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MATING BEHAVIOUR AND REPRODUCTIVE MECHANISMS OF TWO SPECIES
OF PREDACIOUS MITES, PHYTOSEIULUS PERSIMILIS ATHIAS-HENRIOT
AND AMBLYSEIUS ANDERSONI (CHANT) (ACARINA : PHYTOSEIIDAE)

BY

Hiroshi Amano * and D. A. Chant *

ABSTRACT

The mating behaviour and reproductive mechanisms for two species of phytoseiid mites, Phytoseiulus persimilis and Amblyseius andersoni, were observed in the laboratory. The different mating patterns of the two species seemed to reflect their generic differences. In both species the fecundity of females increased with the duration of copulation. Most male P. persimilis inseminated females with only one endospermaphore transferred to only one of the female spermathecae, whereas males of A. andersoni transferred two endospermaphores, one to each spermatheca, in single matings that lasted for the full duration.

RÉSUMÉ

Le comportement d’accouplement et les mécanismes de la reproduction de deux espèces d’acariens phytoséidiens, Phytoseiulus persimilis et Amblyseius andersoni, ont été observés en laboratoire. Les différentes tendances d’accouplement des deux espèces semblent refléter leurs différences génériques. Chez les deux espèces, la fécondité de la femelle augmente avec la durée de la copulation. La plupart des mâles de P. persimilis ont inséminé les femelles avec un seul endospermaphore transféré à une seule des spermathèques de la femelle, tandis que les mâles d’A. andersoni ont transféré deux endospermaphores, un pour chaque spermatheque, durant un seul accouplement de pleine durée.

INTRODUCTION

The reproductive behaviour of the family Phytoseiidae has not been studied extensively, perhaps because of the small size of these mites (about 300-450 μ in body length of the adult females) and their rather monotonous behaviour patterns. However, fragmentary observations which have been reported suggest that phytoseiids generally have little or no pre-mating behaviour, and that mating takes place in a venter-to-venter position with the male beneath the female. The duration of copulation depends on the species studied and the experimental conditions (Ballard, 1954; Herbert, 1956; El-Badry & Zaher, 1961; Prasad, 1967; Muma & Denmark, 1967; Laing, 1968, 1969; El-Badry & Elbenhawy, 1968; Lee & Davis, 1968; Zaher & Shehata, 1971).

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It has been widely recognized among taxonomists of the Phytoseiidae that the shape and size of the so-called spermatheca have considerable value for species recognition. Oudemans (1930) was the first to draw attention to this organ. Since then it has been referred to as the receptaculum seminis, coxal gland, or the seminal receptacle by various authors (Hughes, 1948; Smith & Summers, 1949; Nesbitt, 1951). Womersley (1954) referred to this organ as the spermatheca, although its actual role in the reception of male cells was not studied until Dosse's work (1959).

Except for the female spermatheca, other reproductive organs in phytoseiid mites have not been studied and the structure of the internal reproductive system is still unknown. Furthermore, it is questionable if the term "spermatheca" is appropriate for the organ as it is known in phytoseiid mites, because this term usually applies to the storage organ for sperm or spermatozoa in the female body. To date there is no evidence that the "spermatheca" of phytoseiids functions as a sperm storage organ, as distinct from an organ for sperm reception.

The aim of the present paper, which is the second in a series, is to describe the mating behaviour of two species of phytoseiids quantitatively and to contribute to a better understanding of the reproductive mechanisms of species in this family.

Materials and Methods

Two species of phytoseiid mites, Phytoseiulus persimilis Athias-Henriot and Amblyseius andersoni (Chant), were used for this study, with the spider mite Tetranychus pacificus McGregor as prey. Details of maintaining these mites were described in a previous paper (Amano & Chant, 1977).

Observations were made with a stereoscopic microscope with a 20-watt fluorescent lamp as a light source, installed about 30 cm above and at a 45° angle to the mites. A virgin female and an unmated male, both of which had moulted to adults within 24 hours, were introduced to a 1 x 1 cm piece of black construction paper placed on water-saturated absorbent cotton. The temperature on the surface of the paper was 25° C throughout the observations.

The mites were observed continuously after their introduction to the paper and behaviour was recorded for both sexes. After copulation began (timed from the completion of the venter-to-venter position), observations of one minute duration were made every 15 minutes until the mites finally separated. Records included the time from initial contact to the commencement of copulation, and the duration of copulation. Fifteen pairs of each species were observed to record intraspecific as well as interspecific variations in mating behaviour.

