Diversity in the copulatory behaviour of comb-footed spiders (Araneae, Theridiidae)

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Abstract: Main elements of the copulatory behaviour of comb-footed spiders are presented from personal observations of c. 70 species. For 45 species copulatory behaviour is analysed and compared in detail, for 30 of them for the first time. According to the time at which sperm induction occurs two main types of copulation exist. In the plesiomorphic *Steatoda*-type sperm induction takes place independently of copulation and is a rather long process, whereas in the *Theridion*-type it is part of copulation and therefore proceeds swiftly. Theridiidae exceed all hitherto known spiders in number of sperm inductions. Some representatives of the *Steatoda*-type exhibit a more ritualised form of courtship behaviour, with construction of a mating web and continuous stridulation, until the female approaches. In *Theridion* species the male approaches for copulation. Males of the *Theridion*-type interrupt copulation several times in order to charge their palps with sperm. Thus, sequences of insertions alternate with sperm uptake. Copulation generally involves more insertions in the *Theridion*-type than in the *Steatoda*-type, whereas actual time needed for sperm transfer is comparatively low. Species of the *Theridion*-type invest a considerable part of copulation in functions other than sperm transfer, such as pseudocopulation, mate guarding, sperm uptake and formation of mating plug.

Copulatory patterns differ considerably between species and appear to be specific within the *Theridion*-type. Representatives of the *T. melanurum*-group start insemination with the first insertion. Their copulatory sequences are comparatively uniform. In the *Theridion varians*-group the copulatory pattern is more complex, as the copulatory sequences are differentiated and reflect different functions. The first sequence does not result in sperm transfer and is a pseudocopulation. Insemination starts after the first sperm induction with the next insertions. During the last copulatory sequence a mating plug is produced. Integration of sperm induction may have evolved by rapid repetition of copulations. After each copulation palps are recharged with sperm. Such repeated copulations may help to increase reproductive success, as shown by the high number of copulatory sequences in some *Theridion*-species. By this means, the female is kept away from further males for a rather long time.

Male and female genital organs of entelegyne spiders are morphologically correlated. In most cases, one male palp can insert only into one female duct, either ipsilaterally or contralaterally. In contrast to most other entelegyne spiders, some representatives of the *Theridion*-type show contralateral insertion (left embolus inserts into right introductory duct and vice versa). Interestingly, all types of insertion are present within Theridiidae. *Argyrodes argyrodes* and *Steatoda bipunctata* insert ipsilaterally. Furthermore, males of the one-palped spiders (*Echinotheridion*, *Tidarren*) are able to do both, so that they can choose the still virgin receptaculum.

Many comb-footed spiders produce a mating plug at the end of copulation, which may be temporary or permanent and of varied origin, coming from the mouthparts in *Steatoda triangulosa*, from glands of the male palp in *Argyrodes argyrodes* and *Steatoda bipunctata*, and from secretions of the male and female genital tract in the *T. varians*-group. In the last named, the male secretion is transferred to the palps via the sperm web and to the epigyne by palpal application.

Taxonomy: For two species a new combination is proposed: *Keijia kijabei* (BERLAND 1920) nov. comb. (from *Theridion*) and *Theridion ohlerti* THORELL 1870 (nec *Achaearanea o.*).

Key words: Copulation, sperm induction, insertion, pseudocopulation, amputation, emasculation, sexual cannibalism, mating plug.

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Introduction

Comb-footed spiders are one of the largest spider families, with about 2200 species in c. 80 genera, and are highly diverse in morphology and also in behaviour. They have a wide array of morphological, ecological and behavioural traits. For a first impression of their manifold general appearance see KNOFLACH & PFALLER (this volume) and KNOFLACH & THALER (1998). Considerable diversity is exhibited also in mating behaviour (GERHARDT 1927, BRAUN 1963, KNOFLACH 1998). Sperm induction may take place independently of copulation or may be part of copulation. Some species initiate sperm transfer only after a pre-insemination phase (pseudocopulation, KNOFLACH 1998). Copulation may involve only two insertions, but up to 400 in *Theridion*. It may last for a few seconds only, as in *Achaearanea*, or for several hours, as in *Theridion*. In some species construction of a mating thread is essential. A mating plug, which seals the female's genital organ, may be present or not, may be permanent or not and originates from various parts of the male body. Sexual cannibalism occurs facultatively in the famous widow spiders (FORSTER 1992, ANDRADE 1996, KNOFLACH & VAN HARTEN 2001b), but appears to be absent in many other theridiids. Unique among spiders are the one-palped genera *Tidarren* and *Echinotheridion*, which exhibit numerous outstanding phenomena: self-amputation of a male palp, sudden sexual death, sexual cannibalism and emasculation (KNOFLACH & VAN HARTEN 2000a, 2001a; KNOFLACH 2002a, b).

In the present paper, theridiid copulatory behaviour is discussed from personal observations on c. 70 species in 24 genera. At first, in the general part, the main elements of copulation, like sperm induction, courtship, general pattern, copulatory posture and insertion type, mating plug and mating system, are analysed and compared. In the specific part the copulatory behaviour of 45 species is described, for 30 of them for the first time. Observations already published have also been taken into consideration (see KNOFLACH 1994, 1996, 1997, 1998, 1999, 2002a, b; KNOFLACH & BENJAMIN 2003, KNOFLACH & VAN HARTEN 2000a, b, 2001a, b).

Material and methods

Taxonomic references according to PLATNICK (2003). Material is given for each species in the descriptive part. For numbers of observations see descriptive part. Observations were based on virgin pairs, if not indicated otherwise.

The specific descriptions of the copulatory behaviour of 45 species are arranged in alphabetical order, but separated according to copulatory type (*Theridion* and *Steatoda*-type). Members of a species group are subsumed for better comparison. The following species were analysed:

Theridion-type: 1 *Chrysso cambridgei*, 2 *Keijia kijabei*, 3 *K. tincta*, 4 *Nesticodes rufipes*, 5 *Paidiscura orotavensis*, 6 *P. pallens*, 7 *Rugathodes bellicosus*, 8 *Simitidion lacuna*, 9 *S. simile*, 10–15 *Theridion melanurum*-group: 10 *T. betteni*, 11 *T. melanurum*, 12 *T. musivivum*, 13 *T. mystaceum*, 14 *T. ochreolum*, 15 *Theridion* sp. (close to *T. melanurum*), 16 *T. conigerum*, 17 *T. grancanariense*, 18 *T. incanescens*, 19 *T. ohlerti*, 20 *T. pinicola*, 21–22 *T. sisyphium*-group: 21 *T. impressum*, 22 *T. sisyphium*.

Steatoda-type: 23 *Achaearanea lunata*, 24 *A. simulans*, 25 *A. tepidariorum*, 26 *Anelosimus aulicus*, 27 *Argyrodes argyrodes*, 28–31 *Enoplognatha ovata*-group: 28 *E. afrodite*, 29 *E. latimana*, 30 *E. ovata*, 31 *E. penelope*, 32 *E. verae*, 33–35 *E. diversa*-group: 33 *E. diversa*, 34 *E. macrochelis*, 35 *E. sattleri*, 36 *E. quadripunctata*, 37 *E. thoracica*, 38 *Episinus maculipes*, 39 *Euryopis episinoides*, 40 *Steatoda bipunctata*, 41 *S. castanea*, 42 *S. grossa*, 43 *S. paykulliana*, 44 *S. triangulosa*, 45 *Theridion* (?) *nigrovariegatum*.

Penultimate and young instar specimens were housed separately in plastic boxes (7/4/2.5 cm) at room temperature until they reached maturity. For copulatory observations, males were introduced into the female's web. Copulations were observed with a stereo microscope with horizontal objective body (Nikon SMZ–2B), magnification up to x50. In addition, copulations were videotaped with a SONY DXC–325P equipped with a macroobjective and microlenses. Duration of insertion duration and sperm induction were recorded with a stopwatch. Total insertion time is given for each species as the maximal possible time invested in actual sperm transfer.

All photos and figures by the author, unless indicated otherwise.

SEM micrographs were made with a Zeiss DSM 950 by K. PFALLER (Institute of Anatomy, Histology and Embryology; Department of Histology and Molecular Cell Biology, University of Innsbruck) and Figures 60e–g with a Leitz AMR 1000 by S. TATZREITER (Institute of Botany, Innsbruck). The principal coordinate analysis (Fig. I–III, appendix) was provided by A. LOCHS (Central Information Centre, Innsbruck).

Abbreviations: C 1–12 = copulatory sequence 1–12, MP = mating plug, P = pseudocopulation, s.e. = standard error of the mean.

Terminology: Embolus: distal intromittent sclerite of the male palp. Haematodochae: inflatable palpal membranes. Pseudocopulation: sequence of insertions without sperm transfer (VAN HELSDINGEN 1983). Copulatory sequence: sequence of insertions after sperm induction, initiated and terminated by the male in the *Theridion*-type of copulation. Insertion: functional contact between male palp and female epigyne, followed by haematodochal inflation (Fig. 5d, 7c, 8a, 11a, 13b, 16, 29a, b, 32c, d, 33c, 35d, 65c, d, 72b, 85a, b, 95). Insertion attempt: genital contact not functional, without haematodochal expansion (Fig. 65e). Copulatory courtship: courtship during or after copulation (EBERHARD 1996).

Sperm induction

For sperm induction the male at first has to construct a sperm web, see Figures 1a–f. He starts with a few longitudinal threads, which then are connected by some cross threads (bridge) forming a frame. The web then becomes a dense layer by spinning movements of the spinnerets (sideways swaying movements), alternating with rubbing the epigaster against the bridge. Construction of the sperm web is completed by intensive epigastric rubbing, until the sperm droplet is released and pressed from below against the anterior side of the web. The sperm web is kept in tension by the male's hind legs, only legs I remain on the female web. Shortly after deposition of the sperm droplet the male moves backwards, while holding the sperm web, so that the palps reach the droplet (Fig. 1, 8b, 28b, c, 32b, 33f, 35a, 38d, 40a, b, 43e, f, 49e, f, 50d, 57d, 60a, 83a, 89a, b). By alternate dipping movements of left and right palp the sperm droplet is absorbed. After induction the male chews his palps. There are considerable differences in size of the sperm droplet. *Theridion varians* and related species produce a large droplet (Fig. 1a–d, 8b), whereas in species of the *T. melanurum*-group it is tiny and hard to recognise (Fig. 1e, f, 43e, f).

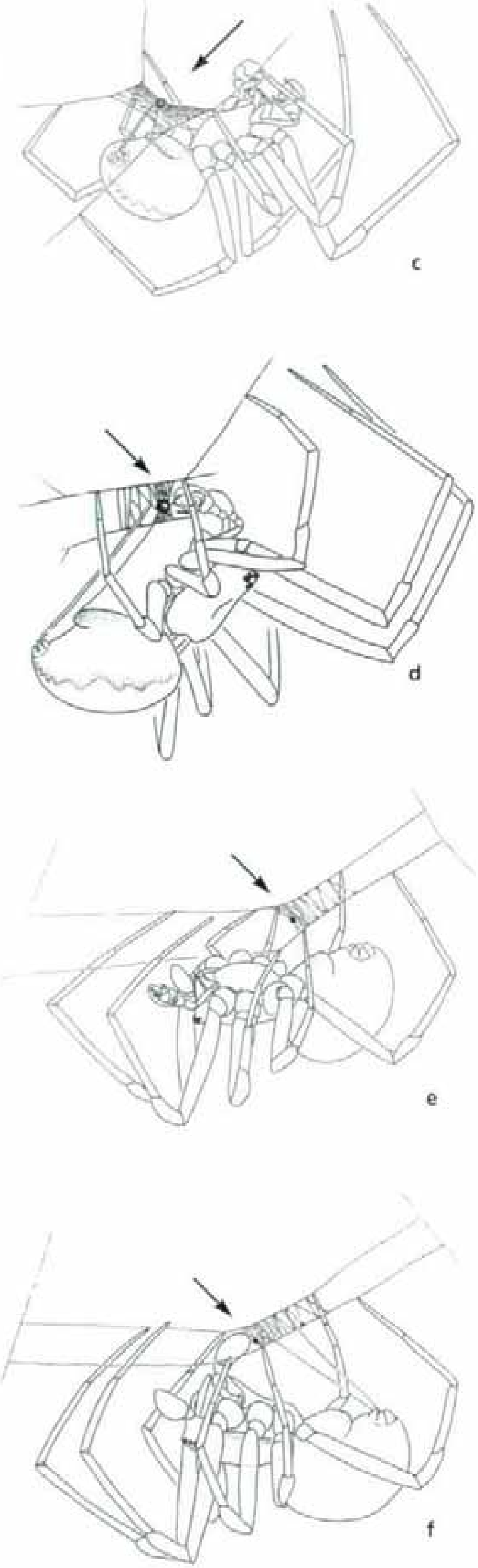


Fig. 1a–f: Sperm induction in *Theridion pinastri* (a, b), *T. petraeum* (c, d) and *T. adrianopoli* (e, f), construction of sperm web already terminated. Deposition of sperm droplet (a, c, e). Induction by alternate palpal dips, when male has moved backwards (b, d, f). Spinnerets and epigastric glands are connected to sperm web by long threads (d, f). Note small size of sperm droplet in *T. adrianopoli*. c, d after KNOFLACH (1998); e, f after KNOFLACH (1997).

According to the time at which sperm induction occurs two main types of copulation exist (Fig. 2; KNOFLACH 1998). In the *Steatoda*-type sperm induction takes place independently of copulation, as in most spiders, and therefore has been observed less frequently. It proceeds some time after the final moult and again after copulation. Sperm induction is rather long, 12.9 min ± 1.2 s.e. on average (range = 6.6–24.0; 15 species assessed; Fig. 3). Therefore, the sperm is stored in the palps for a rather long time, at least for a few days. As palps are 'emptied' by copulation, sperm induction often follows some time afterwards. In *Dipoena melanogaster* and *Lasaeola tristis* males even built two sperm webs in succession, exceptionally even three (KNOFLACH 2000). The *Steatoda*-type represents the widespread pattern and largely includes genera with colulus and hook-like paracymbium, characters which are considered as plesiomorphic (FORSTER *et al.* 1990). Also a few genera of the lost-colulus-clade of Theridiidae (AGNARSSON, in press) follow the *Steatoda*-type, such as *Achaearanea*, *Echinotheridion*, *Tidarren*. One species hitherto placed among *Theridion*, *T. nigrovariegatum*, does not agree at all with the *Theridion*-type of copulation, but shows a long sperm induction independent of copulation.

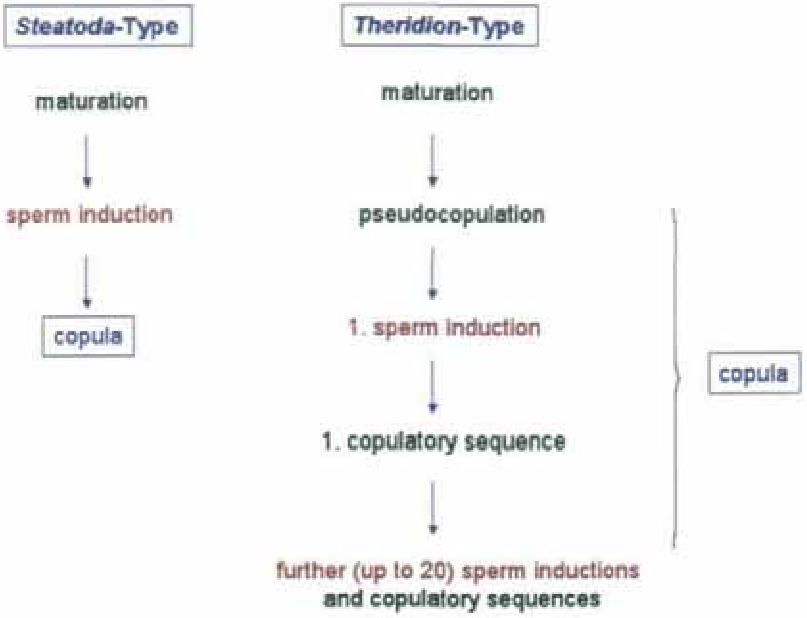
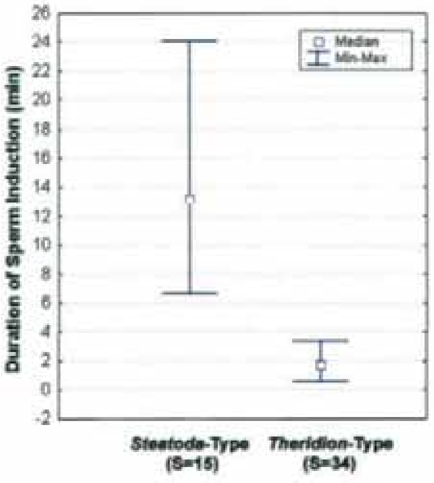


Fig. 2: Main types of copulation in comb-footed spiders.

