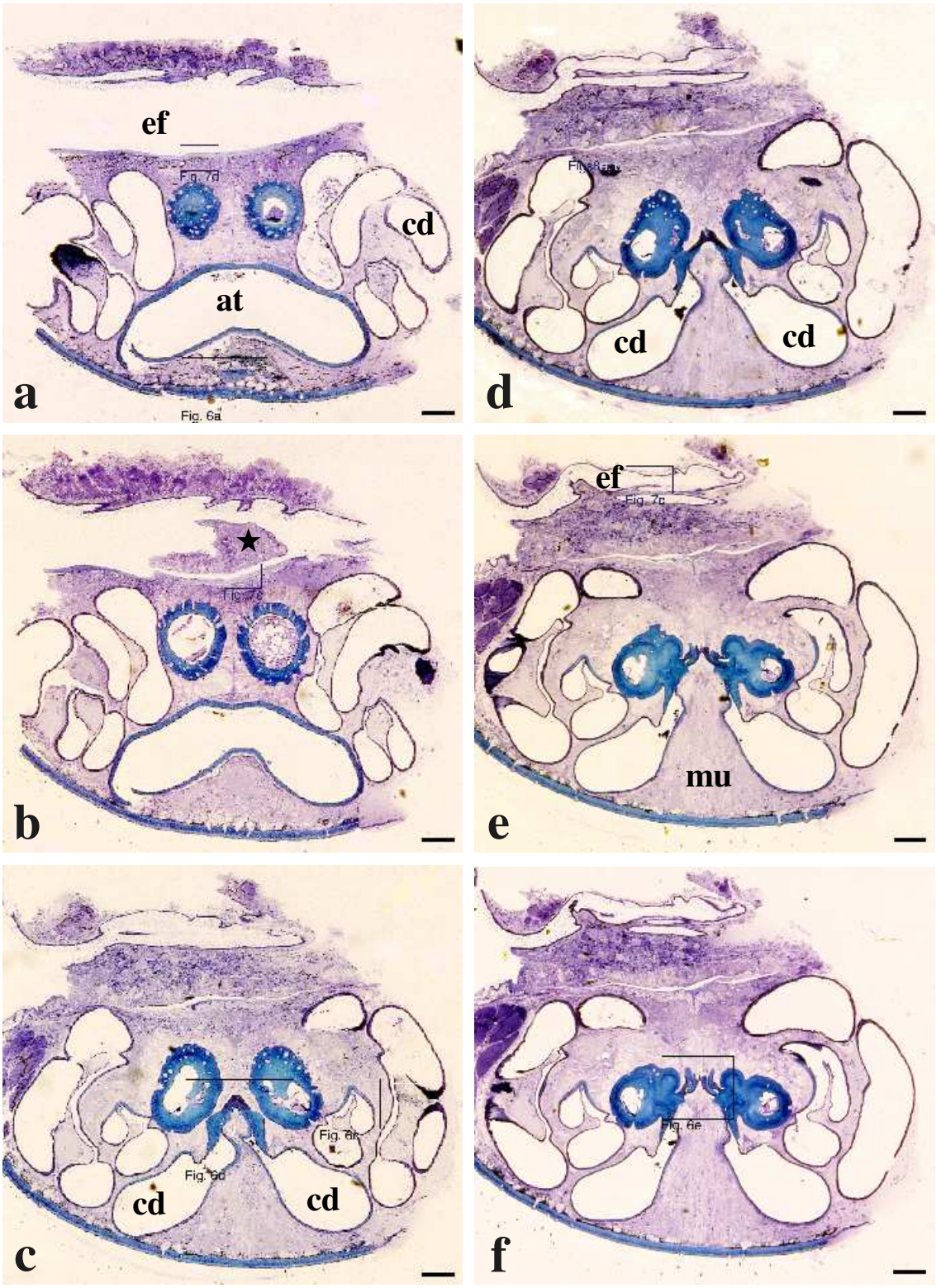
Fig. 4b The most posterior part of the dorsal wall of the uterus externus forms a tongue-like protrusion (asterisk). Scale bar: 100 µm.

Fig. 4c The ventral wall of the atrium bends upwards, forming a cone-shaped protuberance fitting into the pit created by the dorsal wall. Scale bar: 100 µm.

Fig. 4d The two lumina created by the median separation represent the beginning of the paired copulatory ducts (cd). Scale bar: 100 µm.

Fig. 4e Muscle fibres (mu) extend from the ventral side of the common fertilisation duct to the epigynal plate. Scale bar: 100 µm.

Fig. 4f The dorsal wall of the common fertilisation duct is heavily sclerotised (see Fig. 6e). Scale bar: 100 µm.


ef
cd
at
a
Fig. 6a
cd
cd
d
★
b
ef
mu
e
Fig. 6d
cd
cd
c
f

Figs. 5a-f Serial sections (LM) of a virgin female epigynum from the middle portion to the anterior. The squares refer to the corresponding figures showing details.

Fig. 5a The common fertilisation ducts connect to the uterus externus (see Fig. 6f). Scale bar: 100 µm.

Fig. 5b Towards the end, the copulatory duct form a narrow, heavily-sclerotised tube (see Figs. 6g, h). Scale bar: 100 µm.

Fig. 5c The cuticle of the end of the copulatory duct fuses with the spermathecal cuticle. Scale bar: 100 µm.

Fig. 5d The copulatory ducts entwine the spermathecae. Scale bar: 100 µm.

Fig. 5e The anterior lobes of the spermathecae are rounded. Scale bar: 100 µm.

Fig. 5f Laterally, the epigynal ducts and spermathecae are enclosed by the ventral (vd) and dorsal anterior dilators (dd) of the genital aperture. The uterus internus (ui) lies dorsally. Scale bar: 100 µm.

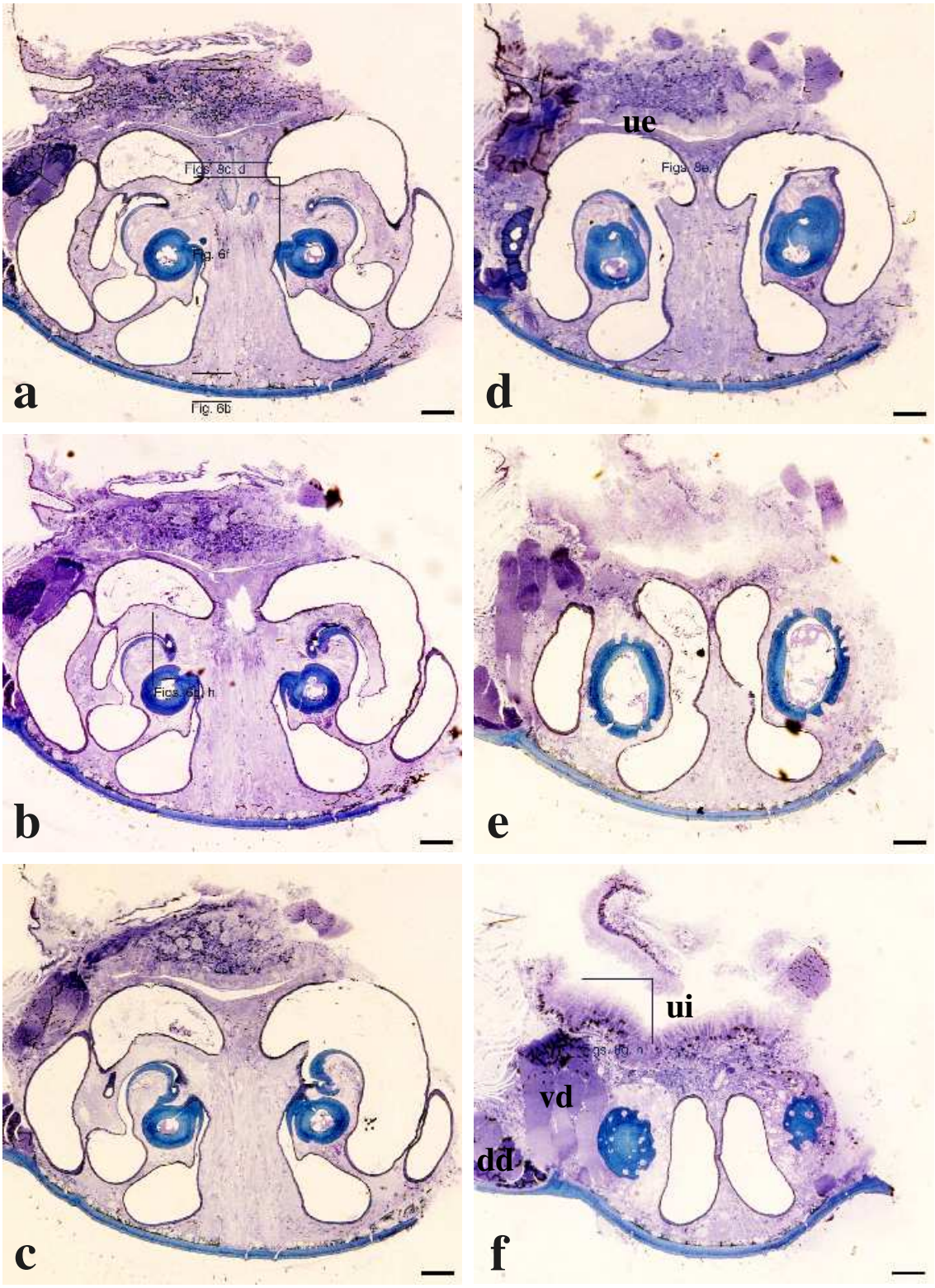

a
b
c
d
e
f
ue
ui
vd
dd

Fig. 6a The epidermis underlying the fluid-filled extra-cellular space of the tactile hair contains large amounts of crystalline deposits (black asterisk). The neighbouring cuboidal cells are filled with pigment granules (white asterisk). Scale bar: 20 µm.

Fig. 6b The tactile hair (arrow) is suspended in a socket in the cuticle of the epigynal plate. The extra-cellular space of the hair is fluid-filled (black asterisk). The adjacent cuboidal cells are filled with pigment granules (white asterisk). The cuticle can be divided into exo (ex)-, meso (me) and endocuticle (en). Scale bar: 5 µm.

Fig. 6c The cuticle of the copulatory ducts appears striated due to the numerous pore canals (arrow). The lumina of the dilations of the ducts are connected. Scale bar: 20 µm.

Fig. 6d At its anterior end, the ventral cuticle of the atrium bends upwards, forming a cone-shaped protuberance fitting into the pit created by the dorsal wall. The cuticle of the ventral and dorsal walls fuse medially. The copulatory ducts (cd) are formed. Scale bar: 20 µm.

Fig. 6e The dorsal wall of the common fertilisation duct is heavy sclerotized (asterisk) forming a valve that is pressed to the ventral epithelium which is covered by a thin cuticular lining only. Scale bar: 20 µm.

Fig. 6f Laterally, the narrow lumen of the common fertilisation duct (cf) is restricted by cells that form cushion-like flaps (asterisks). Muscle fibres (mu) connect the ventral wall of the common fertilisation duct to the epigynal plate. Scale bar: 20 µm.

Fig. 6g Muscle fibres (arrows) connect the end of the copulatory duct (cd) to the common fertilisation duct (cf). Scale bar: 20 µm.

Fig. 6h Muscle fibres (arrows) connect the end of the copulatory duct (cd) to the common fertilisation duct (cf) and the epigynal plate. Scale bar: 20 µm.

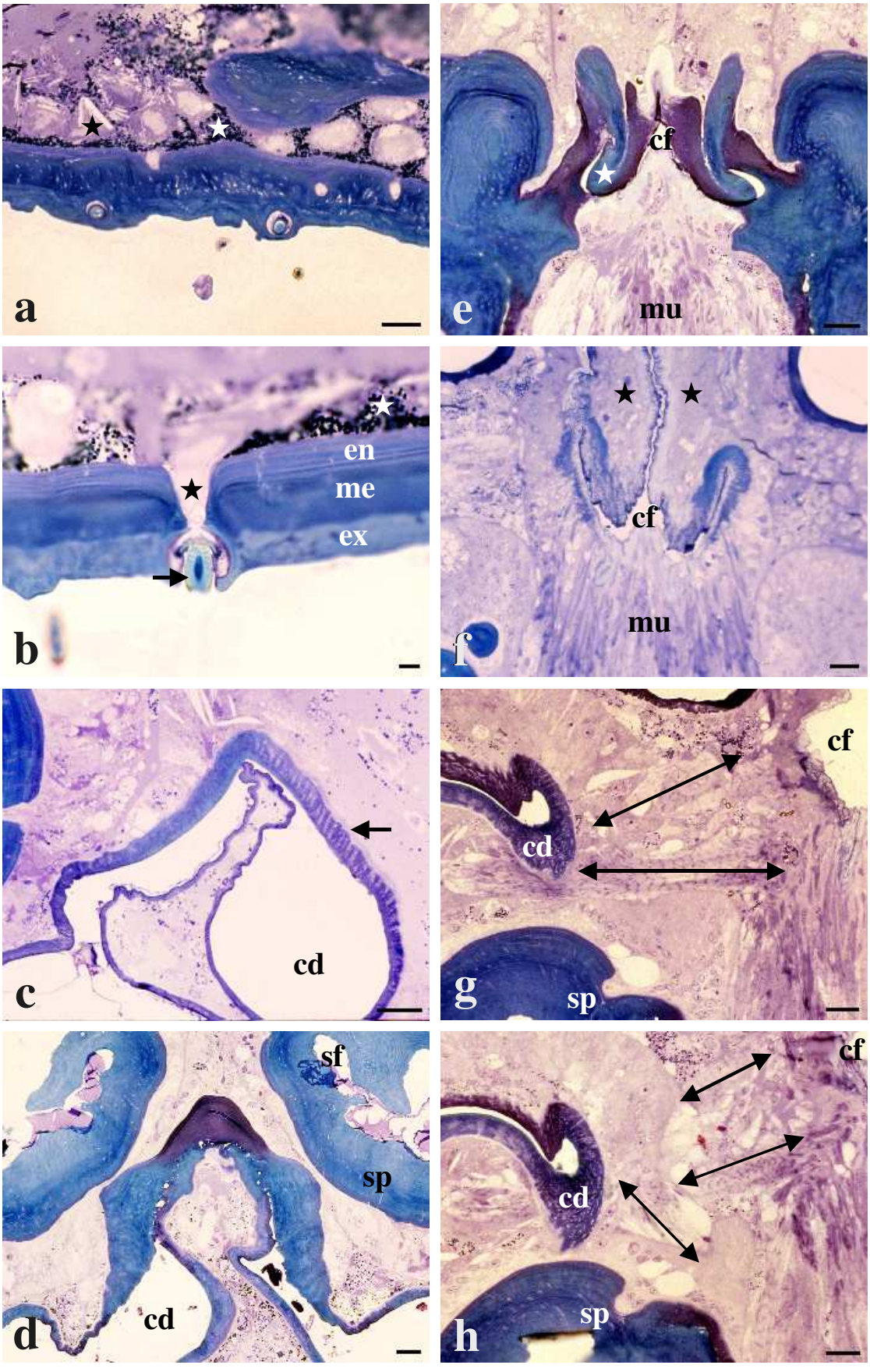

a
e
cf
mu
b
en
me
ex
f
cf
mu
c
cd
g
cf
cd
sp
d
sf
sp
cd
h
cf
cd
sp

Fig. 7a Spermathecal cuticle (LM, toluidine blue). A laminated exo- (ex), meso- (me) and endocuticle (en) can be distinguished. Scale bar: 5 µm.

Fig. 7b Spermathecal cuticle cleaned with KOH. The endocuticular laminae (en) appear less densely packed. Scale bar: 5 µm.

Fig. 7c Cast of spermathecal cuticle previously cleaned with KOH. The low-viscosity resin penetrated into spaces of the endocuticle (asterisks). Scale bar: 5 µm.

Fig. 7d The outer surface of the spermathecal lobes shows more or less regularly distributed protuberances. Openings of the ductules of the glands (arrow head). Scale bar: 5 µm.

Fig. 7e Spermathecal cuticle comprised of endo- (en) and exocuticle (ex). Note the large pore containing a cluster of glandular units. Scale bar: 2 µm.

Fig. 7f Spermathecal cuticle. The laminae show the typical parabolic pattern. Scale bar: 1 µm.

Fig. 7g Spermathecal cuticle. Electron-dense and -light layers indicate the changing orientation of the microfibres within a lamina. Scale bar: 1 µm.

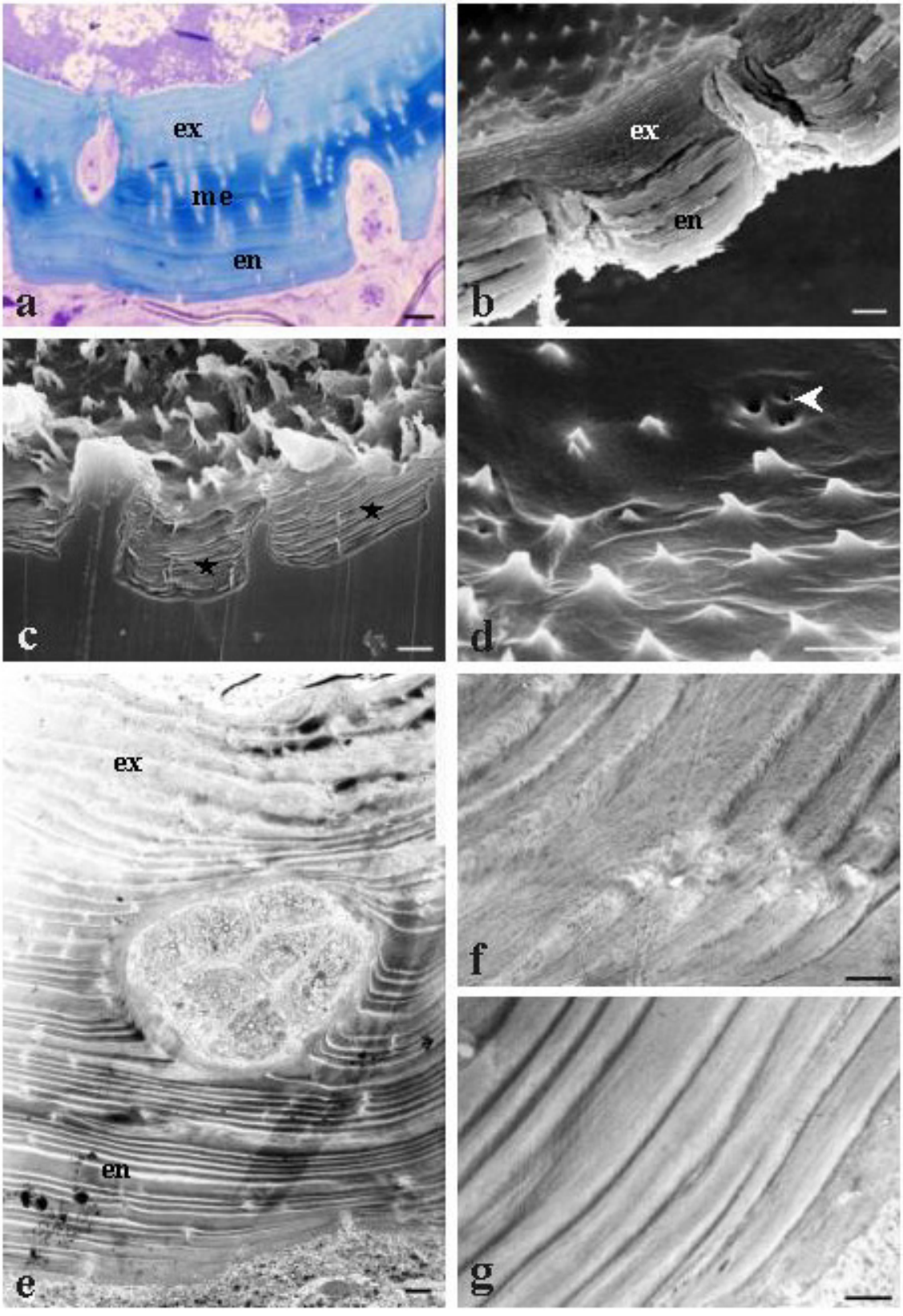

ex
me
en
a
ex
en
b
c
d
ex
en
e
f
g

Fig. 8a Fracture of the spermathecal cuticle. Each protuberance is penetrated by a pore canal (arrow). Scale bar: 2 µm.

Fig. 8b Spermathecal cuticle, apical. The dense homogenous inner epicuticle (white arrow head) can be distinguished from the thin electron-dense outer epicuticle (black arrow head). The protuberance is penetrated by a pore canal (arrow). Scale bar: 1 µm.

Fig. 8c Pore canal in a fracture of KOH treated cuticle. The two tubes laying within the pore canal are twisted along their longitudinal axes (arrow). Scale bar: 1 µm.

Fig. 8d The cast of the pore canals have a twisted-ribbon shape. Scale bar: 1 µm.

Fig. 8e Spermathecal cuticle. Basally, the relatively wide pore canal is filled with a cytoplasmic extension of the intercalary cell (asterisk). In the region of the exocuticle (ex), the pore canal contains a twisted tube (arrow). Pore canal and tube are dilated apically (arrow head) Scale bar: 1 µm.

Fig. 8f The pore canal and the hollow tube within (arrow) are dilated apically. Wax canals traverse the inner layers of the epicuticle, but do not open into the spermathecal lumen (arrow head). Scale bar: 0.2 µm.

Fig. 8g The two tubes lying within the pore canal are twisted along their longitudinal axes (arrow). Scale bar: 0.5 µm.

Fig. 8h Pore canal, transvers. In the basal region of the endocuticle, the plasma membrane of the cytoplasmic extension of the intercalary cells is clearly seen (arrow). The cytoplasm is filled with numerous filaments. Scale bar: 0.2 µm.

Fig. 8i Pore canals, transvers. Further apically in the endocuticle, the cytoplasmic extensions (arrows) of the pore canal is separated from the surrounding cuticle by a granular substance. Scale bar: 0.2 µm.

Fig. 8j Pore canals, transvers. In the region of the exocuticle, a pore canal contains one or more electron-dense tubes (arrow). Scale bar: 0.5 µm.