To study insemination behaviour, mites in copula were forcibly separated by dipping them into distilled water for a few seconds at various times after the initiation of copulation. The times of separation were 5, 10, 30, 60 and 90 minutes after initiation of copulation for both species, and in addition 120 minutes for A. andersoni because of the longer average duration of copulation in this species. Twenty pairs of each of the two species were studied at each separation time. After separation, half of the females were killed in 90 percent alcohol and the other half were reared to determine their fecundity. The ten females which were killed in alcohol were mounted in Hoyer's medium and their spermathecae were examined. Also, ten virgin females and 10 fully-mated females which had just completed copulation were killed and their spermathecae were examined as controls.

For the examination of spermathecae, the following categories were established to express the different degrees of insemination (Fig. 1): (0-0), neither spermatheca was inflated or inse-
minated; (1-0), one of the spermathecae was inflated but not inseminated; (1-1), one of the spermathecae was inflated and inseminated; (2-1), one of the spermathecae was inflated and the other was both inflated and inseminated; and (2-2), both spermathecae were inflated and inseminated. The term "inflated" was used when the vesicle had expanded like a balloon but no endospermatophore could be observed within it. If the vesicle was expanded and an endospermatophore was observed in it, the term "inseminated" was applied. Terminology for the detailed structure of the spermatheca used in the present study follows SCHUSTER and SMITH (1960).
Results and Discussion

In the present study, in both species mating occurred as soon as the mites reached the adult stage. This does not agree with observations reported by Laing (1968). He studied the life history of P. persimilis and reported that mating was never observed immediately after the last moult: usually there was a six to twelve hour feeding period prior to mating in both sexes. Similar observations were reported for males of Typhlodromus pyri Scheuten by Zaher and El-Badry (1971). In the present study there was a tendency to feed heavily immediately prior to mating in P. persimilis, especially with the males, but this was not obligatory.

Males of both species frequently were observed waiting near, or sometimes on, female deutonymphs in the cultures. This phenomenon is common with many phytoseiid mites. Also, it was often observed that the males of P. persimilis were strongly attracted to the nearly-moulted skin of female deutonymphs. These observations suggest that there may be a sex-attractant produced by female deutonymphs.

Little is known about sex pheromones in the subclass Acari, and there is only one recorded indication of a sex pheromone in phytoseiid mites: males of A. fallacis (Garman) displayed a strong response to ether extracts of females (Rock et al., 1976). However, observations in the present study suggest that males of the two species were not attracted to females or female deutonymphs from a distance. If females produce a chemical attractant, it probably plays a role only when the sexes physically encounter one another. Individuals of one species showed no interest when they met individuals of the other.

The mating behaviour of both species is shown schematically in Fig. 2, with their intraspecific as well as interspecific variations. Prior to mating, the males of both species actively search for females, whereas the females remain mostly stationary. Twelve out of 15 pairs of P. persimilis and 11 out of 15 pairs of A. andersoni had their first encounter face to face (A-1 and a-1 in Fig. 2).

Interesting differences in behaviour were recorded between the two species. With P. persimilis all the pairs eventually made contact in a face to face position with their palps and first pairs of legs touching each other (B). The males then inverted themselves, with three different variations (C-1, C-2 and C-3), and crawled underneath the females with their ventral surfaces facing those of the females. The average time required from the initial contact (A-1, A-2 or A-3) to the final venter-to-venter position (E) was 62 seconds, and no significant differences were observed between the variations.

With A. andersoni, in 4 of the 15 pairs there was no face to face contact before the male climbed over the dorsum of the female. Ten out of 15 males climbed over the females laterally (b-2), 2 males climbed from the front (b-1) and 3 from behind (b-3). The males of A. andersoni spent 20 seconds wandering on the dorsum of the females, and often their mouthparts or first pairs of legs touched (c). Thereafter, the males crawled underneath the females posteriorly (d, e and f). The time required for the males to reach the top of the dorsum of the female after initial contact averaged 25 seconds and it required another 21 seconds to reach the final position.

