European Arachnology 2000 (S. Toft & N. Scharff eds.), pp. 157-167.
© Aarhus University Press, Aarhus, 2002. ISBN 87 7934 001 6
(Proceedings of the 19th European Colloquium of Arachnology, Århus 17-22 July 2000)

Morphology of female and male genitalia of *Latrodectus revivensis* Shulov, 1948 (Araneae, Theridiidae) with regard to sperm priority patterns *

BETTINA BERENDONCK[1,2] & HARTMUT GREVEN[1]
[1]*Zoologie II, Heinrich-Heine-Universität, D-40225 Düsseldorf, Germany*
(bettina.berendonck@uni-duesseldorf.de).
[2]*Jacob Blaustein Institute for Desert Research, Ben Gurion University, Sede Boker, Israel*

Abstract

The shape of the female spermatheca is assumed to play a decisive role in determining the sperm priority patterns in spiders that probably are reflected in the mating behaviour of a given species. To estimate the significance of the shape of the female sperm storage organs with regard to sperm priority patterns and the possible influence of the broken embolus tip for subsequent males in *Latrodectus revivensis* we examined the morphology of virgin and mated females' epigyna and male pedipalps by means of scanning electron- and light microscopy of cleared specimens. The female epigynal plate bears long mechanoreceptors. Her copulatory duct forms a narrow tube that takes up the male embolus during insertion. The spermatheca resembles the conduit type and first male sperm priority would be the expected pattern. However, the male embolus clearly shows a defined breaking point and its position inside the female spermathecal opening after copulation suggests that it might act as a mating plug by establishing a physical barrier against subsequent males.

Key words: *Latrodectus*, genital morphology, sperm priority pattern, mating plug

INTRODUCTION

Austad (1984) suggested that in spiders there exists a fundamental dichotomy of spermathecal morphology that divides them roughly along phylogenetic lines and mainly determines sperm priority patterns. In a 'cul-de-sac' spermatheca a single duct connects the sperm storage organ to the vagina resulting in a 'last in-first out' situation of sperm of subsequent males. In 'conduit' spermathecae there are two separate ducts, one duct through which the male transfers its seminal fluids (copulatory duct) and a second duct from which sperm is released into the uterus externus during oviposition (fertilisation duct). The resulting 'first in-first out' situation of sperm from two different males should result in a first male sperm precedence.

In the entelegyne spider *Latrodectus revivensis* Shulov, 1948 a conduit type spermatheca should be expected and, thus, a first-male sperm priority pattern. However, Uhl (2002) has shown that the female genital morphology cannot be deduced from the classification into entelegynes or haplogynes. Even the presence of two separate ducts does not necessarily mean that a spermatheca is also 'functionally' of the conduit type (Uhl and Vollrath 1998). For

---

* In memory of Merav Ziv, Jacob Blaustein Institute for Desert Research, Ben Gurion University, Sede Boker, Israel

L. hasselti Thorell, 1870, Uhl and Vollrath (1998) assume a conduit female spermatheca of the cul-de-sac type (entrance and exit lie close to each other) judging from the illustrations of the genitalia of the related *L. curacaviensis* Müller, 1776 that were shown by Bhatnagar and Rempel (1962). However, illustrations of female spermathecae of various *Latrodectus* species by other authors (Levi 1959, 1983; Wiehle 1961, 1967; Abalos & Baez 1963, 1967; Kaston 1970; Levy & Amitai 1983; Müller 1985) suggest a spatial separation of the entrance and exit.

Males of many *Latrodectus* species are known to frequently lose the apical part of their embolus (= embolus tip) inside the female genital tract during copulation (Dahl 1902; Smithers 1944; Levi 1959; Wiehle 1961; Bhatnagar & Rempel 1962; De Biasi 1962; Abalos & Baez 1963, 1967; Kaston 1970). It is generally taken for granted that this embolus tip does not keep subsequent males from copulating with an already inseminated female (Abalos & Baez 1963; Breene & Sweet 1985). However, so far there is no evidence that a male successfully transfers sperm into a spermatheca that already has one embolus tip in its opening (not only in the copulatory ducts). In the present paper we give a detailed overview of the male and female genitalia of *L. revivensis* to gain more information about the structural prerequisites for sperm priority patterns. We studied the gross morphology of the female epigynal plate, the spermatheca and the connected ducts, the structure of the male embolus and the position of broken embolus parts inside the female genitalia by using light and scanning electron microscopy. Our results are compared with observations on other *Latrodectus* species.

MATERIAL AND METHODS

Latrodectus revivensis occurs in the central Negev desert of Israel (Levy & Amitai 1983). In the 1998 season, 30 mated females which had already built at least one egg-sac in the field, ten subadult females, ten subadult males and three adult males of unknown mating history, were collected in the vicinity of Sede Boqer, Israel. Immature females and males were reared to adulthood.