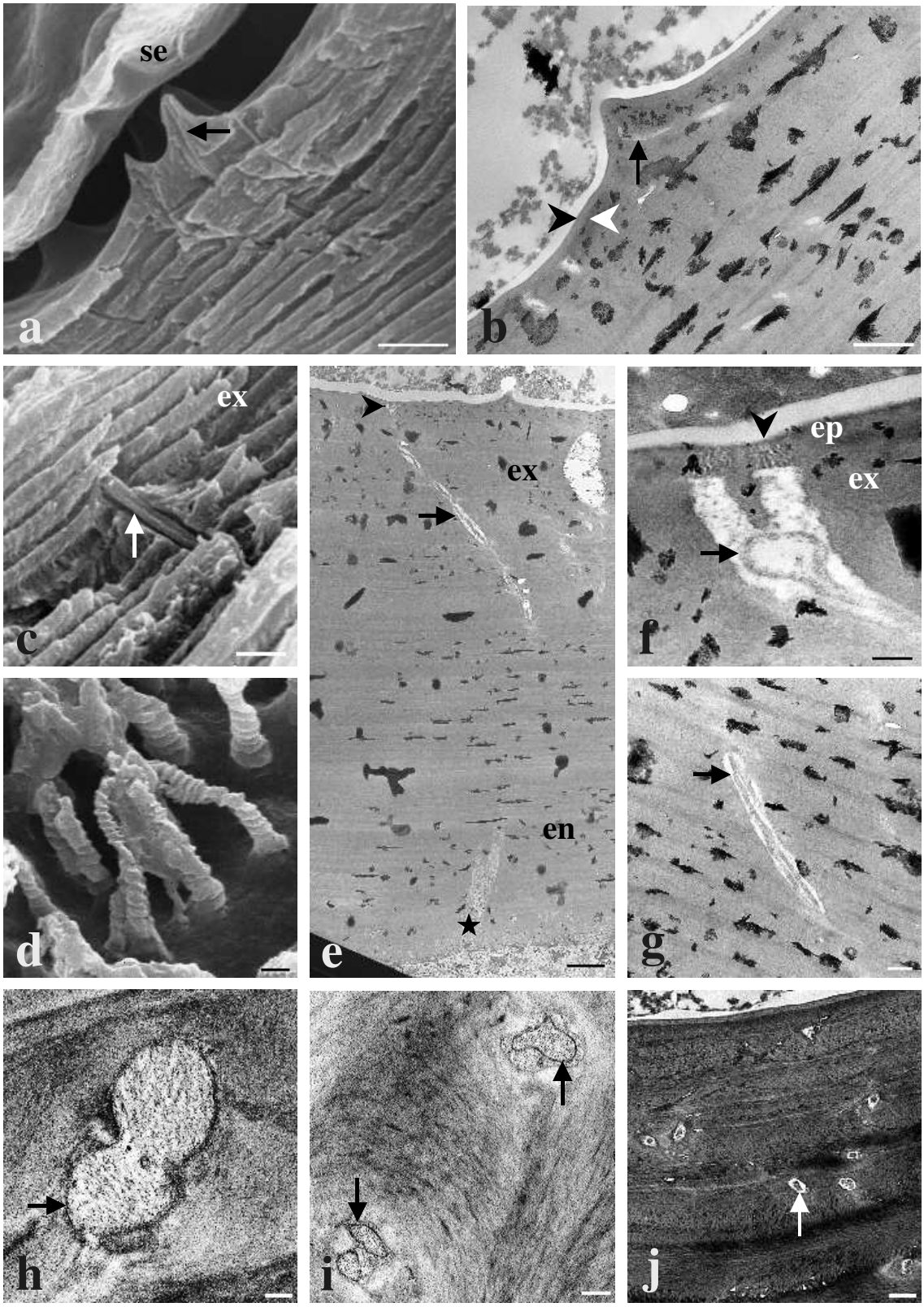

se
a
b
ex
c
ex
en
e
ep
ex
f
d
g
h
i
j

Fig. 9a The anterior (al) and posterior lobes (pl), but not the middle portion (mp) of the cleaned spermatheca (medial view) are penetrated by numerous primary pores. Scale bar: 100 µm.

Fig. 9b The epithelium that surrounds the spermathecal lobes comprises glandular units that penetrate the pores and regular epithelial cells (toluidine blue). Secretory canal cell 1 (C1); envelope cell (E); gland cell 1 (G1); hemolymph (he); intercalary cell (I). Scale bar: 10 µm.

Fig. 9c In the pore of the cleaned cuticle, several cuticular ductules are visible (arrow) that are dilated apically (arrow head). Scale bar: 2 µm.

Fig. 9d Each ductule enters its own cuticular indentation. The apical portion of the cuticle ductule bears numerous short protuberances. Scale bar: 2 µm.

Fig. 9e Fracture of cleaned cuticle. Most apically, the cuticle of the ductule (du) fuses with the cuticle (c) of the spermathecal wall. Scale bar: 1 µm.

Fig. 9f Apically, the cuticular duct (du) is dilated and surrounded by an envelope cell (E). Scale bar: 1 µm.

Fig. 9g The pores of the ductules open onto the spermathecal surface. Scale bar: 1 µm.

Fig. 9h The apical portion of the cuticular ductule bears numerous short protuberances. Scale bar: 1 µm.

Fig. 9i Apically, the ductule bears short protuberances (arrow) and is surrounded by an envelope cell (E). The most apical portion of the pore is made up by the spermathecal wall itself (arrow head). Scale bar: 0.5 µm.

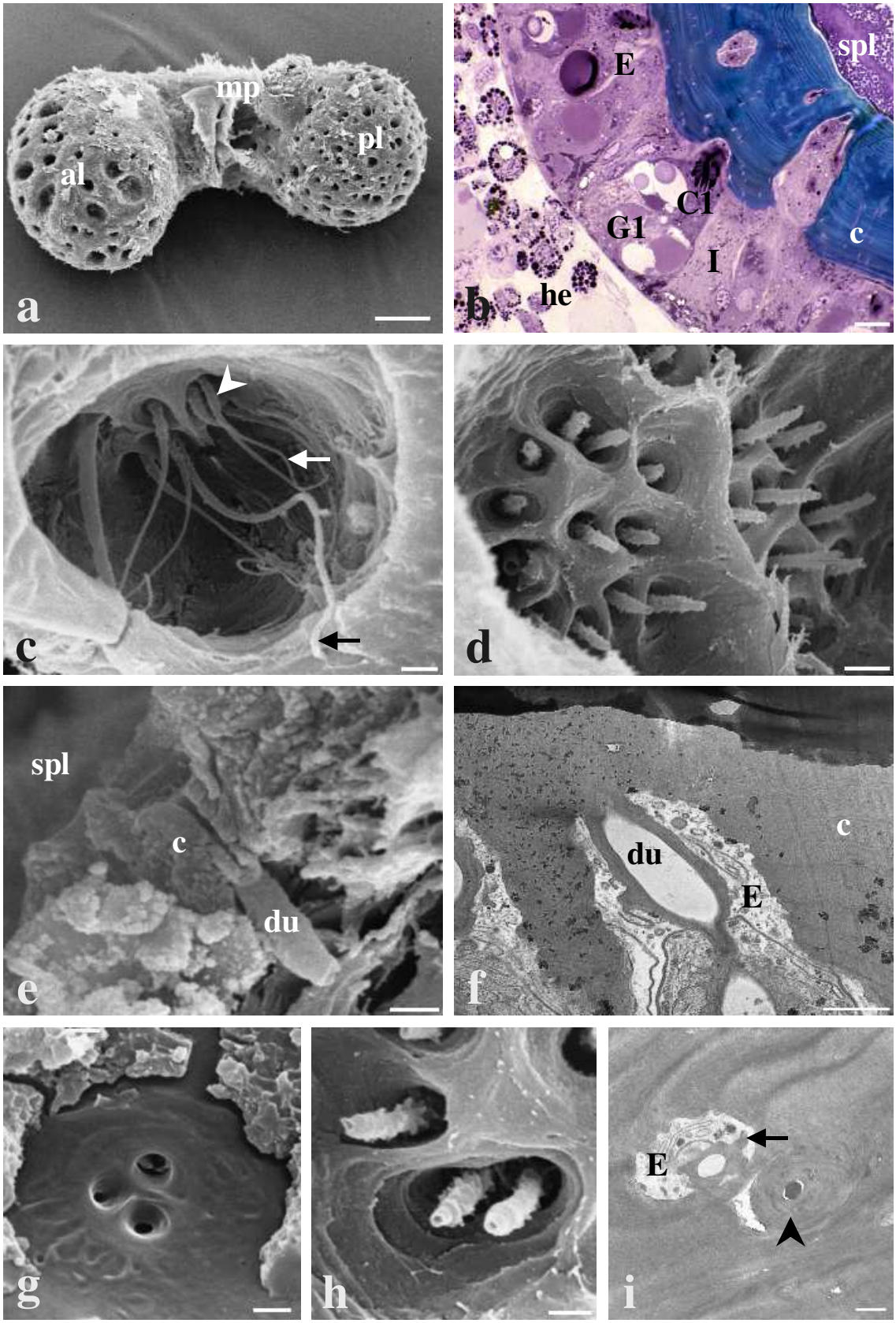

mp
pl
al
a
E
spl
C1
G1
c
I
he
b
c
d
spl
c
du
e
c
du
E
f
g
h
E
i

Fig. 10a Reconstruction of a glandular unit of type I and the associated cells. The red square indicates the part of the neck of the gland cell not unequivocally identified: (bi) basal infoldings; (bm) basement membrane; (c) cuticle; (C1) secretroy canal cell 1; (d) dictyosome; (du) ductule; (E) envelope cell; (fi) filaments; (G1) gland cell 1; (I) intercalary cell; (m) mitochondrium; (mv) microvilli; (mt) microtubuli; (nC1) nucleus of secretory canal cell 1; (nE) nucleus of envelope cell; (nI) nucleus of intercalary cell; (pc) pore canal; (rer) rough endoplasmic reticulum; (v) vesicle.

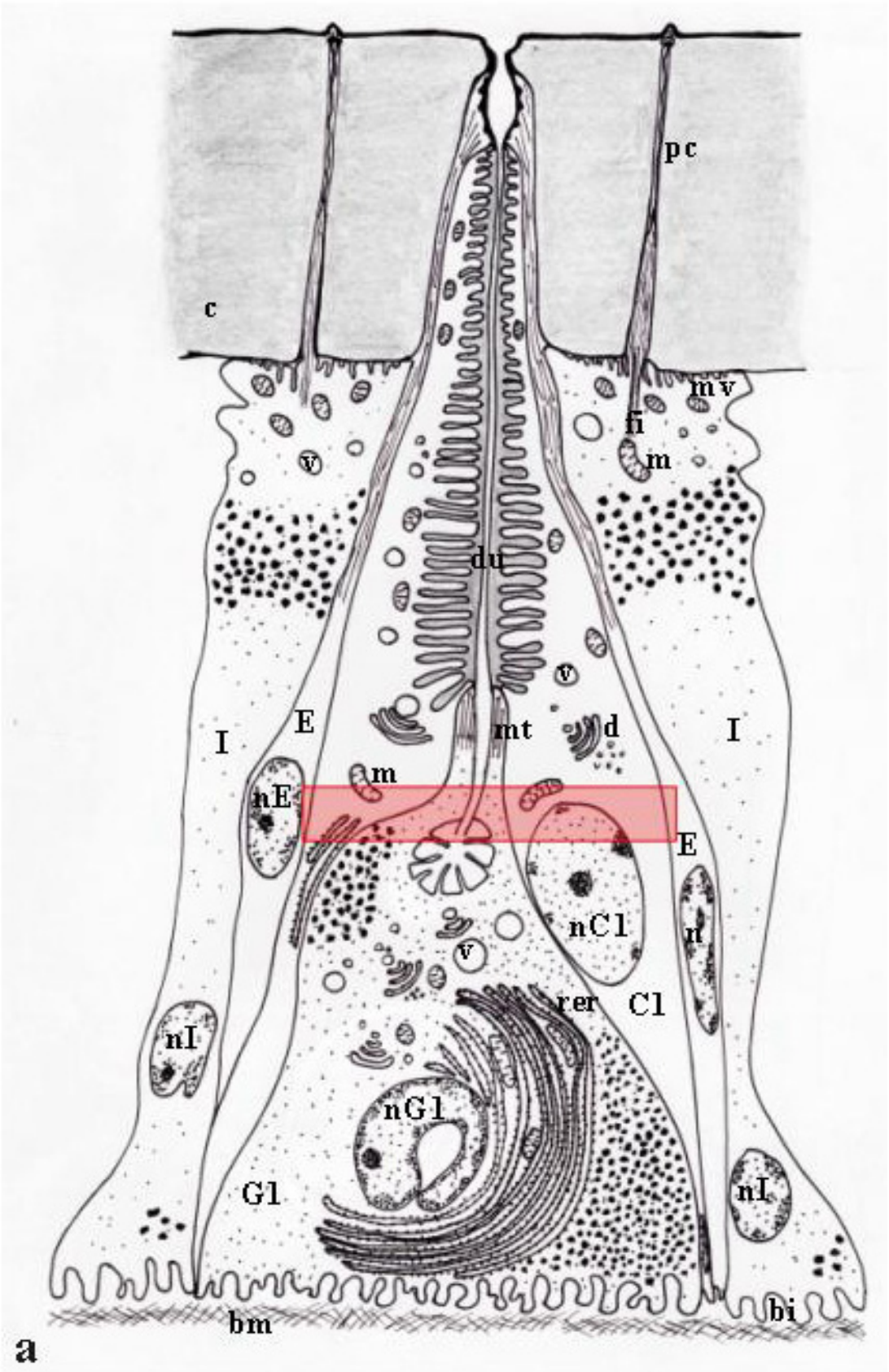

pc
c
mv
fi
m
v
du
v
I
E
mt
d
I
m
nE
E
nCl
n
v
rer
Cl
nI
nGl
Gl
nI
bm
bi
a

Fig. 11a Longitudinal section. The intercalary cell (I) extends from the basement membrane to the spermathecal cuticle. The cytoplasm contains aggregations of glycogen. The arrow indicates the neck of the gland cell (G1) that surrounds the ductule. Scale bar: 2 µm.

Fig. 11b Longitudinal section. The gland cells (G1) lie basally. The secretory canal cells (C1) surround the gland cells and extend from the basement membrane into the pores. Their ovoid nuclei (nC1) lie apically from the main cell body of the gland cells (G1). The arrow indicates the neck of the gland cell (G1) that is penetrated by a ductule. Scale bar: 2 µm.

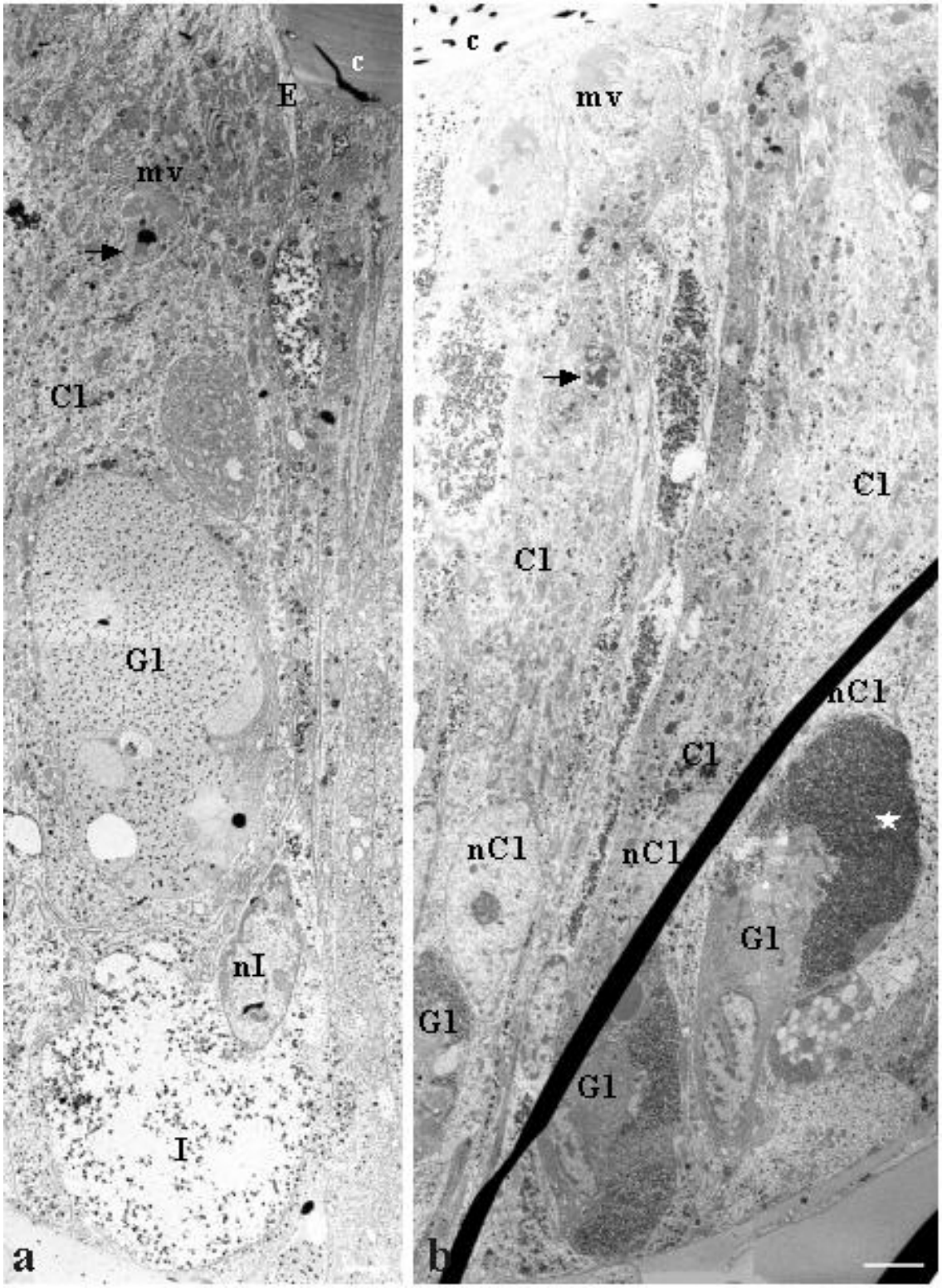

c
E
mv
Cl
Gl
nI
I
a
c
mv
Cl
Cl
nCl
Cl
nCl
nCl
Gl
Gl
Gl
b

Fig. 12a Cross-section very flat above the spermathecal cuticle. Each secretory canal cell (C1) cell and the cluster of the five C1 cells are surrounded by envelope cells (E). The surrounding intercalary cells (I) contain aggregations of glycogen. Apical microvilli and bundles of pore canal filaments (arrows) that reach into the cytoplasm of I are visible. Scale bar: 2 µm.

Fig. 12b Longitudinal section of the basal region. The secretory canal cell (C1) rests upon the basement membrane and surrounds the gland cell (G1). Cisterns of the rough endoplasmic reticulum (rer) are arranged along the plasma membrane that faces the gland cell. Basally, the envelope cells and intercalary cells look similar and the assignment to a given cell type is difficult. Scale bar: 2 µm.

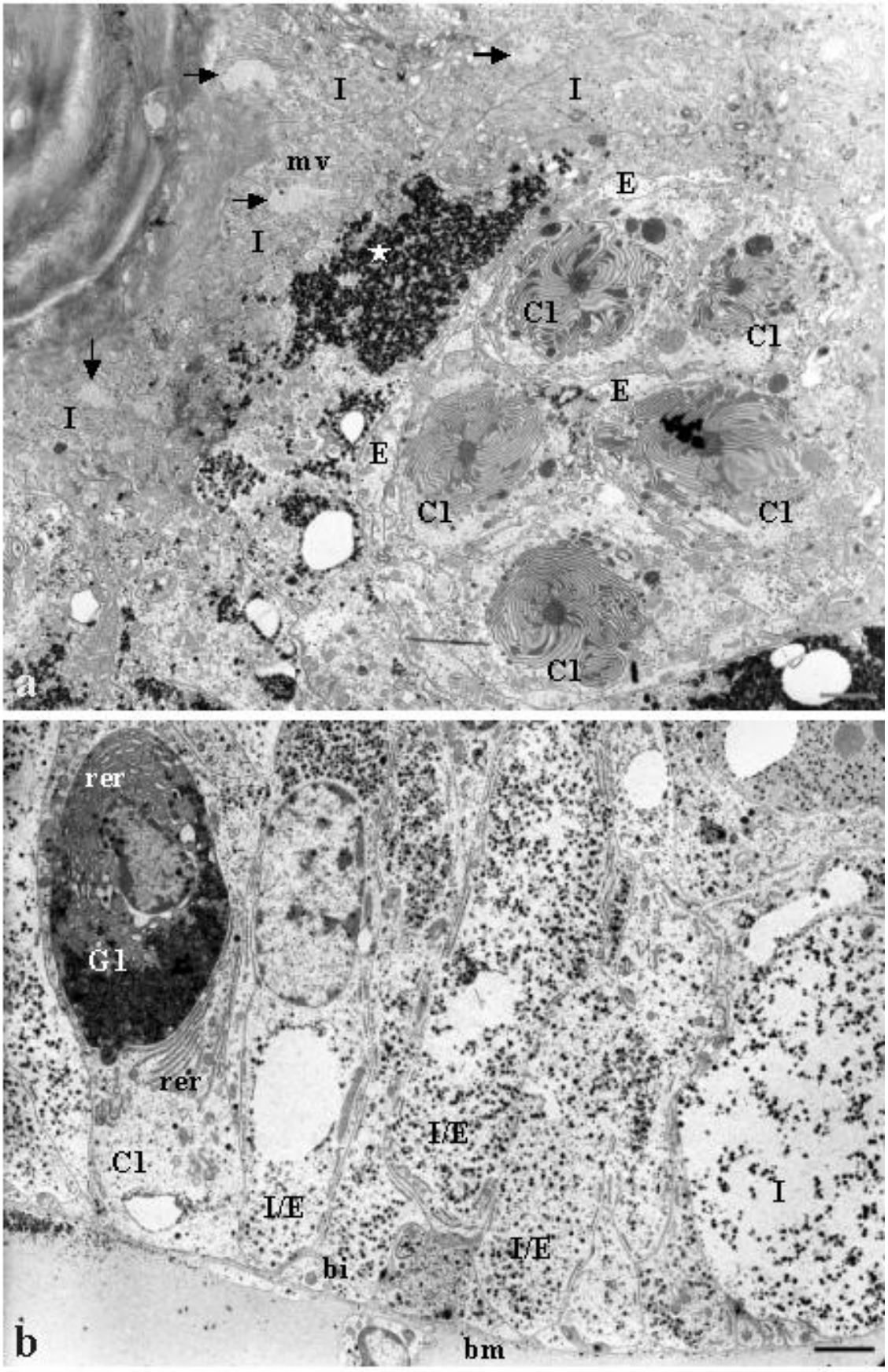

I
I
mv
I
E
Cl
Cl
I
E
E
Cl
Cl
Cl
a
rer
Gl
rer
Cl
I/E
I/E
I
I/E
bi
b
bm

Fig. 13a Cross-section. The lobed heterochromatic nucleus of G1 lies on the same plane as the ovoid nucleus with microvilli-like projections (arrow) of the surrounding C1 cell (nC1). Scale bar: 2 µm.

Fig. 13b Cross-section. Large areas of the gland cell (G1) are filled with glycogen (white asterisk). G1 is surrounded by the secretory canal cell (C1). The ovoid nucleus of the neighbouring C1 (nC1) shows microvilli-like projections (arrow). Scale bar: 2 µm.