The mating behaviour exhibited by A. andersoni, characterized by the climbing movement of the male on the dorsum of the female, is common in the phytoseiids studied to date. These include: A. fallacis (Ballard, 1954), A. cucumeris (Oudemans) (El-Badry & Zaher, 1961), A. gossypi El-Badry (El-Badry & Elbennawy, 1968), T. occidentalis Nesbitt (Lee & Davis, 1968), and T. pyri (Zaher & Shehata, 1971). The present authors have observed this mating pattern for A. degenerans (Berlese), as well. This form of mating behaviour also has been recorded...
Fig. 2: Diagram of mating behaviour in *P. persimilis* and *A. andersoni*. The number in brackets indicates the total number of pairs observed in each category out of 15 replicates. Stippled larger animals represent females.
in other families of mesostigmatid mites, such as the families Laelapidae (Jakeman, 1961), Macrocheilidae (Oliver & Krantz, 1963), Uropodidae (Radinovskv, 1965), Haemogamasidaceae (Young, 1968) and Rhodacaridae (Lee, 1974). On the other hand, only P. macropilis (Banks) has been reported to have the same mating behaviour as P. persimilis among the phytoseiid species studied to date (Prasad, 1967).

This rather exceptional mating pattern in both Phytoseiulus species may be significant to the classification and phylogeny of phytoseiid mites, in addition to its biological significance. It seems that members of the genus Phytoseiulus generally exhibit rather consistent biological characteristics compared to other genera: all species of this genus studied are obligate predators on other mites (mostly spider mites); their larvae do not feed; and they have high predation and oviposition rates (van der Meerwe, 1968; McMurtry et al., 1970).

For convenience, the terms "Amblyseius-Typhlodromus type" and "Phytoseiulus type" are proposed for the patterns of mating behaviour exhibited by A. andersoni and P. persimilis respectively, and they are used in the present and later papers.

Actual insemination occurred in both species in the final venter-to-venter position. No other mating positions have been reported for the Phytoseiidae. The mites remained in this position for an average of 131.07 ± 20.83 (mean ± standard deviation) and 185.00 ± 19.01 minutes in P. persimilis and A. andersoni respectively. During copulation, the males of both species were seen continuously extending their mouthparts to the ventral abdominal region of the females, with periodic jerking movements. On the other hand, females in copula were stationary and usually fed on prey, if any were available. It seems that the entire mating process was accomplished by the efforts of the males and that the only overt movement by the females was kicking or pushing the males with their fourth pair of legs, which eventually separated the two sexes when copulation was complete.

The duration of copulation in the present two species was almost the average among the phytoseiids reported to date. Lang (1968 & 1969) found extremely variable durations of mating in both P. persimilis and T. occidentalis, from a few minutes to several hours. However, such variations were not observed in the present study. This may have been because only unmated males and virgin females were selected for the present study.

The actual act of insemination by the phytoseiids could not be observed in living mites because of their small size and because the act was screened from sight by their bodies. Therefore it was necessary to examine the mounted females and males which were killed at different stages of copulation. Fortunately the spermathecae of P. persimilis and A. andersoni, which are located internally between coxae III and IV on each side of the body, are well sclerotized and it is easy to observe them microscopically.

Figure 3 shows the external reproductive organs of phytoseiids and their positions on the body. Legs are omitted from the figure. As mentioned above, Dosse (1959) was the first to determine the function of the spermatheca experimentally, and he also described the role of the male chelicera in transferring the ectospermatophore from the male genital opening to the female spermatheca. He studied both P. persimilis and T. zwölf eri Dosse. However, his report was not accurate: he stated that the spermatophore was introduced into the genital opening of the female instead of into the sperm induction pore.

The results of observations of spermathecae in females mounted at different stages of copulation are shown in Table I. The average insemination pattern for each species can be described as follows. Males of P. persimilis inflated the vesicle of one of the spermathecae within 10 minutes after mating commenced, and then began to inject spermatophoral material into the vesicle. Seven out of 10 females which mated for the full time were inseminated with only one endo-
spermatophore deposited in one spermatheca during a single mating. The other three were inseminated in both spermathecae, but only one endospermatophore was deposited in each. The males which inseminated both spermathecae of the female had moved from one to the other within 30 to 60 minutes of the initiation of mating.

On the other hand, the males of *A. andersoni* required about 5 minutes to inflate the vesicle and finished insemination of one spermatheca about 90 minutes after mating commenced. Without exception, the males of this species continued to mate and proceeded to inseminate the other spermatheca of the females. However, no spermatheca was inseminated with more than one endospermatophore.