In the *Theridion*-type, sperm induction is part of copulation. Males of *Chrysso*, *Keijia*, *Neottiura*, *Nesticodes*, *Paidiscura*, *Rugathodes*, *Simitidion* and *Theridion* interrupt copulation several times in order to charge their palps with sperm. Thus, sequences of insertions alternate with sperm uptake. Sperm induction proceeds swiftly. The whole procedure of construction of sperm web and induction lasts only 1.7 ± 0.1 min on average (mean ± s.e., range = 0.5–3.4; assessed for 34 species; Fig. 3), much quicker than in the *Steatoda*-type, as this interruption implicates a certain risk for copulatory success. To avoid any delay the male builds the sperm web in the immediate vicinity of the female (Fig. 49e, f). These species do not store the sperm in their palps for a long period, since sperm transfer immediately follows sperm induction. This mating type includes almost exclusively genera of the lost colulus clade (AGNARSSON, in press). They also all have a hood-like paracymbium. In *Paidiscura* behavioural elements do not fully coincide with morphology. Species of the genus *Paidiscura* belong to the *Theridion*-type according to the time of sperm induction, they also lack a colulus, but have a hook-like paracymbium (KNOFLACH & THALER 2000). Males interrupt copulation three times for sperm uptake, see specific part. Probably, shift of sperm induction into copulation occurs in different lineages of Theridiidae.

Integration of sperm uptake into copulation is widespread in Linyphiidae (VAN HELSDINGEN 1983) and is present also in the uloborid spider *Octonoba sinensis* (SIMON 1880) (PEASLEE & BECK 1983), in the desid *Badumna longinqua* (L. KOCH 1867) (according to PEASLEE & BECK 1983) and in the theridiosomatid *Theridiosoma gemmosum* (L. KOCH 1877) (according to HUBER 1998). As the *Theridion*-type is assumed to show apomorphic characters as compared with *Steatoda*, this behaviour should have evolved independently in these families by shortening the period between sperm induction and next copulation as well as by shifting the first sperm induction into copulation. Theridiidae exceed all hitherto known spiders in the number of sperm inductions (Tab. 1). *Theridion conigerum* and *T. ohlerti* charge their palps even more than 20 times during one copulation. Apparently, they spend even more time in sperm induction than in actual transfer.

Fig. 3: Duration of sperm induction in comb-footed spiders arranged by copulatory type.



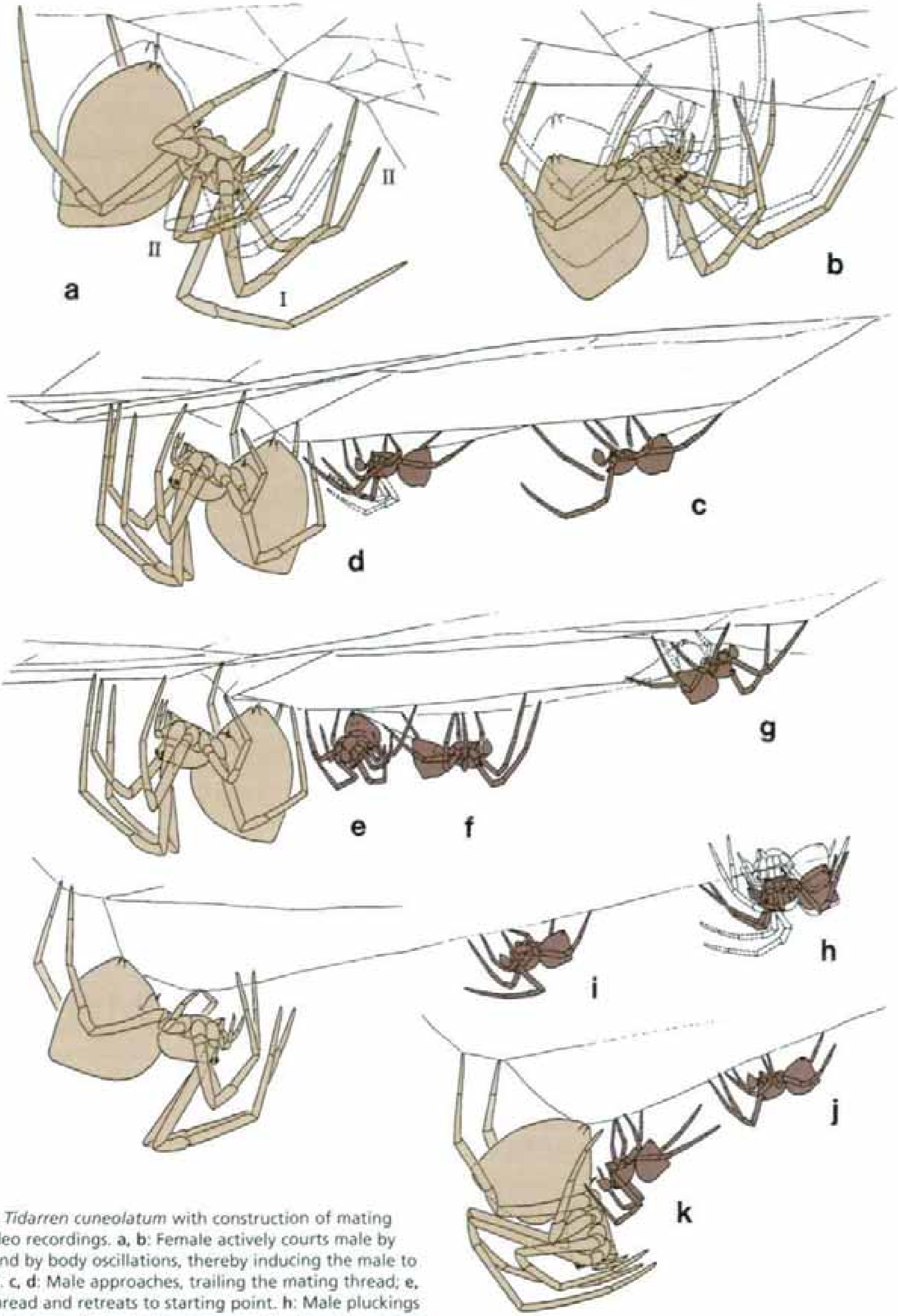


Fig. 4: **a–h**:Courtship in *Tidarren cuneolatum* with construction of mating thread, traced from video recordings. **a, b**: Female actively courts male by twanging with legs II and by body oscillations, thereby inducing the male to spin the mating thread. **c, d**: Male approaches, trailing the mating thread; **e, f, g**: attaches mating thread and retreats to starting point. **h**: Male pluckings cause the female to orient towards the male and approach along the mating thread. **i–k**: Final male approach shortly before insertion. **k**: Female in copulatory posture, perpendicular to mating thread. Solid lines first position, dotted lines second (a, b, d, g, h), finely dotted lines third (a, h). Modified after KNOFLACH & VAN HARTEN (2000a).

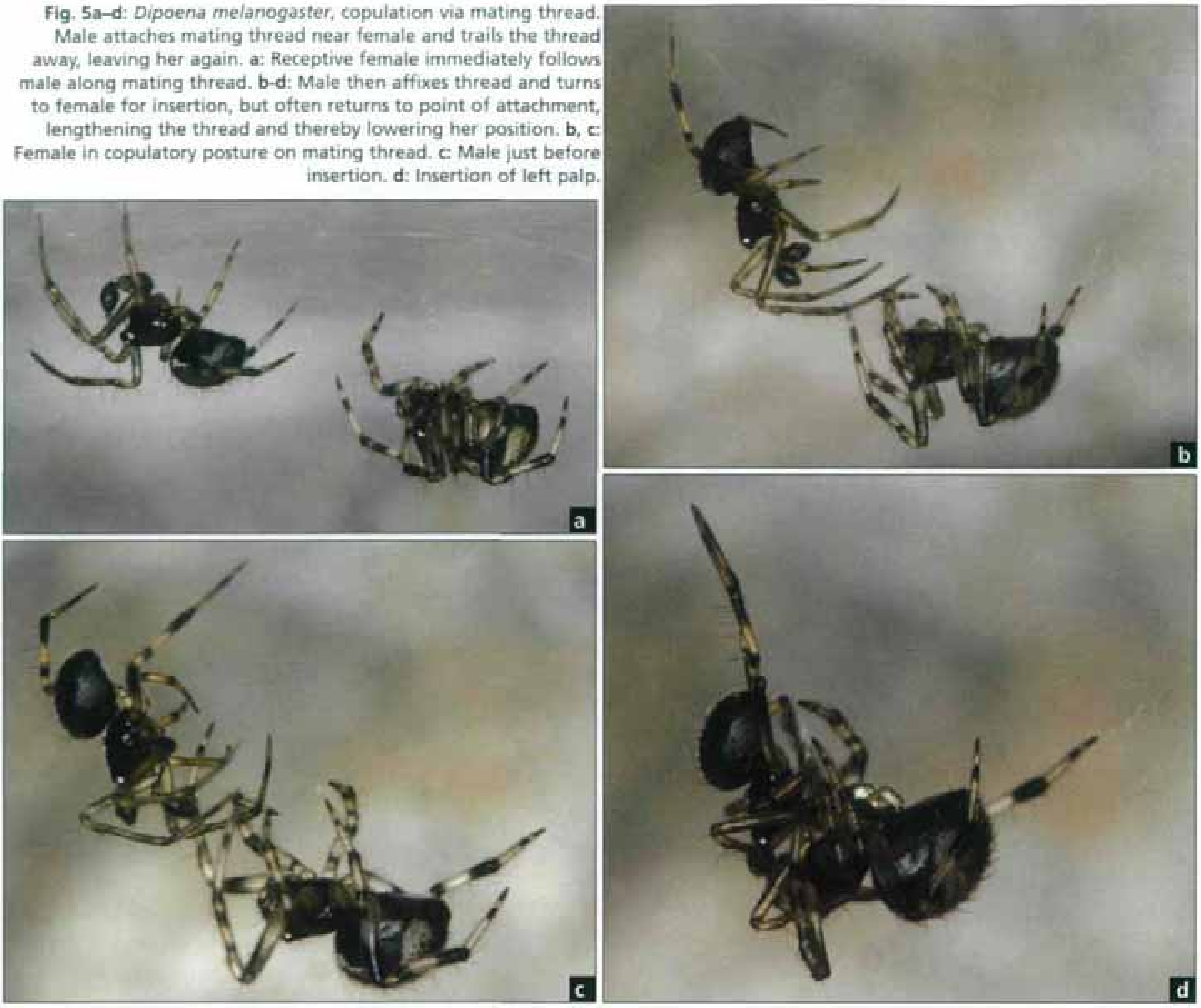


Fig. 5a–d: *Dipoena melanogaster*, copulation via mating thread. Male attaches mating thread near female and trails the thread away, leaving her again. **a**: Receptive female immediately follows male along mating thread. **b-d**: Male then affixes thread and turns to female for insertion, but often returns to point of attachment, lengthening the thread and thereby lowering her position. **b, c**: Female in copulatory posture on mating thread. **c**: Male just before insertion. **d**: Insertion of left palp.

Courtship

An essential function of courtship is the suppression of predatory behaviour, in addition to species recognition, mate choice, stimulation and synchronisation of sperm transfer (PLATNICK 1971). Most comb-footed spiders are sedentary web-builders, so that vibratory and chemical cues are more important for communication than visual sense. Pheromones incorporated into the silk of the female web act as courtship stimulant to the male. Thus, direct contact is not necessary to inform the male. Basic courtship movements of the male are abdominal pulsations and vibrations. Thereby, the abdomen is moved up and down and the anterior sclerotised ridge of the abdomen is rubbed against stridulatory grooves on the posterior part of the prosoma. Such a stridulatory organ (see KNOFLACH & PFALLER, this volume) is present in most theridiids. Courtship repertoire furthermore comprises plucking with forelegs at a distance from the female and mutual palpating with legs and palps during contact phase (Fig. 7a–f). During courtship usually periods of activity alternate rhythmically with periods of quiescence. Courtship apparently lasts longer in the *Steatoda*-type (mean ± s.e. = 24.7 ± 10.9 min for 37 species) than in the *Theridion*-type (mean ± s.e. = 8.4 ± 1.4 min for 31 species).

Some Theridiidae exhibit a more ritualised form of courtship behaviour, with construction of a mating thread and continuous stridulation and plucking, see Fig. 4, 35b, 61a, 72a, 88b, c. The male installs either a 2–4 cm large layer of silk (*Steatoda*,

1	*Theridion lacticolor* (1, n = 2)
2–3	*Chrysso cambridgei* (2–3, n = 7), *Coleosoma floridanum* (2, n = 2), *Neottiura bimaculata* (2–3, n = 4), *Paidiscura orotavensis* (2–3, n = 4), *P. pallens* (3, n = 1), *Theridion melanostictum* (2–3, n = 6), *T. ochreolum* (2–5, n = 8)
3–4	*Keijia tincta* (3–4, n = 4), *Theridion incanescens* (4, n = 1), *T. petraeum* (3–4, n = 19)
4–9	*Keijia kijabei* (5, n = 1), *Simitidion lacuna* (5–7, n = 3), *S. simile* (5–9, n = 6), *T. grancanariense* (4–6, n = 3), *T. impressum* (3–6, n = 3), *T. melanurum* (7–9, n = 2), *T. musivivum* (5–10, n = 10), *T. mystaceum* (5–6, n = 2), *T. pictum* (4–8, n = 11), *T. pinastri* (4–6, n = 6), *T. pinicola* (6–8, n = 3), *T. refugum* (4–9, n = 17), *T. sisyphium* (8, n = 1), *T. varians* (5–8, n = 15)
6–18	*Nesticodes rufipes* (8–17, n = 3), *Rugathodes bellicosus* (6–15, n = 4), *Theridion adrianopoli* (12–18, n = 6), *T. betteni* (10–11, n = 3)
19–25	*Theridion conigerum* (19–20, n = 2), *T. ohlerti* (25, n = 2)

Tab. 1: Numbers of sperm inductions in copulations of Theridiidae (range of sperm inductions and number of observations indicated in brackets)

Enoplognatha), or a 2–4 cm long thread, which may be reinforced several times (*Anelosimus*, *Echinotheridion*, *Paidiscura*, *Tidarren*). On this male-made part of the web he then starts to vibrate and pluck rhythmically, until the female approaches. As a result, copulation takes place on the mating web, outside the retreat of the female. Without female approach copulation cannot be accomplished. Thus, the female decides on the progress of copulation. Courtship via a mating web appears to filter aggressive tendencies of the female and facilitates appropriate orientation of the partners. It may also help to locate the female genital organ. In some species females cooperate by assuming a particular posture, her legs III being flexed and forming a circle, the tarsi being close together on the mating thread (Fig. 4, 61a, b). When the male approaches her along the mating thread he is guided by her legs to the epigynum. The male of *Dipoena melanogaster* also constructs a mating thread, but copulation proceeds in an acrobatic way. In contrast to other species, the female is not lured to this thread by plucking movements and vibrations, but follows the male immediately along the thread (Fig. 5a–d), which the male is just releasing and drawing away. The male attaches the mating thread and is able to manipulate the female's position by lengthening the thread (Knoflach 2000). The unusually rapid tempo of copulation is reminiscent of that in Araneidae. *Dipoena melanogaster* exceeds all comb-footed spiders hitherto studied in rapidity of movements. The pair seem to perform a high-wire act, which does not last longer than a minute. Actual courtship is indistinct. Anyway, males should not be in danger of being preyed upon, as *D. melanogaster* is a specialised ant feeder like other *Dipoena*-species sensu lato.

