Acarologia is proudly non-profit, with no page charges and free open access

Please help us maintain this system by encouraging your institutes to subscribe to the print version of the journal and by sending us your high quality research on the Acari.

Subscriptions: Year 2022 (Volume 61): 450 €
http://www1.montpellier.inra.fr/CBGP/acarologia/subscribe.php
Previous volumes (2010-2020): 250 € / year (4 issues)
Acarologia, CBGP, CS 30016, 34988 MONTFERRIER-sur-LEZ Cedex, France
ISSN 0044-586X (print), ISSN 2107-7207 (electronic)

The digitalization of Acarologia papers prior to 2000 was supported by Agropolis Fondation under the reference ID 1500-024 through the « Investissements d’avenir » programme (Labex Agro: ANR-10-LABX-0001-01)

Acarologia is under free license and distributed under the terms of the Creative Commons-BY.
FINE STRUCTURE OF THE MALE GENITAL SYSTEMS, SPERMATOPHORES AND UNUSUAL SPERM CELLS OF SAXIDROMIDAE (ACARI, ACTINOTRICHIDA)

Gerd ALBERTI\textsuperscript{1}, Yves COINEAU\textsuperscript{2}, Nestor A. FERNANDEZ\textsuperscript{3} and Pieter D. THÉRON\textsuperscript{4}

(Received 28 December 2009; accepted 15 March 2010; published online 30 June 2010)

\textsuperscript{1} Zoologisches Institut und Museum, Ernst-Moritz-Arndt-Universität Greifswald, Johann-Sebastian-Bach-Str. 11/12, 17487 Greifswald, Germany. alberti@uni-greifswald.de

\textsuperscript{2} Muséum National d’Histoire Naturelle, Arthropode, Case Postale 53, 61 rue de Buffon, F-75231 Paris Cedex 05, France

\textsuperscript{3} Faculty of Exact Sciences and Natural Sciences, University of La Pampa, 6300, Santa Rosa, La Pampa, Argentina. nesfernan@yahoo.fr

\textsuperscript{4} School of Environmental Sciences and Development, North-West University, Potchefstroom Campus, 2520, South Africa. pieter.Theron@nwu.ac.za

ABSTRACT — The early derivative actinedid Saxidromidae, Saxidromus delamarei, Bovidromus roussouwi, and Rhinodromus lootsi perform indirect spermatophore transfer by means of a peculiar mating behaviour. The anatomy and fine structure of the male genital systems are described and are shown to exhibit the organisation considered to be fundamental in Actinotrichida: paired testes with germinal and glandular parts, paired vasa deferentia, unpaired ejaculatory duct, progenital chamber containing genital papillae. The genital system is located ventral of the digestive tract. The testes produce relatively few or even very few aflagellate sperm cells, which represent synspermia consisting of likely four undivided sperm cell equivalents in a common cytoplasm. Whereas \textit{S. delamarei} produces a rather large stalked spermatophore containing many synspermia, both the other species produce very tiny stalked spermatophores with a spherical head representing only one synspermium. Thus, in these latter species only one synspermium is transferred to the female at a time, but the male can convey several (possibly five or more) spermatophores to the female during the mating session. A scenario is suggested which could describe the evolution of this remarkable mating system and behaviour.

KEYWORDS — evolution; mating behaviour; mating economy; sperm priority; synspermia; ultrastructure

INTRODUCTION

Saxidromidae comprising three genera, \textit{Saxidromus}, \textit{Bovidromus} and \textit{Rhinodromus}, is a family of mites regarded to be close to the basis of the species-rich and highly diverse Prostigmata (Coineau, 1979; Coineau \textit{et al.}, 2006). However, some authors include the few species known into the Adamystidae, which is considered to represent an early derivative group within the very diverse Anystidae (Evans, 1992; Krantz and Walter, 2009). All species known occur on bare rocks, which are exposed to bright sunlight. They live in rock crevices but appear on rock surfaces from early summer to mate. Despite the different systematic views on their rather basal position, they are known to perform a very unusual mating behaviour (Coineau, 1976; Coineau \textit{et al.}, 2006).