Dosse (1959) reported up to 5 endospermatophores in a single spermatheca in *T. zwölferi*. However, no spermatheca of the single mated females contained more than one endospermatophore in either species in the present study. The examples of (1-1) type spermathecae are shown in Fig. 4, for both phytoseiid species studied. In both photographs, the spermathecae of the left side (SP-1) were inseminated and the others (SP-2) were not. Endospermatophores and inflated vesicles can be observed in the inseminated spermathecae.

The relationship between the duration of copulation and egg production in the two species of phytoseiids is summarized in Table II. In Fig. 5 the total egg production of the females is plotted against the duration of copulation. The age-specific oviposition curves of the females at each duration of copulation are shown in Figs. 6 and 7, for each species separately. It is obvious
Fig. 4: Spermathecae of *P. persimilis* (A) and *A. andersoni* (B) females. COX. II, COX. III and COX. IV indicate coxae II, III and IV, respectively.
from the table and figures that oviposition occurred in females mated for 30 minutes or longer and increased with the duration of copulation in both species. This was consistent with the observation that the size of the endospermaphore inside the spermatheca increased in proportion to the duration of copulation and that both spermathecae usually contained endospermaphores after 90 minutes of copulation, especially in A. andersoni. However, an unexpected and interesting observation was made in the females that had mated for only 10 minutes in both species. As shown in Table I, it appeared that the spermathecae of these females already contained a small endospermaphore within 10 minutes after the initiation of mating. However, in spite of this, females which mated only 10 minutes did not oviposit, and even females which mated 30 minutes produced only 2.7 and 5.1 eggs in P. persimilis and A. andersoni respectively.

Table I. — Relationship between duration of copulation and degree of insemination of the female spermathecae in P. persimilis and A. andersoni.

<table>
<thead>
<tr>
<th>Duration of copulation (minutes)</th>
<th>No. females examined</th>
<th>0-0</th>
<th>1-2</th>
<th>2-1</th>
<th>2-2</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>P. persimilis</strong></td>
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<tr>
<td>0 (virgin)</td>
<td>10</td>
<td>10</td>
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<tr>
<td>5</td>
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<td>10</td>
<td>10</td>
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<td>3</td>
<td>7</td>
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<td>30</td>
<td>10</td>
<td></td>
<td>9</td>
<td>1</td>
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<td>60</td>
<td>10</td>
<td></td>
<td>6</td>
<td>2</td>
<td>1</td>
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<tr>
<td>90</td>
<td>10</td>
<td></td>
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<td></td>
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<tr>
<td>131 (full time)</td>
<td>10</td>
<td></td>
<td>7</td>
<td>3</td>
<td></td>
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<tr>
<td><strong>A. andersoni</strong></td>
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<td></td>
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<tr>
<td>0 (virgin)</td>
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<tr>
<td>90</td>
<td>10</td>
<td></td>
<td>2</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>120</td>
<td>10</td>
<td></td>
<td>1</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>185 (full time)</td>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td>10</td>
</tr>
</tbody>
</table>

1) For categories, see Fig. 1.

The fecundity of A. andersoni did not increase notably when mating exceeded 120 minutes (Table II and Fig. 5). In Fig. 7 the oviposition curve of the females which mated 120 minutes closely overlaps that of the females which mated for the full duration. It is assumed from these results that the last hour of copulation in A. andersoni had little importance to the actual transfer of spermatozoa by the males or to female fecundity.
Fig. 5: Relationship between duration of copulation and total egg production by female phytoseiids. Values represent means and standard deviations. For the number of females examined, see Table II. * — Data from Amano & Chant (1977).