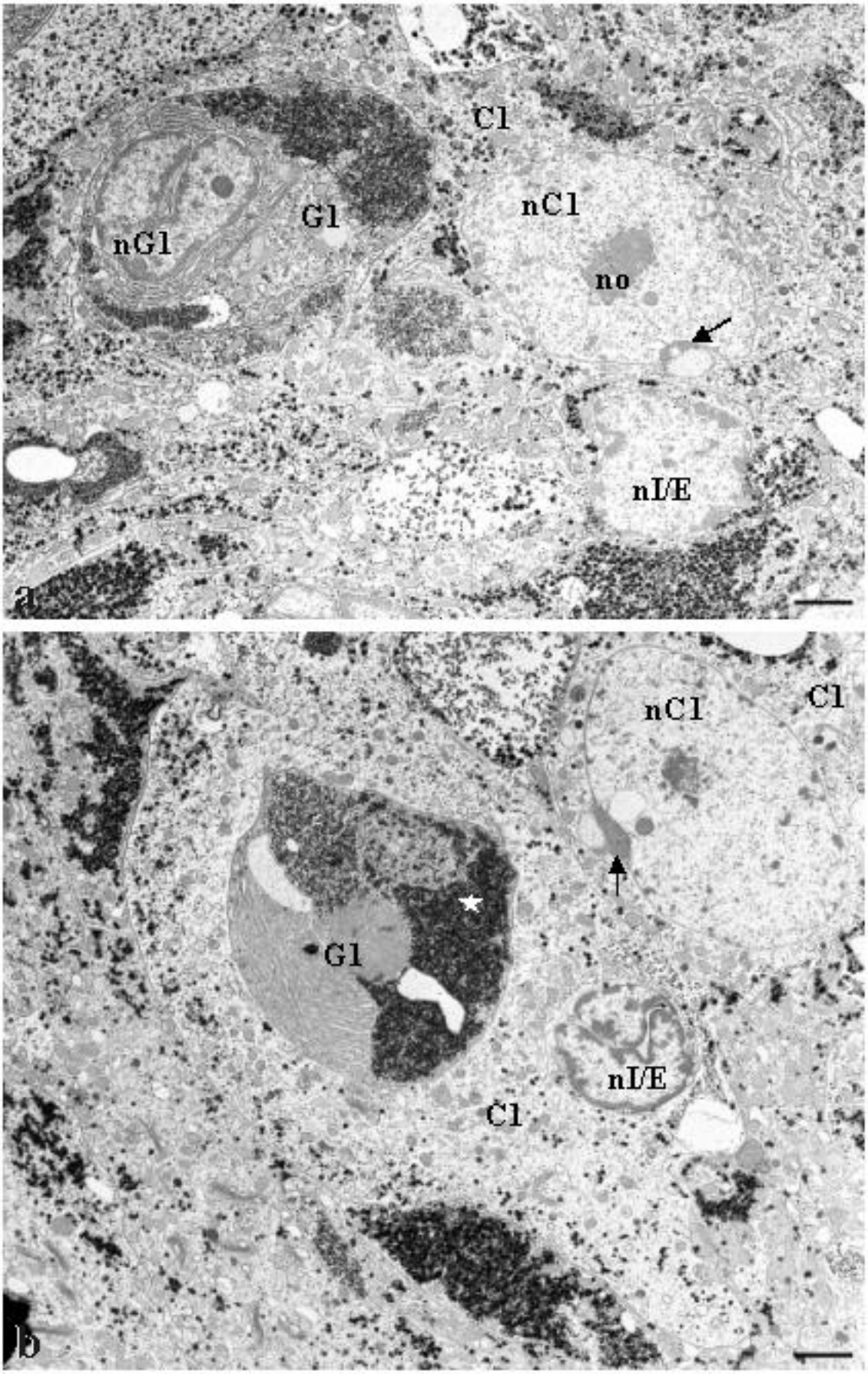

Cl
nCl
Gl
nGl
no
nI/E
a
nCl
Cl
Gl
nI/E
Cl
b

Fig. 14a Longitudinal section of the basal region. The gland cell (G1) show basal infoldings. Rough endoplasmatic reticulum (rer) is abundant and forms tightly packed cisterns around the lobed nucleus. Scale bar: 2 µm.

Fig. 14b Cross-section. The gland cell possesses a lobed heterochromatic nucleus (n), rough endoplasmic reticulum (rer) , numerous dictyosomes (d) , mitochondria (m), vesicles (v) and glycogen. Microvilli extend into the extra-cellular cavity that is filled with granular material (asterisk). Scale bar: 1 µm.

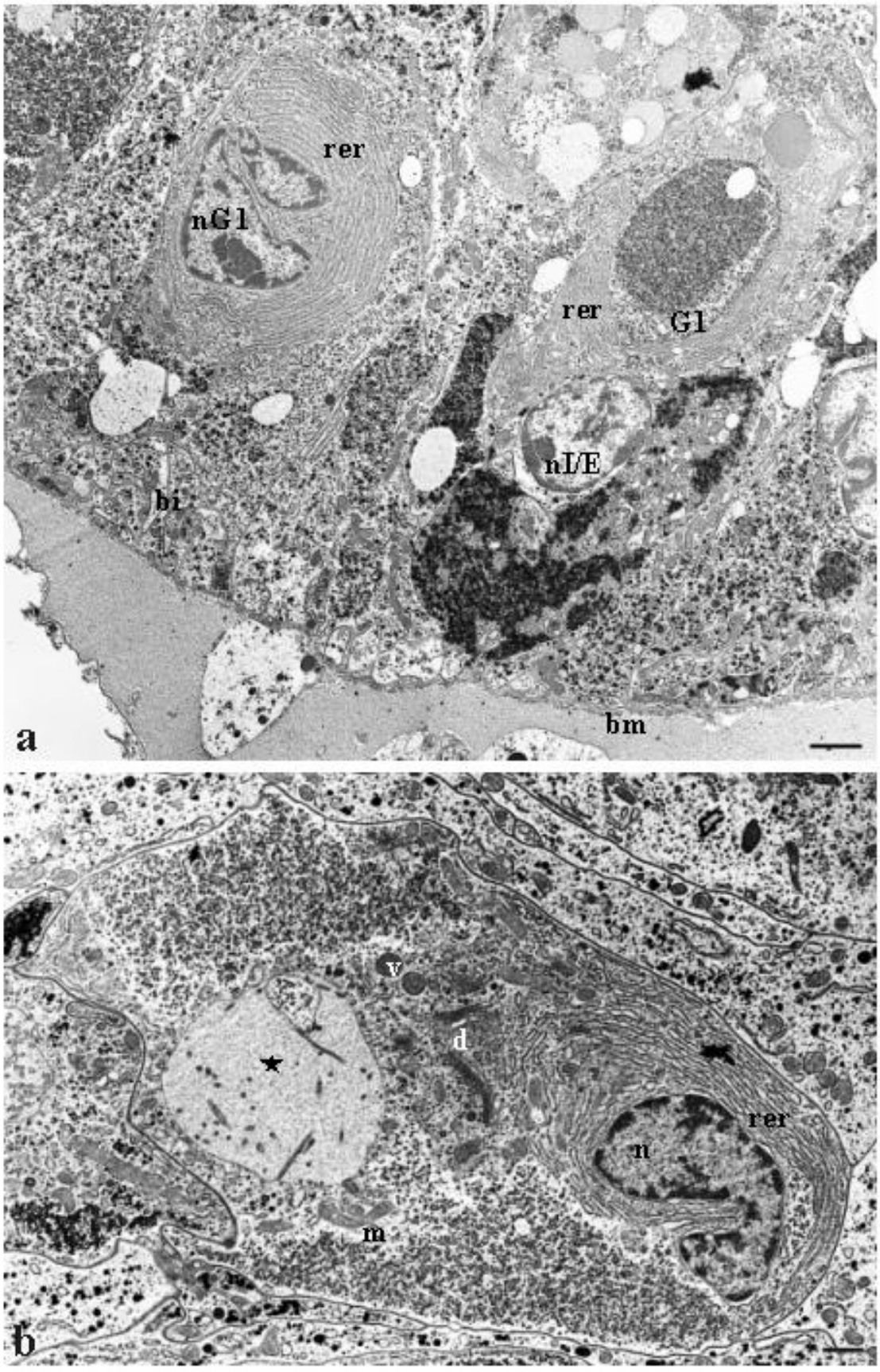

rer
nGl
rer
Gl
nI/E
bi
bm
a
v
d
rer
n
m
b

Fig. 15a Oblique section of gland cell (G1). Mitochondria (m) lie between the partly dilated cisterns of the rough endoplasmic reticulum (rer) around the heterochromatic nucleus (n). The supranuclear region contains dictyosomes (d), mitochondria (m), glycogen aggregations (white asterisk) and many membrane-bound vesicles (v) of varying size and electron-density. The extra-cellular cavity is cut several times (black arrow heads). Scale bar: 1 µm.

Fig. 15b Microvilli extend into the extra-cellular cavity of the gland cell (G1). Scale bar: 0.5 µm.

Fig. 15c The supranuclear region of G1 contains mitochondria (m), vesicles (v) and dictyosomes (d). Scale bar: 0.5 µm.

Fig. 15d Mitochondria (m) lie between the tightly packed cisterns of the rough endoplasmic reticulum (rer) around the heterochromatic nucleus of G1 (nG1). Scale bar: 0.5 µm.

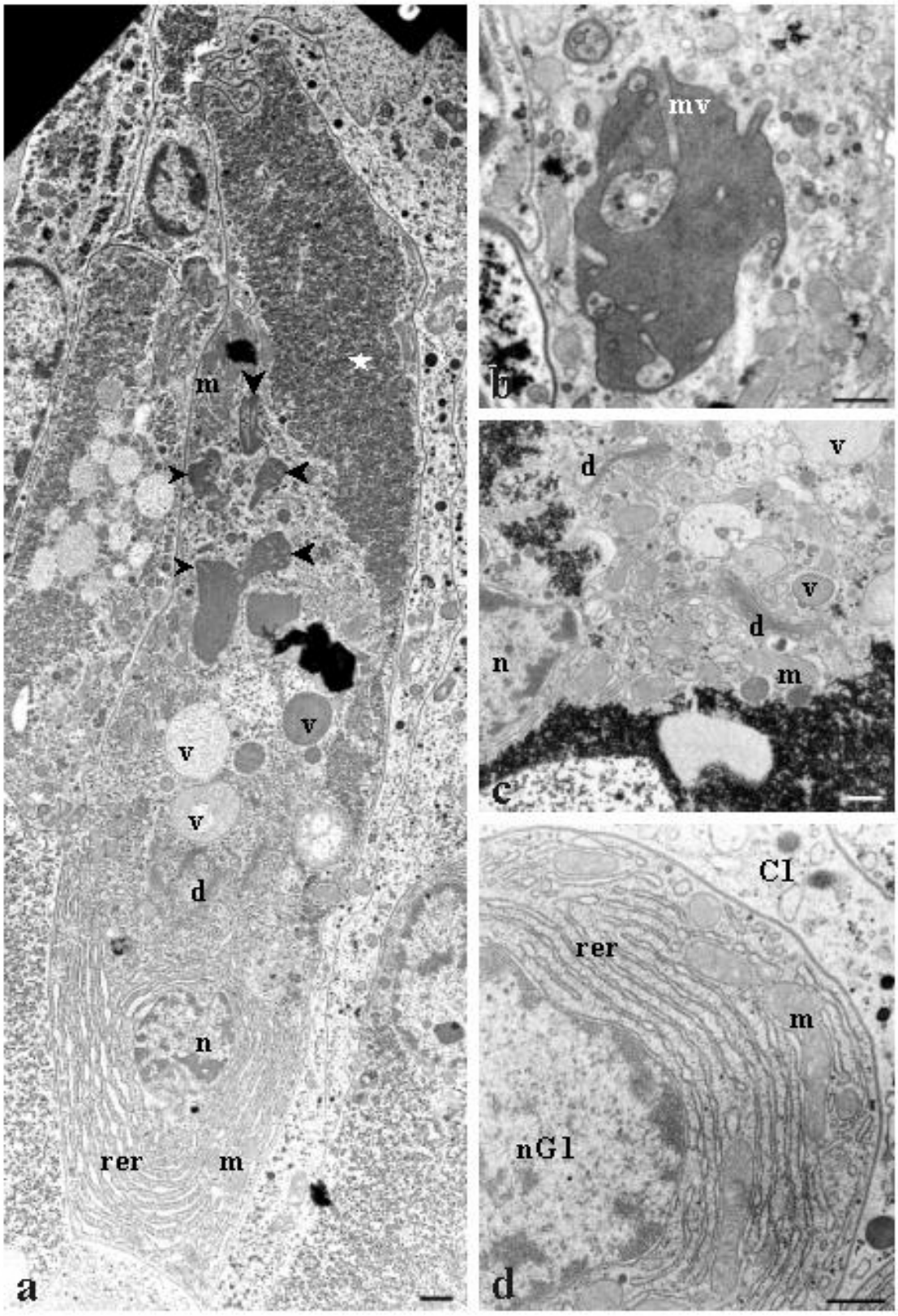

a
m
v
v
v
d
n
rer
m
b
mv
c
d
v
v
d
n
m
d
Cl
rer
m
nGl

Fig. 16a Longitudinal section. At least five glandular units (C1, 1 -5) enter a single pore. Microvilli extend towards the cuticular ductules (du) that traverse up to two-thirds of the cells' lengths. G1 lies basally and is surrounded by C1. Scale bar: 2 µm.

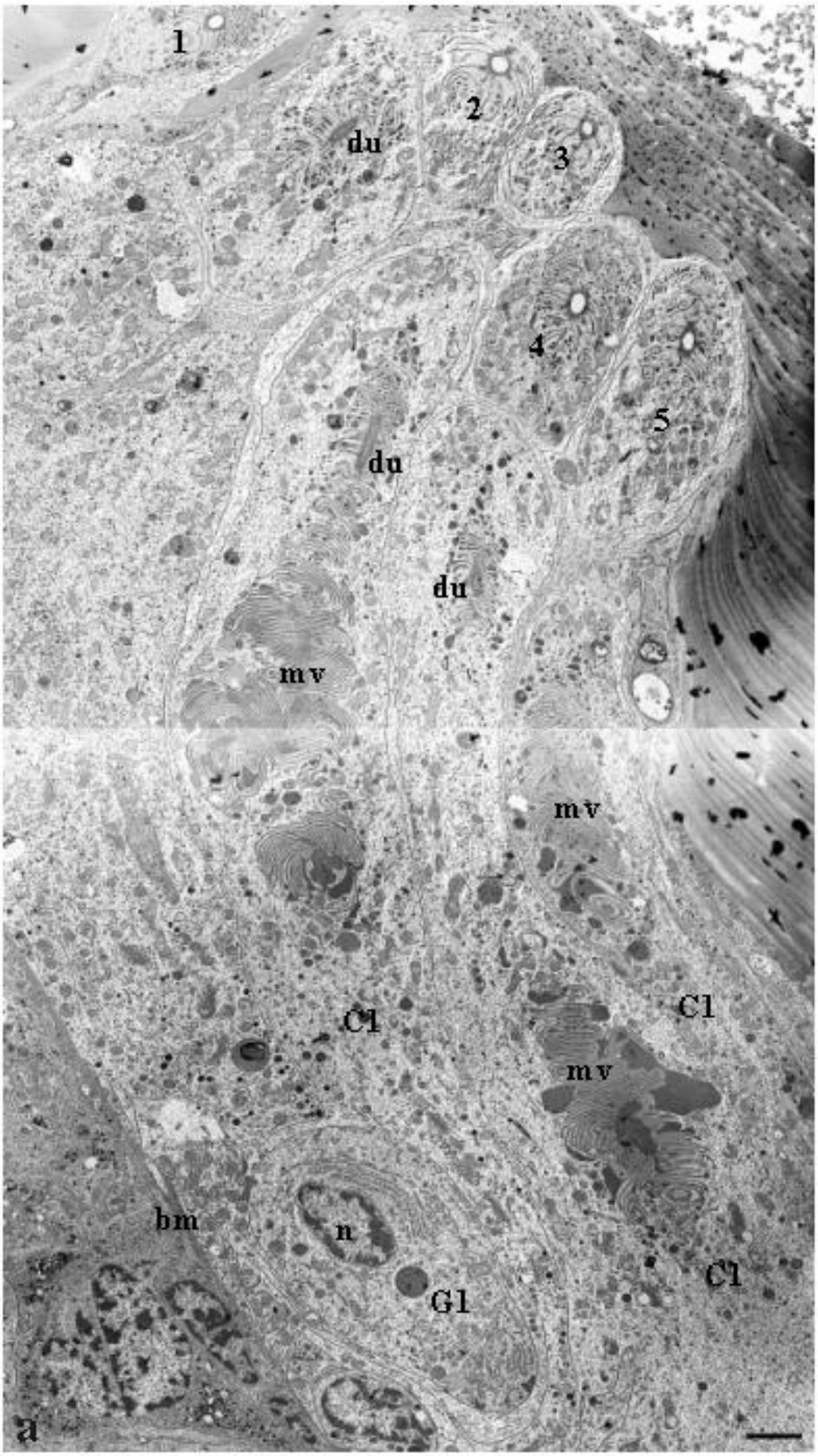

1
2
3
4
5
du
du
du
mv
mv
Cl
Cl
Cl
mv
bm
n
Gl
a

Fig. 17a The ductule that reaches into the neck of the gland cell (G1) (asterisk) has an irregular outline. Scale bar: 1 µm.

Fig. 17b The ductule that reaches into the neck of the gland cell (G1) (asterisk) has an irregular outline. Its wall consists of a homogenous, moderate electron-dense layer. The lumen is filled with a homogenous, more electron-dense material. Scale bar: 0.5 µm.

Fig. 17c Oblique section of the basal end of the ductule of C1. Electron-dense material fills the space outside the microvilli (mv). Microtubules run along the ductule that reaches into the neck of G1. Scale bar: 1 µm.

Fig. 17d The cytoplasm of the neck of the gland cell (G1) that is connected to the most basal end of the ductule of C1 contains mitochondria (m), small vesicles and electron-dense particles (glycogen and ribosomes). The glandular unit is ensheathed by an envelope cell (E). Scale bar: 1 µm.

Fig. 17e The cytoplasm of the neck portion of G1 contains small vesicles and electron-dense particles (glycogen and ribosomes). Parallel-arranged microtubules (mt) run along the part of the ductule that reaches into the neck of G1. The secretory canal cell C1 contains conspicuous dictyosomes (d), numerous mitochondria (m), free ribosomes and vesicles. Scale bar: 1 µm.

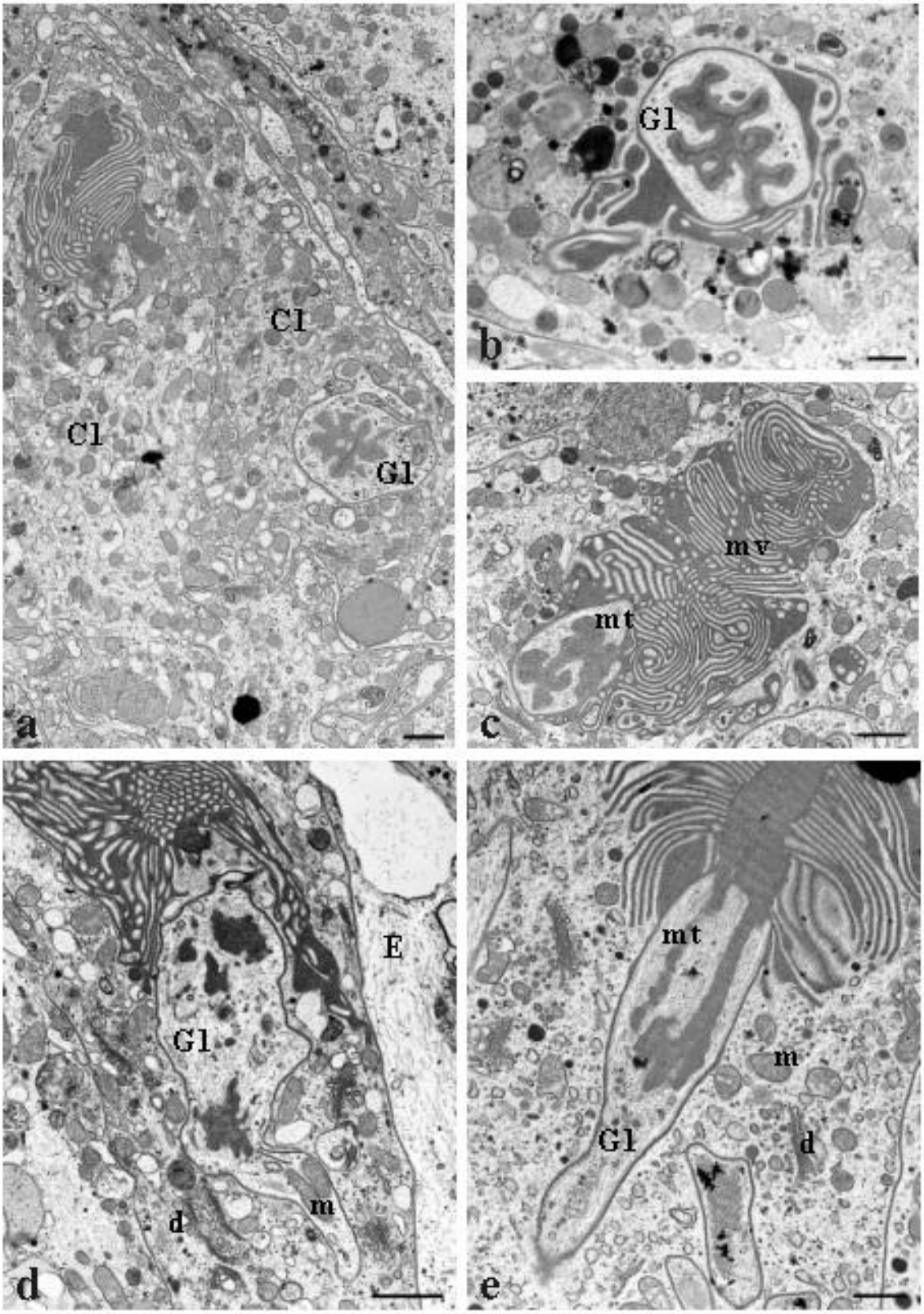

Cl
Cl
Gl
a
Gl
b
mv
mt
c
E
Gl
m
d
d
mt
m
Gl
d
e

Fig. 18a Longitudinal section of the cuticular ductule of the secretory canal cell (C1) inside the pore. On the luminal side, the ductule is covered by a thin electron-dense layer (white arrow). Microtubuli (mt) run along the cell periphery and lie between the microvilli that reach towards the ductule (black arrow head). Scale bar: 1 µm.

Fig. 18b Cross-section of the cuticular ductule of C1. Electron-dense material fills the space between the microvilli and the cuticular ductule. The ductular lumen contains granular material. Scale bar: 0.5 µm.

Fig. 18c On one side, the inner membrane of the nucleus (nC1) forms regularly-arranged microvilli-like projections (mv). Scale bar: 0.5 µm.

Fig. 18d The cytoplasm of C1 contains conspicuous dictyosomes (d), numerous mitochondria (m), free ribosomes and many membrane-bound vesicles (v) of varying size and electron-density. Scale bar: 1 µm.