The male catches a female with its forelegs and impales it (\textit{S. delamarei}) onto or place it over a sper-
matophore previously produced. Males of B. rous-
souwi provided with two and R. lootsi possessing
one dorsoanteriad projecting processus of the idio-
soma insert these into the female’s progenital cham-
ber prior to spermatophore deposition. In con-
trast to S. delamarei, which deposits a rather large
stalked spermatophore, these latter two species de-
posit very tiny spermatophores bearing a small
spherical droplet. The female takes only the droplet
and the stalk can be replenished several times by the
male with a further droplet, which contains sperm
material. Following a first investigation on Saxidro-
mus delamarei (Alberti et al., 2007), we have studied
the fine structure of the male genital systems, the
spermatophores and sperm of two further species
and found remarkable and peculiar similarities but
also pronounced differences.

**MATERIALS AND METHODS**

Specimens of Saxidromus delamarei Coineau, 1974
were collected in June 2003 by Y.C. and N.A.F. close
to Banyuls-sur-Mer (France), whereas specimens of
Bovidromus roussouwi Coineau, Théron and Fernan-
dez, 2006 were sampled near Pofchefstroom (South
Africa) and Rhinodromus lootsi Coineau, Théron and
Fernandez, 2006 near Rustenburg (South Africa) by
P.Th and G.A. in March 2005.

Transmission electron microscopy (TEM) and light
microscopy (LM): The living mites were transferred
into a drop of cold fixative (3.5% buffered glu-
taraldehyde; phosphate or cacodylate buffer 0.1M;
pH 7.4) and transversely cut into halves. The speci-
mens were immediately transferred into small vials
containing the fixative and placed into a refrigera-
tor for about two hours. They were then rinsed sev-
eral times with the buffer solution and transferred
for postfixation into 2% buffered OsO₄ solution,
where they were left for another two hours. The
South African specimens were transferred into di-
luted glutaraldehyde (1:4 with buffer solution) and
were further processed after return of G.A. to Greif-
swald. Following the OsO₄-fixation the specimens
were rinsed several times with buffer solution and
finally dehydrated using graded ethanols. Embed-
ding occurred either in Araldite with propyleneoxide
as intermedium or in Spurr’s mixture (Spurr 1969).
The living mites were found to be very hydropho-
bic, hence the process of fixation was slightly var-
tied to improve the results when working with the
South African species. These mites were briefly
immersed into isopropanol to break the hydropho-
bic barrier and thus to facilitate the access of the
fixatives. These problems did not occur with the
spermatophores of S. delamarei, which were col-
lected immediately after deposition and treated as
described. Because of the tiny size of the sper-
matophores of the South African species, it was
not possible to collect individual spermatophores.
However, we were able to obtain mating mites dur-
ing spermatophore transfer and hence got the heads
of the spermatophores. They were fixed together
with the mites.

Sectioning was done with a Leica ultracut UCT
microtome, whereby ultrathin sections were pro-
duced (70 nm) - and from time to time semithin sec-
tions (400 nm) - using a Diatome diamond knife.
The ultrathin sections were stained with uranylac-
etate and lead citrate according to Reynolds (1963)
and studied in a Zeiss EM10A or (mostly) JEOL-
JEM-1011 (80 kV) transmission electron microscope.
The semithin sections after staining according to
Richardson et al., (1960) served for general orien-
tation using a light microscope (for further tech-
nical details see, e.g., Alberti and Nuzzaci, 1996).

Micrographs of these semithin sections were taken
with an Olympus BX60 microscope provided with
an Axio Cam MRC - Zeiss digital-camera connected
with the Axio Vision Rel. 4.8 program.

**RESULTS**

**Male genital system**

The male genital system of all three species con-
sts of two tubular testes located in the posterior
of the body which continue anteriad into a pair of
vasa deferentia extending beyond the genital open-
ing (Figure 1a). A transversal bridge shortly in front
of the genital opening connects both of the defer-
ent ducts (Figure 1b). This unpaired structure opens
posteriorventrad into the cuticle-lined dorsal cham-
ber of the ejaculatory duct, which descends almost
Figure 1: Light micrographs of transverse sections through the posterior part of the idiosoma of *Rhinodromus lootsi*. (a) – Shortly in front of the genital opening. The two vasa deferentia located below the midgut are seen containing several synspermia. (b) – Slightly posterior, the genital opening is appearing. The vasa deferentia are connected by a transverse bridge (asterisk indicates a shrinkage artifact). (c) – More posteriorly, the ejaculatory duct with its dorsal chamber appears (asterisk indicates artifact). (d) – The paired testes are seen consisting of germinal and glandular parts. The dorsomedian excretory organ (i.e. the postcolon; e.g., Alberti and Coons 1999) is seen. Note that all parts of the genital system are located ventral of the digestive system. Scale bar: 50 \( \mu m \).