Fig. 6a, b: *Latrodectus geometricus*, courtship with leg-binding. Male coats female legs and body with weak strands of silk.

Remarkably, genera with courtship via a mating thread belong to different theridiid lineages (Latrodectinae, Pholcommatinae, Anelosiminae, Theridiinae and Hadrotarsinae, respectively; classification according to Agnarsson, in press). Apart from *Paidiscura* they all follow the *Steatoda*-type of copulation. Production of silk is also of importance in the courtship of widow spiders (*Latrodectus*), but not in forming a mating web. The male ties the comparatively giant female by throwing strands of silk on her legs and body (Fig. 6). These leg-binding threads probably activate the cataleptic state of the female, but do not actually restrict her. She is able to remove the weak strands of silk by a few movements. A similar, less distinct behaviour is sometimes present also in *Steatoda* species, see descriptive part. Here, some males throw strands of silk onto the female but more often onto her web (Fig. 88a). *Euryopis* males and females also briefly threw silk towards each other before copulation, see descriptive part.

In most species studied here courtship occurs without a mating thread and is therefore less ritualised. The male approaches the female for copulation, often in the retreat (Fig. 7a–f). Courtship is performed with

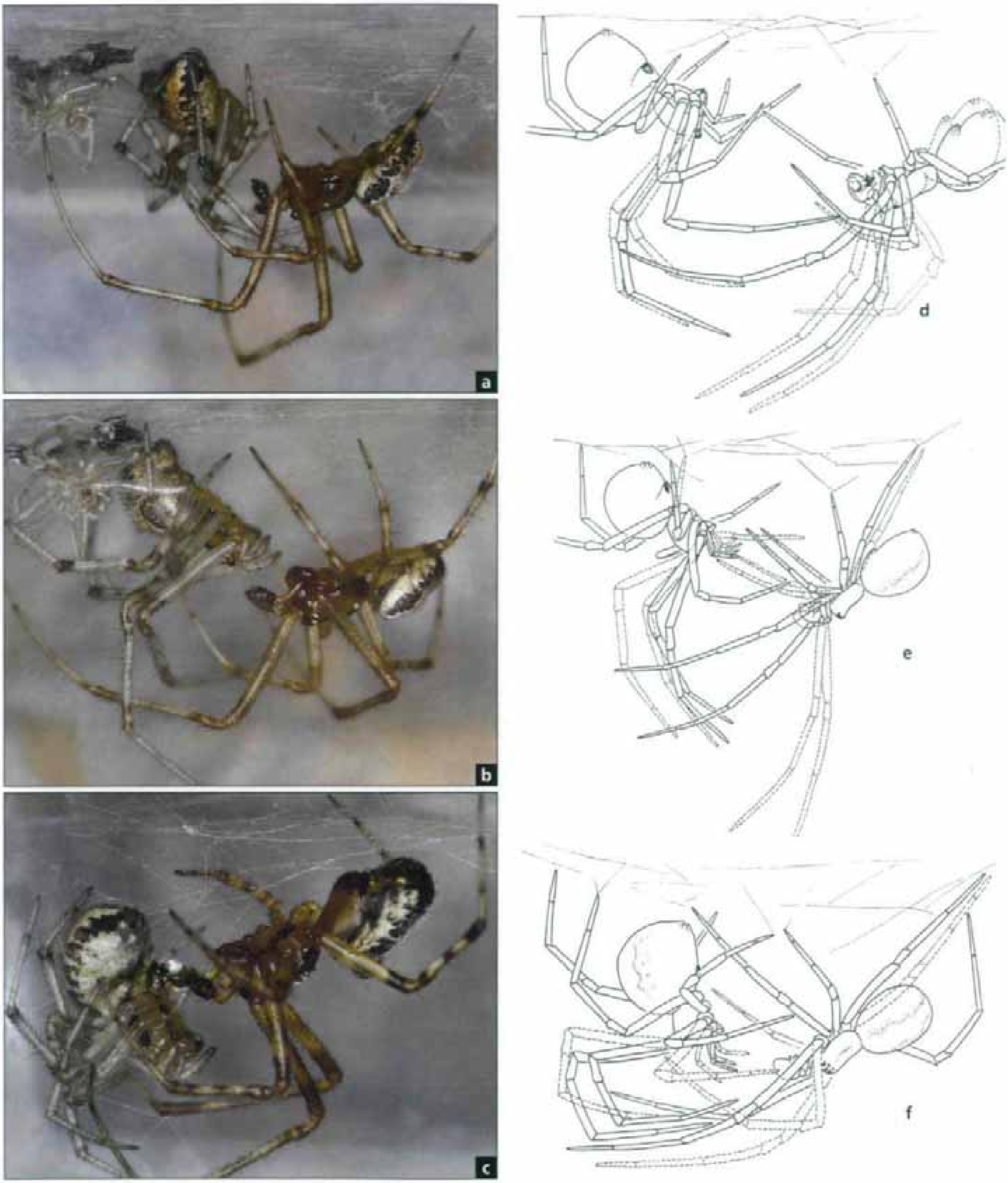


Fig. 7a–f: Male approach for copulation in *Theridion pictum* (a–c). Courtship in *T. varians*, traced from video recordings (d–f). Male approach and contact courtship by mutual palpating. Note light colour and exuvium of freshly moulted female in a–c.

considerable individual variation, and may even be missing. This type of courtship occurs in all representatives of the *Theridion*-type (except *Paidiscura*) and in some of the *Steatoda*-type (*Achaearanea*, *Argyrodes*, *Crustulina*, *Episinus*, *Euryopis*, *Lasaeola tristis*, *Theridion nigrovariegatum*). In *Argyrodes* male courtship movements are more ritualised, with rhythmic body oscillations, see descriptive part. Apparently, in species with reduced webs also a mating web is missing (*Argyrodes*, *Episinus*, *Euryopis*). Genera lack-

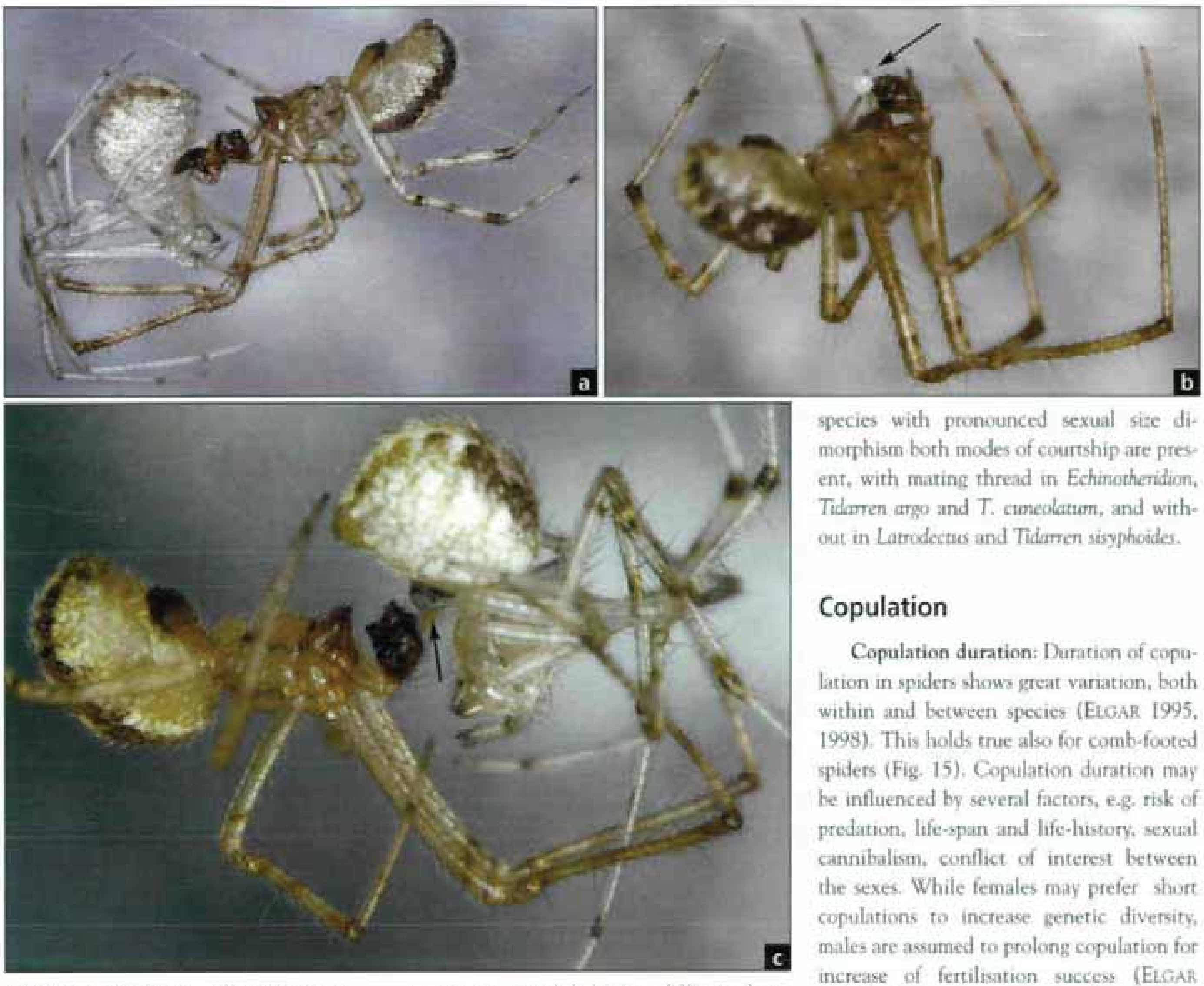


Fig. 8 a–c: Three stages of copulation in *Theridion varians*. a: Insertion of left palp. Forelegs of male in contact with female's legs. b: Sperm induction, arrow points to sperm droplet. c: Late phase of mating plug sequence. Secretion droplet protrudes from the epigyne (arrow).

ing a mating web belong to different theridiid lineages (Hadrotarsinae, Latrodectinae, Spintharinae, Argyrodinae, Theridiinae; classification according to AGNARSSON, in press), but the subfamily Theridiinae constitutes a considerable part. Courtship via a mating thread is present in many araneid spiders and there was considered as derived by ROBINSON & ROBINSON (1980), as it represents an additional construction. Many 'derived' Theridiidae (in the sense of LEVI & LEVI 1962 and AGNARSSON, in press) court at the hub (e.g. *Achaearanea*, *Chrysso*, *Coleosoma*, *Nesticodes*, *Neottiura*, *Rugathodes*, *Theridion*; all subfamily Theridiinae), whereas more basal ones construct mating threads (e.g. *Steatoda*, *Enoplognatha*, *Anelosimus*). Probably, the establishment of a mating web is plesiomorphic and has been reduced several times within Theridiidae. In species with pronounced sexual size dimorphism both modes of courtship are present, with mating thread in *Echinotheridion*, *Tidarren argo* and *T. cuneolatum*, and without in *Latrodectus* and *Tidarren sisyphoides*.

Copulation

Copulation duration: Duration of copulation in spiders shows great variation, both within and between species (ELGAR 1995, 1998). This holds true also for comb-footed spiders (Fig. 15). Copulation duration may be influenced by several factors, e.g. risk of predation, life-span and life-history, sexual cannibalism, conflict of interest between the sexes. While females may prefer short copulations to increase genetic diversity, males are assumed to prolong copulation for increase of fertilisation success (ELGAR 1998). In many species copulation lasts longer than necessary for actual sperm transfer and therefore has additional functions (EBERHARD 1985, ELGAR 1998).

Pseudocopulation: Some theridiid species start copulation with a pseudocopulation, which is a sequence of insertions without sperm transfer. In the *Theridion varians*-group, this was proved by absence of egg-laying and by empty receptacula of females, which had undergone pseudocopulation only (KNOFLACH 1998). Just after this pre-insemination period the first sperm induction takes place. Insemination starts with the second sequence of insertions. Females of *T. varians* dissected after the first insertion of this second sequence had one of their copulatory ducts filled with sperm. Pseudocopulation differs from the following true copulatory sequences by lower mean insertion duration and by an increased number of insertions (Fig. 9, 10). It is known also in Linyphiidae (KULLMANN 1964, VAN HELSDINGEN 1965, 1983, STUMPF 1990). Such a pre-insemination phase is assumed to serve as courtship and therefore to stimulate and synchronise sperm transfer (EBERHARD 1985).

Nevertheless, pseudocopulation does not necessarily occur in all theridiid species, which integrate sperm induction into copulation (contra KNOFLACH 1998). In the *Theridion melanurum*-group sperm transfer starts immediately with the first insertion (see descriptive part). At least it was proved for two species, *T. musivivum* and *T. ochreolum*. Females, which had undergone the first copulatory sequence only, laid fertile egg-sacs. Sperm transfer obviously is reflected by longer duration of insertions. In the *T. melanurum*-group insertions are equally long and frequent at the beginning (Fig. 41, 42, 44, 46, 48), while in the *T. varians*-group insertions are distinctly shorter and more frequent during pseudocopulation than in following sequences (Fig. 9, 10). *Theridion grancanariense*, *T. incanescens*, *T. pinicola*, and *Simitidion* clearly follow the *Theridion varians*-group (Fig. 39, 51, 52, 56). Judging from the insertion pattern, pseudocopulation may be assumed also for *T. lacticolor* (Fig. 12a). In *Nesticodes rufipes* at least the number of insertions is greatly increased in the first sequence, which probably indicates a pseudocopulation as well (Fig. 34). Anyway, this is a suggestion only and has to be proved for each species. In species with pseudocopulation there is no further sperm induction at the end of copulation. According to the insertion pattern pseudocopulation apparently is missing in *Chrysso*, *Keijia*, *Neottiura*, *Paidiscura*, *Rugathodes*, *Theridion impressum*, *T. sisyphium* (see Fig. 30, 31, 37, 58), perhaps also in *Theridion conigerum* and *T. ohlerti*. Furthermore, absence of pseudocopulation appears to be correlated with the male's sperm uptake behaviour. Males were observed to charge their palps with sperm at the end of copulation (see Fig. 30, 31, 41, 42, 44, 46, 48, 58). The sperm obviously is used for another copulation, which then starts with immediate sperm transfer.