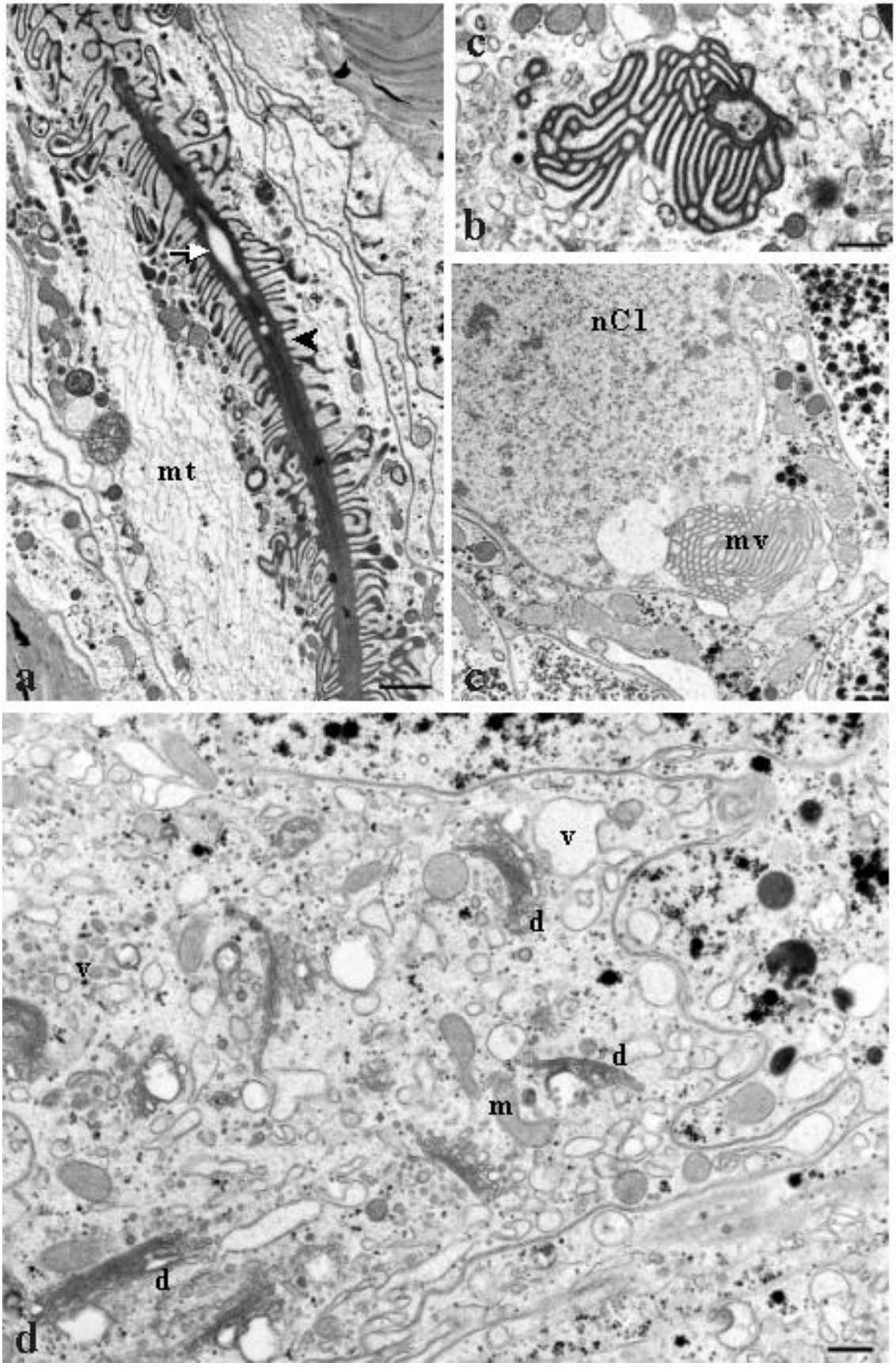

a
mt
b
c
nCl
mv
d
v
d
v
d
m
d

Fig. 19a Longitudinal section. Secretory canal cells C1 and C2 enter a single pore. Both types are ensheathed by envelope cells (E). The less densely packed microvilli that surround the ductule of C2 create a large extra-cellular space (asterisks). Scale bar: 2 µm.

Fig. 19b Cross-section. A cluster of secretory canal cells (C1) and a single secretory canal cell (C2) enter a single pore. Each single cell and the cluster are ensheathed by envelope cells (E). The widely-spaced microvilli of C2 create a large extra-cellular space (asterisk). Scale bar: 0.5 µm.

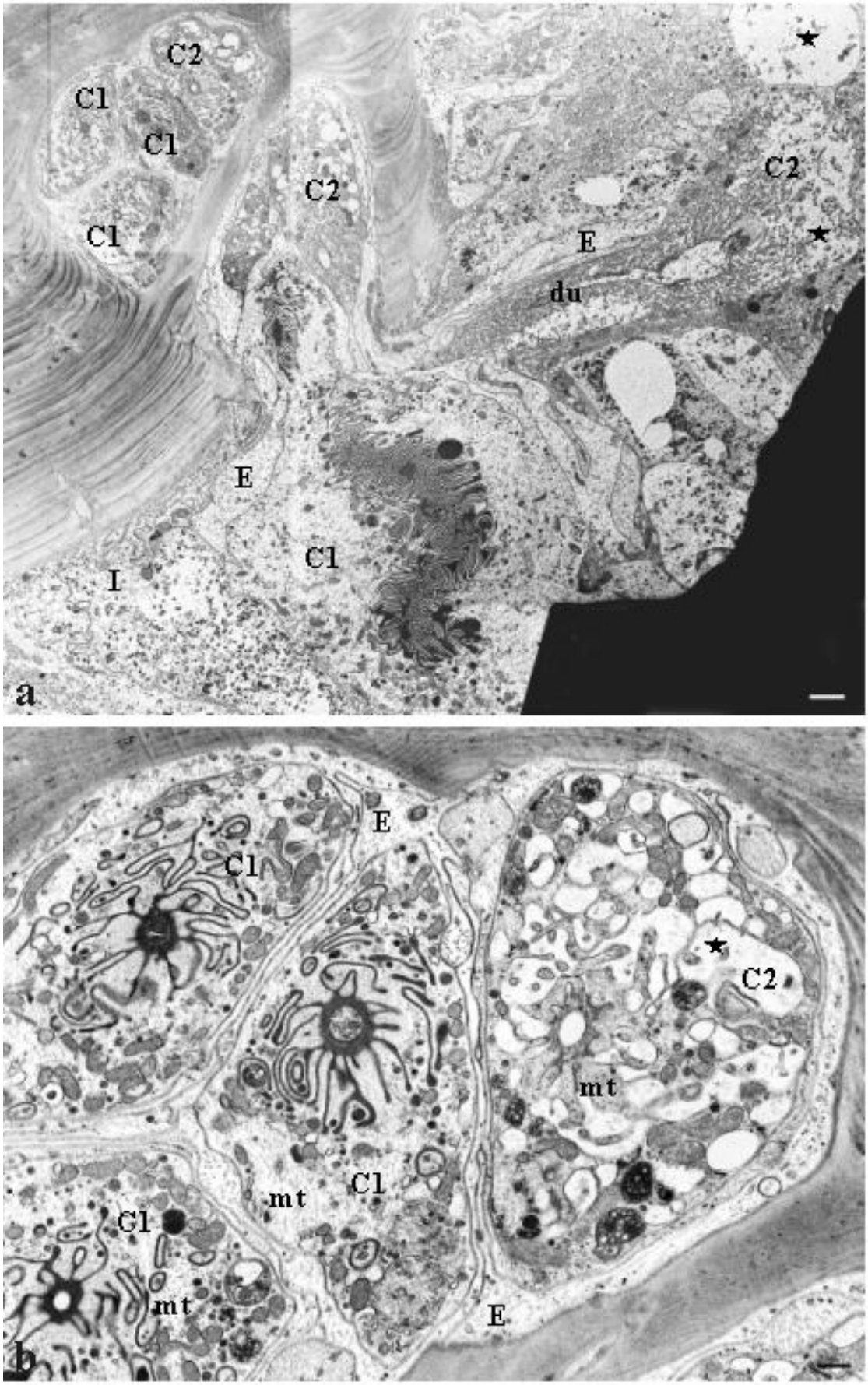

C2
C1
C1
C1
C2
E
du
C2
E
C1
I
a
E
C1
C2
mt
C1
mt
C1
mt
E
b

Fig. 20a Overview of the region comprising a glandular unit of type II (G2/C2). In the basal region the cell membranes appear to have been destroyed by fixation processes. The cytoplasm contains extra-cellular reservoirs (black arrow heads) of the gland cells (G2) each with a central ductule. Cell extensions that contain nuclei (n) of various other cells are visible. Scale bar: 2 µm.

Fig. 20b Microvilli (mv) extend into the extra-cellular reservoir of G2. The lumen contains moderate electron-dense material. Scale bar: 0.5 µm.

Fig. 20c Microvilli extend into the extra-cellular reservoir of G2. The lumen contains moderate electron-dense material and a central ductule (du). Scale bar: 0.5 µm.

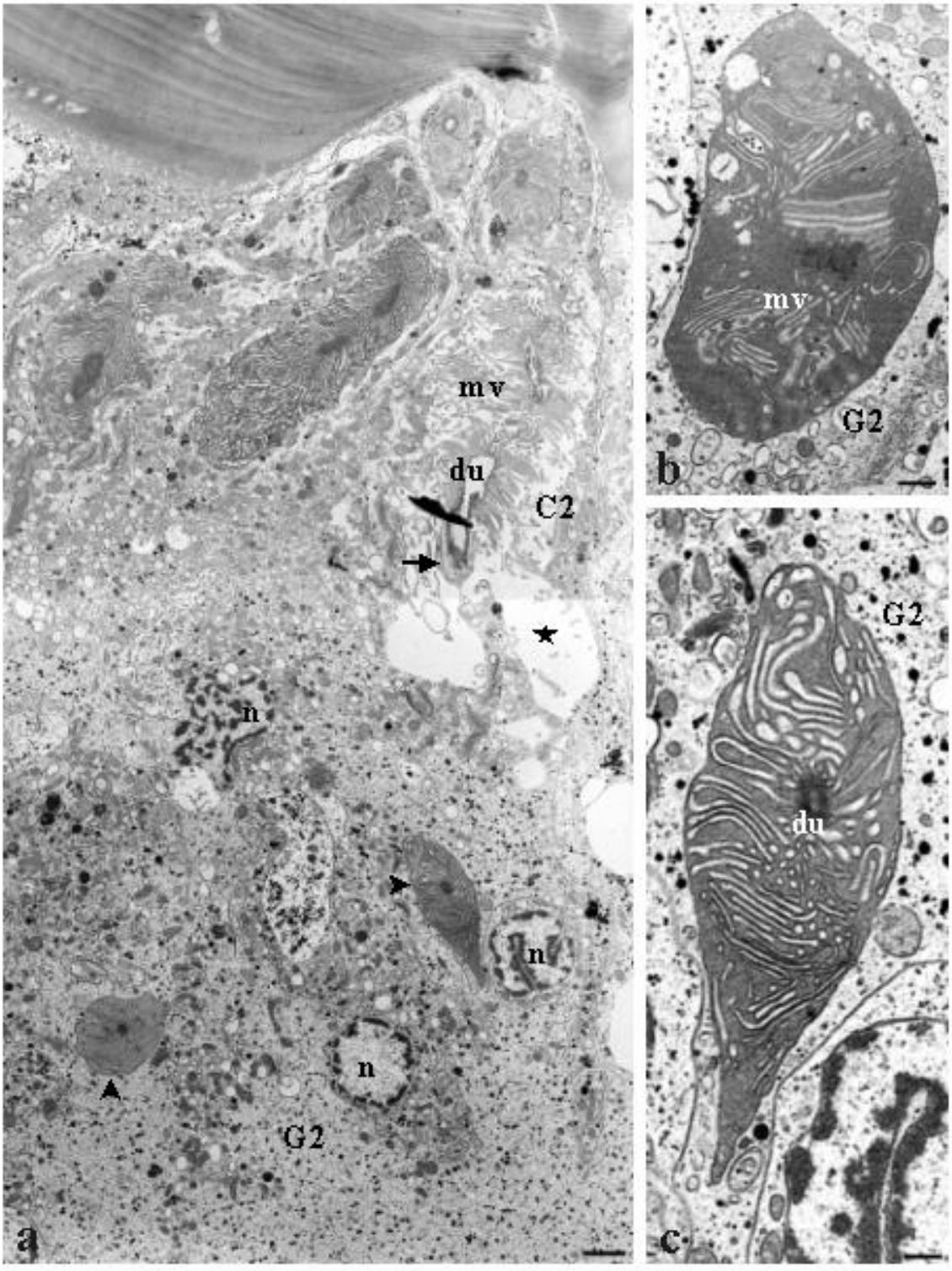

mv
du
C2
n
n
n
G2
a
mv
G2
b
G2
du
c

Fig. 21a The cuticular ductule of the secretory canal cell (C2) takes a curved course through the cytoplasm and passes into the plane of section in two places. The thin, electron-dense cuticle (arrow) of the more apical portion of the ductule is surrounded by a fibrous mass. The extra-cellular space is filled with granular material (black asterisk). In the neck of G2 microtubules (mt) are arranged in parallel along the ductule that reaches into it. Scale bar: 1 µm.

Fig. 21b The secretory canal cell (C2) contains mitochondria (mt), dictyosomes and vesicles. Microtubules (mt) run along its periphery. The luminal side of the basal portion of the ductule is conspicuously sculptured (arrow). The ductular lumen and the extra-cellular space are filled with a granular material. The cytoplasm of the neck of G2 contains mitochondria (m), vesicles, electron-dense granules and microtubules (mt). Scale bar: 0.5 µm.

Fig. 21c Cross-section of the ductule of C2 that reaches into the neck of G2 (black asterisk). The ductular lumen is filled with a granular material. Scale bar: 1 µm.

Fig. 21d Cross-section of the ductule of C2 that reaches into the neck of G2. The lumen is filled with a granular material. Scale bar: 1 µm.

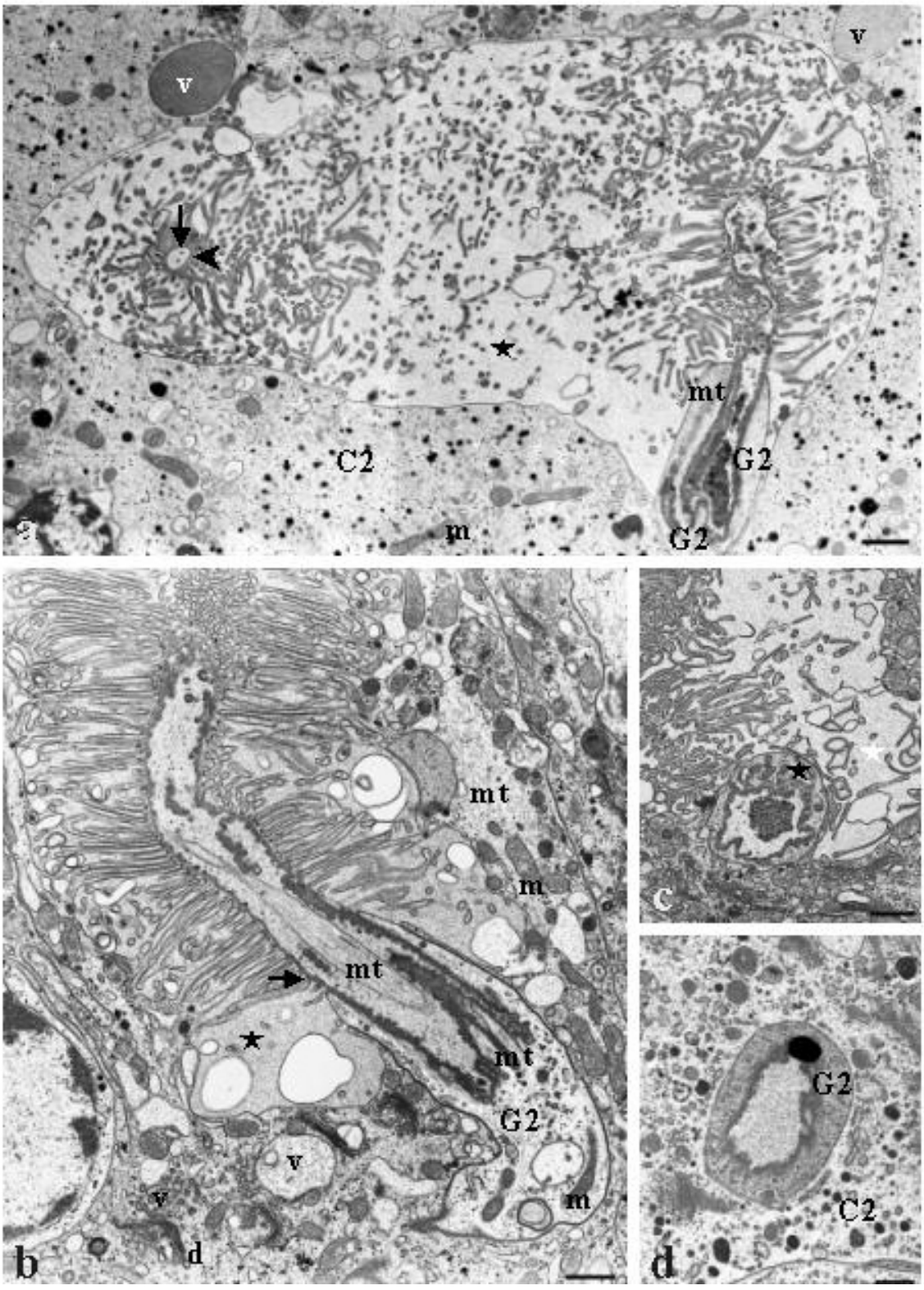

v
v
mt
C2
G2
m
G2
mt
m
mt
mt
G2
v
v
m
d
b
c
G2
C2
d

Fig. 22a Longitudinal/oblique section. Most apically, the microvilli that extend towards the ductule of C2 are supported by numerous microtubules (mt). The thin ductule cuticle (black arrows) is surrounded by a fibrous mass (black arrow heads). Envelope cells (E) ensheath the C2 cells and the apical part of the ductule. Here, the cuticle comprises a thin, electron-dense outer epicuticle (white arrows) and a thicker homogenous inner epicuticle (white arrow heads). Scale bar: 1 µm.

Fig. 22b Longitudinal section. The secretory canal cells (C2) contain mitochondria (m) and microtubules (mt). The spaced microvilli extending towards the cuticular ductule of the secretory canal cells (C2) are also supported by microtubules. The microvilli create large extra cellular spaces to the outside, filled with granular material. The thin, electron-dense ductule cuticle (arrows) is surrounded by fibrous material (arrow heads). Scale bar: 0.5 µm.

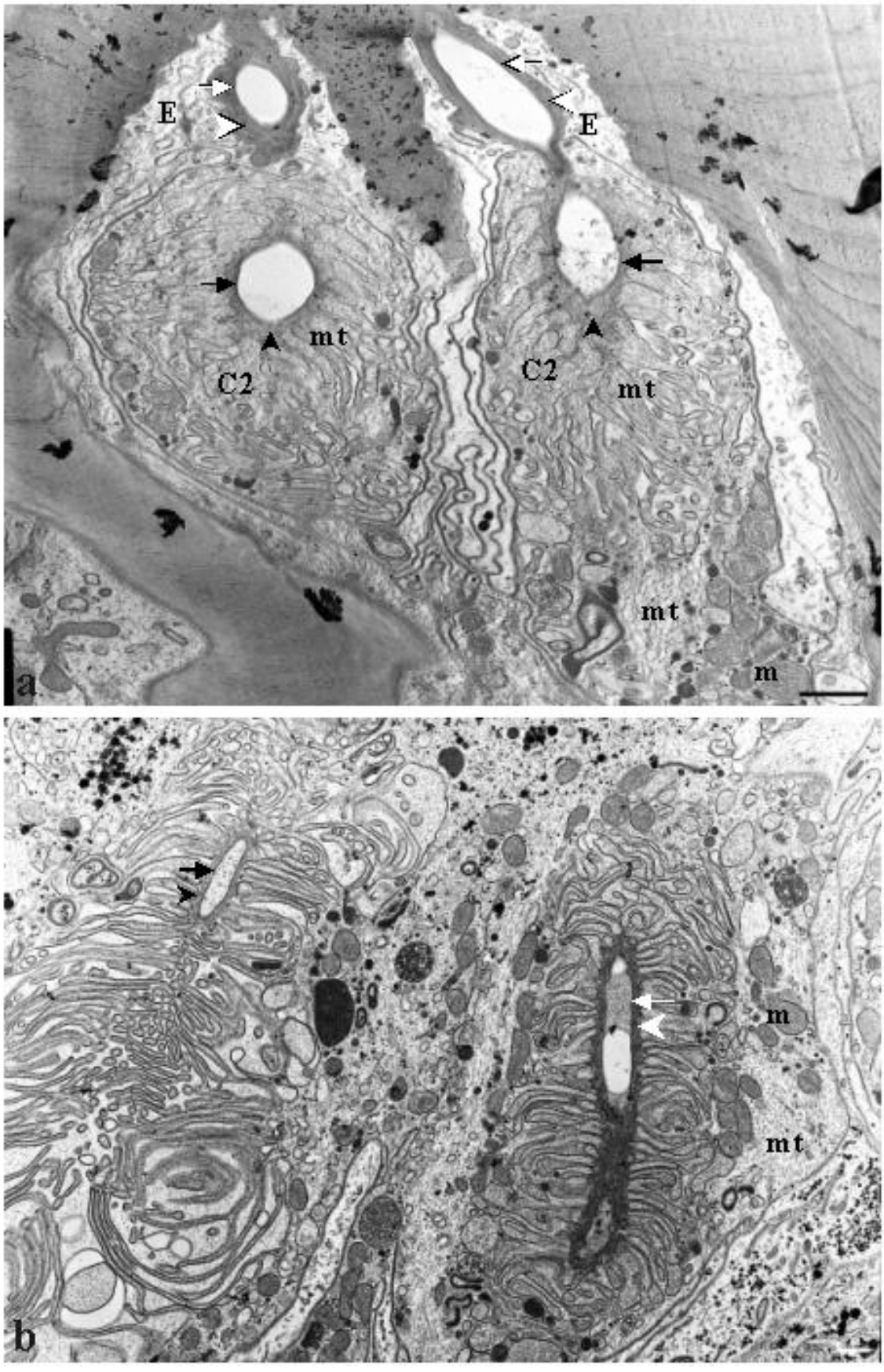

E
E
mt
C2
C2
mt
mt
m
a
m
mt
b

Fig. 23a Longitudinal section. The electron-lucent cytoplasm of the envelope cell (E) contains sparse cell organelles. The irregular-shaped, heterochromatic nucleus (nE) has a basal position. Scale bar: 1 µm.

Fig. 23b Longitudinal section. The secretory canal cell (C1) contains conspicuous dictyosomes, numerous mitochondria and vesicles of varying size and electron-density. The adjacent envelope cell (E) contains glycogen, small vesicles and an irregular shaped nucleus (nE). Scale bar: 2 µm.

Fig. 23c Cross-section. Inside the pore, the secretory canal cell (C1) contains numerous mitochondria (m) and microtubules (mt). The thin, electron dense ductule cuticle (white arrow) is surrounded by electron-dense material in continuation with the electron-dense material that surrounds the microvilli on the outside. The envelope cells (E) that surround C1 contain numerous microtubules (mt). Scale bar: 0.5 µm.