Abbr.: Cae, caecum of midgut; ED, ejaculatory duct; Ex, excretory organ; GO, genital opening; Lu, lumen of testis; MG, midgut; Mu, dorsoventral muscles; Sp, synspermia; TB, transversal bridge; Tge, germinal part of testis; Tgl, glandular part of testis; VD, vas deferens.

Vertically (Figures 1c,d and 3). The primary or eugenital opening is located within a progenital chamber, which includes aside of eugenital setae two pairs of genital papillae and is closed by progenital lips (terms acc. to van der Hammen, 1980). The genital system is located ventral of the digestive tract (Figure 1a-d).

The testes consist of two parts both extending longitudinally through the structure, a small germinal part and a prominent glandular part. Within the germinal part only few or even very few germ cells were seen (Figures 1d and 2a). Because of the rarity of germ cells, spermatogenesis could not yet be studied in detail. In any case, these cells are rather large and do not separate at the end of spermiogenesis into individual cells (spermatooza).

Hence aggregates containing (most likely in all three species) four sperm equivalents in a common cytoplasm are delivered into the lumen of the testis. These structures represent so-called synspermia.
The glandular part consists of large epithelial cells, which are provided with large nuclei containing a prominent nucleolus. The cytoplasm is dominated by rough endoplasmic reticulum and small electron-lucent Golgi bodies (dictyosomes) (Figures 1d and 2a,c).

A secretion is produced by these cells and fills the lumen of the testes, vasa deferentia and unpaired chamber of the ejaculatory duct together with the mature sperm cells (Figure 1).

The secretion consists of several components. In, e.g., *Saxidromus delamarei* it consists of large electron-dense droplets and a matrix of peculiar, probably fibrous, substructure (Figure 5a). It con-
FIGURE 3: TEM micrographs of vas deferens and ejaculatory duct of Bovidromus roussouwi. (a) – Composed figure showing complex structure of ejaculatory duct in cross section. Note large synspermium in dorsal chamber lined by peculiar cuticle. Arrow points to eugenital (primary) genital opening. Scale bar: 20 µm. (b) – Vas deferens. Note flat epithelium. Scale bar: 20 µm. (c) – Detail of epithelium of vas deferens with irregularly shaped microvilli. Cells contain many mitochondria and are underlain by a muscular layer. Scale bar: 2 µm. (d) – Dorsal chamber of ejaculatory duct with cuticular fringes and secretion. Scale bar: 10 µm. (e) – The ejaculatory duct is surrounded by a thick muscular layer. Scale bar: 10 µm. (f) – Eugenital opening (arrow) and accessory gland. Scale bar: 20 µm.

Abbr.: aGL, accessory gland; Cu, cuticle; Du, duct of accessory gland; ED, ejaculatory duct; Ep, epithelium; euS, eugenital seta; Mi, mitochondria; Mu, muscle; Mv, microvilli; pCh, progenital chamber; Se, secretion; Sp, synspermium; Vd, vas deferens.

tributes to the formation of a secretion layer around each synspermium (Figure 3a,b).

Due to technical problems with the fixation (see Materials and methods), the distal parts of the genital system were best observed in the South African species and the following description of these parts are largely based on these species (Figures 1, 3 and 4).
The vasa deferentia have a wide lumen which is surrounded by a flat epithelium. The epithelial cells bear irregularly shaped microvilli. Rather many mitochondria are obvious in these cells, which are underlain by a muscular layer. The transversal bridge collects the mature sperm prior to transfer and delivers them into the dorsal chamber of the ejaculatory duct (Figure 3). The epithelium of this duct is cuticle-lined. The cuticle shows numerous spines or fringes which reach into the lumen of the duct. It is differently sclerotized according to the region within the duct. The shape of the ejaculatory duct is rather complex and could not yet be reconstructed completely. However, towards the genital opening
a funnel-like, narrow passage, is formed which terminates at the eugenital opening. Also this part of the duct is provided with a very complex arrangement of cuticular structures. The ejaculatory duct is surrounded by a strong muscular layer.

The genital papillae protruding laterally into the progenital chamber are located in deep pouches between proximal folds bordering the eugenital opening and the inner wall of the progenital lips. The few epithelial cells comprising the genital papillae show membrane folds, many mitochondria and microtubules. The overlying cuticle is conspicuously thicker and "cushion-like" when compared to the adjacent cuticle (Figure 4a-c).