Fig. 6: Age-specific oviposition curves for the females of P. persimilis which mated with males for various durations. Numbers in brackets are the number of females examined. * — Data from Amano & Chant (1977).
Table II. — Relationship between duration of copulation and female oviposition behaviour in P. persimilis and A. andersoni. 1

<table>
<thead>
<tr>
<th>Duration of copulation (minutes)</th>
<th>No. females examined (N)</th>
<th>Females which oviposited at least one egg of N females</th>
<th>Average total egg production of N females</th>
<th>Average oviposition period (days)</th>
<th>Average daily egg production of N females during the oviposition period</th>
</tr>
</thead>
<tbody>
<tr>
<td>P. persimilis</td>
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<tr>
<td>5</td>
<td>10</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>10</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>30</td>
<td>10</td>
<td>7</td>
<td>2.70± 2.50</td>
<td>1.10± 1.17</td>
<td>1.30± 0.99</td>
</tr>
<tr>
<td>60</td>
<td>10</td>
<td>9</td>
<td>36.20± 6.73</td>
<td>7.30± 4.81</td>
<td>2.14± 2.04</td>
</tr>
<tr>
<td>90</td>
<td>10</td>
<td>10</td>
<td>39.20± 3.26</td>
<td>15.40± 3.26</td>
<td>2.68± 0.33</td>
</tr>
<tr>
<td>131 (full time) 2)</td>
<td>16</td>
<td>16</td>
<td>66.25± 35.34</td>
<td>22.94± 6.15</td>
<td>2.91± 0.17</td>
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<tr>
<td>A. andersoni</td>
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<td></td>
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<td></td>
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<tr>
<td>5</td>
<td>10</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>10</td>
<td>10</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
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<tr>
<td>30</td>
<td>10</td>
<td>8</td>
<td>5.10± 5.18</td>
<td>5.30± 4.28</td>
<td>0.78± 0.60</td>
</tr>
<tr>
<td>60</td>
<td>10</td>
<td>7</td>
<td>12.90± 12.38</td>
<td>11.10± 9.41</td>
<td>0.82± 0.67</td>
</tr>
<tr>
<td>90</td>
<td>10</td>
<td>10</td>
<td>27.30± 8.65</td>
<td>23.40± 9.58</td>
<td>1.26± 0.30</td>
</tr>
<tr>
<td>120</td>
<td>9</td>
<td>9</td>
<td>41.11± 7.28</td>
<td>33.44± 8.31</td>
<td>1.24± 0.15</td>
</tr>
<tr>
<td>185 (full time) 2)</td>
<td>6</td>
<td>6</td>
<td>46.33± 5.47</td>
<td>35.33± 5.32</td>
<td>1.32± 0.09</td>
</tr>
</tbody>
</table>

1) All values in the three right-hand columns are means± standard deviations.
2) Data from Amano and Chant (in press).
* Significantly different from the full-time mated females (bottom row of each species). For statistical procedures, the equality of variances was first examined, and the t-test or 'the approximate t-test' (p=0.05) was conducted depending on the results of equality of variances (see Sokal and Rohlf, 1969).

The results in Table II and Figs. 5-7 show that the total egg production of females decreased with the shorter duration of copulation as a consequence of both reduced oviposition periods and lowered daily egg production rates.

After copulation, the endospermatophores deposited in the spermathecae quickly disappeared. Figure 8 shows the spermathecae of the females that were killed after a 24 hour post-mating feeding period. There was a significant difference between P. persimilis and A. andersoni: no endospermatophore was observed in the spermathecae of P. persimilis (Fig. 8A), whereas a vestige of the endospermatophore could still be seen in A. andersoni (Fig. 8B). However, even in
the latter species, it can be seen that the endospermatophore in the spermatheca had become reduced in size and that the wall-like structure of one of the endospermatophores had partially disappeared.

**Fig. 7**: Age-specific oviposition curves for the females of *A. andersoni* which mated with males for various durations. Numbers in brackets are the number of females examined. *— Data from Amano & Chant (1977).

The spermathecae of mated females of *P. persimilis* had the same appearance 2 days after copulation as in the virgin females (0-0 type in Fig. 1). On the other hand, a transparent residue of the endospermatophore could be seen even 2 days after mating in *A. andersoni*, although this structure disappeared 2 to 4 days after mating, except for the heavily sclerotized wall-like portion at the base of the endospermatophore. This wall-like structure did not disappear completely for another 4 days.

These observations suggest that after several days there are no morphological differences between the spermathecae of mated females and of virgin females, especially in *P. persimilis*. The presence of endospermatophores inside the spermathecae of females has been used as one of the indicators of the fertilization of female phytoseiids. However, the present study shows that the absence of endospermatophores does not necessarily indicate that mating has not taken place. Furthermore, in females which mated only 10 minutes, even the presence of an endospermatophore in the spermatheca is not positive evidence that normal mating has occurred and that oviposition will follow. In a series of studies on overwintering phytoseiids, Wysoki & Swirski 1971a & b) used this character to determine the overwintering mode of several species in Israel, and they wisely adopted the presence of endospermatophores in the spermatheca as positive evidence of the act of fertilization, combined with the presence of developing ova. They did not interpret the absence of an endospermatophore as conclusive evidence of non-fertilization.