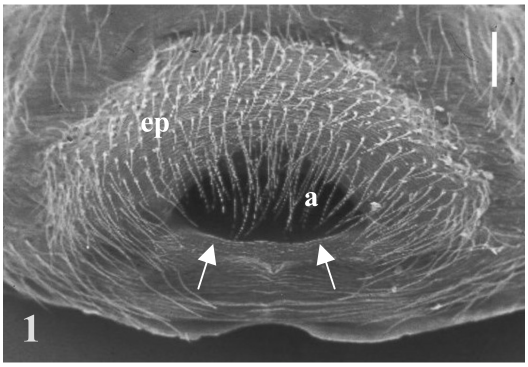
The genitalia of the 24 females which had mated in the field were isolated and kept in 5 % KOH solution for several days until the tissue was dissolved. Cleared specimens were finally transferred into glycerine and checked with a light microscope. The spermatheca of five adult virgin females and the pedipalps of five virgin males were treated similarly.

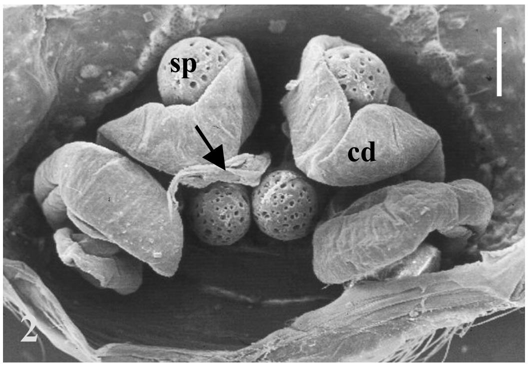
The epigyna of three mated females from the field and the isolated spermathecae of five virgin and three mated females were isolated and cleaned with 5% KOH and contact lens cleaner. The cleaned spermathecae of two of the mated females were transversally cut with a razor-blade in the region where the copulatory duct opens into the spermatheca. The female epigyna, the spermathecae and the pedipalps of the five virgins and the three males of unknown mating history were dehydrated in a graded series of ethanol, critical-point dried, sputter-coated with gold and examined with a Jeol JSM-5400 scanning electron microscope.

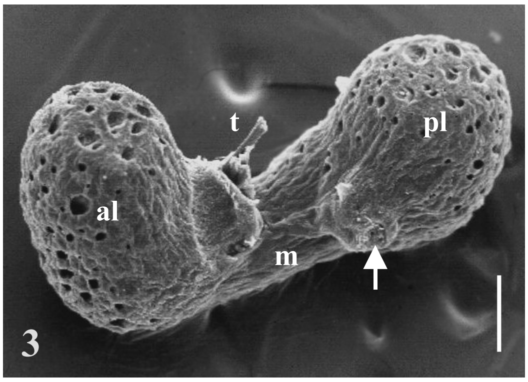
RESULTS

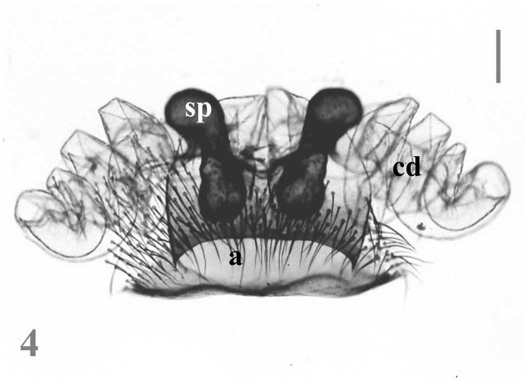
Female epigynum

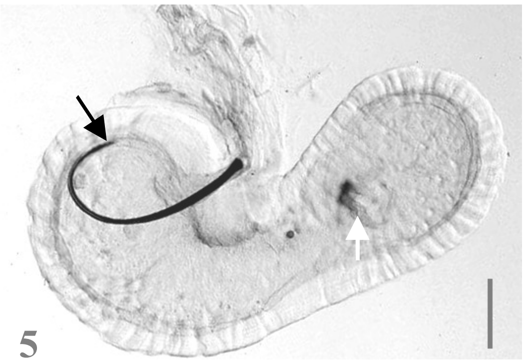
The epigynum of *L. revivensis* is an arched and heavily sclerotised plate which is situated on the ventral side of the female's opisthosoma immediately in front of the epigastric furrow. The epigynal plate is transverse, suboval and densely covered with thin hairs that partly overhang the nearly triangular opening of the atrium. The posterior margin of the opening is slightly curved backwards forming very probably a guide for the male pedipalp during genital coupling (Fig. 1). From each side of the atrium an opening leads into one of the paired copulatory ducts (synonymous with the 'bursae copulatrices' in Bhatnagar & Rempel 1962). Each duct twines around the spermatheca on that side (Fig. 2, not seen in Fig. 4 due to preparation). After two coils in a posteriolateral direction each duct makes a sharp turn back towards the spermatheca, completing another two coils. Along its main course the