A pair of accessory glands opens proximal to the eugenital opening into the ejaculatory duct. The cells of the accessory glands seem to be quite large and are full of electron-lucent lipid inclusions. A highly branching system of thin cuticle-lined ducts penetrates deeply into the gland (Figures 3a,f and 4d-f). Aside of the eugenital opening, eugenital setae are located (Figure 3a). The progenital lips border the (secondary) genital opening with sharp longitudinal cuticular keels (Figure 3a,d).

**Spermiogenesis and sperm structure**

The sperm cells of the three species are similar in so far as they represent synspermia as mentioned already (Figure 5). As in other spermatophore producing actinotrichid mites, the (syn)spermia are provided with a secretion layer (Alberti, 1980b; Alberti and Coons; 1999). Comparing the saxidromid synspermia, it is evident, that the sperm of the European species differ remarkably from the sperm of the two South African species being more similar to each other than to those of *S. delamarei*. The synspermia are aflagellate and spherical and show acrosomal complexes consisting of an acrosomal vacuole and an acrosomal filament (perforatorium), condensed nuclear material devoid of a nuclear envelope (so-called chromatin bodies), and a number of mitochondria. In each synspermium, several acrosomal complexes and chromatin bodies are present, likely four (indicating the spermatids which have not separated).

*S. delamarei* has the most complex sperm of the three species. Details have already been published elsewhere. Here only some characteristics are reported for comparison (Figure 5a-c; see Alberti et al., 2007). The synspernum is rather small (diameter about 2.5 µm) and surrounded by a rather thin secretion layer (about 0.075 µm thick). Most conspicuous is the acrosomal complex which protrudes slightly against the secretion layer producing small bulges at the surface of the cell. The acrosomal vacuole of each sperm equivalent is highly structured showing a complex shape and including different components. It is underlain by a flat extension of the sausage-shaped chromatin body. The extension is penetrated by the acrosomal filament, which runs into the cytoplasm. Chromatin bodies and acrosomal filaments are sectioned many times because of their length and their meandering course within the cytoplasm (Figure 5a-c). The acrosomal filament is relatively thick (about 0.09 µm in diameter). Spermatids show many tubular invaginations of the plasmalemma (Figure 5b), which later are hardly visible in the mature sperm.

The sperm of *B. roussouwi* (diameter about 50 µm) and *Rh. lootsi* (diameter about 28 µm) are much larger due to an increased amount of cytoplasm and provided with a much thicker secretion layer (*B. roussouwi* about 4.6 µm, *Rh. lootsi* about 6.45 µm thick) (Figure 5d,g). In contrast to *S. delamarei*, the acrosomal complexes and chromatin bodies are rather small and inconspicuous in both species. They are also located at the cell periphery, but do not project. The acrosomal vacuoles are irregularly shaped, flat cisternae containing electron-dense material (Figure 5f,j). That of *R. lootsi* was rarely seen and my be very small (Figure 5h-j). They are underlain by numerous small filaments. Similar filaments were also seen adjacent to parts of the chromatin bodies. The acrosomal filament (in *B. roussouwi* about 0.19 µm, *Rh. lootsi* about 0.13 µm thick) starts more or less underneath a central invagination of the vacuole and runs into the cytoplasm after penetrating a similar irregularly shaped flat chromatin body. Since sections of the acrosomal filament were only seen close to the acrosomal complexes and chromatin bodies, the filament is likely
FIGURE 5: See next page
relatively short. A thick mantle of numerous mitochondria is located underneath the cell periphery. The centre of the synspermium seems to be largely devoid of organelles. In contrast to _S. delamarei_, the cell surfaces of the synspermia of both South African species are provided with numerous conspicuous interdigitating cell protrusions which are covered by the secretion layer mentioned above.

The layer is composed of several sublayers (most conspicuous in _Rh. lootsi_) as is obvious from Figure 5d and g.

**Spermatophore structure**

As with the synspermia, the spermatophores produced by the three species are more alike in the two South African species, whereas those of _S. delamarei_ differ considerably (Figure 6). In this latter species, rather conventional stalked spermatophores (about 300 µm high) are deposited. They are rather simple, stout structures with a thick stalk and an elongated head which ends with a short attenuating tip. The sections reveal that the spermatophore is not much structured. There is an indistinctly delimited chamber in the upper third of the spermatophore which contains a dense secretion and numerous synspermia (Figure 6b) and is surrounded by a considerable amount of additional electron-lucent secretion.