The copulatory pattern is determined by the number and duration of insertions and

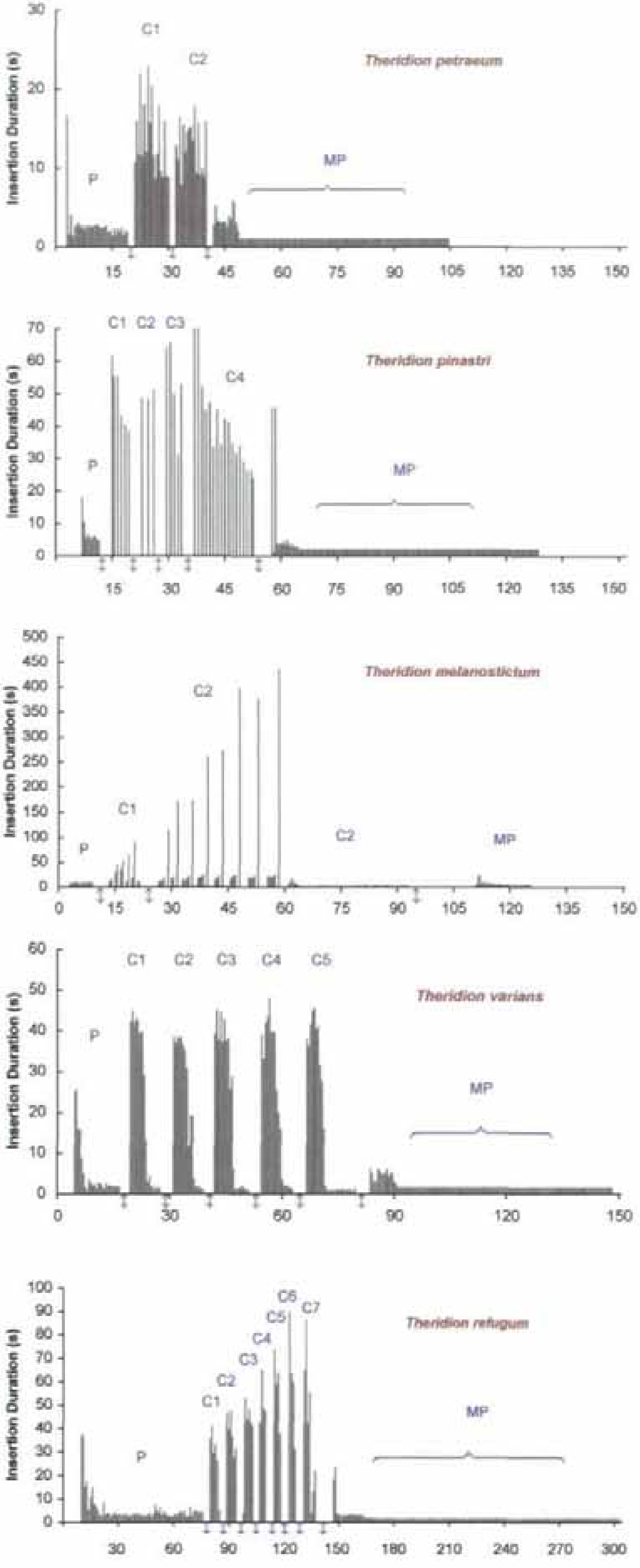


Fig. 9a–e: Copulation and insertion pattern in species of the *Theridion varians*-group, *Theridion petraeum*, *T. pinastri*, *T. melanostictum*, *T. varians* and *T. refugum*. Each bar represents an insertion. Sperm induction indicated by double arrows. Mating plug sequence shown as short insertions. Gap before pseudocopulation indicates courtship. P = pseudocopulation; C1–7 = copulatory sequences; MP = mating plug sequence. After KNOFLACH (1998).

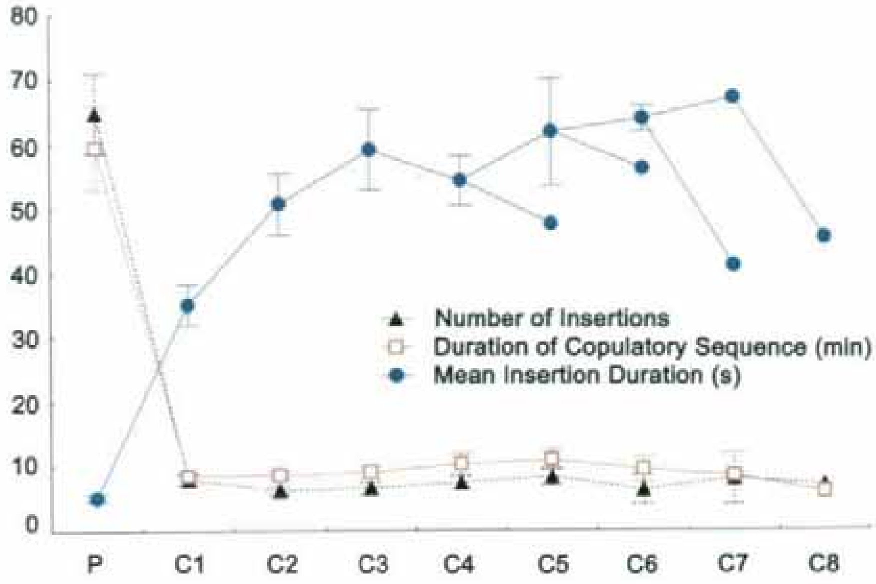


Fig. 10: Copulation of *Theridion refugum*. Mean values of number of insertions (triangles), duration of insertion sequences (squares) and mean insertion duration (circles) of pseudocopulation (P) and copulatory sequences (C1–8), with respective standard error (whiskers) for 14 copulations. Last sequence of short copulations given as additional point, when deviating from the pattern of maximal sequence. After KNOFLACH (1998).

of copulatory sequences as well as by their temporal occurrence. Copulatory patterns differ considerably between species and appear to be specific (see Fig. 9, 12 and specific part), especially in the *Theridion*-type. As they interrupt copulation several times for sperm uptake, copulation is divided into well-defined copulatory sequences. Despite some individual variation (see Fig. 44, 46), most species can be characterised by at least one part of the copulatory pattern: duration, number of insertions, number of sperm inductions and insertion pattern of sequences. Number of insertions is low in *Chrysso* (Fig. 30), *Keijia* (Fig. 31), *Neottiura*, *Rugathodes* (Fig. 37), *T. adrianopoli* (Fig. 12b), *T. conigerum*, some species of the *T. melanurum*-group (*T. betteni*, *T. mystaceum* and *Theridion* sp., see Fig. 41, 48), *T. impressum* and *T. sisyphium* (Fig. 58), with a total of only 10–30 insertions, 2 insertions per sequence. Accordingly, these species are assumed to lack pseudocopulation. Insertion pattern of each sequence is rather uniform in most of these species. *Theridion varians* and relatives perform a high number of insertions, up to 400 in *T. varians*, in *T. lacticolor* even more than 440 (Fig. 12a; KNOFLACH & VAN HARTEN 2000b). Insertion patterns differ greatly between copulatory sequences (Fig. 9a–e), indicating different processes, such as pseudocopulation, sperm transfer and formation of mating plug. In this respect some species of the *T. melanurum*-group differ from the above-mentioned representatives, as they show one or more final copulatory sequences with completely differing insertion patterns (*T. melanurum*, *T. musivivum* and *T. ochreolum*, see Fig. 42, 44, 46). The function of these final short insertions is unclear, since a mating plug was not discernible. Representatives of the *Theridion varians*-group produce a considerable amount of mating plug secretion in the last sequence (Fig. 8c, 21, 22). In *T. adrianopoli* several final copulatory sequences with short palp-epigynum contacts result in formation of an inconspicuous mating plug (Fig. 12b; KNOFLACH 1997).

After sperm induction the male usually returns immediately to the female in order to resume copulation. This is not the case in some species of the *Theridion melanurum*-group as well as in *T. sisyphium*, *T. impressum* and *T. adrianopoli*. These males remain motionless for a specific period near the female. Only after this period of rest do they again return to the female for the next insertions: *T. impressum* after 9 min, *T. adrianopoli*, *T. betteni* and *T. sisyphium* after about 20 min, *T. mystaceum* after c. 30 min and *Theridion* sp. (*melanurum*-group) even not before 2.3 h on average! In this last-mentioned Mediterranean species copulation continues for more than 24 h. This species therefore has the longest copulation within the comb-footed spiders studied, albeit its entire duration has not been recorded up to now. Indeed, only a small fraction of this time serves for sperm transfer.

Also in the *Steatoda*-type of copulation considerable differences exist with regard to number and duration of insertions. However, species with few insertions prevail (mean ± s.e. = 36.9 ± 10.7 insertions for 38 species), see also Figures 14, 15 and Tables 2, 3. In *Achaearanea* only a few insertions of a few seconds take place, as well as in *Dipoena melanogaster*. *Crustulina* and some *Steatoda*-species insert each palp for 1–2 h, *Robertus lividus* even for 3 h (HIRSCHBERG 1969), whereas some *Enoplognatha*-species change their palps over 200 times in a rapid sequence. A male of *Anelosimus aulicus* would hardly be able to achieve such a rapid sequence of insertions. This species has a remarkably long embolus, which is three times longer than the male's body (see also

Fig. 11a, b: Copulation in *Theridion melanostictum*. **a:** Insertion of left palp. Forelegs of male in contact with female's legs. **b:** Mating plug sequence, palpal applications without haematodochal inflation.

KNOFLACH & PFALLER, this volume). Insertion of the embolus requires much precision and also withdrawal of the thread-like embolus is done cautiously (Fig. 61, 62). Afterwards, the embolus is completely disarranged and needs special treatment by the legs and the other palp in order to regain the original condition (Fig. 61f).

Total duration of all insertions is the maximal possible time spent in sperm transfer. Copulation generally involves more insertions in the *Theridion-type* than in the *Steatoda*-type (mean ± s.e. = 81.1 ± 15.1 insertions for 31 species; see also Fig. 14, 15; Tab. 2, 3), whereas actual time of insemination is comparatively low (Fig. 15). Thus, males of the *Theridion*-type change palps more frequently, but invest less time in actual sperm transfer. Entire copulation duration varies considerably in both types and averages 91.1 ± 17.5 min for 38 species of the *Steatoda*-type and 144.2 ± 25.5 min for 31 species of the *Theridion*-type (mean ± s.e.). In the *Theridion*-type „actual" sperm transfer requires only a fraction of the entire copulation duration (on average 0.25 ± 0.04 s.e. for 31 species), whereas in the *Steatoda*-type they appear to coincide at a larger scale (on average 0.5 ± 0.06 s.e. for 38 species). The remaining time is used for courtship or resting. Species of the *Theridion*-type invest a considerable part of copulation in functions other than mere sperm transfer, as

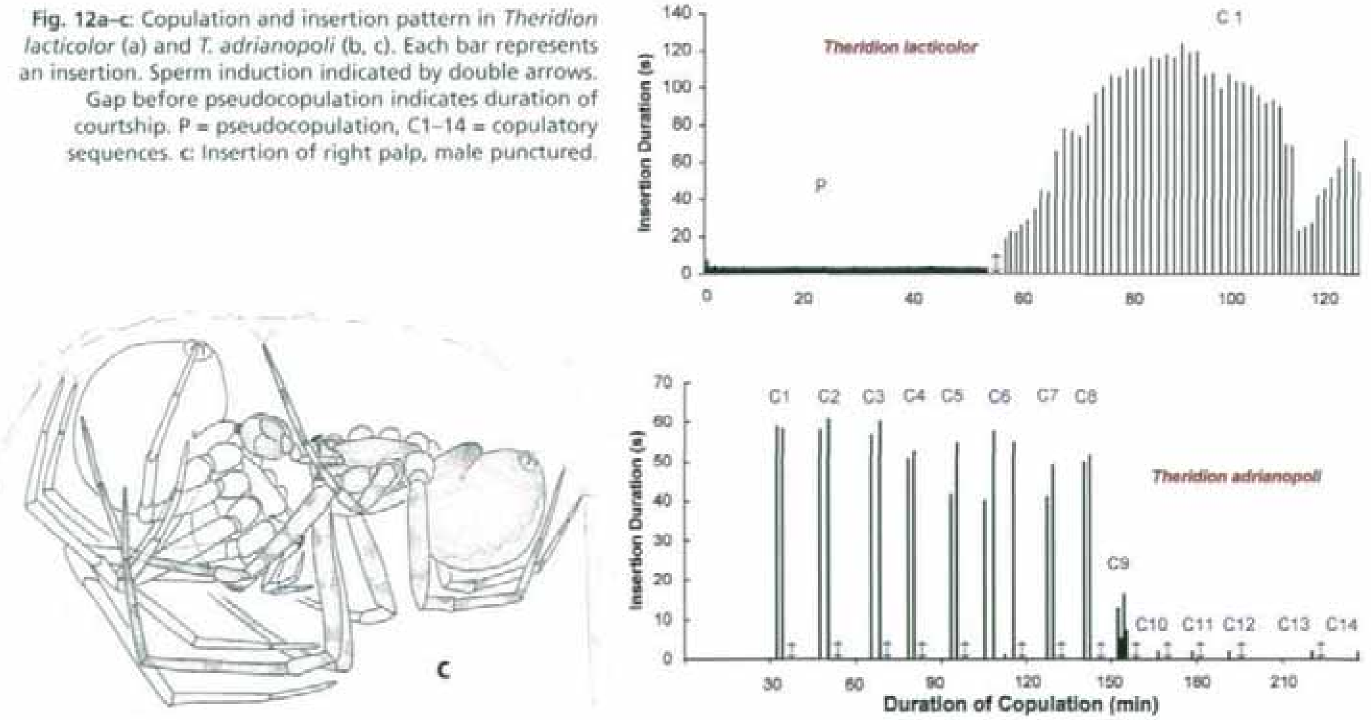
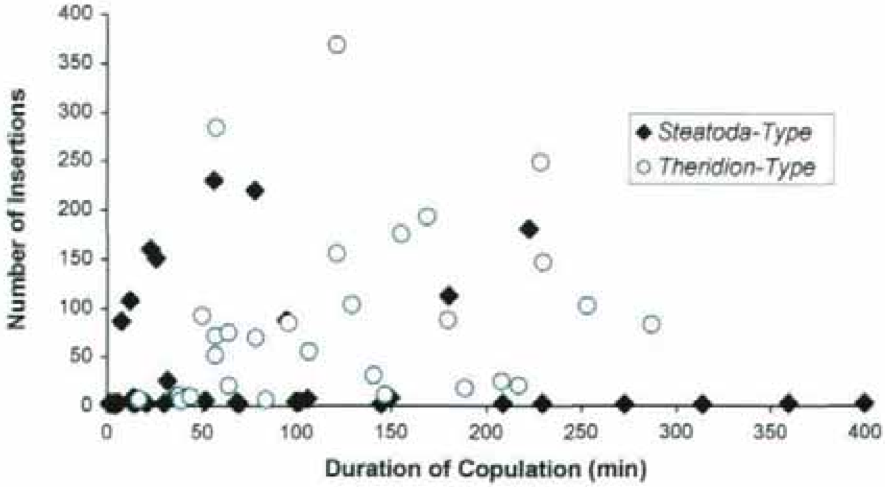


Fig. 12a–c: Copulation and insertion pattern in *Theridion lacticolor* (a) and *T. adrianopoli* (b, c). Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates duration of courtship. P = pseudocopulation, C1–14 = copulatory sequences. **c**: Insertion of right palp, male punctured.

Fig. 13a, b: Copulation in *Neottiura bimaculata*. **a:** Male approach for insertion. **b:** Insertion of left palp. Note absence of leg contact.

Fig. 14: Relationship between number of insertion and duration of copulation in 70 theridiid species separated by copulatory type, outliers excluded. Each point represents a species.



courtship in terms of pseudocopulation, mate guarding, sperm uptake and formation of mating plug.

In most theridiid species of this study haematodochae inflate only once per insertion (Tab. 2). During the long-lasting insertions of *Crustulina* and *Steatoda* haematodochae inflate and deflate rhythmically (GERHARDT 1923, 1924, 1925; KNOFLACH 1994). These rhythmic haematodochal pulsations may stimulate the female and perhaps correspond to a sequence of short insertions and repeated withdrawals of the palp. Within the genus *Enoplognatha* both insertion types are present, few long-lasting insertions with haematodochal pulsations in the *E. diversa*-group and permanent change of palps in the *E. ovata*-group. Such rhythmic haematodochal movements are less common in the *Theridion*-type. They occur only in *Keijia* (see descriptive part) and in advanced copulatory sequences in *Neottiura bimaculata* (see KNOFLACH 1999). According to HUBER (1998) numerous short insertions may produce similar stimuli in the female as rhythmic movements during one insertion. Absence of haematodochal pulsations does not imply that no movements take place. In many species the male shows regular pumping movements, which appear to achieve and maintain maximal haematodochal expansion and which let the female passively move. The males also pivot and vibrate their abdomen against the carapace, thereby indicating stridulatory activity.

Principal Coordinate Analysis (Fig. I–III, appendix): The two types of copulation are not clearly separated in the Principal Coordinate plot, but instead show some degree of overlap. Alignment mainly is influenced by two variables, number of insertions and duration of copulation (Fig. 1b, c). Thus, the three rough clusters represent more or less one group with few insertions of short duration (lower midline, mainly *Steatoda*-type), one group with few insertions of long duration (upper left, mainly *Steatoda*-type) and one group with numerous insertions and long copulation duration (upper right, only *Theridion*-type). Further subgroups given in Table 2 (e.g. copulation via mating web or presence of pseudocopulation) cannot be recognised in Fig. I–III (appendix). The *Steatoda*-type contains noticeably more species with large body size and hence pronounced sexual size dimorphism. These are irregularly scattered in both

Steatoda-clusters. This mating type also includes a larger number of ground-dwelling species, which appear to be more aggregated in the long copulation cluster.