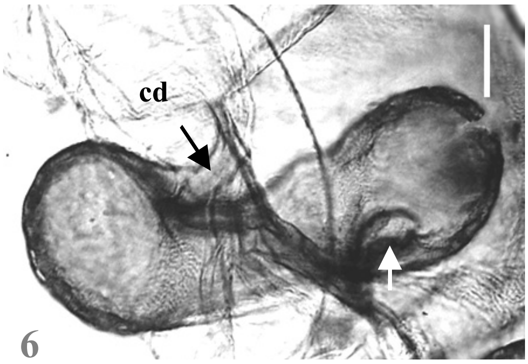


Fig. 1. Epigynal plate (ventral view).The posterior margin of the nearly triangular opening is slightly curved backwards (arrows). a: atrium, ep: epigynal plate. Scale bar: 200 µm. **Fig. 2.** Female egigynum (dorsal view) with copulatory ducts and cuticular lining of the duct that opens into the uterus externus (arrow). cd: copulatory duct, sp: spermatheca. Scale bar: 200 µm. **Fig. 3.** Left spermatheca (medial view). Note the embolus tip lodged inside the spermathecal opening. The outer cuticular papilla indicates the exit of the fertilisation duct (arrow). al: anterior lobe, m: narrow middle portion, pl: posterior lobe, t: embolus tip. Scale bar: 100 µm. **Fig. 4.** Cleared epigynum (ventral view) with slightly sclerotized copulatory ducts. a: atrium, cd: copulatory duct, sp: spermatheca. Scale bar: 200 µm. **Fig. 5.** Cleared spermatheca (medial view) with a male embolus tip in the opening. The opening of the pointed end of the embolus tip rests at the most anterior inner wall of the spermatheca (black arrow). Fertilisation duct (white arrow). Scale bar: 100 µm. **Fig. 6.** Cleared spermatheca (medial view). Close to the spermatheca the flat copulatory duct forms a heavily sclerotised tube on one side (black arrow). The funnel-shaped fertilisation duct originates from the apical, lateral wall of the posterior lobe, slightly bends anteriorly with its exit finally opening on the basal surface (white arrow). cd: copulatory duct. Scale bar: 100 µm.

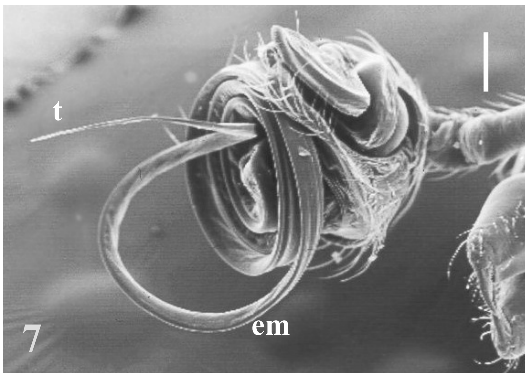
copulatory duct is slightly sclerotised (Fig. 4). In its last part, close to the entrance of the spermatheca, the duct becomes very flat and one side forms a heavily sclerotised tube (Figs. 6, 16, 17). This organisation is retained in that section where the cuticle of the copulatory duct fuses with the cuticle of the spermatheca (Fig. 18). 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 (Fig. 18). As in the copulatory duct, the slit is slightly widened laterally (not exceeding 17 µm) forming a tube (Figs. 18, 19) that takes up the male embolus tip during copulation (Figs. 5, 15, 16, 17).

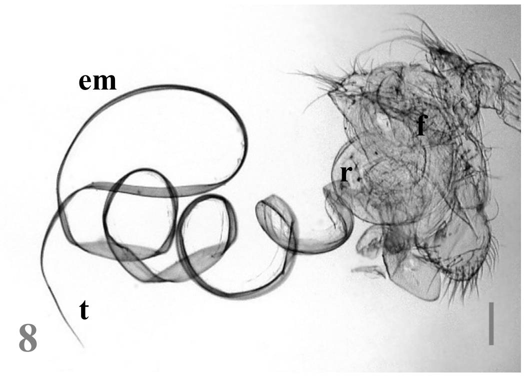
The paired spermathecae are dumb-bell shaped and lined by very thick and heavily sclerotised walls (Figs. 3, 18). Each spermatheca consists of two rounded lobes that are connected by a narrow middle region (Figs. 3, 5, 6). The cuticle is penetrated by numerous pores of variable size (Figs. 2, 3). In the anterior and posterior lobes they have a diameter up to 40 µm. The fertilisation duct is formed by the spermathecal wall itself. It originates from the lateral apical wall almost in the middle of the posterior lobe (Figs. 5, 6). The lumen of the fertilisation duct is funnel-like; it is wide at the beginning and becomes narrower towards the end (Fig. 6). The whole duct bends slightly anteriorly; it finally opens on a cuticular papilla on the basal surface (Fig. 3) connecting the spermatheca to the uterus externus via a cuticula lined duct(Figs. 2, 6).