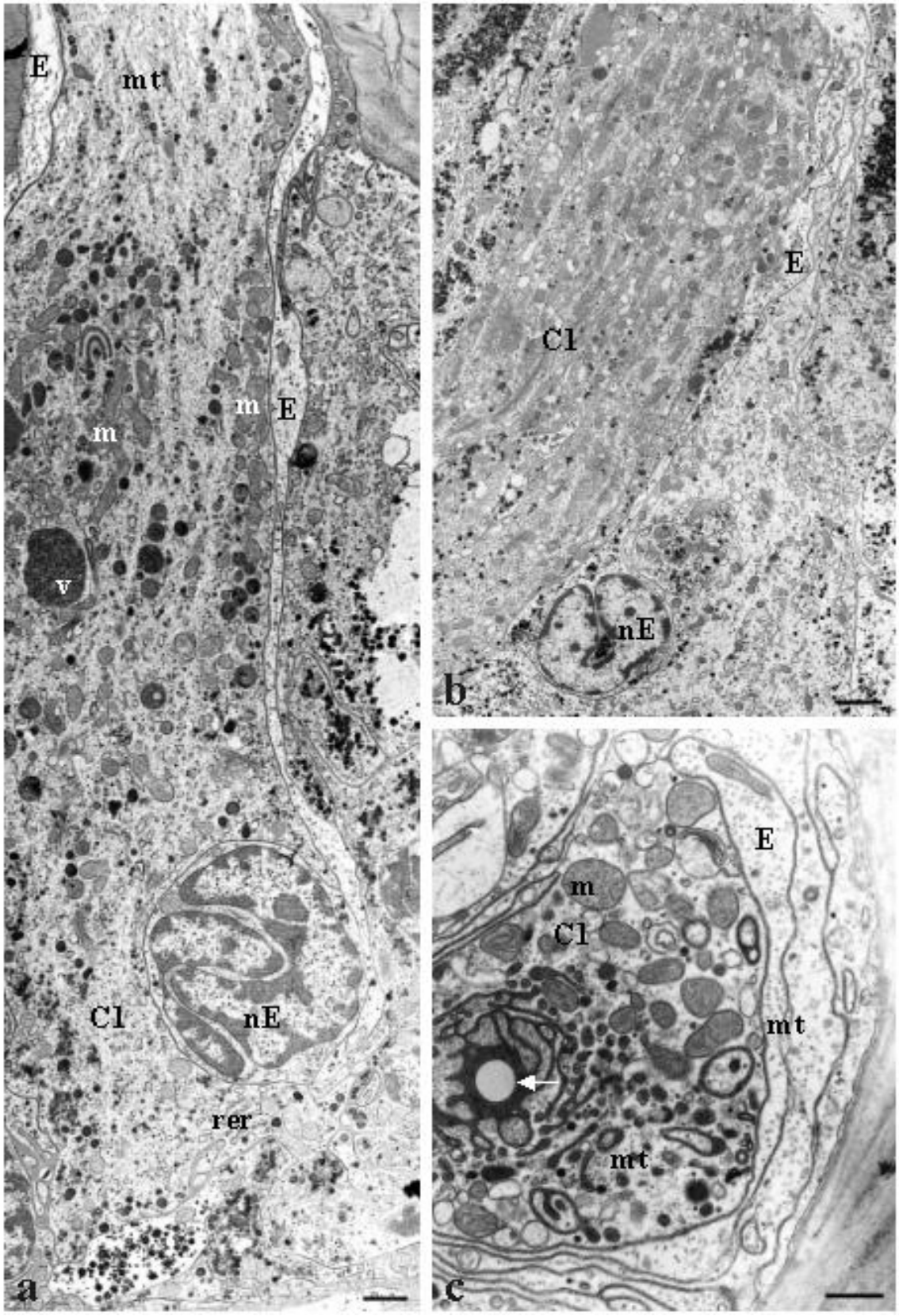

E
mt
m
m
E
v
Cl
nE
rer
a
E
Cl
nE
b
E
m
Cl
mt
mt
c

Fig. 24a Apically, the intercalary cells I exhibit microvilli (mv) and send finger-like cell extensions into the pore canals of the spermathecal cuticle. The cell extensions are densely filled with tubular filaments (arrow heads). The apical cell body contains mitochondria (m) and glycogen aggregations (white asterisk). The plasma membranes of the intercalary cells (I) interdigitate. Scale bar: 1 µm.

Fig. 24b Mitochondria (m) lie in the proximity of a bundle of pore canal filaments (fi) that reach far into the cytoplasm of the intercalary cell (I). Scale bar: 1 µm.

Fig. 24c The cell membrane of the filament (fi) filled, finger-like cell extension of the intercalary cell is clearly visible (arrow). Scale bar: 0.5 µm.

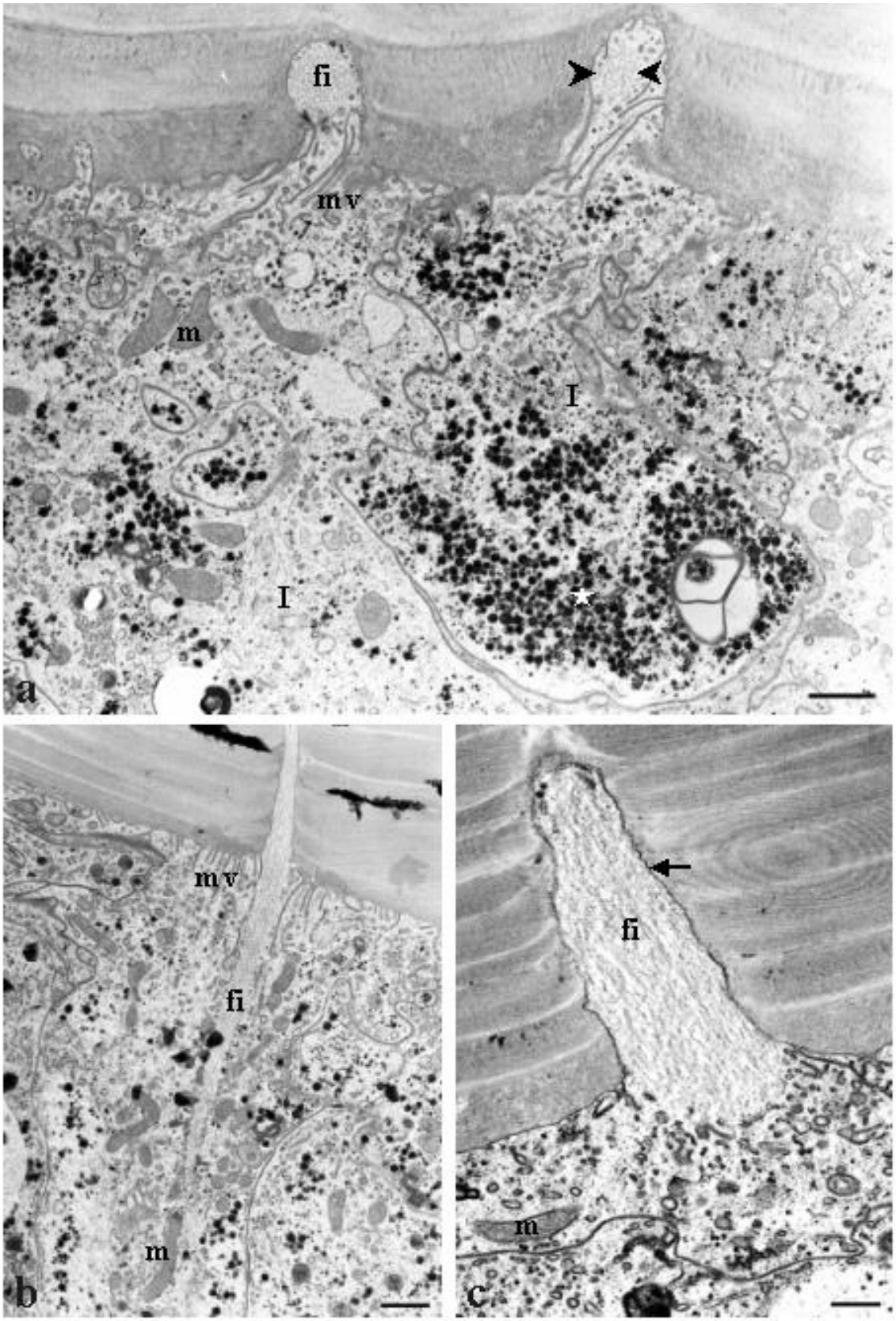

fi
mv
m
I
I
a
mv
fi
m
b
fi
m
c

Fig. 25a The ordinary epithelial cells around the middle portion of the spermatheca and the end of the copulatory duct possess irregular-shaped, heterochromatic nuclei. The cytoplasm is packed with glycogen particles (arrow). The elongated, spindle-shaped, more electron-lucent regions (asterisks) are not bound by cell membranes. Scale bar: 2 µm.

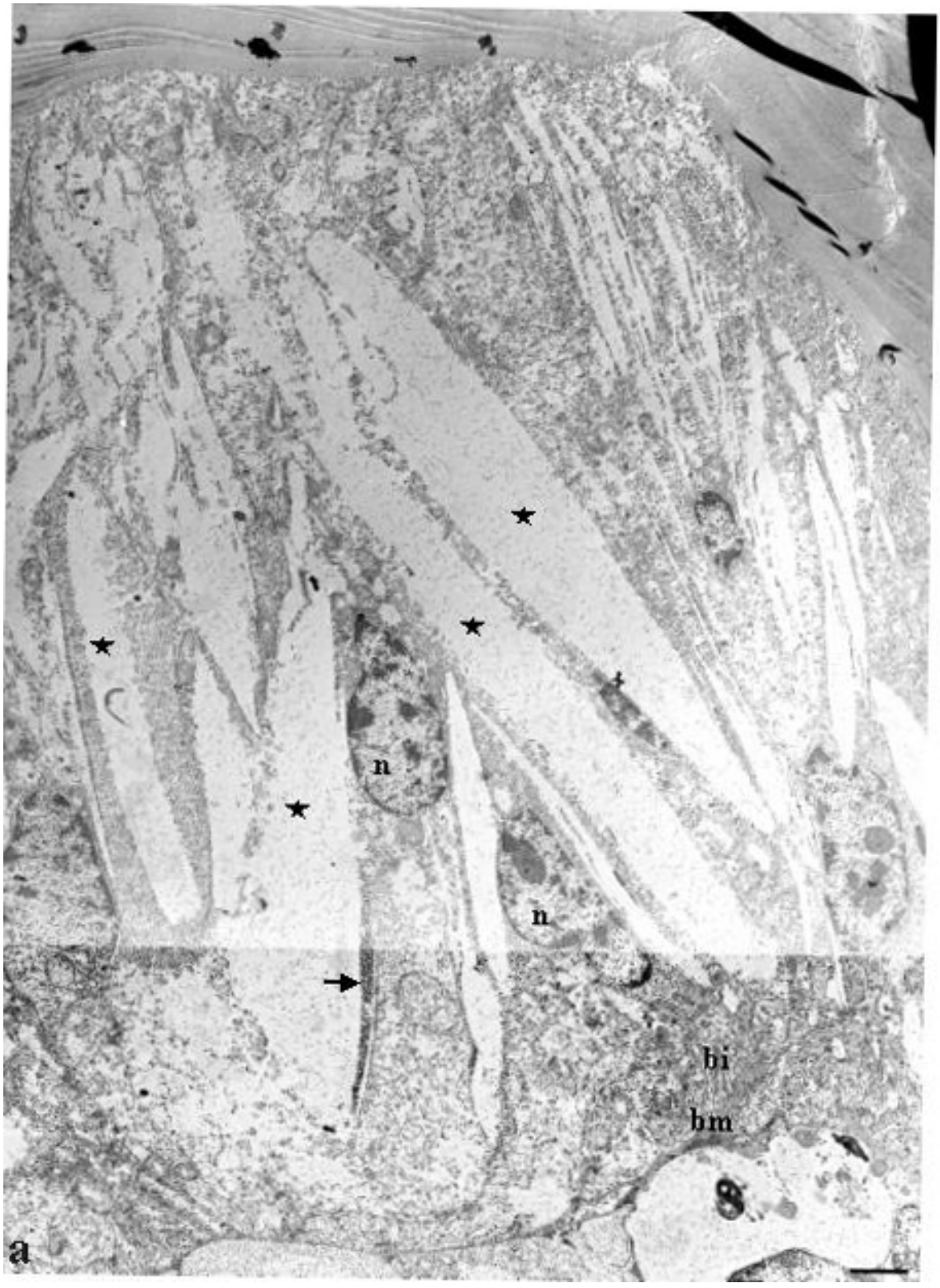

n
n
bi
bm
a

Fig. 26a Schematic drawing of the longitudinally-cut female genitalia: (at) atrium; (cd) copulatory duct; (ef) epigastric furrow; (go) gonopore; (sp) spermatheca; (ue) uterus externus; (ui) uterus internus.

Fig. 26b The cuticular lining of the epigastric furrow exhibits vertical extensions. Scale bar: 5 µm.

Fig. 26c The thin cuboidal epithelium of the epigastric furrow (ef) is covered by a cuticle with vertical extensions (see Fig. 26b). Scale bar: 20 µm.

Fig. 26d Close to the opening of the epigastric furrow, the ventral wall is made up of a thin cuboidal epithelium with pigment granules (asterisk). Scale bar: 10 µm.

Fig. 26e At the opening of the gonopor, the amount of pigment granules of the ventral cuboidal epithelium decreases, whereas the degree of vacuolisation increases (asterisk). Scale bar: 10 µm.

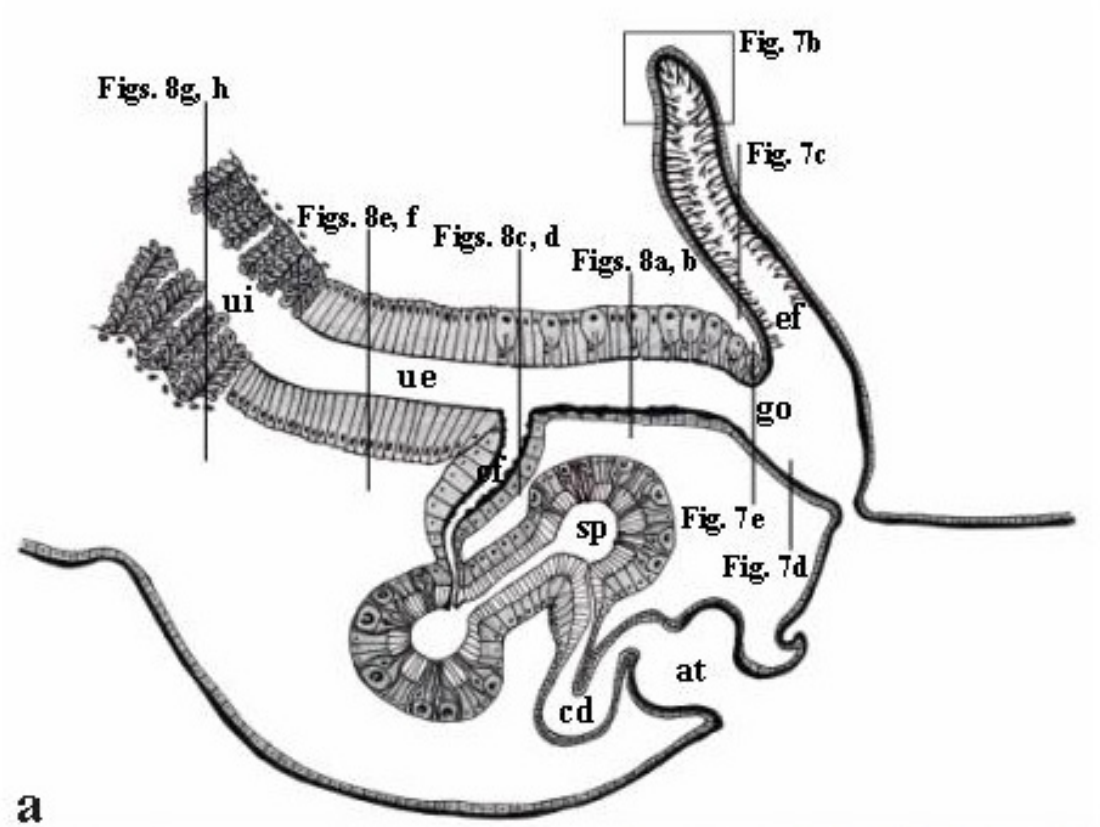
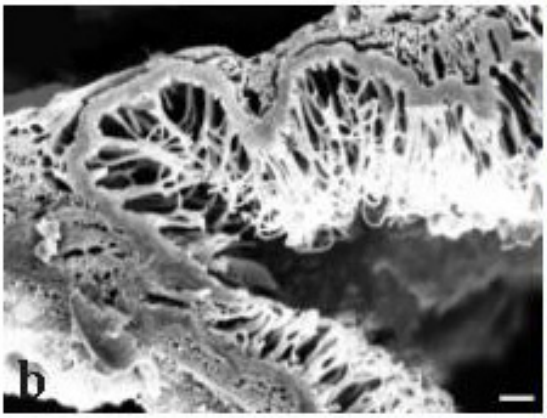
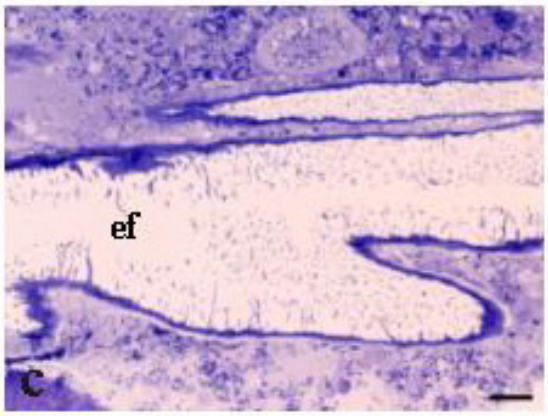
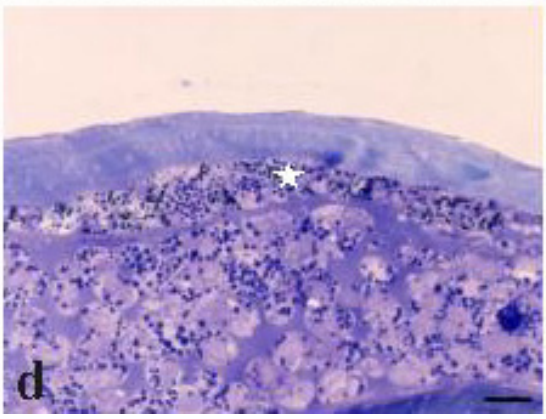


Fig. 7b
Figs. 8g, h
Fig. 7c
Figs. 8e, f
Figs. 8c, d
Figs. 8a, b
ui
ef
ue
go
of
sp
Fig. 7e
Fig. 7d
at
cd
a


b


ef
c


d

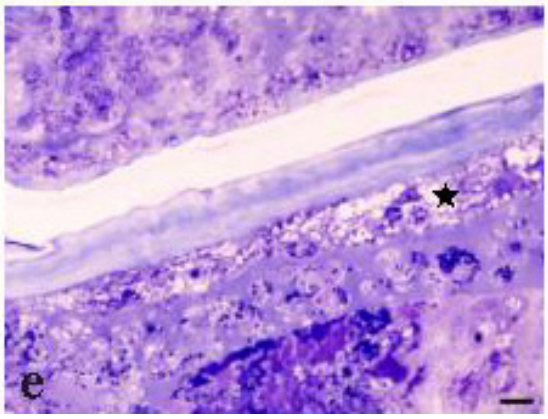

e

Fig. 27a The epithelium of the posterior wall of the gonopor consist of huge glands (asterisks) that are surrounded by prismatic epidermal cells that contain many vacuoles (or secretory granules?). The secretion (se) in the uterus externus, most probably produced by the glands, stains extensive blue with toluidine blue. Scale bar: 20 µm.

Fig. 27b The terminal gland cell (asterisks) has an invagination which seems to be in contact with a conducting canal of a more apical cell (black arrow head). The canal traverses the cuticle and opens into the lumen of the uterus externus (white arrow head). Scale bar: 5 µm.

Fig. 27c At the height of the junction of the common fertilisation duct and the uterus externus, the lumen is filled with light blue droplets imbedded in a homogenous, light pinkish secretion (se). The pouches of the common fertilisation (cf) duct are covered by a relatively thick cuticle. Scale bar: 20 µm.

Fig. 27d At the high of the junction of the common fertilisation duct and the uterus externus, the epithelium of the dorsal wall only contains few glands among numerous, highly-vacuolised (secretory granules?) epidermal cells. Scale bar: 5 µm.

Fig. 27e Anterior to the junction with the common fertilisation duct, the dorsal wall of the uterus externus (ue) comprises a high columnar epithelium. Scale bar: 20 µm.

Fig. 27f The high columnar epithelium of the uterus externus shows pronounced basal infoldings (bi) and secretory granules (asterisk). The thin cuticle is covered by a light pinkish secretion (toluidine blue). Scale bar: 5 µm.

Fig. 27g The uterus internus (ui) is formed by a secretory epithelium devoid a cuticular lining. Transversally-sectioned muscle fibres (mu) accompany the epithelium. Scale bar: 20 µm.

Fig. 27h The cells of the uterus internus (ui) have a small basis and a broad apex. Secretion is visible among the cells as light blue droplets (toluidine blue) of various sizes (arrow heads). Scale bar: 5 µm.

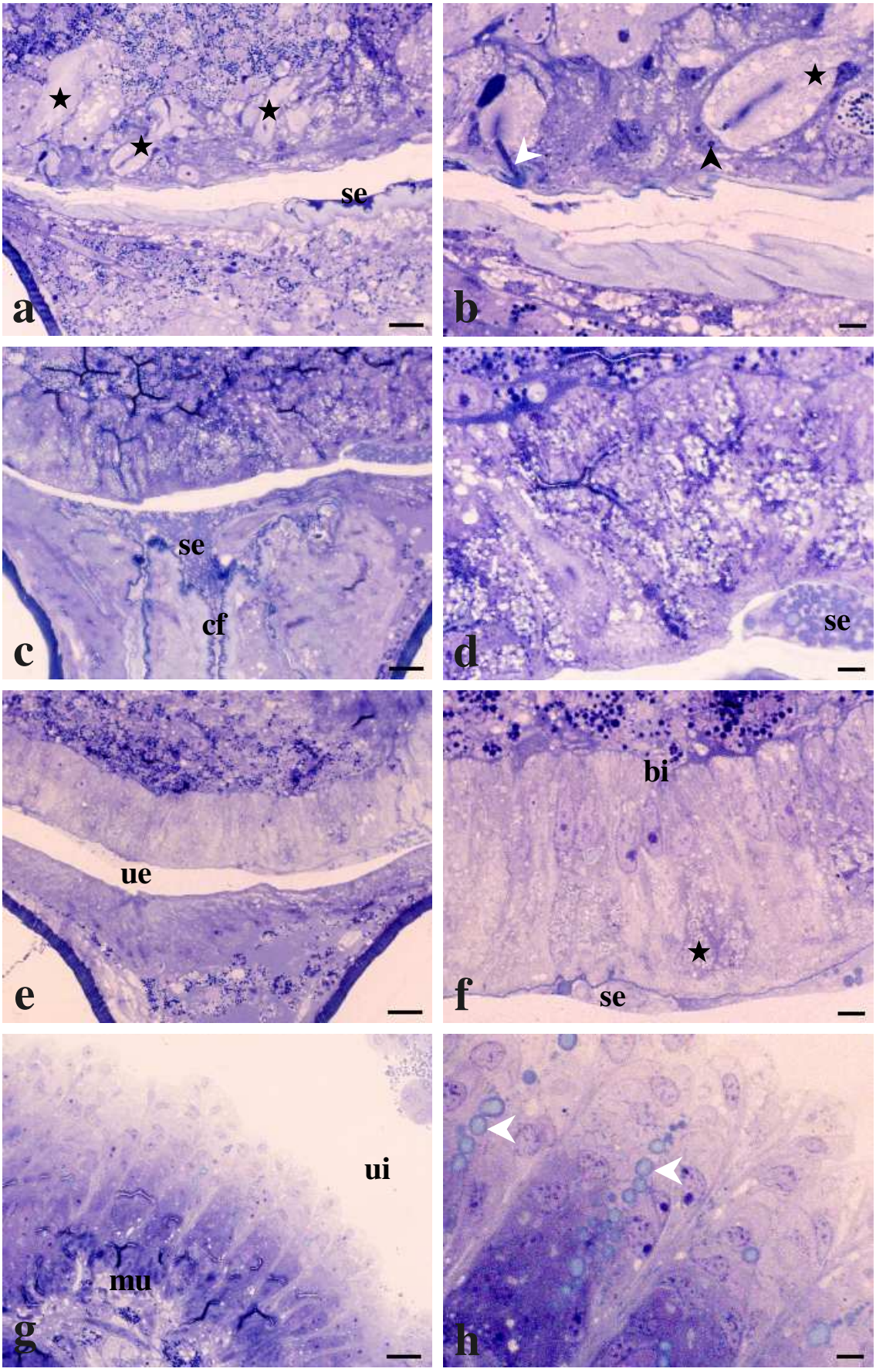

a
se
b
c
se
cf
d
se
e
ue
f
bi
se
g
ui
mu
h

Fig. 28a The vessel (ve) close to the spermathecal epithelium (spe) contains a hemocyte. Scale bar: 2 µm.