Special case of one-palped spiders: palp-amputation, sudden sexual death and emasculation

The unique case of the one-palped spider genera *Tidarren* and *Echinotheridion* was recently studied more closely (KNOFLACH & VAN HARTEN 2000a, 2001a, KNOFLACH 2002a, b, KNOFLACH & BENJAMIN 2003). Their minute males amputate one of their palps a few hours after the penultimate moult (see KNOFLACH & PFALLER, this volume), left and right at random. They therefore are semi-emasculated and spend the rest of their lives with a single palp only. Anyway, for copulation two palps are not necessary, since the males die from a sudden sexual death during insertion. It seems that for genitalia coupling a considerable part of the haemolymph is shifted from the male's body into the palpal organ (Fig. 17, 20b). Also the prosoma of the male becomes shrivelled, apparently owing to contraction of prosoma muscles. Copulation involves a single insertion and is associated with cannibalism of the dwarf male in most species hitherto studied. In *Tidarren cuneolatum* the male is devoured after a few minutes of insertion (Fig. 17, KNOFLACH & VAN HARTEN 2000a). Such postcopulatory sexual cannibalism is not present in all species. *T. argo* and *Echinotheridion gibberosum* synchronise sperm transfer and sexual cannibalism by emasculation, by breaking off the single male palp (Fig. 18, 19; KNOFLACH & VAN HARTEN 2001a, KNOFLACH 2002a, b). The separated gonopod remains attached to the epigynum for several hours (4–5 on average, up to 10 h) and apparently continues to function independently of the male, while the female feeds on the palpless, emasculated male (Fig. 18, 19). In this way genitalia contact is prolonged considerably. The separated palp of *T. argo* reveals a peculiar holdfast structure, as the palpal membranes are highly modified (KNOFLACH & VAN HARTEN 2001a). In *E. gibberosum* the palp is fastened to the epigynum by palpal sclerites only.

Tab. 2: Overview and arrangement of comb-footed spiders according to copulatory elements. Species groups and genera with same features were subsumed. 1: Sperm induction independent of copulation; 2: Duration of sperm induction long; 3: Courtship via mating web; 4: Copulation by male approach; 5: Sperm induction as part of copulation; 6: Duration of sperm induction short; 7: Haematodochae inflate only once per insertion; 8: Haematochae pulsate during insertion; 9: Pseudocopulation present; 10: Number of insertions low <10; 11: Number of insertions high, more than 10; 12: Mating plug present. Origin of mating plug: ep = epigastric, o = oral, pg = palpal secretion, po = entire palp.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12
Enoplognatha diversa–group	+	+	+	–	–	–	–	+	–	+	+	–
Steatoda bipunctata	+	+	+	–	–	–	–	+	–	+	–	pg?
Steatoda castanea	+	+	+	–	–	–	–	+	–	+	–	o?
Steatoda grossa	+	+	+	–	–	–	–	+	–	+	–	–
Steatoda paykulliana	+	+	+	–	–	–	–	+	–	+	–	–
Steatoda triangulosa	+	+	+	–	–	–	–	+	–	+	–	o
Anelosimus aulicus	+	?	+	–	–	?	+	–	–	+	–	–
Dipoena melanogaster	+	+	+	–	–	–	+	–	–	+	–	–
Echinotheridion gibberosum	+	?	+	–	–	?	+	–	–	+	–	po
Tidarren argo	+	?	+	–	–	?	+	–	–	+	–	po
Tidarren cuneolatum	+	?	+	–	–	?	+	–	–	+	–	–
Enoplognatha ovata-group	+	+	+	–	–	–	+	–	–	–	+	–
Enoplognatha thoracica-group	+	?	+	–	–	?	+	–	–	–	+	–
Achaearanea	+	+	–	+	–	–	+	–	–	+	–	–
Theridion nigrovariegatum	+	+	–	+	–	–	+	–	–	+	–	–
Episinus	+	+	–	+	–	–	+	–	–	+	–	–
Euryopis episinoides	+	?	–	+	–	?	+	–	–	+	–	–
Latrodectus	+	?	–	+	–	?	+	–	–	+	–	po
Argyrodes argyrodes	+	+	–	+	–	–	+	–	–	–	+	pg
Lasaeola tristis	+	+	–	+	–	–	+	–	–	–	+	–
Crustulina	+	?	–	+	–	?	–	+	–	+	–	–
Paidiscura	–	–	+	–	+	+	+	–	– ?	+	–	–
Keijia	–	–	–	+	+	+	–	+	– ?	+	–	–
Neottiura bimaculata	–	–	–	+	+	+	+	+	– ?	+	–	–
Theridion impressum	–	–	–	+	+	+	+	–	– ?	+	–	–
Chrysso cambridgei	–	–	–	+	+	+	+	–	– ?	–	+	ep?
Rugathodes bellicosus	–	–	–	+	+	+	+	–	?	–	+	–
Theridion adrianopoli	–	–	–	+	+	+	+	–	– ?	–	+	ep?
Theridion conigerum	–	–	–	+	+	+	+	–	– ?	–	+	–
Theridion melanurum-group	–	–	–	+	+	+	+	–	–	–	+	–
Theridion ohlerti	–	–	–	+	+	+	+	–	?	–	+	–
Theridion sisyphium	–	–	–	+	+	+	+	–	– ?	–	+	–
Coleosoma floridanum	–	–	–	+	+	+	+	–	+ ?	–	+	–
Nesticodes rufipes	–	–	–	+	+	+	+	–	+ ?	–	+	ep?
Simitidion	–	–	–	+	+	+	+	–	+ ?	–	+	ep
Theridion lacticolor	–	–	–	+	+	+	+	–	+ ?	–	+	–
Theridion grancanariense	–	–	–	+	+	+	+	–	+ ?	–	+	ep?
Theridion incanescens	–	–	–	+	+	+	+	–	+ ?	–	+	ep
Theridion pinicola	–	–	–	+	+	+	+	–	+ ?	–	+	ep
Theridion varians-group	–	–	–	+	+	+	+	–	+	–	+	ep

Tab. 3: Copulation data of 69 species of comb-footed spiders. Mean values are given when numbers of observations exceed 1. For detailed data see specific part of this study. 1: Number of observations; 2: Duration of precopulatory courtship (min); 3: Entire copulation duration (min); 4: Time of actual sperm transfer (min); 5: Number of insertions; 6: Number of sperm inductions during copulation; 7: Number of dipping movements during sperm uptake; 8: Duration of pseudocopulation (min); 9: Duration of formation of mating plug (min); 10: Type of mating plug (0) absent. (1) oral. (2) part of palp. (3) entire palp. (4) palpal secretion. (5) epigastric; 11: Sexual cannibalism (0) not observed. (1) facultative. (2) obligatory; 12: Source.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12
Achaearanea lunata	2	1.3	13.0	0.1	5.0	–	–	–	–	0	1	present study
Achaearanea simulans	5	4.1	1.8	0.0	2.2	–	–	–	–	0	1	present study
Achaearanea tepidariorum	3	17.3	30.3	0.0	2.0	–	20.0	–	–	0	1	present study
Anelosimus aulicus	4	17.7	85.5	9.4	6.3	–	–	–	–	0	0	present study
Argyrodes argyrodes	8	14.3	176.7	18.7	111.7	–	–	–	18.7	4	0	present study
Chrysso cambridgei	7	1.0	84.1	3.5	6.0	2.0	64.9	–	1.6	5	0	present study
Coleosoma floridanum	2	3.5	57.5	34.0	183.5	2.0	20.5	26.0	–	0	0	Knoflach (1999)
Crustulina guttata	2	80.0	360.0	350.0	2.0	–	–	–	–	0	0	Knoflach (1994)
Crustulina scabripes	4	65.0	209.3	199.8	2.0	–	–	–	–	0	0	Knoflach (1994)
Dipoena melanogaster	9	2.3	6.1	0.3	2.6	–	12.5	–	–	0	0	Knoflach (2000)
Dipoena sp.	1	4.0	14.0	0.2	2.0	–	–	–	–	0	0	Knoflach, unpubl.
Echinotheridion gibberosum	17	12.5	314.3	314.3	1.0	–	–	–	6.3	3	2	Knoflach (2002a)
Enoplognatha afrodite	4	31.0	56.5	19.9	229.5	–	–	–	–	0	1	present study
Enoplognatha diversa	2	8.0	102.0	77.8	4.0	–	–	–	–	0	1	present study
Enoplognatha latimana	1	2.5	23.0	12.0	159.0	–	35.0	–	–	0	1	present study
Enoplognatha macrochelis	5	26.0	150.0	130.4	7.6	–	–	–	–	0	1	present study
Enoplognatha ovata	5	13.2	23.6	10.0	125.0	–	–	–	–	0	1	present study
Enoplognatha penelope	2	0.5	12.3	3.8	106.5	–	26.0	–	–	0	1	present study
Enoplognatha sattleri	1	c. 0.1	95.0	76.2	87.0	–	–	–	–	0	1	present study
Enoplognatha thoracica	1	2.5	32.0	19.5	25.0	–	–	–	–	0	1	present study
Enoplognatha quadripunctata	2	3.8	78.5	45.4	219.0	–	–	–	–	0	1	present study
Enoplognatha verae	1	–	223.0	60.0	180.0	–	–	–	–	–	0	present study
Episinus maculipes	1	c. 0.1	3.5	3.0	2.0	–	6.0	–	–	0	0	present study
Episinus truncatus	1	0.0	6.3	6.1	2.0	–	–	–	–	0	0	Locket (1926)
Euryopis episinoides	1	0.1	c. 15.0	2.5	2.0	–	–	–	–	0	0	present study
Euryopis flavomaculata	1	0.0	5.0	1.3	2.0	–	–	–	–	0	0	Hirschberg (1969)
Keijia kijabei	1	1.0	38.0	7.3	10.0	5.0	14.0	–	–	0	0	present study
Keijia tincta	3	15.3	43.2	4.8	9.3	3.3	12.2	–	–	0	0	present study
Lasaeola tristis	5	0.0	8.3	1.9	74.8	–	28.5	–	–	0	0	Knoflach (2000)
Latrodectus dahli	1	50.0	70.0	31.0	2.0	–	–	–	0.2	2	1	Knoflach & van Harten (2001b)
Latrodectus geometricus	1	60.0	100.0	33.0	4.0	–	–	–	0.2	2	0	Knoflach & van Harten (2001b)
Neottiura bimaculata	3	1.5	39.0	13.7	4.7	2.3	33.5	–	–	0	0	Knoflach (1999)
Nesticodes rufipes	3	8.0	169.3	5.4	192.0	11.7	11.3	20.0	93.5	5?	1	present study
Paidiscura orotavensis	1	4.0	30.0	0.4	6.0	3.0	19.0	–	–	0	0	present study
Robertus lividus	1	5.0	395.0	390.0	2.0	–	–	–	–	0	0	Hirschberg (1969)
Rugathodes bellicosus	4	29.0	60.8	1.9	19.5	10.5	13.0	–	–	0	0	present study
Simitidion lacuna	1	0.1	57.0	31.4	71.0	5.0	22.0	8.0	22.0	5	0	present study
Simitidion simile	5	7.3	57.2	18.8	51.3	6.4	17.5	8.1	14.7	5	0	present study
Steatoda bipunctata	1	c. 400	c. 230	c. 200	2.0	–	–	–	50.0	4	0	present study
Steatoda castanea	1	5.0	36.0	5.0	9.0	–	–	–	10.0	–	1	present study
Steatoda grossa	4	9.9	68.6	28.2	2.8	–	–	–	–	0	1	present study
Steatoda nobilis	1	18.0	52.0	22.5	5.0	–	–	–	–	0	1	Locket (1979)
Steatoda paykulliana	3	37.0	14.3	7.2	7.7	–	–	–	–	0	1	present study
Steatoda triangulosa	4	12.0	15.8	3.5	2.3	–	66.0	–	12.0	1	1	present study
Theridion adrianopoli	2	17.0	208.5	17.1	24.5	12.5	20.5	–	6.0	5	0	Knoflach (1997)
Theridion betteni	3	1.8	217.3	9.2	20.3	10.3	12.0	–	–	0	0	present study

(continued)

Theridion conigerum	2	7.5	141.0	10.0	30.0	19.5	22.0	–	–	0	0	present study
Theridion grancanariense	2	13.5	230.0	129.6	146.0	5.5	16.5	40.0	45.8	5	0	present study
Theridion impressum	3	3.0	44.0	1.0	8.7	4.3	11.0	–	–	0	0	present study
Theridion incanescens	1	3.0	96.0	21.2	85.0	4.0	24.0	2.0	31.5	5	0	present study
Theridion lacticolor	2	1.3	121.5	82.5	367.5	1.0	55.0	45.5	–	0	0	present study
Theridion melanostictum	5	4.2	155.5	88.2	174.4	2.2	25.3	10.4	9.9	5	0	KNOFLACH (1998)
Theridion melanurum	2	6.9	180.0	110.3	87.0	8.0	25.0	–	–	0	0	present study
Theridion sp. melanurum-group	3	19.7	c. 1400	9.0	14.0	5.3	32.0	–	–	0	0	present study
Theridion musivivum	9	1.4	50.1	32.2	91.3	7.3	16.4	–	–	0	0	present study
Theridion mystaceum	2	8.0	147.0	4.0	10.5	6.0	25.0	–	–	0	0	present study
Theridion nigrovariegatum	5	12.7	21.0	8.7	2.2	–	–	–	–	0	0	present study
Theridion ochreolum	8	6.0	78.8	69.0	54.4	2.8	17.3	–	–	0	0	present study
Theridion ohlerti	2	31.0	287.0	2.5	82.0	25.0	15.5	–	–	0	0	present study
Theridion petraeum	17	9.7	121.6	19.4	154.5	2.9	28.5	17.5	53.9	5	0	KNOFLACH (1998)
Theridion pictum	11	8.9	129.6	34.6	102.5	6.2	22.5	6.1	47.1	5	0	KNOFLACH (1998)
Theridion pinastri	5	7.0	106.8	20.1	55.2	5.0	19.3	3.1	63.0	5	0	KNOFLACH (1998)
Theridion pinicola	3	17.0	64.0	20.3	74.0	7.0	7.0	7.7	34.4	5	0	present study
Theridion refugum	13	9.5	253.3	34.1	101.4	6.4	16.2	57.6	126.6	5	0	KNOFLACH (1998)
Theridion sisyphium	1	3.0	189.0	6.5	17.0	8.0	8.0	–	–	0	0	present study
Theridion varians	10	7.7	228.8	44.5	248.2	6.9	31.4	14.9	82.0	5	1	KNOFLACH (1998)
Tidarren argo	12	13.4	272.9	272.9	1.0	–	–	–	0.6	3	2	KNOFLACH & VAN HARTEN (2001a)
Tidarren cuneolatum	25	4.3	4.0	4.0	1.0	–	–	–	–	0	2	KNOFLACH (2002a)
Tidarren sisyphoides	12	1.6	145.0	145.0	1.0	–	–	–	–	3	0	KNOFLACH & BENJAMIN (2003)

Tidarren argo performs emasculation immediately after genitalia contact is achieved, *Echinotheridion gibberosum* not until a few minutes after insertion. These differences may indicate that emasculation behaviour could have evolved convergently in the two genera.

In the American *Tidarren sisyphoides* copulation also is accompanied by the death of the male (Fig. 20a). Remarkably, the female removes the dead male from the epigynum and casts him away without consuming him. As sexual size dimorphism is much larger in *T. siyphoides* (Fig. 20a, b), consumption of the dead male may therefore have been lost in this species (KNOFLACH & BENJAMIN 2003).

According to the time of sperm induction one-palped spiders belong to the *Steatoda*-type. Copulation proceeds via a mating thread and female approach in *Echinotheridion gibberosum*, *Tidarren argo* and *T. cuneolatum* (Fig. 4), but not in *T. sisyphoides*. In the latter species, the male directly mounts the female's venter without web-spinning activities. Females are polyandrous (Fig. 26) and males monogynous owing to their sudden sexual death and mate consumption. As the male can use his single palp only once, females have to copulate at least twice to get both receptacula inseminated.