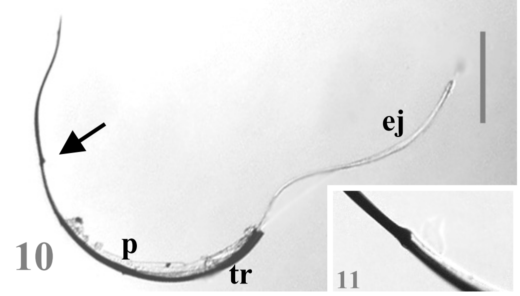
Male pedipalp

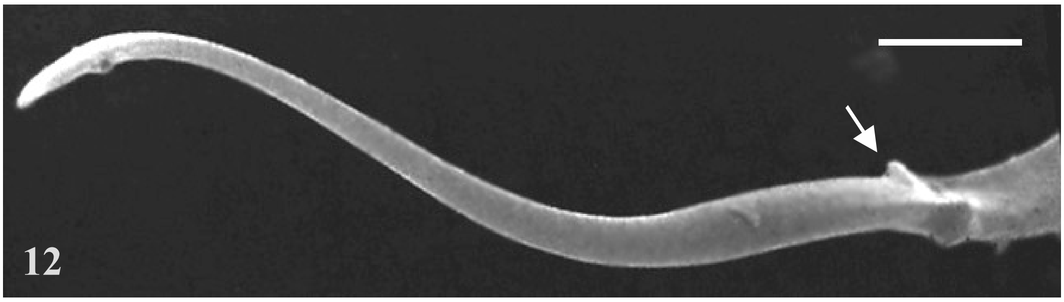
The two distal segments, the tarsus and pretarsus of the male pedipalp are modified and form the copulatory organ. The cymbium (tarsus) is spoon-shaped and covered with various sense organs such as tactile hairs, slit sensilla and trichobothria. The genital bulb (pretarsus) consists of various sclerites connected by membranous parts (haematodochae) (Figs. 7, 8). They surround the internal parts of the spermophore (synonymous to the male 'receptaculum seminis' in Wagner 1887, see Bhatnagar & Rempel 1962 for citation). The spermophore (Fig. 8) consists of the fundus, the reservoir and the ejaculatory duct. The fundus and the reservoir form a sclerotised spiral coil, with one end overlapping the other. From the reservoir originates the transparent and slender ejaculatory duct (Fig. 10) which has an outer diameter of approx. 4 µm and an inner diameter of about 3 µm (Fig. 14). 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. 15). The long spirally coiled part of the embolus can be clearly divided into the dark brown and heavily sclerotised truncus and the membranous pars pendula that runs along its inner concave side (Figs. 8, 10, 11). In cross section the truncus forms a U-shaped channel closed by the pars pendula (Fig. 14). Inside the channel lies the ejaculatory duct originating from the reservoir (Figs. 10, 14). Apically, the embolus possesses a solid S-shaped sclerite, the embolus tip (Figs. 7, 8, 10, 12). SEM pictures show that the transition between the embolus tip and the rest of the embolus is marked by a saddle-like thickening (Fig. 12). The thickening is also visible in the embolus tips inside the female genital tract and indicates the site of fracture (Figs. 3, 5, 15, 16, 17). The total length of the tip varies among individuals (approx. 300-400 µm). The outer diameter of the tip is approximately 13 to 16 µm at the breaking point and 8 to 10 µm just beyond it (Figs. 12, 13). From here the diameter remains constant

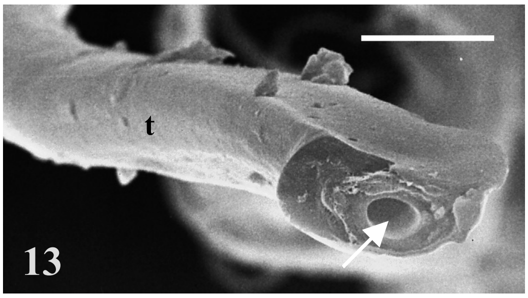
Fig. 7. Right male pedipalp (lateral view) with its long spirally coiled embolus. em: embolus, t: embolus tip. Scale bar: 200 µm. **Fig. 8.** Cleared male pedipalp (lateral view). The genital bulb consists of various sclerites connected by membranous parts. The receptacle consists of the fundus, the reservoir and the ejaculatory duct inside the embolus. em: embolus, f: fundus, t: embolus tip, r: reservoir. Scale bar: 200 µm. **Fig. 9.** Opening of the embolus tip with a maximum diameter of approx. 6 µm. Scale bar: 10 µm. **Fig. 10.** Apical portion of the male embolus. The main part of the embolus, that ends at the breaking point (arrow)