Fig. 28b A granular hemocyte that contains electron-dense vesicles lies closely attached to the basement membrane (bm) of the basal infoldings (bi) of the spermathecal epithelium. Scale bar: 1 µm.

Fig. 28c The granular hemocyte exhibits rough endoplasmic reticulum around the nucleus (arrow). The hemocyte is surrounded by the basal infoldings (bi) of the spermathecal epithelium. The basement membrane appears thinner (arrow head). Scale bar: 1 µm.

Fig. 28d A granular hemocyte appears incorporated into a gland cell (G1) of the spermathecal epithelium. Basally, a cell (asterisk) containing myelin-like bodies (arrows) partly surrounded by the basement membrane. Scale bar: 2 µm.

Fig. 28e A cell filled with myelin-like bodies lies inside the spermathecal epithelium. Scale bar: 1 µm.

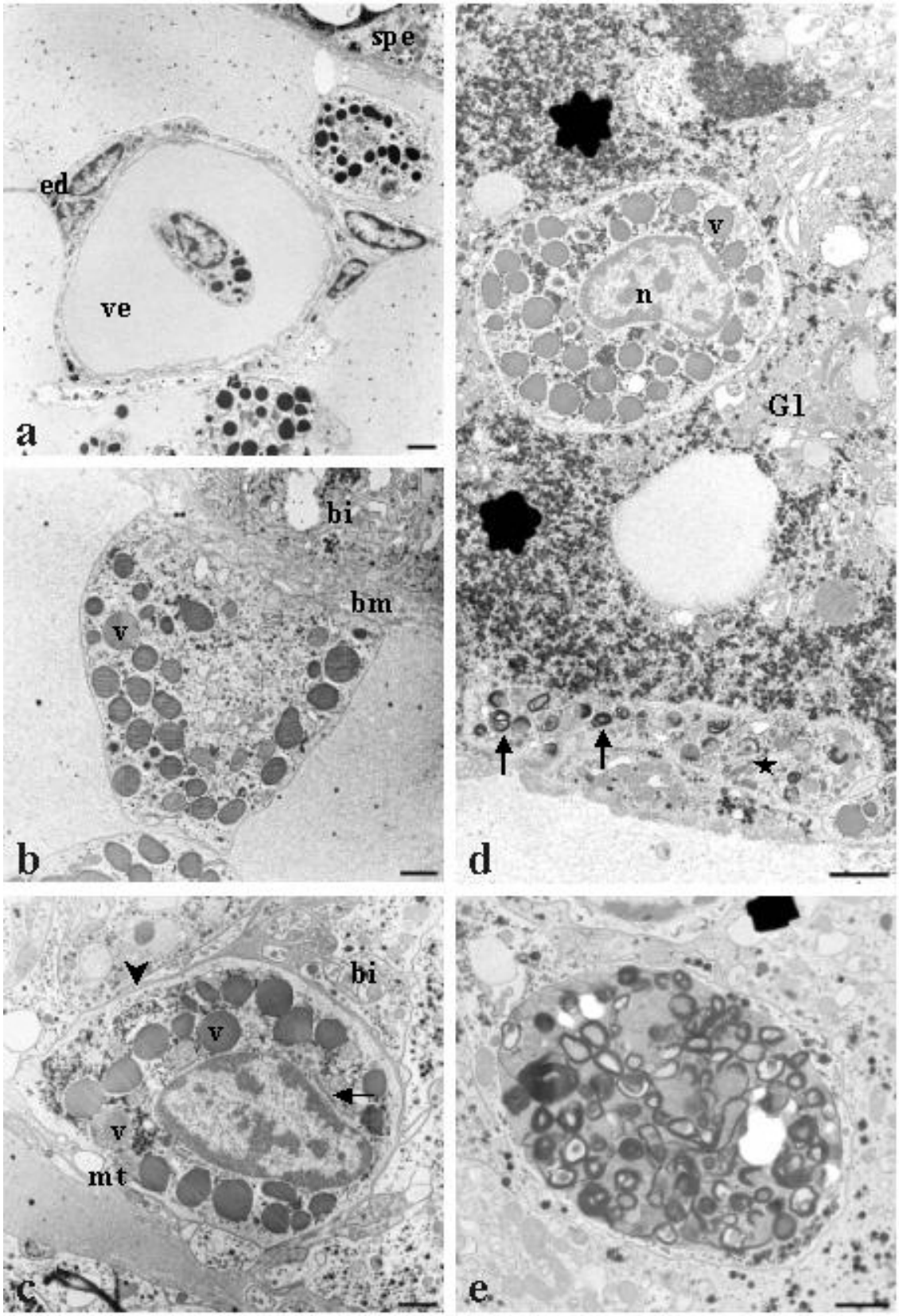

spe
ed
ve
a
bi
bm
v
b
v
n
Gl
d
bi
v
v
mt
c
e

Fig. 29a The granular hemocyte exhibits rough endoplasmic reticulum around the nucleus (arrow). Furthermore, the cytoplasm contains moderate electron-dense vesicles (v), small particles and lysosomes (ly). Scale bar: 1 µm.

Fig. 29b The granular hemocyte contains moderate electron-dense vesicles (v), small particles and a large lysosome (ly). Scale bar: 1 µm.

Fig. 29c The hemolymph contains almost no cell organelles apart from the nucleus with a prominent nucleolus (no). Scale bar: 1 µm.

Fig. 29c The axons (ax) of the nerve fibre that is closely attached to the endothel (ed) of a blood vessel contain microtubules, vesicles and granules. The ensheathing glial cell extensions (gl) contain glycogen and are surrounded by a basement membrane (bm). Scale bar: 0.2 µm.

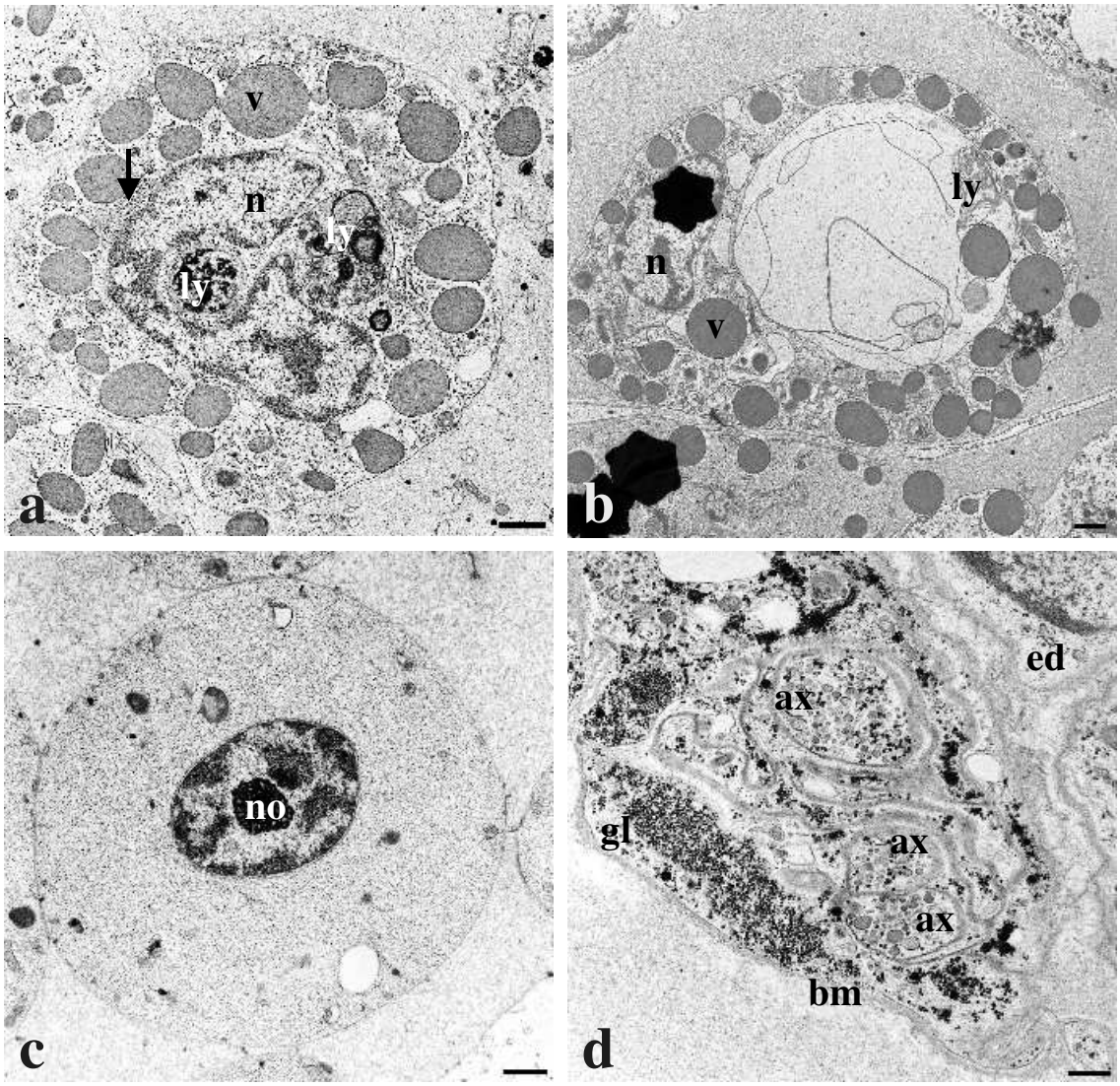

v
n
ly
ly
a
ly
n
v
b
no
c
ed
ax
gl
ax
ax
bm
d

Fig. 30a Male *Latrodectus revivensis* (dorsal view). Scale bar: 2 mm.

Fig. 30b Male pedipalps (ventrofrontal view). The embolus tip rests on the conductor (arrow). Scale bar: 200 µm.

Fig. 30c Male pedipalp (retrolateral view): (cy) cymbium. Scale bar: 200 µm.

Fig. 30d Male pedipalp (ventral view). Scale bar: 200 µm.

Fig. 30e Male pedipalp (prolateral view). Scale bar: 200 µm.

Fig. 30f Male pedipalp (dorsal view). Scale bar: 200 µm.


a
b
cy
c
d
e
f

Fig. 31a The tibia (dorsal view) bears trichobothria (tr), tactile hairs (tc) and slit sense organs (sl). Scale bar: 20 µm.

Fig. 31b Male (frontal view). The thickened base of the embolus (asterisk) is joined to the radix by a delicate cuticle. Scale bar: 300 µm.

Fig. 31c The cymbium (cy) (dorsal view) is covered with hairs of varying size. The bowl-shaped tibia (ti) bears one dorsal and two retrolateral trichobothria (arrows). Scale bar: 100 µm.

Fig. 31d The cymbium bears tactile hairs (tc) and numerous slit sensilla (sl). Scale bar: 10 µm.

Fig. 31e So far undescribed structures (arrows) of unknown function are situated on the frontally directed surface of the cymbium. Scale bar: 50 µm.

Fig. 31f A pit-like tarsal organ (arrow) lies in the middle of the lobed surface of the cymbium. Scale bar: 100 µm.

Fig. 31g The ampulla-shaped parts of the so far undescribed structures are directed towards the inside of the cymbium (arrow head). The club-shaped portion protrudes from the cymbial surface (arrow). Scale bar: 20 µm.

Fig. 31h The ampulla-shaped parts of the so far undescribed structures are directed towards the inside of the cymbium (arrow head). The club-shaped portion protrudes from the cymbial surface (arrow). Scale bar: 20 µm.

Fig. 31i The club-shaped portion of the so far undescribed structures protrudes from the cymbial surface (arrow). Scale bar: 20 µm.

Fig. 31j Pit-like tarsal organ of the cymbium. Scale bar: 5 µm.

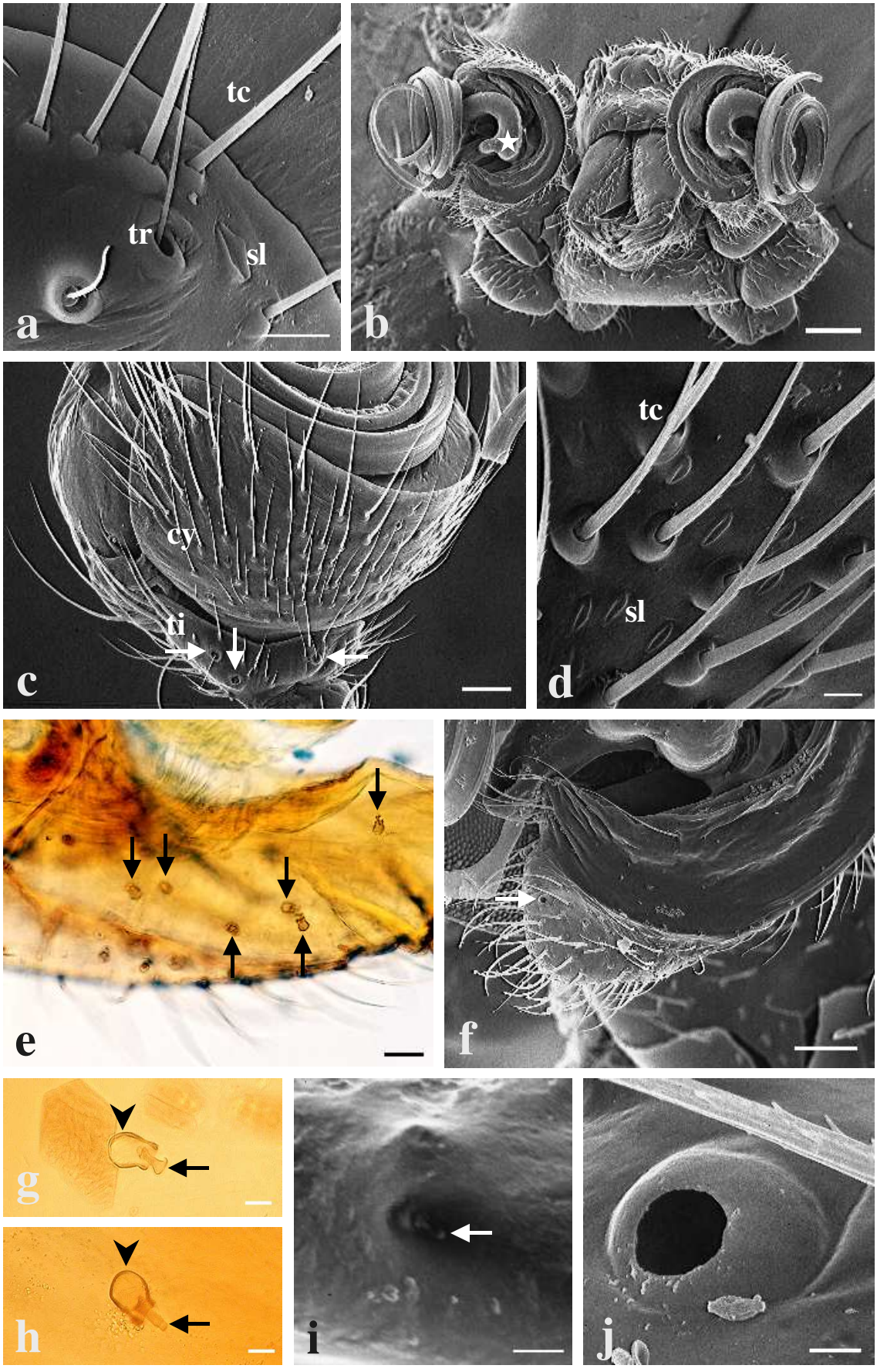

tc
tr
sl
a
b
cy
ti
c
tc
sl
d
e
f
g
h
i
j

Fig.32a Male pedipalp (ventral view). The embolus (em) with its intact embolus tip (t) is dislodged due to preparation. Scale bar: 200 µm.

Fig. 32b Cleared pedipalp. The genital bulb consists of various sclerites connected by membranous parts (hematodochae). The spermophor consists of the fundus (f), the reservoir (r) and the ejaculatory duct inside the embolus (better visible in Fig. 32d). Scale bar: 200 µm.

Fig. 32c The apex of the embolus tip is slightly flattened and bears the oval opening. Scale bar: 2 µm.

Fig. 32d Cleared apical portion of the embolus. The main part of the embolus that ends at the breaking point (arrow) before the embolus tip (t) can be divided into the dark truncus (tu) and the membranous *pars pendula* (pp). They surround the ejaculatory duct (ej). Scale bar: 100 µm.

Fig. 32e Breaking point of the embolus. Scale bar: 10 µm.

Fig. 32f The embolus tip is an S-shaped sclerite. The transition between the tip and the rest of the embolus is marked by a saddle-like thickening (arrow). The opening (arrow head) lies approx. 30µm from the apex. Scale bar: 50 µm.

Fig. 32g Broken off embolus tip. A canal with a diameter of approx. 4 µm runs through the tip. Scale bar: 5 µm.

Fig. 32h Broken embolus. The truncus (tu) forms an U-shaped channel closed by the *pars pendula* (pp). Inside lies the ejaculatory duct (ej) originating from the reservoir. Scale bar: 5 µm.

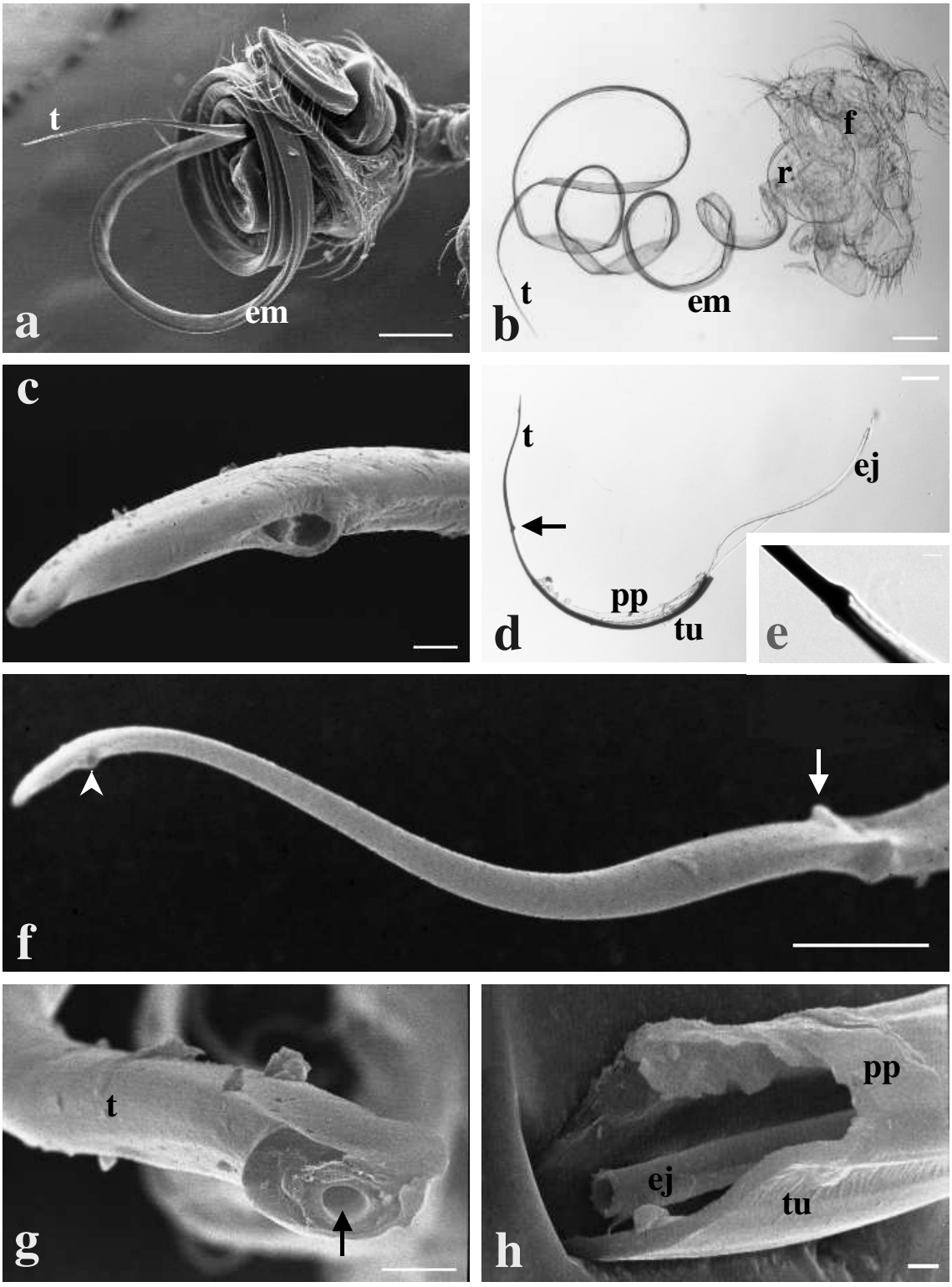

t
em
a
f
r
t
em
b
c
t
ej
pp
tu
d
e
f
t
g
pp
ej
tu
h

Fig. 33a Male tarsus (ventral view). The serrated bristles (sb) possess many small teeth on their ventral side. Tactile hairs (tc) cover all sides of the tarsus. Chemoreceptive hairs (ch) are arranged in more or less longitudinal lines. Scale bar: 30 µm.

Fig. 33b The smooth surfaced, S-shaped chemoreceptive hairs arise at a steep angle. Their tips each have a small opening to the outside (arrows). Scale bar: 20 µm.