In contrast to _S. delamarei_, the spermatophores of the two South African species are smaller and much more slender (in _B. roussouwi_ about 240 µm; _Rh. lootsi_ about: 130 µm high; estimates according to drawings from Coineau _et al._, 2006) consisting of a thin stalk and a spherical head. Hence we could only obtain the heads of the spermatophores (see Materials and methods). These heads were found to represent one synspermium as described above (Figures 1a-c, 3a,b and 5d,g).

**DISCUSSION**

The male genital system of Saxidromidae is fundamentally structured as in other actinotrichid mites. Most distinct is the organization of the testes into germinal and glandular parts and the location of the system ventral to the digestive tract (see, e.g., Alberti and Coons, 1999, Alberti, 2006). The ejaculatory duct opens into the progenital chamber which contains genital papillae, which are considered to play a role in water- and/or osmoregulation (Alberti, 1979; Alberti and Coons, 1999).

Except for the ejaculatory duct, which is highly structured, the entire system may be regarded as rather simple when compared to other actinotrichid mites, e.g., Bdellidae, Erythraeidae (Michael, 1896; Alberti, 1974; Witte, 1975). This may correlate with the rather simple structure of the spermatophores. Spermatophores occur in actinedid and oribatid mites and numerous have been described light microscopically (see, e.g., Alberti and Coons, 1999). In contrast, only few spermatophores have been studied with regard to fine structure, e.g., those of several Oribatida (e.g., Alberti _et al._, 1991; Fernandez _et al._, 1991). It turned out that these spermatophores,
Figure 6: Comparison of mating by Saxidromus delamarei and Rhinodromus lootsi and their corresponding spermatophores as seen in TEM (that of Rh. lootsi partially reconstructed; a, d from Coineau et al., 2006, b from Alberti et al., 2007). (a) – Some details of the mating sequence from above to below: S. delamarei male (black) has captured a female with its forelegs and deposits a rather large spermatophore (arrow). The male then turns round and impales the female onto the spermatophore. The spermatophore almost fills the "entire" female. The male has to separate the upper part of the spermatophore (which is more or less in the female) from the lower part which is attached to the ground. (b) – Longitudinal section of spermatophore of S. delamarei. Note the considerable amount of secretion forming the spermatophore and the rather small sperm chamber containing dense secretion and many synspermia. (c) – Spermatophore of Rh. lootsi drawn to same scale as that of S. delamarei. The head is (largely) represented by one synspermium. Stalk added schematically. Scale bar for b and c: 50 µm. (d) – Mating sequence seen in Rh. lootsi. Note that the spermatophore (arrow) produced by the male is considerably smaller bearing a very small head (i.e., mainly the synspermium). The male can use the same stalk several times depositing further synspermia on it. The male inserts its dorsoanterioria protruding processus into the female's genital opening prior to spermatophore deposition (not shown; see Coineau et al., 2006 for more details).

Abbr.: SpC, sperm chamber.
regarded previously to be of the "primitive" droplet type, show a remarkable diversity and structural complexity, which exceeds at least in some species that of the studied Saxidromidae. Hence, it may be justified to classify even the spermatophore of _S. delamarei_, which is the most complex of the family, as rather simple.

In contrast, the sperm cells and the mating behaviour are certainly much derived and complex. In all three species, synsperma are produced. These peculiar sperm aggregates were until recently only known from few haplogyne spiders and comprise "fused" sperm enclosed in a common secretion sheath (Alberti and Weinmann, 1985; Alberti, 2000). In fact, it was shown for spiders, that the spermatids do not separate at the end of spermiogenesis (Michalik et al., 2004) as is the case in Saxidromidae. In any case, Saxidromidae represent only the second taxon in the animal kingdom known to possess synsperma (Alberti et al., 2007). Each synspermiu contains a number of nuclei, acrosomal complexes and, in the case of spiders, axonemata in a common cytoplasm. Acari have aflagellate sperm cells and Actinotrichida have condensed nuclear material which has lost the nuclear envelope during spermatogenesis (hence called chromatin bodies) (Alberti 1980a, b, 1991, 2000, 2006; Alberti and Coons, 1999; Coons and Alberti, 1999). Accordingly, synsperma of Saxidromidae do not contain axonemata and possess chromatin bodies.