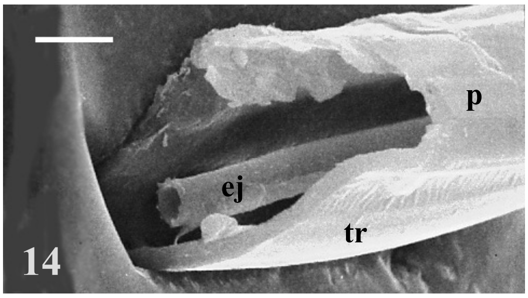












can be clearly divided into the dark truncus and the membranous pars pendula. They surround the ejaculatory duct. ej: ejaculatory duct, p: pars pendula, tr: truncus. Scale bar: 200µm. **Fig. 11.** Breaking point of the embolus, 4 x larger than Fig. 10. **Fig. 12.** The embolus tip is a S-shaped sclerite. The transition between the tip and the rest of the embolus is marked by a saddle-like thickening (arrow). Scale bar: 50 µm. **Fig. 13.** Broken off embolus tip. A canal with a diameter of approx. 3 µm runs through the tip (arrow). t: embolus tip. Scale bar: 10 µm. **Fig. 14.** Broken embolus. The truncus forms a U-shaped channel closed by the pars pendula. Inside lies the ejaculatory duct originating from the reservoir. ej: ejaculatory duct, p: pars pendula, tr: truncus. Scale bar: 10 µm.