To investigate more accurately the mechanisms of insemination by the male, mounted slides of the pairs in *copula* were examined microscopically. Unfortunately, it was not possible to obtain slides of a pair of *A. andersoni* while in copulation. The killing technique using chloroform solution was effective for *P. persimilis* but not entirely for *A. andersoni*, and the pairs of this species separated in the solution. Perhaps the degree of union during the insemination was
Figs. 8-9: 8) Spermathecae of *P. persimilis* (A) and *A. andersoni* (B) after a 24 hour post-mating feeding period. E, developing egg; 9) Ectospermatophores of *P. persimilis* (A) and *A. andersoni* (B) observed on the slides of the pairs which mated 15 and 5 minutes, respectively.
looser with *A. andersoni*, or this species was able to survive in the chloroform long enough to separate. In spite of this, ectospermatophores detached from the chelicerae of the males were observed on the slides of the pairs for both species.

Figure 9 shows the ectospermatophores of each species which became separated from the spermatodactyls during the preparation of the slides. The ectospermatophores of the two species appeared to be similar and to be composed of a spherical chamber and a projecting neck. The diameter of the former was about 30 μ. However, it is not known whether these ectospermatophores had been distorted in size, either by the insemination effort of the male or by pressure from the coverglass on the slides. In any event, the five or more ectospermatophores observed for each species were consistent in shape and size. Ectospermatophores of similar shape have been reported for other mesostigmatids (Radinovsky, 1965; Young, 1968; Lee, 1974).

![Figure 10](image)

**Fig. 10**: Male spermatodactyl in position to inseminate the female spermatheca. This pair mated 10 minutes before being killed in chloroform. CH, male chelicera; MA.d, major duct of the spermatheca; SP.d, spermatodactyl of the male chelicera; V, vesicle of the spermatheca.

In the specimen shown in Fig. 10, the spermatodactyl (SP.d) is clearly inserted into the major duct (MA.d) of the female spermatheca, although the ectospermatophore was separated from the spermatodactyl during the preparation of the slide. It was observed on other slides that the ectospermatophores were attached to the chelicera, the spermatodactyl, which confirmed Dosse’s observations (1959). He reported in *P. persimilis* that the ectospermatophores were attached to the proximal end of the spermatodactyls of the males during the insemination process.

The method by which male phytoseiids remove the ectospermatophores from their genital openings and attach them to their spermatodactyls is not known. Moreover, the actual mechanism of transfer of the endospermatophore from the spermatodactyl into the female spermatheca has not been determined. The presence of an internal canal through the spermatodactyl has...
been reported for phytoseiids (Wainstein, 1973), as well as for other mesostigmatid families (Young, 1968; Lee, 1974). The endospermatophores probably move through this canal, although no spermatozoa have been observed in the canal of phytoseiids to date.

Young (1968) reported in his study of the family Haemogamasidae that the downward-pressing movements of the male chelicerae pressed the ectospermatophore, which was attached to the base of the chelicera, to the female venter and transferred the contents inside. This method of transference may be possible in phytoseiids, although attempts to observe it were not successful in the present study.

Since Dosse (1959), it is common among researchers of phytoseiids to refer to the endospermatophore deposited in the spermatheca as the "spermatophore". In other words, they believe that the whole spermatophore (ectospermatophore in this paper), including its outer sac, is deposited in the female spermatheca.

From the observations of the slides of both phytoseiid species in the present study, however, the ectospermatophores were often observed around the chelicera of the male even after the spermatheca was seen to contain endospermatophores. This suggests that the ectospermatophore remains at the base of the chelicera of the male during and after insemination, which is consistent with the observations on other mesostigmatid families (Young, 1968; Lee, 1974).

If this observation is correct, another question arises concerning the wall-like structure of the endospermatophores inside the spermathecae. Dosse (1959) studied this structure and reported that the injected spermatozoa inside the spermatheca were surrounded by a strong, chitinized covering and that this covering was not destroyed even by maceration of the whole mite in lactic acid with heat.