Copulatory posture and genitalia coupling: ipsilateral or contralateral insertion

Copulatory posture: Most Theridiidae show a mating position typical of web-spiders. The mates are directed towards each other, assuming an inclined posture, with the prosoma lower than the abdomen (Fig. 7c, 8a, 11, 12c, 13, 21, 29, 32, 33, 35, 36, 38, 40, 43, 45, 49, 50, 54, 55, 57, 59–61, 65, 72b, 75, 77, 85a, 87, 88d, 90c, 91, 92, 95). Apart from genitalia coupling, further body contact is often achieved by the forelegs of the male, which push aside the female's legs. In many species, leg contact is maintained during the entire copulation and appears to be an important trigger of copulatory posture. On the other hand, some Theridiidae do not show such continuous leg contact, e.g. *Neottiura bimaculata* (Fig. 13). In some species, contact between the partners is formed by genitalia only, as in *Crustulina* (Fig. 16). Furthermore, species of the genus *Crustulina* and some *Steatoda* species assume

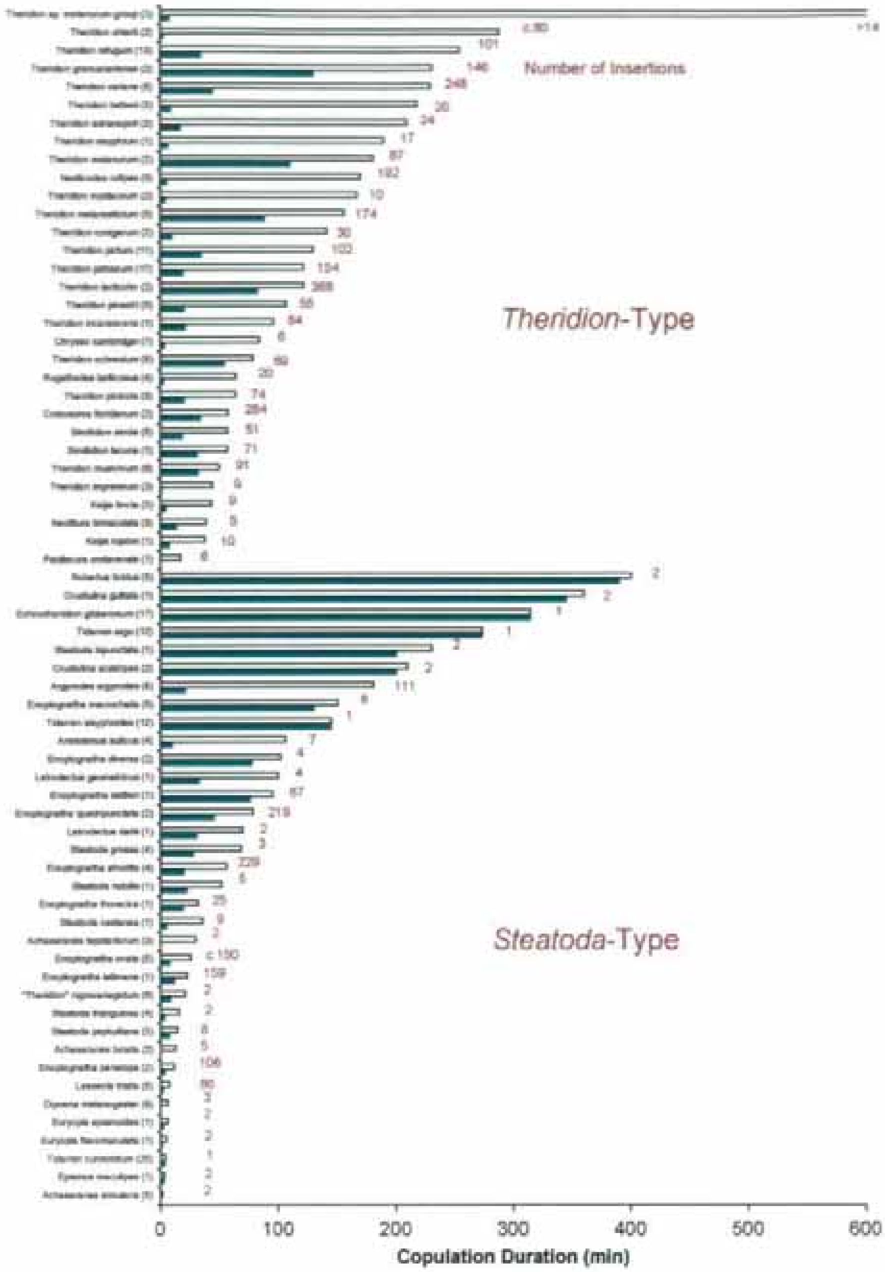


Fig. 15: Overview of copulations of 66 theridiid species. Open bars show entire copulation duration, coloured bars maximal time spent in sperm transfer (sum of insertion duration). Numbers indicate mean numbers of insertions, numbers in brackets following species names indicate number of observations. Entire copulation duration varies considerably in both types. In the *Theridion*-type „actual" sperm transfer requires only a fraction of the entire copulation duration. A considerable part of copulation is used for functions other than mere sperm transfer, such as courtship in terms of pseudocopulation, sperm induction, mate guarding and mating plug.

an unusual posture. Soon after application of the palp the female turns through 180°, so that the mates face the same direction during the entire insertion, in an upright position, the prosoma being higher than the abdomen. A female of *Episinus maculipes* also rotated during insertion (Fig. 82b). In *Steatoda bipunctata* copulatory posture may vary considerably owing to repeated female turns during insertion (GWINNER-HANKE 1970; see also descriptive part). Variant postures are less surprising in species with considerable sexual size dimorphism, e.g. in *Tidarren sisyphoides* and *Latrodectus*, where the male climbs on the venter of the female from behind, so that male and female are venter to venter, both facing in the same direction (Fig. 20a, 23a).

Type of embolus: WIEHLE (1961) distinguished two types of emboli, an introductory embolus (Einfuhrungsembolus), which is deeply inserted into the female copulatory duct, and a connecting embolus (Anschlußembolus), which is docked to the copulatory orifice without penetrating the duct. Most theridiid species seem to introduce their embolus, see also Figure 24. This is also indicated by the corresponding lengths of copulatory duct and embolus and by the relatively wide lumen of the female duct. In the *Theridion melanurum*-group the embolus apparently cannot be introduced. The ducts are too narrow to allow insertion and the short embolus does not correspond with the long, convoluted duct, e.g. in *T. mystaceum*. It is assumed to be a docking system. It is unclear how the sperm fluid is pushed through this long way to the receptaculum.

Ipsilateral or contralateral insertion? Genital organs of entelegyne spiders are generally strictly correlated, so that one palp fits only to one side of the female genital organ. The palp may be inserted either into the same-sided, ipsilateral, or into the opposite, contralateral female copulatory duct. Ipsilateral insertion has been considered as characteristic for all entelegyne spiders (HELVERSEN 1976; HUBER 1995) and is known in most araneoid spiders. This means that the right embolus enters the right side of the epigynum and vice versa.

However, comb-footed spiders appear to be heterogeneous also in this respect. In *Theridion varians* and relatives contralateral insertion was observed (KNOFLACH 1998), in *T. melanostictum* the embolus was clearly visible through the microscope as the female duct became dark when the embolus was inserted. In addition, females of *T. varians* were dissected after the first insertion with sperm transfer. Their respective contralateral copulatory duct was filled with sperm. This obviously is an exception among entelegynes. *Theridion* apparently shares this feature with some Tetragnathidae (HUBER & SENGLET 1997). *Argyrodes argyrodes* and *Steatoda bipunctata* were clearly observed to insert their palps ipsilaterally (see also Fig. 66). In *S. bipunctata* ipsilateral insertion was confirmed by the presence of a mating plug. After insertion of the right palp the right side of the epigynum was plugged and vice versa. GERHARDT (1926) also reported ipsilateral insertion in *Steatoda castanea*. The one-palped spiders are even able to switch, and therefore to choose a certain side of the female genital organ. *Tidarren cuneolatum* showed contralateral insertion in copulations with virgin females (KNOFLACH 2000a). Those females which copulated with a left-palped male had their right receptaculum filled with sperm secretion, while in right-palped males the left receptaculum was filled. This was not the case when a virgin copulated with two right-palped or two left-palped males in succession. As both female receptacula contained sperm fluid, the second male must have inserted ipsilaterally. This optional switch to the ipsilateral and still virgin side of the vulva is apparently made possible essentially by reduction of a functional distal haematodocha. Consequently, in these species the palpal sclerites do not rotate much, but maintain a similar position to each other as in the unexpanded palp. As sclerites are not forced in a certain direction, palpal insertion appears to be more flexible.

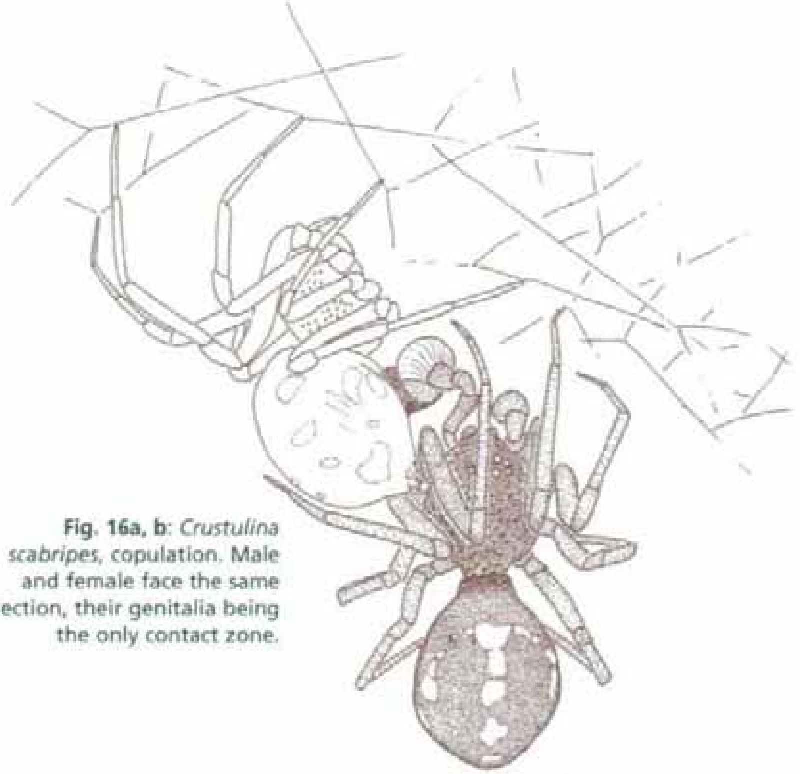


Fig. 16a, b: *Crustulina scabripes*, copulation. Male and female face the same direction, their genitalia being the only contact zone.

Mating plugs

Mating plugs occur in many insects and arachnids (EBERHARD 1985) and also in many spider families (SUHM et al. 1996). About 30 % of the comb-footed spiders investigated in this study show a plug. Mating plugs may be of different origins.

In *Steatoda triangulosa* the plug secretion comes from the mouthparts. It is transferred to the palps by palpal chewing and finally to the epigynum (BRAUN 1956, see also descriptive part, Fig. 93, 94).

In *Theridion varians* and relatives the mating plug originates from secretions of the male and female genital tract and is a result of male and female interaction. The male secretion responsible for hardening the „female" secretion droplet is transferred from the genital tract to the palps via the final „sperm web" and to the epigyne by numerous palpal applications during a long-lasting sequence (KNOFLACH 1998, see Fig. 8c, 9, 11b, 21). The fluid finally hardens and appears to prevent a further copulation (Fig. 22). Without male secretion the mating plug cannot be formed. When the last sperm

Fig. 17: Post-copulatory mate consumption in the one-palped spider *Tidarren cuneolatum*. Right palp of male still inflated owing to irreversible deformation of the prosoma by contracted musculi laterales.

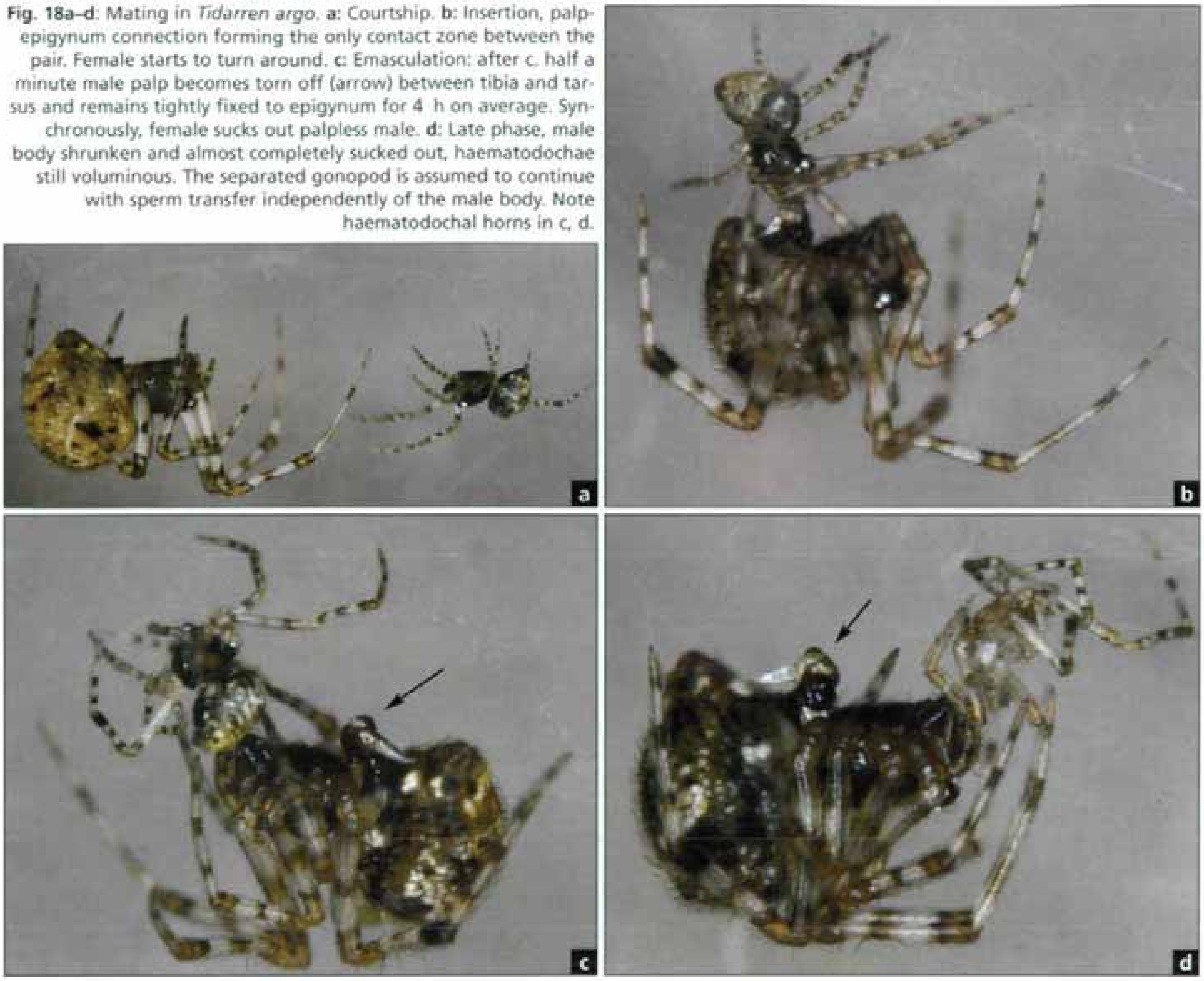


Fig. 18a–d: Mating in *Tidarren argo*. **a**: Courtship. **b**: Insertion, palp-epigynum connection forming the only contact zone between the pair. Female starts to turn around. **c**: Emasculation: after c. half a minute male palp becomes torn off (arrow) between tibia and tarsus and remains tightly fixed to epigynum for 4 h on average. Synchronously, female sucks out palpless male. **d**: Late phase, male body shrunken and almost completely sucked out, haematodochae still voluminous. The separated gonopod is assumed to continue with sperm transfer independently of the male body. Note haematodochal horns in c, d.

web with the plug droplet was removed before absorption, males nonetheless performed an imaginary induction and mating plug sequence as usual. However, the secretion droplet in the epigyne did not harden at the end of this sequence and the fluid was reabsorbed by the female, so that the epigynum remained unplugged.