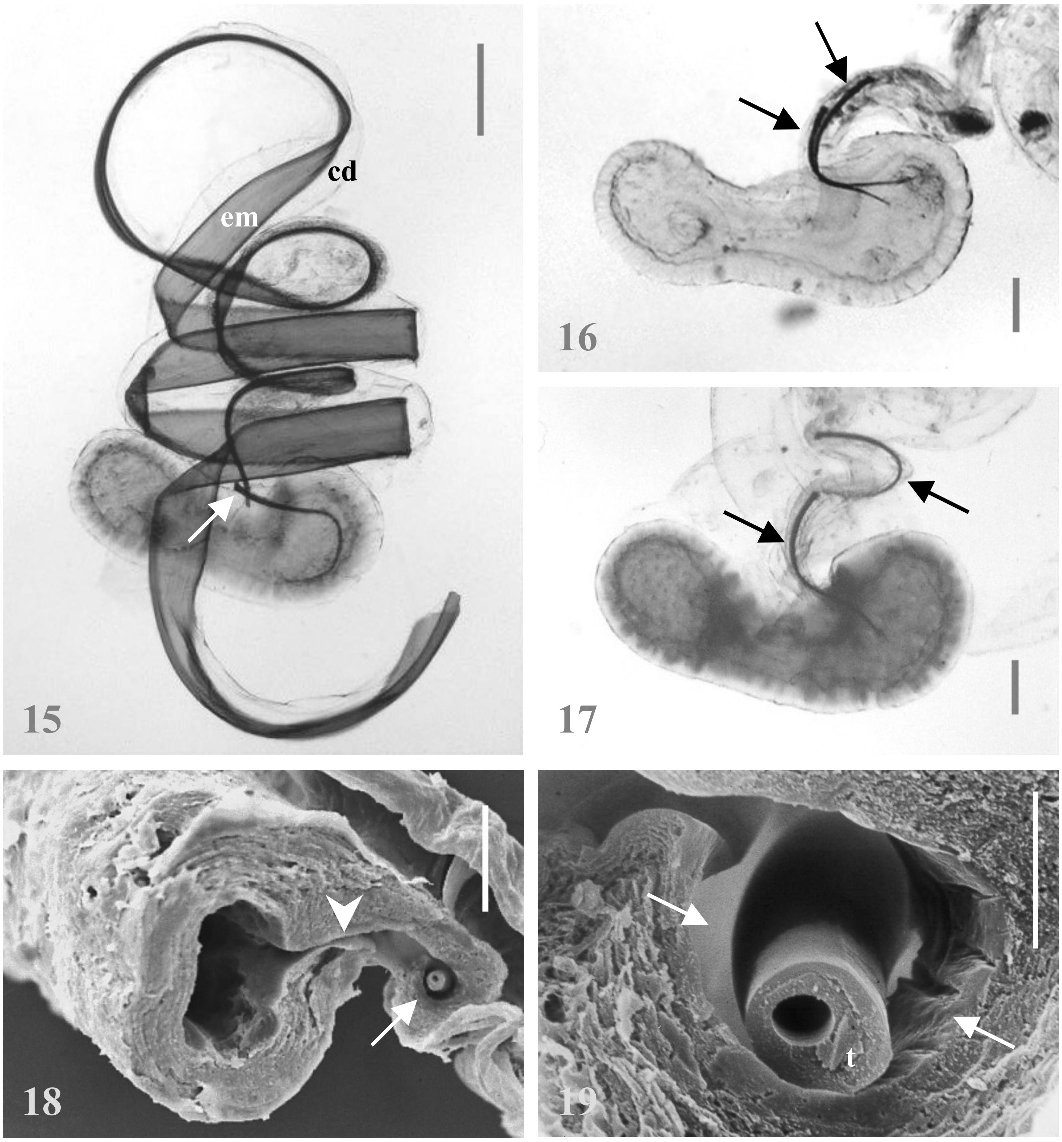


Fig. 15. The male lost its complete embolus inside the female copulatory duct. Clearly visible is the well-defined breaking point of the embolus (arrow). The tip is lodged deep inside the spermathecal opening. cd: copulatory duct, em: embolus. Scale bar: 200 µm. **Fig. 16.** Cleared spermatheca (lateral view) with two tips (arrows) reaching into the spermathecal lumen. Scale bar: 100 µm. **Fig. 17.** Cleared spermatheca (lateral view) with one tip in the opening (left arrow) and second tip (right arrow) lying in the copulatory duct behind the first one. Scale bar: 100 µm. **Fig. 18.** 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: 200 µm. **Fig. 19.** The embolus tip lies in the tube-like opening of the spermatheca. Secretion fills the space between tip and cuticle (arrows). t: embolus tip. Scale bar: 10 µm.

for the proximal third of the tip. Distally, the diameter decreases steadily towards the opening and tapers to the slightly flattened apex (Fig. 12). A canal with a diameter of approx. 3 µm runs through the tip (Figs. 13, 19). This canal is continuous with the ejaculatory duct which ends at the breaking point (Fig. 14). 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 (Fig. 9).

Position of the male embolus tip inside the female spermathecal opening

In most mated females a part of the male embolus, in some cases even the whole embolus, was found inside the female genital tract (Fig. 15). It becomes obvious that the male screwed its coiled embolus completely into the similarly coiled copulatory duct of the female. The embolus tip was lodged deeply inside the lateral part (tube) of the slit-like opening of the female spermatheca (Fig. 18), where it finally snapped off at the breaking point. The space between the tip and the cuticle of the spermathecal opening was filled with a secretion (Fig. 19). In those cases where the tip broke off at the breaking point and the rest of the embolus was retreated after copulation only the wider part close to the saddle-like thickening of the tip remained lying inside the distal part of the copulatory duct (Figs. 3, 5, 15). About 2/3 of the embolus tip's length extended into the anterior lumen of the spermatheca. The actual site where the seminal fluid was expelled was found at the most anterior wall of the spermatheca (Fig. 5). Here the opening of the pointed end of the male embolus came to rest during insemination. In most females not more than one tip was found in each spermathecal opening. In two females two tips were seen in the opening, but neither of these tips was positioned deeply inside the opening as described before (Fig. 16). Only between 1/3 to 1/2 of the tips' lengths reached into the spermathecal lumen. In other specimens a second tip could be observed lying in the copulatory duct, behind a tip that had been already positioned in the spermathecal opening by another male (Fig. 17).

DISCUSSION

Our description of the female and male genitalia of *L. revivensis* revealed many similarities to other *Latrodectus* species described by various authors in greater or lesser detail throughout the last century. The most detailed studies were undertaken for *L. curacaviensis* by Bhatnagar and Rempel (1962) and *L. geometricus* C.L. Koch, 1841 by Abalos and Baez (1963, 1967). In the present study, the use especially of the scanning electron microscope revealed some new details, e.g. about the epigynal plate, the female copulatory duct, the spermatheca and the male embolus.

None of the authors who have characterised the outer aspects of any *Latrodectus* species mention the long and thin hairs that cover the epigynal plate and partly overhang the opening of the atrium (Shulov 1940, 1948; Levi 1959, 1966, 1983; Bhatnagar & Rempel 1962; Abalos & Baez 1963, 1967; Mackay 1972; Levy & Amitai 1983). These hairs are innervated and represent typical mechanoreceptors (unpubl.) that may enable the female to perceive stimuli provided by the male during courtship (Shulov 1940; Ross & Smith 1979; Anava & Lubin 1993) and, through this, information about his quality. In addition, the female might be able to obtain information about the success of the coupling process itself.

The copulatory ducts of *L. revivensis* are not simple tubes as described for other *Latrodectus* species (Bhatnagar & Rempel 1962; Kaston 1970; Breene & Sweet 1985). Close to the spermatheca the 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 may form a guidance system for the male embolus during copulation and might act as a bottle-neck which the male embolus has to pass, before the tip can enter the spermatheca to deposit the seminal fluids. In addition, musculature in this region appears more complex than suggested (see

Whitehead & Rempel 1959) and is now under investigation.