Fig. 33c Cleared tarsus (lateral view). The serrated bristles are situated on the ventral side, opposite the three moveable claws. One of the two ventrolateral situated slit sensilla ('claw slits') is visible (arrow). Scale bar: 50 µm.

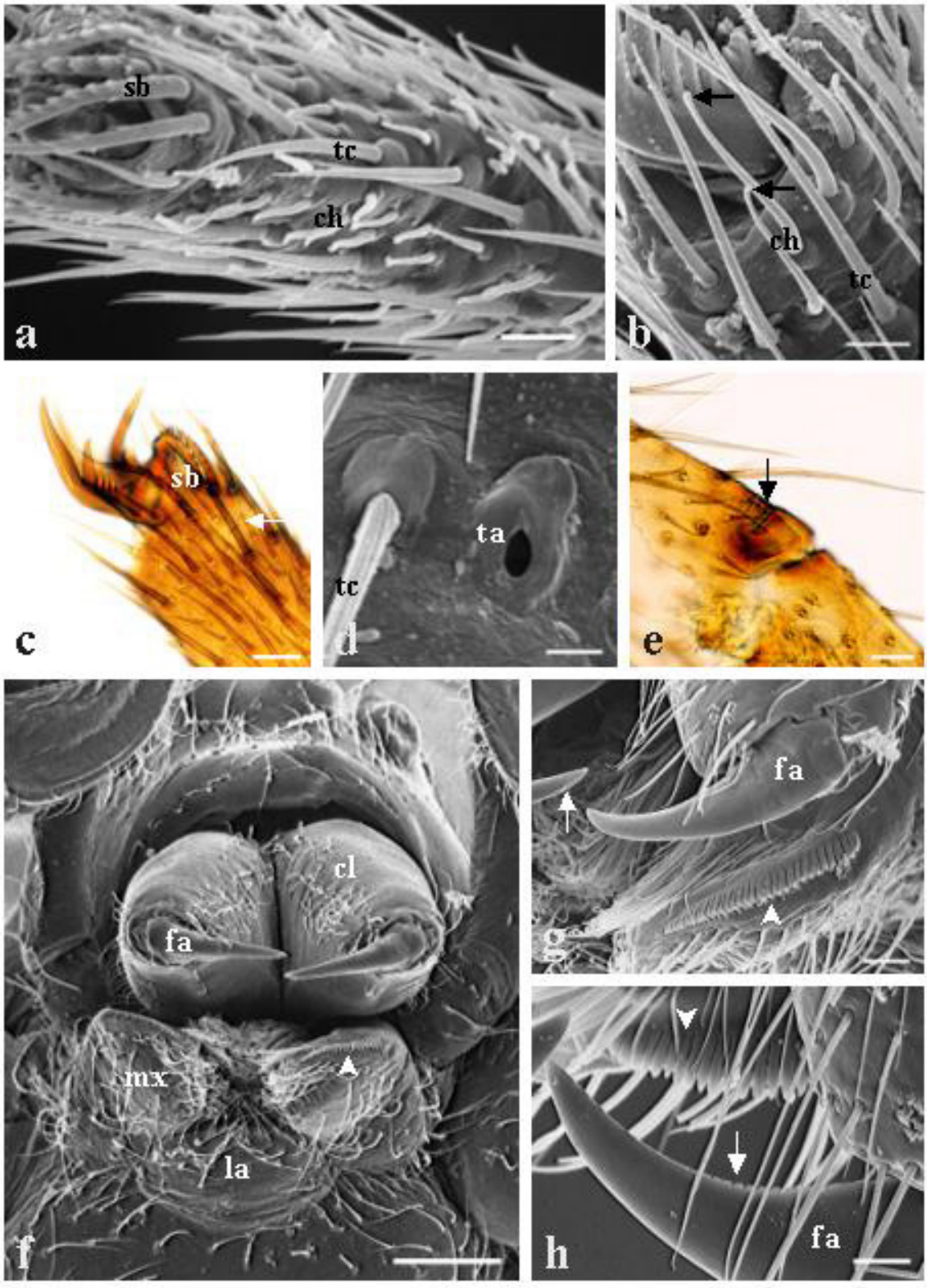
Fig. 33d The tarsal organ (ta) resembles a circular pit. The tactile hair (tc) has a ribbed surface and arises at a steep angle. Scale bar: 10 µm.

Fig. 33e The metatarsal lyriform organ (arrow) consists of parallel slit sensilla oriented perpendicular to the long axis of the leg. Scale bar: 50 µm.

Fig. 33f Male, mouth region (ventral view). The mouth opening is bordered laterally by the maxillae (mx) and at the back by the labium (la). The anterior rim of the maxilla bears a serulla (arrow head). The chelicerae (cl) consists of a stout basal part and a moveable fang (fa). Scale bar: 200 µm.

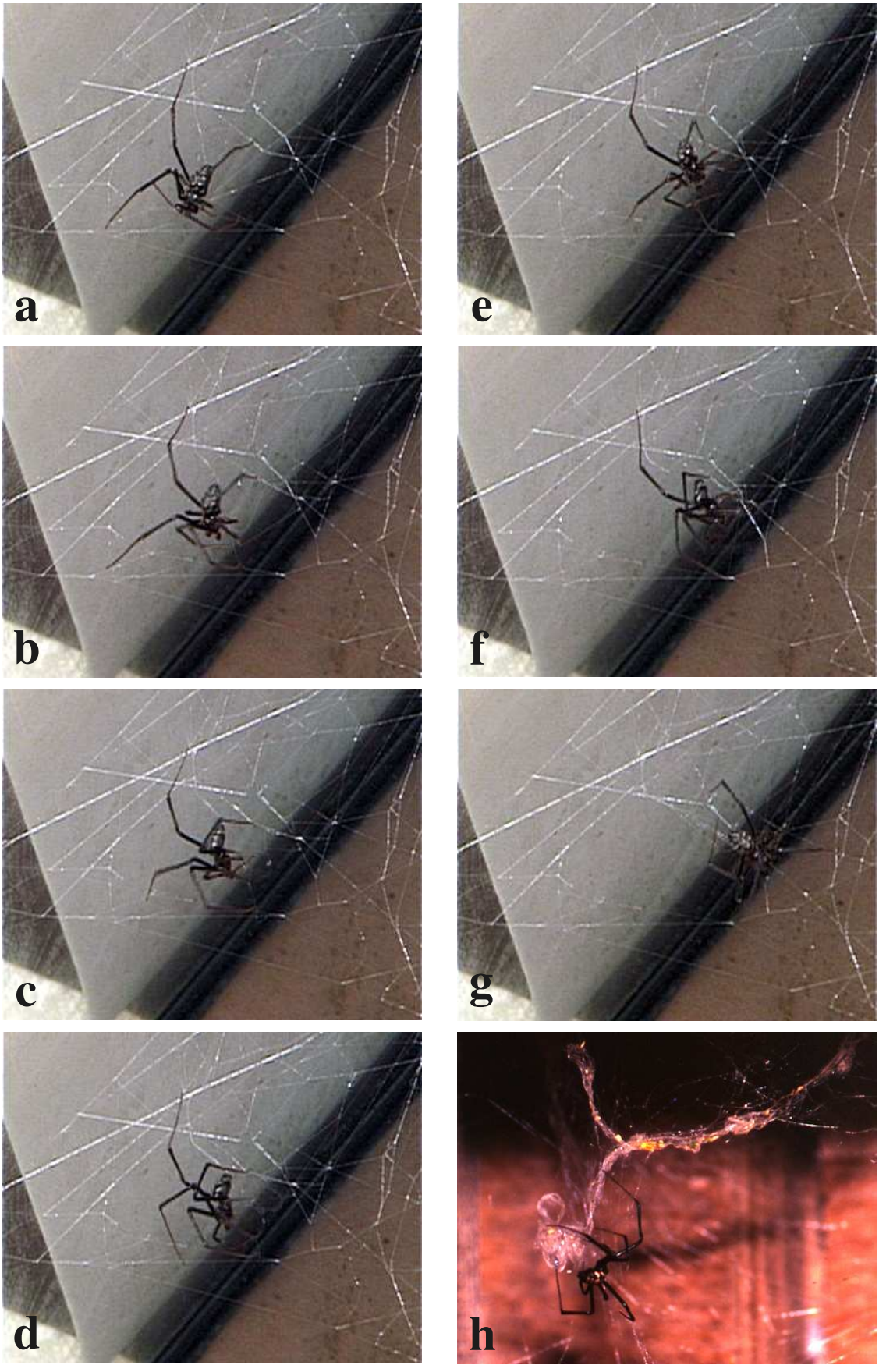
Fig. 33g The anterior rim of the maxilla bears a serulla (arrow head). The opening of the fang (fa) is situated at the tip (arrow). Scale bar: 40 µm.

Fig. 33h The inner edge of the fang (fa) is finely serrated (arrow). The arrow head indicates the serulla of the maxilla. Scale bar: 20 µm.


sb
tc
ch
a
ch
tc
b
sb
c
ta
tc
d
e
cl
fa
mx
la
f
fa
g
fa
h

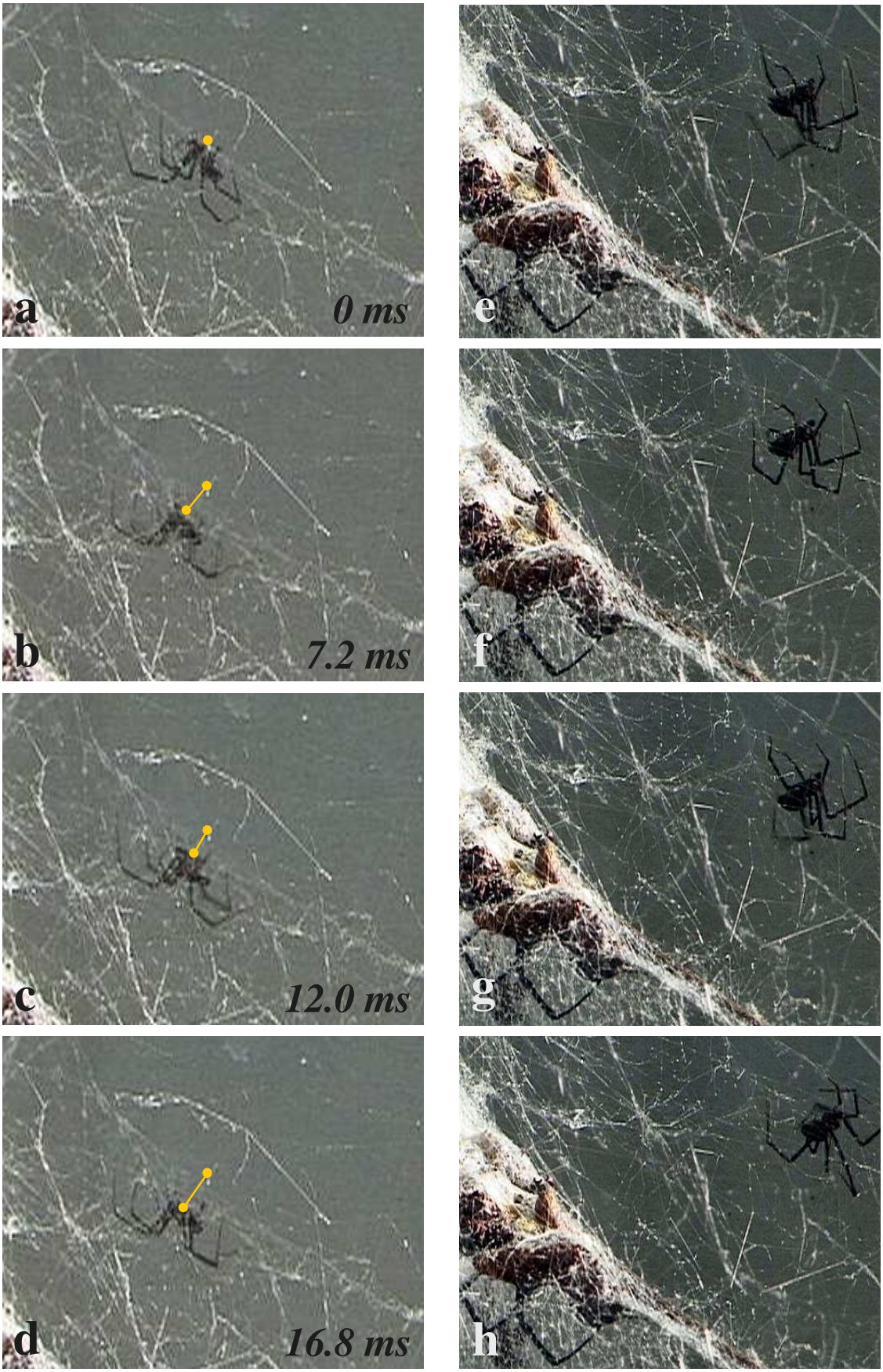
Figs. 34a-g Cutting, bundling: After cutting the threads of the female web (a-d) the male gathers the loose threads with his mouthparts (e, f) and covers them with his own silk (g).

Fig. 34h Bundling: The cut female's threads are compressed into bands and sheets and covered with the male's own silk.


a
e
b
f
c
g
d
h

Figs. 35a-d Cutting: After cutting a supporting thread the male bounces up and down over a distance of approx. 4 mm (yellow marking).

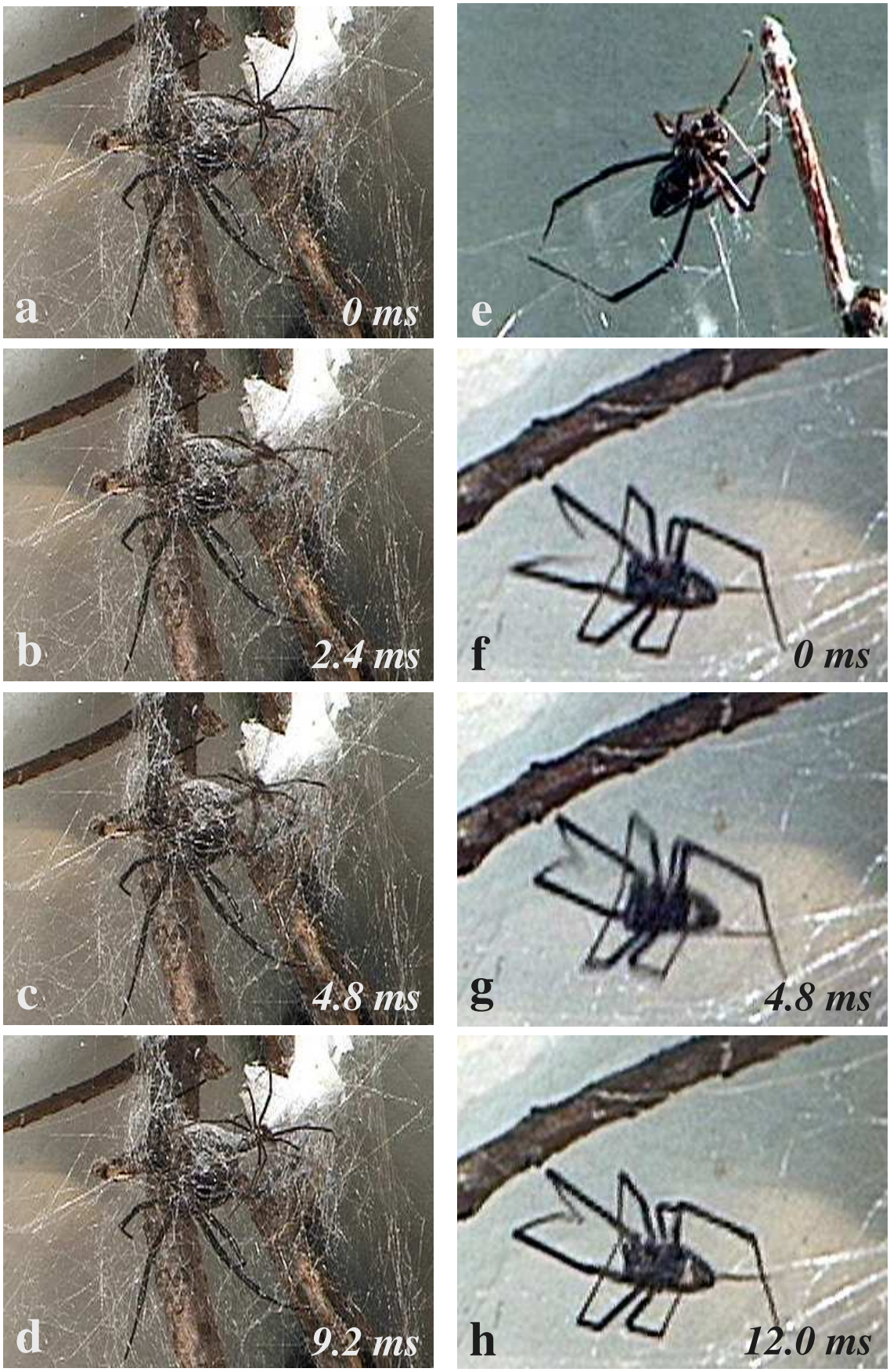
Figs. 35e-h Spinning/trailing silk: After cutting (a-d) the male makes a turn of approx. 180° on the same plane. After spinning the loose threads (e-g) the male starts walking by trailing further silk (h).


a
0 ms
b
7.2 ms
c
12.0 ms
d
16.8 ms
e
f
g
h

Figs. 36a-d Jerking: Following a rejecting movement by the female, the male jerks by means of a quick and vigorous flexion of the legs without releasing the lines of the web.

Fig. 36e Strumming sequence/mouthpart tugging: The male takes the typical position for a strumming sequence. The first pair of legs is stretched out and grasps the main thread. The tarsi of legs II almost touch each other in front of the pedipalps forming a loop. Tarsi of legs III meet under the sternum of the prosoma. Legs IV are stretched out, grasping threads of the surrounding web. The male tugs the single thread that runs along between the mouthparts.

Figs. 36f-h Strumming sequence/twanging: The main thread is rapidly tensioned and then suddenly released.


a
0 ms
e
b
2.4 ms
f
0 ms
c
4.8 ms
g
4.8 ms
d
9.2 ms
h
12.0 ms

Figs. 37a-d Strumming sequence/palp rubbing: The yellow arrows indicate the brief anterodorso-posteroventral movements of the left pedipalp (yellow asterisk). Anterior of his chelicerae, the left pedipalp is lifted from the silk (a, b), brought posteriorly and back downwards onto the thread just ventrally from the chelicerae (c). Finally, the pedipalp is moved frontally along the thread in a stroking manner (d).

Figs. 37e-h Strumming sequence/stroking: The tarsus (arrows) is moved along the thread in sliding contact with the silk (e-g), lifted off and brought back to a position close to the pedipalps (h).

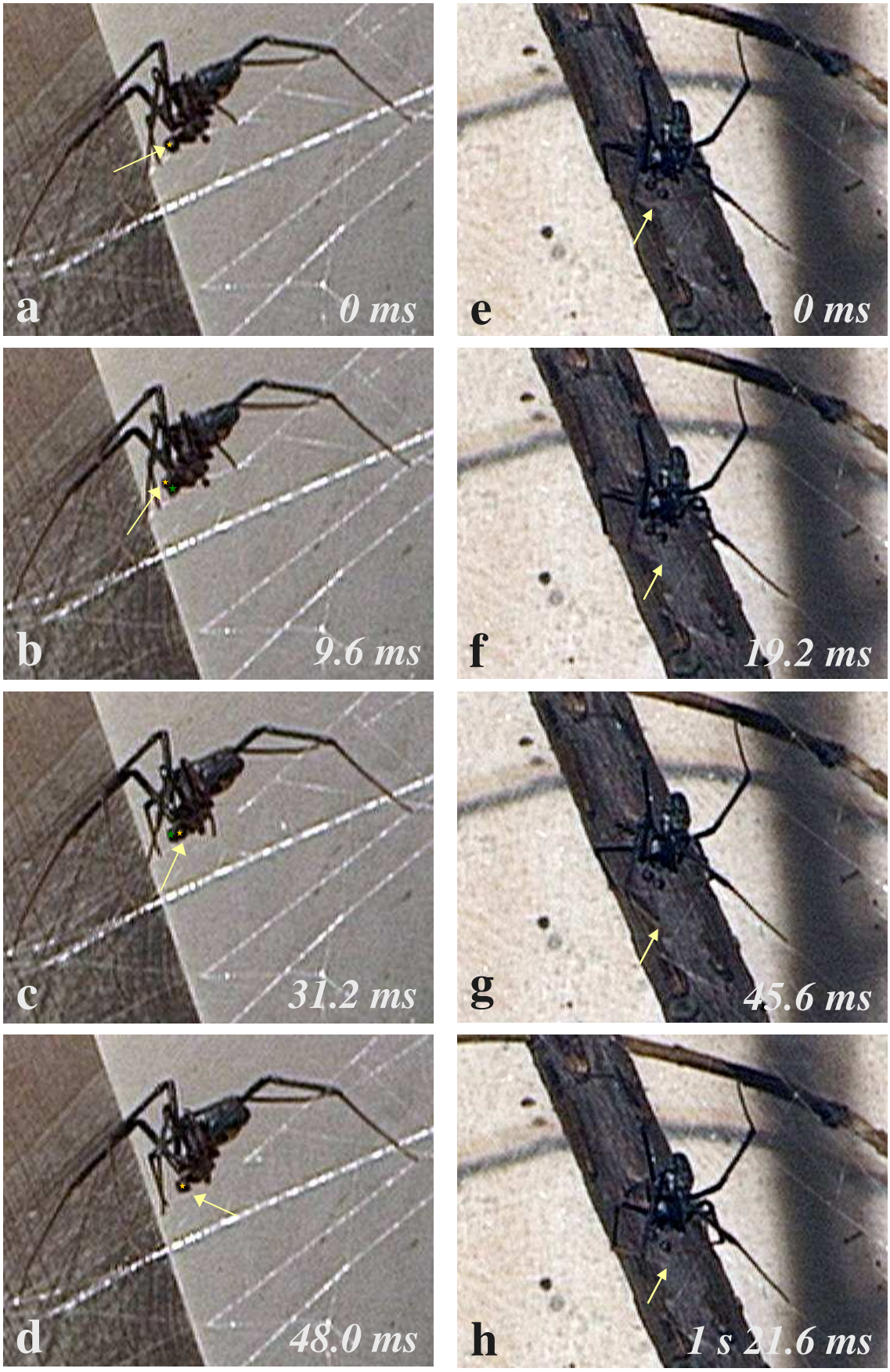

a
0 ms
e
0 ms
b
9.6 ms
f
19.2 ms
c
31.2 ms
g
45.6 ms
d
48.0 ms
h
1 s 21.6 ms

Fig. 38a The male achieves first tactile contact by carefully caressing the female's front legs (arrow).

Fig. 38b Strumming sequence: Strumming sequences are also performed on a single thread (arrow) inside the female retreat.

Fig. 38c Scrabbling/nibbling: During a cheliceral scrabbling/nibbling sequence, the male positions the tarsus of his first leg directly on the mouth region of the female (arrow).

Fig. 38d Cheliceral scrabbling/nibbling: The male sits with his mouthpart directly positioned over the female atrium.