Another possibility for formation of a mating plug comes from the male palp. Evidently, this occurs in *Argyrodes argyrodes* and *Steatoda bipunctata*. The secretion is assumed to come from a palpal gland as in *Amaurobius* (Amaurobiidae, see SUHM et al. 1996). *Argyrodes argyrodes* performs an unusual mode of mating plug production. Interestingly, towards the end of copulation the male actively inflates the haematodochae in the unlocked palp, which presumably causes the mating plug secretion to be discharged (Fig. 67–71, see descriptive part). The conspicuous secretion is then transferred to the epigynum by short palpal applications. In *Steatoda bipunctata* the mating plug apparently is produced during the second phase of the long insertion (c. 2 h, see descriptive part). After insertion a whitish, compact mass fills the copulatory orifice (Fig. 86b). It cannot be excluded that in *S. bipunctata* a female product also forms part of the secretion mass.

The males of some spider species regularly lose the distal part of the embolus during copulation (WIEHLE 1967). These parts may also act as mating plug. In the widow spiders, *Latrodectus*, the tip of the embolus breaks off at a defined breaking point (Fig. 24b) upon withdrawal of the palp and remains in the female receptaculum, thereby plugging the entrance to the receptaculum

Fig. 19a, b: Copulation in the one-palped spider *Echinotheridion gibberosum*. **a:** During insertion both partners are completely motionless. The male's sudden sexual death is indicated by his contracted legs. **b:** Emasculation completed after 3 min on average. Female sucks out palpless male while genital contact is maintained by the separated gonopod.

(Fig. 24b; DAHL 1902; WIEHLE 1967; KNOFLACH & VAN HARTEN 2001b; BERENDONCK & GREVEN 2002). Sometimes the entire embolus breaks off and blocks the copulatory duct in its full length (Fig. 24a). In *Achaearanea tepidariorum* also a small piece of the embolus tip is lost upon insertion (Fig. 60g) and may be left in the receptaculum (ABALOS & BAEZ 1963; LOCKET & LUCZAK 1974), but appears to have no plug function. In *Echinotheridion gibberosum* and *Tidarren argo* even the entire male palp is torn off and apparently serves as a mating plug for a while (Fig. 18, 19; KNOFLACH & VAN HARTEN 2001a, KNOFLACH 2002a, b). The male of *Tidarren sisyphoides* dies with copulation and remains passively coupled to the female for 2.4 h on average (Fig. 20a), until he is removed by her (KNOFLACH & BENJAMIN 2003). Instead of a separated male palp, the entire male body may serve as a temporary mating plug.

A mating plug does not necessarily impede a further copulation as it may be removed by a second male. In many cases they are said to be not resistant enough to prevent a further insertion (EBERHARD 1985, 1996). In *Theridion adrianopoli* plugged females were able to copulate again (KNOFLACH 1997). Also *Argyrodes argyrodes* and *Steatoda bipunctata* were observed to remate (see descriptive part). Thus, the mating plug was dislodged

Fig. 20a, b: Copulation in *Tidarren sisyphoides*. **a:** About 3 min from the onset of insertion the male's legs become contracted, which indicates his death. He remains passively coupled to the female for more than 2 hrs, while she is cataleptic. **b:** Dead male removed from the epigynum without being consumed by female. Note inflated male palp and size of female's tibia IV for comparison.

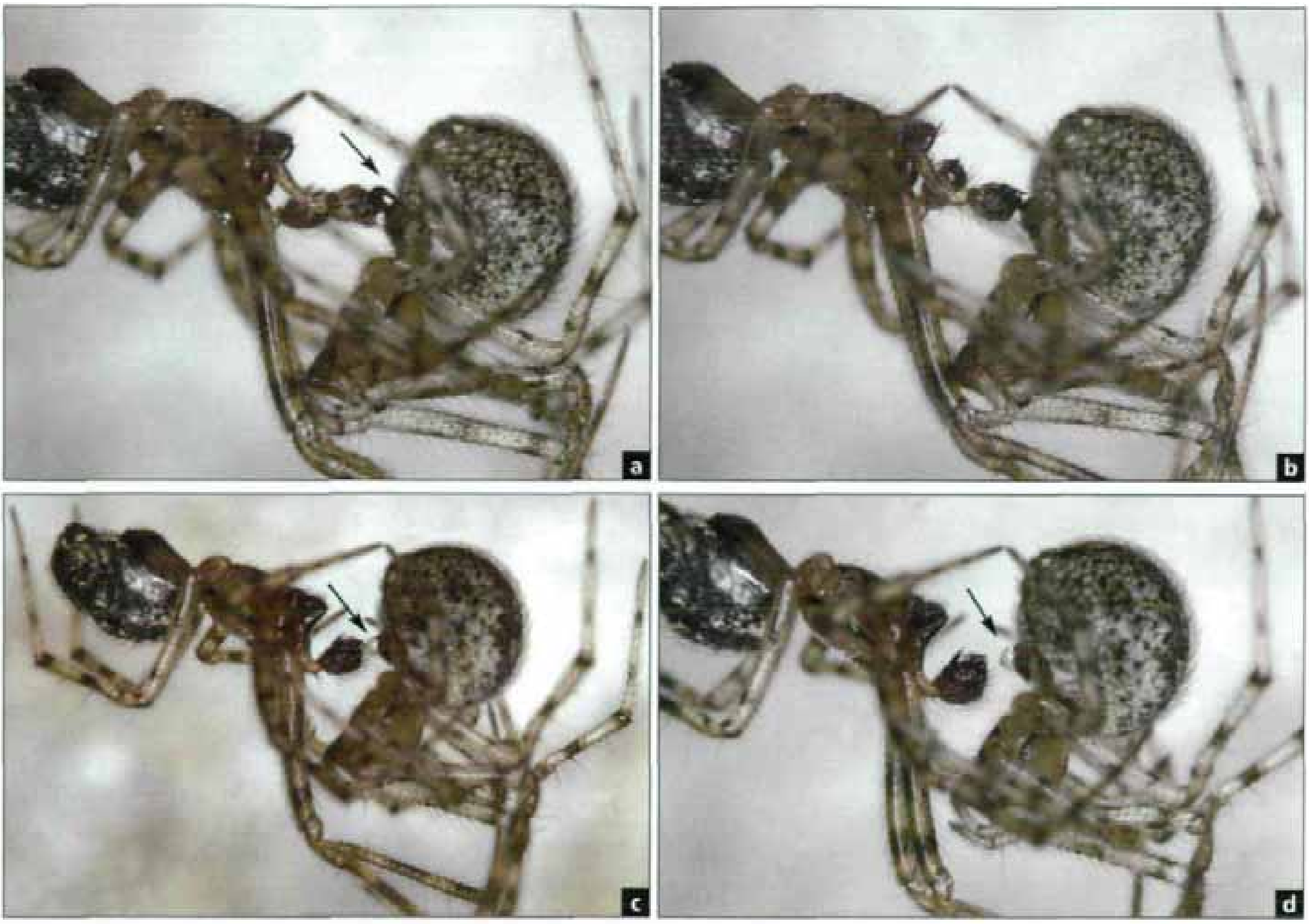


Fig. 21a–d: Formation of mating plug in *Theridion petraeum*. The mating plug is assumed to be a combination of male and female secretions. Apparently, the main part of the droplet is produced by the female. The male secretion produced in the genital tract is responsible for hardening the droplet. It is transferred to the palps via the last sperm web and to the epigynum by palpal applications. Palpal applications differ from the preceding copulatory sequences by gradually diminishing haematochal swelling and by short duration. At the beginning, palpal sclerites still become twisted with minimal inflation, the sickle-shaped tegular apophysis glides into the epigastric furrow (arrow, a), other sclerites into epigynal groove. These movements perhaps stimulate the female to produce her secretion. A few minutes later the male palps alternately touch the epigynal groove without being rotated (b). The actual formation of the mating plug begins. In the epigyne a transparent, viscous droplet appears and enlarges steadily, into which the conductor is continuously immersed (c). Late phase of transfer of the mating plug secretion; the fluid projects from the epigyne (d). Finally, the droplet hardens and becomes a solid, brownish plug.

by the male. In the *Theridion varians*-group the mating plug appears to be permanent. The willingness to pair decreases after copulation, but in several cases a female of *T. varians* and relatives accepted a further copulation attempt. Nevertheless, males were not able to link their palps to the sealed epigyne and stopped insertion attempts after some time (KNOFLACH 1998). The plug of *Latrodectus* appears to be permanent as well. It does not impede a further copulation, but makes access to the female receptacle difficult. In *L. revivensis* the embolus tip is considered to be an effective barrier, as a second male is prevented from reaching the receptaculum (BERENDONCK & GREVEN 2002). For *L. hasselti* such plug function is absent (ANDRADE & BANTA 2002). Apart from paternity assurance mating plugs probably may also prevent backflow and loss of sperm or counteract desiccation of sperm (MASUMOTO 1993, HUBER 1995, SUHM et al. 1996).

Mating systems

Comb-footed spiders exhibit different mating systems according to the number of mating partners. Males of many theridiid species are assumed to be polygynous, which generally is the widespread outcome among animals (THORNHILL & ALCOCK 1983). Nevertheless, the number of copulations

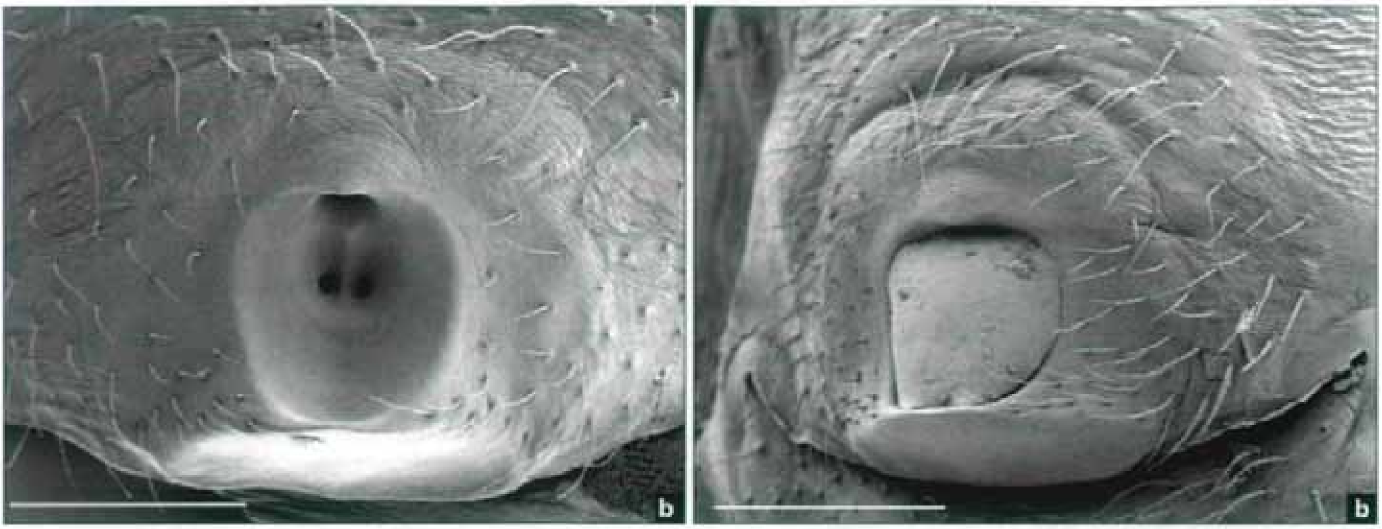


Fig. 22a, b: Epigynum of *Theridion varians*. **a**: Virgin and unplugged female; copulatory orifices visible. **b**: Copulated and plugged female. The mating plug completely fills the epigynal groove. Scale lines: 0.2 mm. Photos: K. PFALLER.

may be rather limited in theridiid males. They appear to be short-lived in many species, but need time for searching and guarding a penultimate female, and for actual copulation, which often is time-consuming. In addition, the period of female receptivity may be quite short as well. In mid-Europe, most Theridiidae mature more or less synchronously within a few weeks in spring and early summer. The chance for further mating opportunities therefore depends highly on the spatial distribution of females. In some habitats, e.g. in stony debris, they apparently are more aggregated. On favourable sites 3–5 females live under one stone, as observed for *Theridion petraeum*, *T. refugum* or *Rugathodes bellicosus*.

Sexual selection may act in the form of intrasexual competition through two widespread behavioural traits, mate guarding (male-male combat) and production of a mating plug (reduction of female receptivity) (THORNHILL & ALCOCK 1983, ELGAR 1998). Mate guarding can be assumed for numerous theridiids. In the field males are found associated with penultimate females which are just approaching their last moult. After a short courtship they rest immobile beside the female, awaiting her maturation and perhaps fending off rivals. Enlarged male chelicerae, as present in *Enoplognatha*, *Rugathodes*, some *Steatoda* species and also in the *Theridion varians*-group, probably reflect morphological adaptations for male-male conflict. At least in *Enoplognatha macrochelis* and *Theridion pictum* severe fights were observed (Fig. 25), which ended in male injury and once even in consumption of the rival. Species without such morphological prerequisites also show male-male conflicts, as known for *Achaearanea wau* LEVI, LUBIN & ROBINSON 1982. Remarkably, in this social species forced copulations take place. A considerable percentage of defenceless females engaged in moulting were mated (24%, see LUBIN 1986).

A mating plug, which seals the epigynum, can help to minimise competition. The relative frequency and different modes of formation of a mating plug (see above) indicate a strong force to exclude competitors. In the *Theridion varians*-group both forms of intrasexual competition apparently occur. Repetition of copulation may be another way to increase reproductive success, as shown by the high number of copulatory sequences in some *Theridion*-species. After each copulation palps are recharged with sperm. By this means integration of sperm induction may have evolved. In the extreme long copulations of *Theridion* sp. of the *T. melanurum*-group (see descriptive part), with hours of pauses, mate guarding and repeated copulations interlock. Thereby, the female is kept away from further males for a long time. In this species an essential prerequisite for direct sperm competition is given, since there is no mating plug and females mate more than once. Some species show rather uniform copulatory sequences, usually with two insertions per sequence (see copulatory pattern). In the *Theridion varians*-group copulation becomes more differentiated and copulatory sequences fulfill different functions, such as pseudocopulation, sperm transfer and formation of mating plug.

Fig. 23 a, b: Copulation in *Latrodectus dahli*. **a:** male on female venter shortly before insertion, nibbling at the epigynal atrium with his mouthparts. **b:** Male cleaning his legs and palps after copulation. Palps become disarranged upon withdrawal, as the embolus tips break off and are left in the female receptacula.

For females the number of mates is little known. Females of the genus *Latrodectus* are polyandrous. After copulation the male leaves the apical part of his embolus in the female copulatory duct upon withdrawal of the palp, thereby often blocking the entrance to the receptacle (Berendonck & Greven 2002). The number of broken male embolar tips filling the female duct may reflect the approximate number of mates. A female of *L. geometricus* probably had copulated at least three times, owing to five embolar tips being found in her vulva (Müller 1985). Abalos & Baez (1967) found among 150 *Latrodectus* females 24 with 3–6 embolar tips. In the social species *Achaearanea wau* from Papua New Guinea moulting females were mated by four males in succession (Lubin 1986). Also females of one-palped spiders definitely mate several times, since one male can inseminate only one receptaculum owing to his sudden sexual death, see above (Knoflach & van Harten 2000a, 2001a, b, Knoflach & Benjamin 2003).