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 to the anterior lobe; the fertilisation duct is part of the posterior lobe. This compartmentation should result in a stratification of sperm inside the lumen. A fair raffle of rival males' sperm proposed for many insects (Parker 1990), implying that the sperm of different males mix inside the spermatheca due to the active movement of the sperm cells, does not occur in *Latrodectus* species. Here, as in most araneomorphs, single coated sperm cells lie immobile inside the spermatheca until oviposition (Alberti 1990; for further references see Foelix 1997). The position of the sperm cells attained during insemination is most probably the decisive factor determining whether they will be used for fertilisation. In case a second male is able to insert his embolus tip in an already filled spermatheca (that seems to happen frequently at least in some *Latrodectus* species such as *L. geometricus* (see Müller 1985) and *L. pallidus* O.P. Cambridge, 1872 (Harari pers. comm.)), he has to develop considerable force to push his sperm from the opening of the embolus tip in the anterior lobe and through the narrow middle portion into the posterior lobe. Only in those sperm cells which lie in close proximity of the fertilisation duct the protective coat is dissolved (unpubl.). Thus, only those spermatozoa can be used for fertilisation. A second male should not only have to displace the rivals' sperm in the anterior and posterior lobes, but also has to push his sperm close to the lumen of the fertilisation duct. When both spermathecae are filled by the first male, a clear first male sperm priority would be expected. The main question is therefore, whether a male is able to fill only one or both spermathecae. Looking at the various combinations in which the spermathecae can be filled by two males (one male inserts his sperm into one spermatheca, a second male inserts his sperm into the second spermatheca; one is subsequently filled by both (e.g. in those females with two tips in one opening), the second spermatheca is just filled by one, etc.), we would expect highly variable P2 values. In case the male is able to deter the intromission of a rival's embolus tip into the spermathecal lumen with his own tip, the situation becomes even more complex, and P2 values ranging from 0.0 to 1.0 as found for *L. hasselti* (Andrade 1996) are not surprising.

The inner basal surface of the spermathecal cuticle showed pores of different sizes. As suggested by Bennet (1992) for theridiid species in general, the large pores in the cuticle of the anterior and posterior lobes of *L. revivensis* are primary pores, 'more or less simple canals which convey gland ducts through the walls of the spermathecal heads' (Bennet 1992, p. 3). Not much is known about the glands of the spermathecal epithelium and the secretions they pass into the spermathecal lumen (short review in Lopez 1987). Possible functions include pheromone release (Kovoor 1981), sperm nutrition and mechanical displacement of sperm. Also the activation of sperm in spiders is mediated by female secretion rather than being time dependent as proposed for *Nephila clavipes* (Brown 1985).

Theridiids including *L. revivensis* possess one of the most complex pedipalps known in spiders (Levi 1961). Although there are several parts of the genital bulb engaged in the coupling process between male and female genitalia, the male embolus is the only part that will be introduced into the female. This was demonstrated in a female of *L. revivensis* that retained long parts of the embolus in one of her copulatory ducts after mating. The loss of the whole embolus was reported for several *Latrodectus* species (Wiehle 1961; Müller 1985). It is assumed that a loss of the entire embolus happens more often in species, whose females possess more coils in their copulatory duct, e.g. *L. geometricus* (Abalos & Baez 1963; Abalos 1968). According to Comstock (1910) the embolus of *Latrodectus* species belongs to the free type and spiral subtype. Wiehle (1961) defined this structure as an 'Einführungsembolus' ('introducing embolus') of the subtype 'Querschleifenembolus 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 at the convex side and accompanied by a membranous 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). The embolus of *L. revivensis* and other *Latrodectus* species perfectly combines rigidity and flexibility which enables the embolus to penetrate the variable copulatory duct of the female. The tip, however, does break off frequently inside the female genital tract (Dahl 1902; Smithers 1944; Levi 1959; Wiehle 1961, 1967; Bhatnagar & Rempel 1962; Abalos & Baez 1963, 1967; Kaston 1970; Breene & Sweet 1985; Andrade 1996) at a definite breaking point ('Sollbruchstelle' Wiehle 1961). As shown in the present study the embolus tip of *L. revivensis* is a solid sclerite with a canal inside. A translucent, circular tube inside the tip described for *L. geometricus*, *L. curacaviensis* and *L. mactans* by Abalos and Baez (1963) could not be found in *L. revivensis*. In the latter species 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 structures might act as barbs when the male tries to retract his embolus, thus facilitating the rupture of the tip. The ejaculatory duct and the canal of the tip of *L. revivensis* are very narrow (approx. 3 μm in diameter) and each encapsulated sperm cell has to pass it one by one during sperm induction and ejaculation. As long as the embolus of a male is not mutilated (e.g. ripped off or uncoiled) after the first insertion a male might be able to copulate with another female (see Breene & Sweet 1985), but for several reasons a successful second copulation using the same pedipalp appears rather doubtful. An embolus devoid 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 could be demonstrated in the female specimen of *L. revivensis* which had an entire embolus in the copulatory duct. 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 Baez (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). Furthermore, the recharge 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. The expected 'sterility' of mated males that have lost their tips could be shown by experiments conducted in *L. hasselti* by Andrade (in press). A successful second insemination with an already used palp without an embolus tip appears impossible. Thereore, a male should invest all his sperm in the first copulation