Figs. 38e, f Scrabbling: The right pedipalp (green asterisks) and left pedipalp (yellow asterisks) are lifted off the female's body and brought down again in an alternating pattern.

Figs. 38g, h Tapping: The left tarsus (leg I; arrow) is lifted off the female's body and brought down again.


a
e
b
f
c
g
d
h

Figs. 39a-d During coupling attempts the male lifts his body up by stilting his legs (a). He moves his abdomen sideways so that his body axis forming an angle of approx. 45° to the body axis of the female. The male lifts the left pedipalp (b, yellow asterisk). He then moves his right pedipalp (green asterisk) even further to the left underneath the left pedipalp (b). With his whole body tilting and finally shifting to the right, he attempts to couple his pedipalp to the carina of the female epigynal opening (c). After the unsuccessful attempt, the male moves a few millimetres backwards on the female opisthosoma (d).

Figs. 39e-g After he has successfully achieved genital coupling, the male shifts to the right, his body slowly tilts to the opposite, left side (f). The white, soft haematodochae inflates (g) (arrow).

Fig. 39h After copulation male and female sit in close proximity.

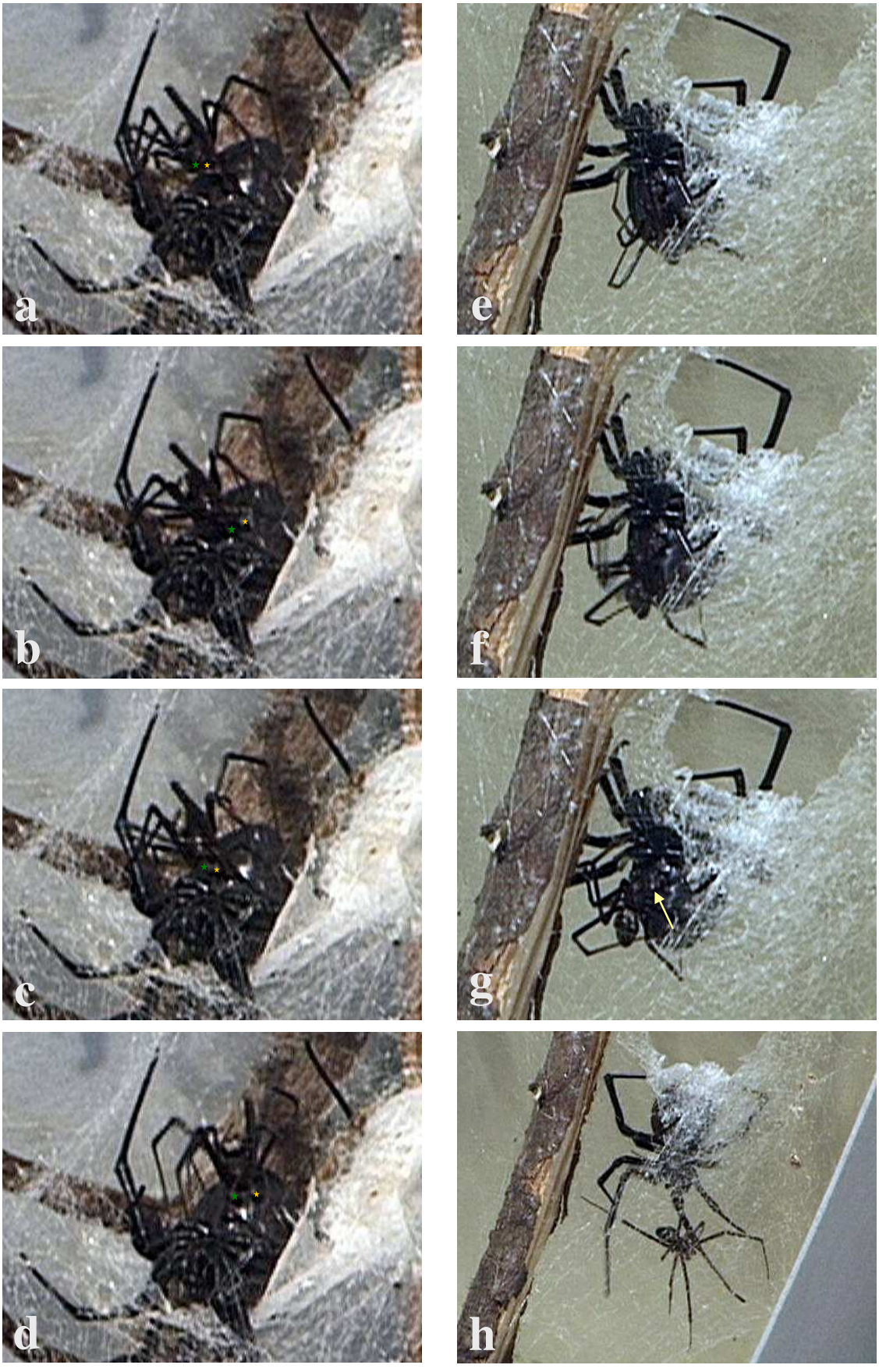

a
e
b
f
c
g
d
h

Fig. 40a The male spermophor is filled with a mass of spermatozoa that lie loosely embedded in secretions. Scale bar: 10 µm.

Fig. 40b The spermatozoa lie loosely embedded in secretions that consist of a homogenous purplish matrix (asterisk) and small droplets (arrow head). Scale bar: 5 µm.

Fig. 40c The spermatozoa form small disks that consist of the tightly-coiled sperm head and the flagellum indistinguishable from the head. Each spermatozoon is surrounded by a capsule. Secretion droplets (arrow head) are distributed among the spermatozoa. Scale bar: 2 µm.

Fig. 40d Virgin female. The spermatheca is filled with granular secretion (se). At the periphery the secretion appears rather homogenous where it is expelled through the gland pores (arrow). Scale bar: 20 µm.

Fig. 40e Virgin female. The spermatheca is completely filled with secretion (se). Scale bar: 20 µm.

Fig. 40f Female approx. 24 h after copulation. In the anterior lobe, only some of the granular female secretion (se) remains lying in isles among the spermatozoa. The majority of the female secretion appears to have been replaced by the sperm mass forming a dense layer covering the cuticle. Scale bar: 20 µm.

Fig. 40g Female approx. 24 h after copulation. The anterior lobe is filled with spermatozoa (s). Scale bar: 20 µm.

Fig. 40h Female approx. 24 h after copulation. The capsules of the spermatozoa (s) appear dilated. Little purplish, liquid secretion remains visible between the capsules. Further isolated isles are formed by blue droplets (se) imbedded in the same purplish, liquid secretion. Scale bar: 5 µm.

Fig. 40i Female approx. 24 h after copulation. The capsules of neighbouring spermatozoa are in direct contact with each other forming a compact mass with an overall structure that is reminiscent of a honeycomb. Scale bar: 2 µm.

Fig. 40j Female approx. 24 h after copulation. The flagellum of the spermatozoon is clearly visible and coiled around the elongated head. Scale bar: 1 µm.

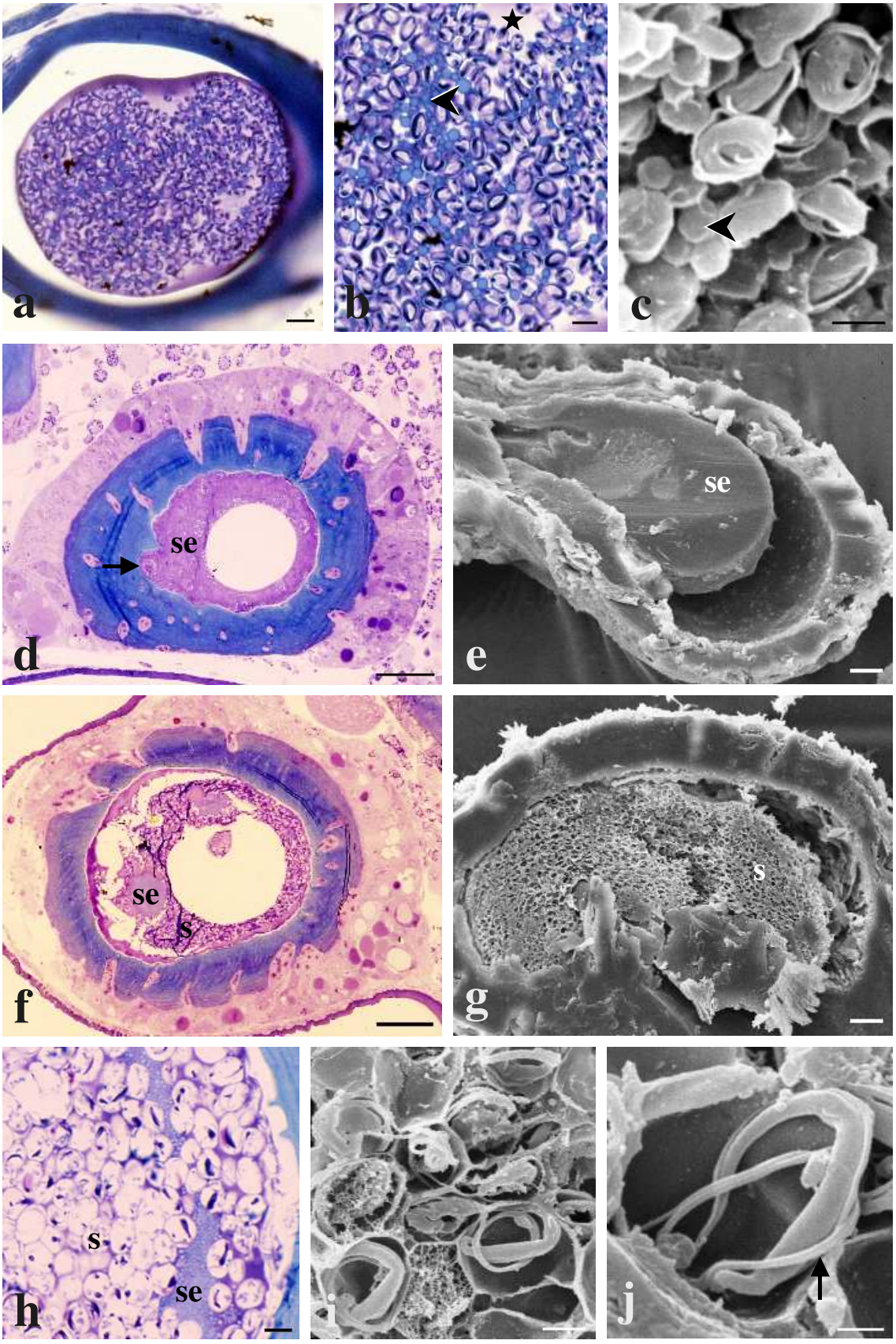

a
b
c
se
d
se
e
se
s
f
s
g
s
se
h
i
j

Fig. 41a Female approx. 12 h after the first oviposition. The posterior lobe is filled with granular secretion that appears less dense in the middle. Scale bar: 50 µm.

Fig. 41b, c Female approx. 12 h after the first oviposition. At the periphery, the secretion (se) appears rather homogenous where it is expelled through the gland pores (arrow). Scale bars: 5 µm, 2µm.

Fig. 41d Female approx. 12 h after the first oviposition. In the region where the small fertilisation duct starts to form the spermatozoa (s) are surrounded by pinkish, granular secretion (se). Scale bar: 50 µm.

Fig. 41e Female approx. 12 h after the first oviposition. In the region where the small fertilisation duct (sf) starts to form the spermatozoa (s) are decapsulated and surrounded by pinkish, granular secretion. Scale bar: 5 µm.

Fig. 41f Female approx. 12 h after the first oviposition. The spermatozoa inside the small fertilisation (sf) duct are decapsulated, but still coiled and inactive. Scale bar: 5 µm.

Fig. 41g Female approx. 12 h after the first oviposition. At the height of the entrance to the copulatory duct into the spermatheca the lumen is filled with decapsulated spermatozoa (s). Two tips lie in the tube-like opening (arrow). The surrounding epithelial cells exhibit light, spindle-shaped areas (asterisk). Scale bar: 50 µm.

Fig. 41h Female approx. 12 h after the first oviposition. At the height of the entrance to the copulatory duct into the spermatheca the lumen is filled with decapsulated spermatozoa (se), granular secretion and isles of blue droplets imbedded in purplish, liquid secretion (arrow). Scale bar: 5 µm.

Fig. 41i Female approx. 12 h after the first oviposition. Isles of droplets imbedded in liquid secretion (arrow) lie between decapsulated spermatozoa. Granular secretion is seen at the periphery (se). Scale bar: 2 µm.

Fig. 41j Female approx. 12 h after the first oviposition. The anterior lobe of the spermatheca is densely filled with encapsulated spermatozoa. Scale bar: 50 µm.

Fig. 41k Female approx. 12 h after the first oviposition. The capsules appear dilated. Little purplish, liquid secretion remains visible between the capsules. Further isolated isles are formed by blue droplets imbedded in purplish, liquid secretion (arrow). Scale bar: 5 µm.

Fig. 41l Female approx. 12 h after the first oviposition. The capsules of neighbouring spermatozoa are in direct contact with each other forming a compact mass with an overall structure that is reminiscent of a honeycomb. Scale bar: 2 µm.

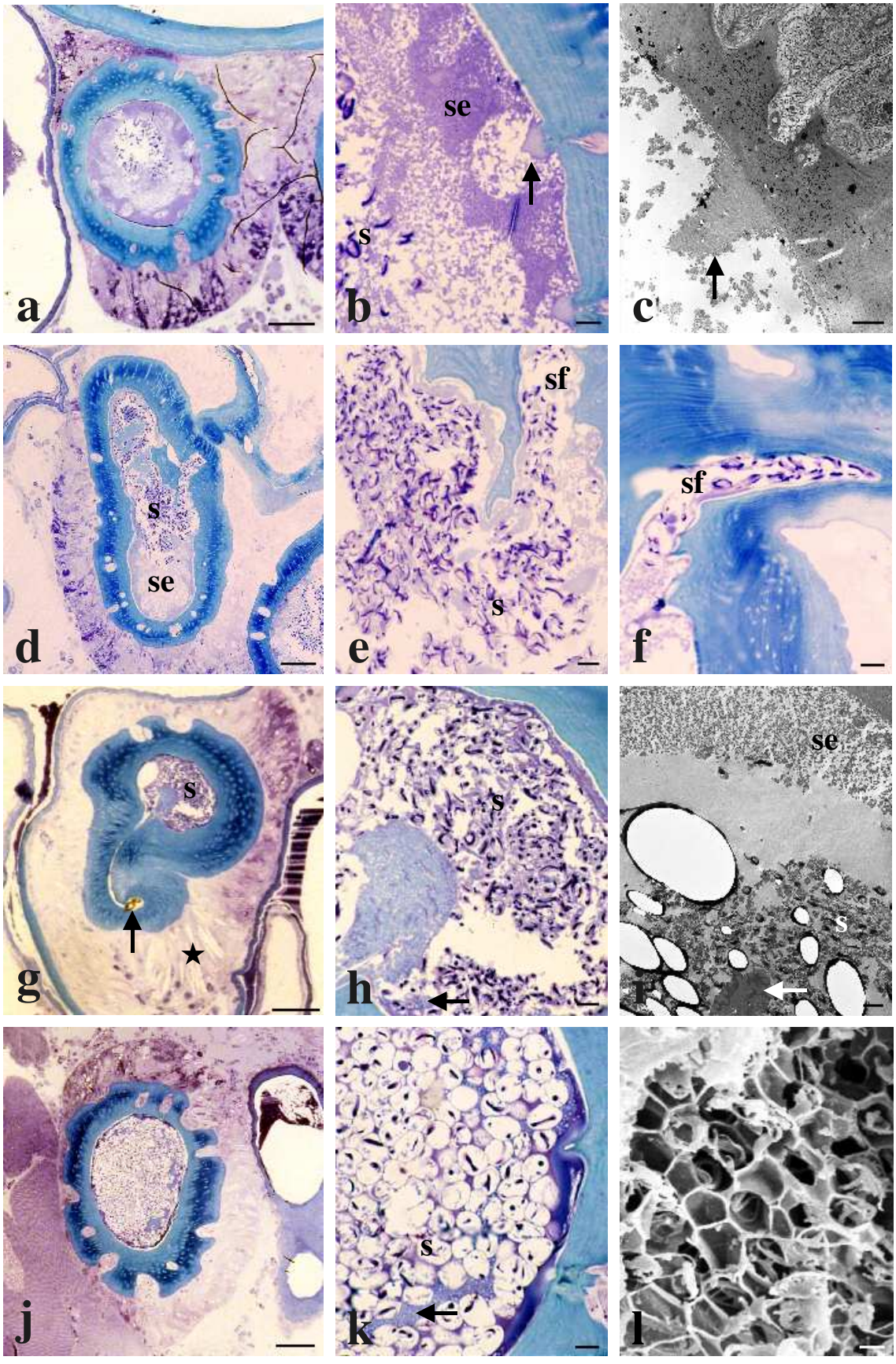

a
se
s
b
c
s
se
d
sf
s
e
sf
f
s
g
s
h
se
s
i
s
j
s
k
l

Fig. 42a Cleared spermatheca with copulatory duct. The male lost its entire embolus (em) inside the female copulatory duct (cd). The well-defined breaking point of the embolus (arrow) is clearly. Scale bar: 100 µm.

Fig. 42b Cleared spermatheca (lateral view) with two tips (arrows) reaching into the lumen. Scale bar: 100 µm.

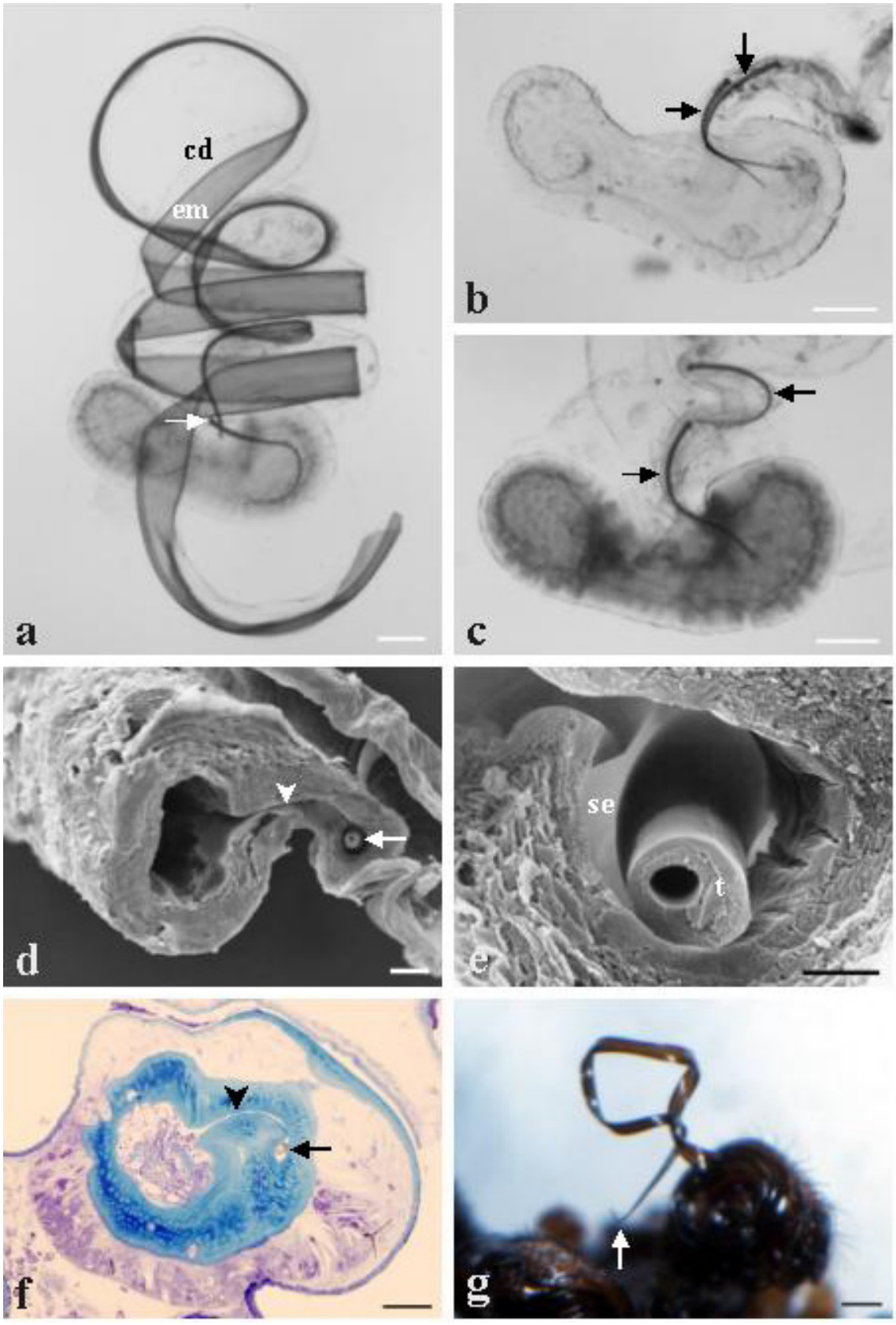
Fig. 42c Cleared spermatheca (lateral view) with one tip in its opening (left arrow) and a second tip lying in the copulatory duct (right arrow) behind the first one. Scale bar: 100 µm.

Fig. 42d Spermatheca cut transversally in the region of the entrance. The narrow slit (arrow head) is slightly widened laterally, forming a tube that takes up the embolus tip (arrow). Scale bar: 20 µm.

Fig. 42e The embolus tip lies in the tube-like opening of the spermatheca. Secretion (se) fills the space between tip and cuticle. Scale bar: 5 µm.

Fig. 42f Semi-thin section of the region near the entrance. The narrow slit (arrow head) is slightly widened laterally forming a tube that takes up the embolus tip (arrow). Scale bar: 50 µm.

Fig. 42g Mated male. The whole embolus is completely uncoiled, but the embolus tip is still present (arrow). Scale bar: 200 µm.


cd
em
a
b
c
d
se
t
e
f
g

Danksagung

Diese Arbeit ist mit Unterstützung zahlreicher Personen entstanden. Mein Dank gilt besonders:

Herrn Professor Dr. Hartmut Greven für die fachkundige und aufmerksame Betreuung der Arbeit.

Herrn Professor Dr. Klaus Lunau, der sich bereit erklärt hat, als Zweitgutachter die vorliegende Arbeit zu beurteilen.

Ofer Eitan, der mir im Feld und Labor hilfreich zur Seite stand.

Meiner Kollegin Merav Ziv, die die Entstehung dieser Arbeit leider nicht mehr miterleben konnte.

Yvonne Müller-Iglisch, Trina Mell und Jason Dunlop für ihre besondere Mühe, mir mit Korrekturen bei dieser Arbeit behilflich zu sein.

Sven Krackow und Thomas Eltz für Hilfe im Märchenwald der Statistik.

Natalia Ruiz, die mir in Israel eine wertvolle Freundin war.

Meinen Freunden Martin Dielmann und Sylvia von Häfen für ihre bedingungslose moralische Unterstützung

Meinem Freund Michael Janßen, für seine liebevolle Geduld und moralische Unterstützung.

Meinen Eltern Irmgard und Norbert Berendonck für die moralische und finanzielle Unterstützung, ohne die diese Arbeit wohl nie zustande gekommen wäre.