At least three possibilities exist about the origin of this covering. First, this wall-like structure was injected by the male in the form of liquid with the spermatozoa. Second, it was produced by a chemical reaction between the contents of the spermatheca and the materials injected by the male. Third, it is a part of the spermatophore structure other than the ectospermatophore, as is the case in ticks (Feldman-Muhsam, 1973).

When considering the solid nature of this wall-like structure as reported by Dosse, it is surprising that this structure disappeared inside the spermatheca so quickly after mating, as described above. This structure did not disappear, however, if females were killed and mounted immediately after copulation. In other words, disappearance occurred only in living mites.

Although the internal female reproductive system is basically uniform among other mesostigmatid families which use the sperm induction pores for the reception of spermatozoa, the Phytoseiidae seem to have a different arrangement of the reproductive organs. The generalized female reproductive system of other mesostigmatid families is shown in Fig. 11A. Data used in the construction of this figure were derived from Michael (1892), Warren (1941), Jakeman (1961), Young (1968), Krantz (1970), Lee (1974) and Treat (1975).

Spermatozoa are deposited in the rami sacculi (R.S.) through the sperm induction pores (SP.i) and the tubuli annulati (T.A.), and stored in the unpaired spermatheca (SP.t). The cells produced by the female in the paired ovaries (OV) are fertilized in the fertilization chamber (F.C.) by the male cells and develop into the large eggs in the uterus (UT). Eggs are deposited from the genital opening (G.O.) through the vagina (VA).

A schematic diagram of the female reproductive system of phytoseiids is shown in Fig. 11B. The endospermatophore is introduced to the so-called spermatheca and spermatozoa probably move through the minor ducts (MI.d) to the as yet unknown central areas of the reproductive system. This spermathecal structure is rarely seen in other mesostigmatid mites: Michael (1892) reported a similar structure in "Laelaps (?) ligniformis", and it also was illustrated for
several species of the family Ascidae (ATHIAS-HENRIOT, 1961; CHANT, 1963; LINDQUIST & CHANT, 1964).

Costa (1966) attempted to homologize the vesicle, and the major and minor ducts of the spermatheca in phytoseiid females with the *sacculus foemineus* (corresponding to the spermatheca in Fig. 11A), *tubulus annulatus* and *cornu sacculus* (part of the spermatheca and/or fertilization chamber in Fig. 11A) of other mesostigmatid females. Perhaps he believed that the minor ducts of phytoseiids connect directly to the ovary. FAIN (1963) presented another hypothesis and suggested the possible presence of a sperm storage organ (spermatheca from the definition in other Acarina and Insecta) between the minor ducts and the ovary in phytoseiid mites.

![Diagram](image)

Fig. 11: Generalized schematic representations of the reproductive systems of female mesostigmatid mites (A) and female phytoseiid mites (B). COX. III and COX. IV, coxae of legs III and IV; F.C, fertilization chamber; G.O, genital opening; MA.d, major duct; MI.d, minor duct; OV, ovary; R.S, *ramus sacculus*; SP.t, spermatheca; SP.i, sperm induction pore; T.A, *tubulus annulatus*; UT, uterus; V, vesicle; VA, vagina.

The present study indicated that the endospermatophore disappeared very quickly after insemination into the spermatheca of the female. Moreover, the spermatheca returned quickly to its original shape, which is the same as that in virgin females. Although there is no evidence that the spermatozoa themselves did not remain in the spermatheca after the endospermatophore disappeared and the vesicle of the spermatheca shrunk, the possibility exists that the spermatozoa moved to another organ in which they were stored until they fertilized the female cells. Structurally, the shrunken spermatheca seems too small to retain all of the spermatozoa with which it was inseminated during the long oviposition period of these mites. If the hypothesis that the spermatozoa are stored in an organ other than the so-called spermatheca is correct, the function of the spermatheca in phytoseiids is restricted to being the reception site for the male cells. If this is the case, other terminology, such as the *bursa copulatoria* from the Insecta, or the *ramus sacculus* shown in Fig. 11A, would be more appropriate.
Only detailed histological studies will resolve this question. If a method of staining the spermatozoa of phytoseiids can be established, it will enable the movement of the injected spermatozoa inside the female body after the act of insemination to be determined. So far, there have been no reports on this matter in phytoseiid mites.

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