It becomes clear by our pictures that a broken embolus tip prevents other males from successfully entering a previously filled spermatheca. As shown in the SEM pictures, the male embolus tip closes the female spermathecal opening very tightly. Only in those cases in which the first male did not position his embolus tip deeply inside the opening a second male managed to enter the lumen with his own tip. More frequently the second male did not reach the spermathecal lumen but lost his tip, and most probably his sperm, inside the copulatory duct. The frequency of the loss of the embolus tip, the number and position of the tips inside the genital tract of mated females from the field and the comparison with other *Latrodectus* species allows us to characterise the embolus tip of

L. revivensis as an effective mating plug (Berendonck et al. in prep.).

Austad (1984) reduced the problem of sperm precedence patterns of entelegyne spiders to a theoretical shape of the female spermatheca. Our findings suggest that females and males of *L. revivensis* have a variety of possibilities to control the outcome of matings that include epigynal structures, spermathecal organisation and embolus tips that close perfectly the spermathecal opening.

ACKNOWLEDGEMENTS

We thank J. Dunlop, G. Uhl and an anonymous referee for valuable comments on the manuscript and the University of Aarhus, Denmark, for the financial support that made it possible to participate in the 19th European Colloquium of Arachnology in Århus.

This research was supported by a graduate fellowship from the Jacob Blaustein Institute for Desert Research, Ben-Gurion University of the Negev, Israel. This is publication No. 320 of the Mitrani Department of Desert Ecology.

REFERENCES

Abalos, J.W. 1968. La transferencia espermática en los arácnidos. *Revista de la Universidad Nacional de Cordoba (Argentina)*, 2d ser. 9, 251-278.

Abalos, J.W. & Baez, E.C. 1963. On spermatic transmission in spiders. *Psyche* 70, 197-207.

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

Alberti, G. 1990. Comparative spermatology of Araneae. *Acta Zoologica Fennica* 190, 17-34.

Anava, A. & Lubin, Y. 1993. Presence of gender cues in the web of a widow spider, *Latrodectus revivensis*, and a description of courtship behaviour. *Bulletin of the British Arachnological Society* 9, 119-122.

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

Andrade, M.C.B & Banta, E.N. In press. Value of male remating and functional sterility in redback spiders. *Animal Behaviour*

Austad, S.N. 1984. Evolution of sperm priority patterns in spiders. In: *Sperm competition and the evolution of mating systems* (R.L. Smith ed.), pp. 223-249. Harvard University Press, Cambridge, Massachusetts.

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.

Bhatnagar, D.S. & Rempel, J.G. 1962. Structure, function and postembryonic development of the black widow spider *Latrodectus curacaviensis* (Mueller). *Canadian Journal of Zoology* 40, 465-510.

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.

Brown, S.G. 1985. Mating behaviour of the Golden-Orb-Weaving spider, *Nephila clavipes*: II. Sperm capacitation, sperm competition and fecundity. *Journal of Comparative Psychology* 99, 167-175.

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

Dahl, F. 1902. Über abgebrochene Kopulationsorgane männlicher Spinnen im Körper des Weibchens. *Sitzungsberichte der Gesellschaft für Naturforschung zu Berlin*, 185-203.

De Biasi, P. 1962. Estrutura interna e presença de segmentos do êmbolo no epígino de Latrodectus geometricus (Araneidae: Theridiidae). *Papéis Avulsos do Departamento de Zoologia* 15, 327-331.

Foelix, R.F. 1997. *Biology of Spiders.* Harvard University Press, Cambridge, Massachusetts.

Kaston, B.J. 1970. Comparative biology of American black widow spiders. *Transactions of the San Diego Society of Natural History* 16, 33-82.

Kovoor, J. 1981. Une source probable de pheromone sexuelles: les glandes tegumentaires de la region genitale de femelles d'araignees. *Atti della Societa Toscana di Scienze Naturali Memorie B* 88, 1-15.

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

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

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

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

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

Parker, G.A. 1990. Sperm competition games: raffles and roles. *Proceedings of the Royal Society of London B* 242, 120-126.

Ross, K. & Smith, R.L. 1979. Aspects of the courtship 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.

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.

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

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

Uhl, G. & Vollrath, F. 1998. Genital morphology of *Nephila edulis*: implications for sperm competition in spiders. *Canadian Journal of Zoology* 76, 39-47.

Wagner, W. 1887. Kopulationsorgane des Männchens als Criterium für die Systematik der Spinnen. *Horae Societatis Entomologicae Rossicae* 22: 3-132.

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.

Wiehle, H. 1961. Der Embolus des männlichen Spinnentasters. *Zoologischer Anzeiger* Suppl. 24, 457-480.

Wiehle, H. 1967. Steckengebliebene Emboli in den Vulven von Spinnen (Arach., Araneae). *Senckenbergiana Biologica* 48, 192-202.