It may be mentioned again, that these clearly apomorphic peculiarities (testis histology, aflagellate sperm, chromatin bodies, chromatin body penetrated by the acrosomal filament) are shared only with Solifugae amongst other Arachnida (Alberti 1980a, b, c; Alberti 2000; Alberti 2006; Alberti and Peretti 2002; Klann et al., 2005, 2009). Anactinotrichid mites (and other Arachnida) are distinctly different (Alberti 1980a, b, 1991, 2000, 2006). Unfortunately, these obvious results were recently incorrectly referred to by Shultz (2007). Interestingly, however, the idea of a sister group relationship of Actinotrichida and Solifugae has recently received a new molecular support (Dabert et al., 2006) and is not really conclusive with respect to these mites. Thus a scenario "explaining" the evolution of synsperma in Saxidromidae may be described in the following way:

1. Actinotrichida likely have indirect spermatophore transfer as the plesiotypic insemination type. This is one mode of sperm transfer securing internal fertilization which is necessary in terrestrial habitats. It may be modified within several taxa in various ways (with or without mating, semidirect sperm transfer with gonopods, direct sperm transfer with penis = perhaps modified spermatopositor) (e.g., Pauly, 1952; Taberly, 1957; Schuster, 1962; Schuster and Schuster, 1966, 1977; Alberti, 1974; Witte, 1975, 1991; Ehrnsberger, 1977; Schaller, 1979; Alberti et al., 1991; Fernandez et al., 1991; Norton et al., 1993; Oldfield and Michalska, 1996; Alberti and
2. Saxidromidae have kept the plesiotypic transfer mode, but have modified it considerably. The male manipulates the female almost by brute force (securing sperm transfer) likely as an adaptation to the adverse habitat (heat, drought) and the resulting high competition for females (limited time due to increasing insolation). Coping with this, *S. delamarei* on the one hand and *B. roussouwi* and *R. lootsi* on the other, apparently evolved two different strategies:

a. *S. delamarei* during one mating event transfers relatively many synspermia, along with a long mating time and a large spermatophore (blocking almost the entire female genital tract) thus securing sperm priority by hindering further couplings and inseminations. However, in case of disturbances through other males, the mating male may be prevented from separating the spermatophore from the substrate which is necessary since the female is not able to do that and will die if the male fails to do this successfully (Coineau and Kovoor 1982). Hence, in this strategy the male may lose the entire invested material (many sperms, much spermatophore secretion) upon disturbance.

b. Both the other species transfer only one relatively small synspermium at a time. Thus at least some genetic material of the male will be transferred relatively fast. In case of disturbance, only a small amount of material is lost for the male (if it is not kept by the female) and the female can free itself from the tiny spermatophore stalk. If there is no disturbance, the male can deposit further synspermia on the same stalk thus transferring further synspermia. The sperm transfer thus is more secure, more effective and more economic. It may be speculated whether these mites are able to test the female’s fertilization state or to remove sperm of previous males with their anterior protuberances thus making their activities even more effective. It seems conclusive to consider the thick secretion layers covering these synspermia (in contrast to those of *S. delamarei*) serve as a protective layer preventing damage caused through such actions by a subsequent male. (It may even be considered whether the thick layer found in *Rh. lootsi* is a protective correlate to the long unpaired processus found in this species).

The testes of all three species apparently contain rather few sperm (compared to other actinedid mites), with the South African species showing an extreme reduction. Evidently, the reduction in sperm and secretion invested by the males, and thus an increase in economy, is possibly due to the complex, effective and secure mating behaviour.

But why synspermia? Since we found synspermia in all three species, the suggested reduction of secretion material alone makes no sense, since the spermatophore of *S. delamarei* requires a lot of secretion as do the conspicuous secretion layers around the synspermia of the South African species. We suggest instead, that the “invention” of synspermia is a means of shortening spermiogenesis and thus is “cheaper” for the male. The latest steps of spermiogenesis are transferred into the female and hence occur only in the case of successful mating. Hence, the synspermia, which are so rarely found in the animal kingdom, may be a further step in making the sperm transfer procedure more economic for the male.

Further studies, in particular of fertilized females, are needed to better understand this peculiar sperm transfer. Such studies are currently being conducted.

ACKNOWLEDGEMENTS

Thanks are due to Elisabeth Lipke (University of Greifswald) for technical help and to Ingrid, Johannes and Matthias Alberti for assistance during the collecting trips in South Africa. The valuable comments of the reviewers are appreciated.

REFERENCES

Alberti G. 1974 — Fortpflanzungsverhalten und Fortpflanzungsgänge der Schnabelmilben (Acarina: Bdellidae, Trombidiformes) — Z. Morphol. Tiere, 78: 111-157.

Alberti G. 1979 — Fine structure and probable function of genital papillae and Claparède organs of