Neither classical precopulatory female choice nor cryptic female choice have hith-

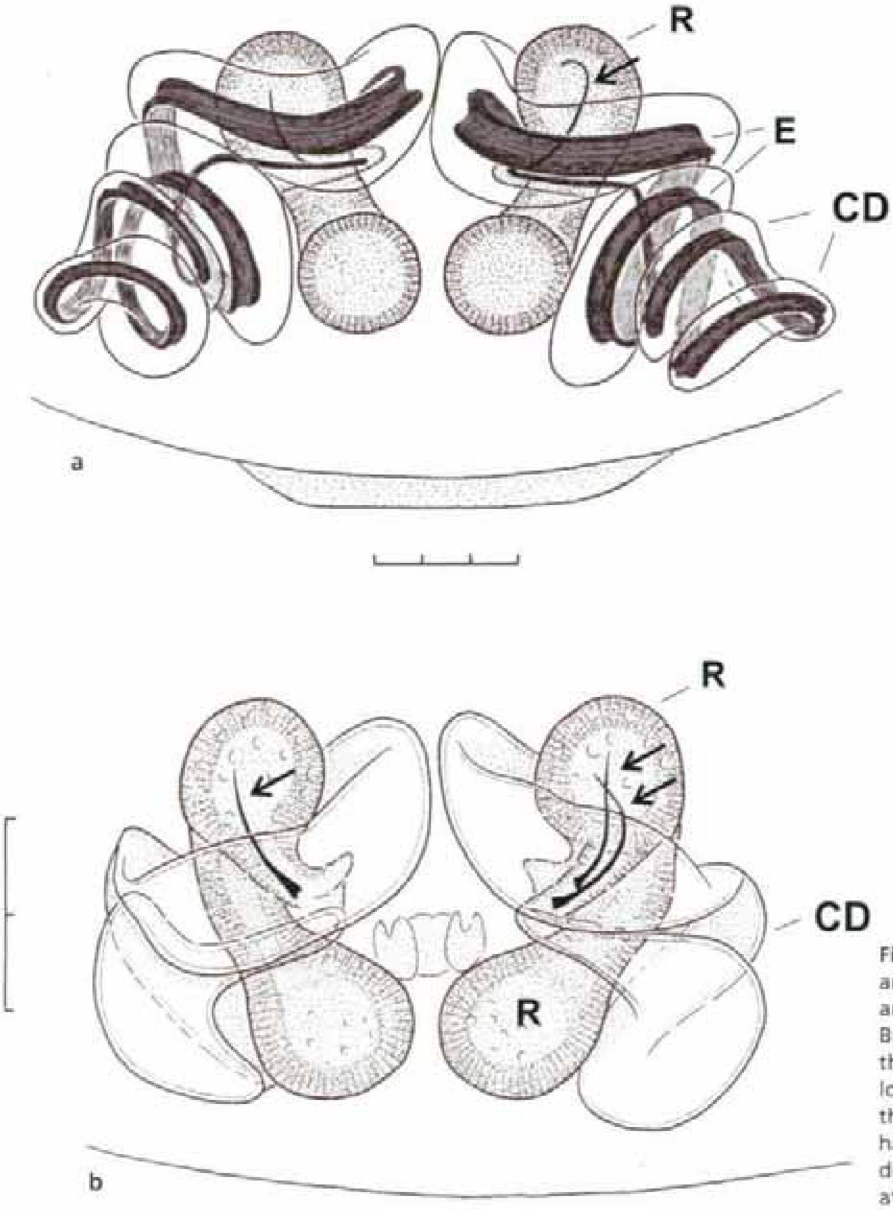


Fig. 24a, b: Vulva of (a) *Latrodectus renivulvatus* and (b) *L. dahli*. **a:** Entire embolus is torn off and completely fills female copulatory duct. **b:** Broken embolus tips remain deeply inserted in the entrance of copulatory ducts into anterior lobe of the receptacula. As the vulva contains three embolus tips (arrows) the female must have mated at least twice. CD = copulatory duct; E = embolus; R = receptaculum. Modified after Knoflach & van Harten (2001b).

Fig. 25a, b: Male-male combat for access to female in *Theridion pictum*. Female legs in the upper-left foreground.

erto been the subject of a study in comb-footed spiders. Both forms of intersexual selection can be assumed to influence the process and outcome of copulation in comb-footed spiders. Occurrence of male copulatory courtship provides evidence of cryptic female choice (EBERHARD 1996). In theridiids, abdominal vibrations during insertion (stridulation), leg movements, pumping movements of the body, and perhaps even insertion attempts and haematodochal pulsations may be interpreted as copulatory courtship and thus indicate cryptic female choice. In this respect also pseudocopulation in *Theridion* may be of relevance as well as gustatorial copulation in *Argyrodes* (see following paragraph). Vibratory and tactile signals via a mating thread may serve as precopulatory assessment criteria to females of the *Steatoda*-type. Females of the *Theridion*-type seem rather passive during courtship and copulation. They apparently copulate with the male which successfully defended her. Further information may be provided by body contact during copulation. Apart from genitalia coupling, in many theridiids the main body contact is achieved by forelegs of the male (Fig. 7c, 8, 11, 12c, 21, 28a, 33, 49, 50, 54, 61, 72, 75, 77, 91, 95 etc.). Leg contact sometimes is maintained during the entire copulation. This leg contact between male and female apparently is very important, as control of copulation seems to be independent of proprioreceptive feedback from the palps (ROVNER 1967). Males of the linyphiid spider *Linyphia triangularis* (CLERCK 1757) were artificially induced to autotomise their palps and then allowed to copulate. Notwithstanding, they displayed complete copulation with its typical phases, pseudocopulation, sperm web construction and copulatory sequences, all with imaginary movements. Females were willing to „copulate" for up to 7 h, although there was no palp-epigyne contact (ROVNER 1967). In theridiid species with a permanent mating plug, as in the *T. varians*-group, female choice may be exhibited by interruption of copulation. Out of c. 80 pairings of the *Theridion varians*-group, two females of *T. varians* preyed on their mates before the mating plug was produced (Fig. 27). Predisposition for female aggressiveness is rather variable. Females of the *Theridion*-type usually do not show signs of aggressiveness. However, in some species female behaviour

Fig. 26: Polyandry in *Tidarren sisyphoides*. Approach of second male, which is the successive mate.

Fig. 27: Sexual cannibalism in *Theridion varians*. One of the rare observations, when a female cannibalised her mate during copulation.

often changes after copulation. Females of *Achaearanea*, *Steatoda*, *Latrodectus* and *Enoplognatha* frequently try to attack their mates when copulation is completed, even though the male continues with courtship.

Disposal of prey as nuptial gift as in *Pisaura mirabilis* (Clerck 1757) (Pisauridae, see Bristowe 1958), *Metellina segmentata* (Clerck 1757) (Tetragnathidae; see Gerhardt 1927) etc. is not known in comb-footed spiders. Instead, the male of *Argyrodes argyrodes* offers a secretion from glands of his clypeal projection (Fig. 64), which is eagerly touched by the female (see also descriptive part). This gustatorial component apparently enables appropriate orientation of the partners. When grasping the male clypeal organ the female assumes the copulatory posture (Fig. 65a–f). As an extreme form of a nuptial gift males of the one-palped spiders *Tidarren* and *Echinotheridion* regularly sacrifice themselves and are consumed by their mates (see above). Sexual cannibalism takes place either after copulation, e.g. in *Tidarren cuneolatum*, or even during copulation. In *T. argo* and *Echinotheridion gibberosum* sexual cannibalism and sperm transfer are synchronised by emasculation. In these species sexual cannibalism appears to be a by-product of the males' sudden sexual death. *Tidarren sisyphoides* females do not consume their mates (Knoflach & Benjamin 2003). In the Australian red-back spider, *Latrodectus hasselti* Thorell 1870, such nuptial sacrifice is facultative (Forster 1992, Andrade 1996): some males shift their body during insertion to the mouthparts of the females and achieve longer copulation by being consumed, whereas other conspecifics escape and avoid consumption. Monogyny occurs facultatively in *Latrodectus*, if the male is consumed after the first copulation. In addition, the breaking of the distal end of the embolus was considered to render a *Latrodectus* male unable to remate (Abalos & Baez 1963, Bhatnagar & Rempel 1962), see also Figure 24b. Such functional sterility was proved for *L. hasselti*; males remated, but without fertilisation success (Andrade & Banta 2002). Nevertheless, males of the American *L. mactans* were observed to remate and fertilise further females (Breene & Sweet 1985). In *L. renivulvatus* a successful further male copulation can be definitely excluded, since the entire embolus is torn off and left in the female genital organ (Fig. 24a; Knoflach & van Harten 2001b).

Monogyny is obligatory in the one-palped spiders as a result of the males' sudden sexual death. Their lives are restricted to one female, while females are polyandrous. As the male can use his single palp only once, females have to copulate at least twice to get both receptacula inseminated (Fig. 26). As a result, sex roles are reversed in these species. Potential reproductive success appears to be higher in females than in males, implicating sex role reversal and also male choice owing to his high investment. This sex role reversal is also indicated by the unusually active role of females in courtship. In many species, females apparently court for males. Males are assumed to prefer well-nourished females. The male's high investment should promise optimal fertilisation success. His body is used directly for production of offspring. Females appear to benefit from multiple copulations in various ways. Apart from an additional meal, genetic diversity of the offspring becomes increased. This may be of special relevance, when the progeny live close together.

Fig. 28a–c: Different stages of copulation in *Chrysso cambridgei*. **a**: Copulatory posture and insertion. **b, c**: Sperm induction. Arrow points to sperm droplet, which is already largely absorbed.

Descriptive part

Theridion-type

1 *Chrysso cambridgei* (Petrunkevitch 1911) (Fig. 28–30)

Material: **Mexico**, Chiapas state, Tapachula, Rosario Itzapa, ♂♀, 6.–12.10.2001, leg. S.P. Benjamin and J.A. Garcia-Ballinas. Offspring was reared to adulthood in captivity in Innsbruck.

Mating behaviour of C. *cambridgei* was observed from seven pairs. Sperm induction is part of copulation. Males constructed two or three sperm webs, the first after the first copulatory sequence and the last either before or after the last sequence. Copulation consisted of three copulatory sequences, each with two insertions. It is assumed that there is no pseudocopulation. According to duration of insertion, sperm transfer appears to start with the first copulatory sequence. During the last sequence a mating plug was produced, which seals the tiny epigynal atrium and perhaps prevents a female from remating.

Courtship behaviour: During precopulatory courtship there were no obvious distant courtship movements of the male. The male either remained motionless or immediately approached the female and initiated direct contact by palpating the female legs and body with forelegs and palps. In response the female palpated as well and adopted the inclined copulatory posture. Some males pushed their palps several times towards the epigynal region. Precopulatory courtship lasted only about 1 min on average (range = 0.3–3.0, n = 7). After sperm induction and during the interval before the next copulatory sequence four males were observed to oscillate their body, with their forelegs bent sidewards. Two males swayed their body up and down very often and intensively. Copulatory posture as typical of other *Theridion* species (Fig. 28, 29). During insertion one male was observed more closely. After some body pulsations he moved his forelegs up and down and then became motionless again.

Sperm induction (Fig. 28b, c): Spinning of the sperm web with induction took about 3.0 min on average (range = 2.5–3.8, n = 7), 1.0 min of which was used for construction of the sperm web. Spinning of the initial longitudinal threads (up to 3 cm) was particularly time- and space consuming. The male absorbed the sperm droplet within 2.1 min on average and by as many as 65

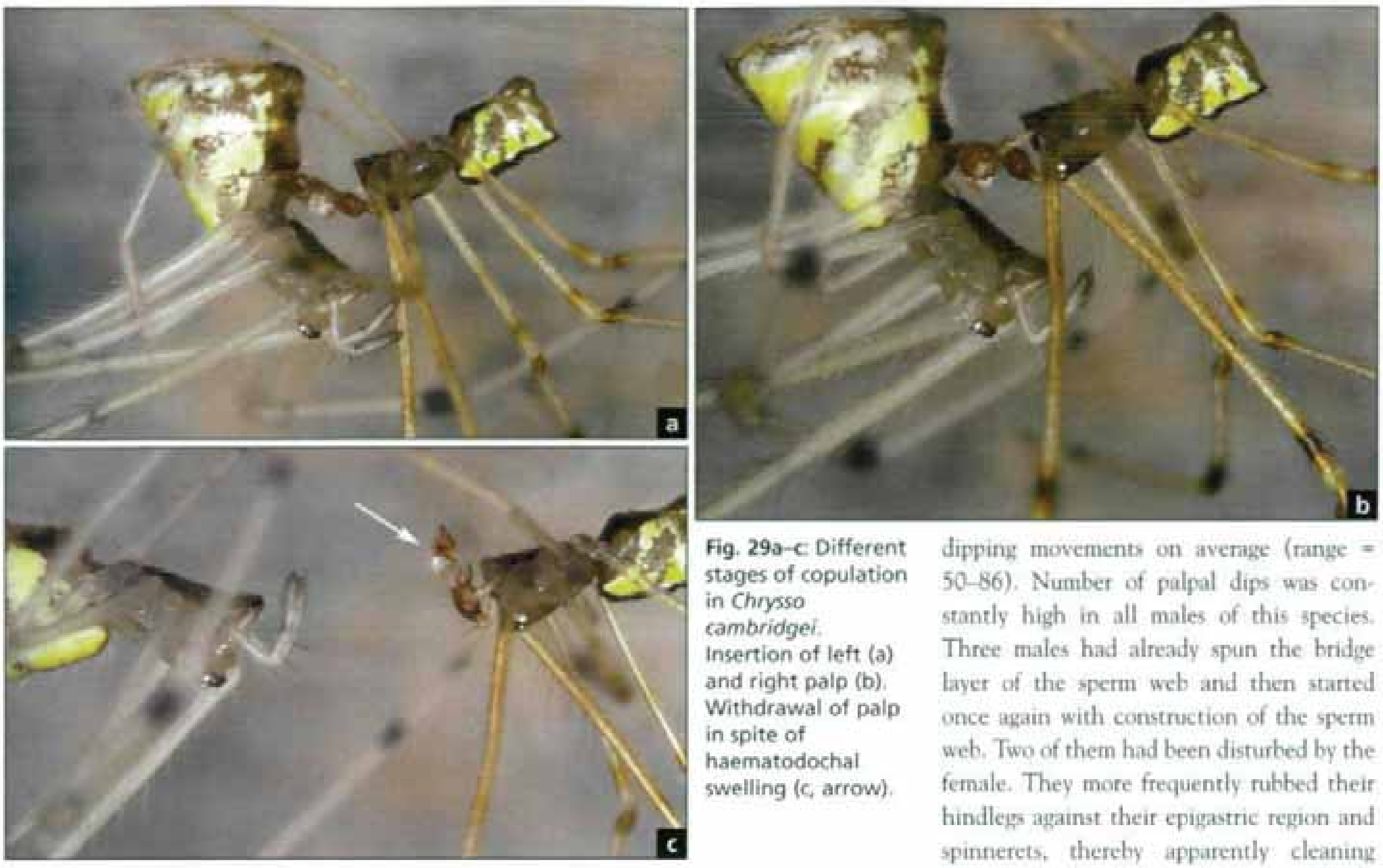


Fig. 29a–c: Different stages of copulation in *Chrysso cambridgei*. Insertion of left (a) and right palp (b). Withdrawal of palp in spite of haematodochal swelling (c, arrow).

dipping movements on average (range = 50–86). Number of palpal dips was constantly high in all males of this species. Three males had already spun the bridge layer of the sperm web and then started once again with construction of the sperm web. Two of them had been disturbed by the female. They more frequently rubbed their hindlegs against their epigastric region and spinnerets, thereby apparently cleaning these body parts. These movements were also present in the other males. Some males (n = 4) were observed to perform a third sperm induction after the final copulatory sequence. Another male did not charge his palps again within a period of 2 h.

Entire copulation duration averaged 84 min (range = 65–120, n = 7). Total number of insertions 6. Total insertion time 3.5 min on average (range = 2.9–4.7, n = 7).

Copulatory pattern (Fig. 30a, b): Each palp was inserted once per copulatory sequence. In the first two sequences insertions lasted 47.4 s on average (range = 32–68, n = 23). These insertions apparently reflect actual sperm transfer. Withdrawal of the palp sometimes proceeded swiftly, despite inflated haematodochae (Fig. 29c). Ultimate haematodochal collapse then took place on the free palp. The first two sequences took about 2–3 min. In the last se-

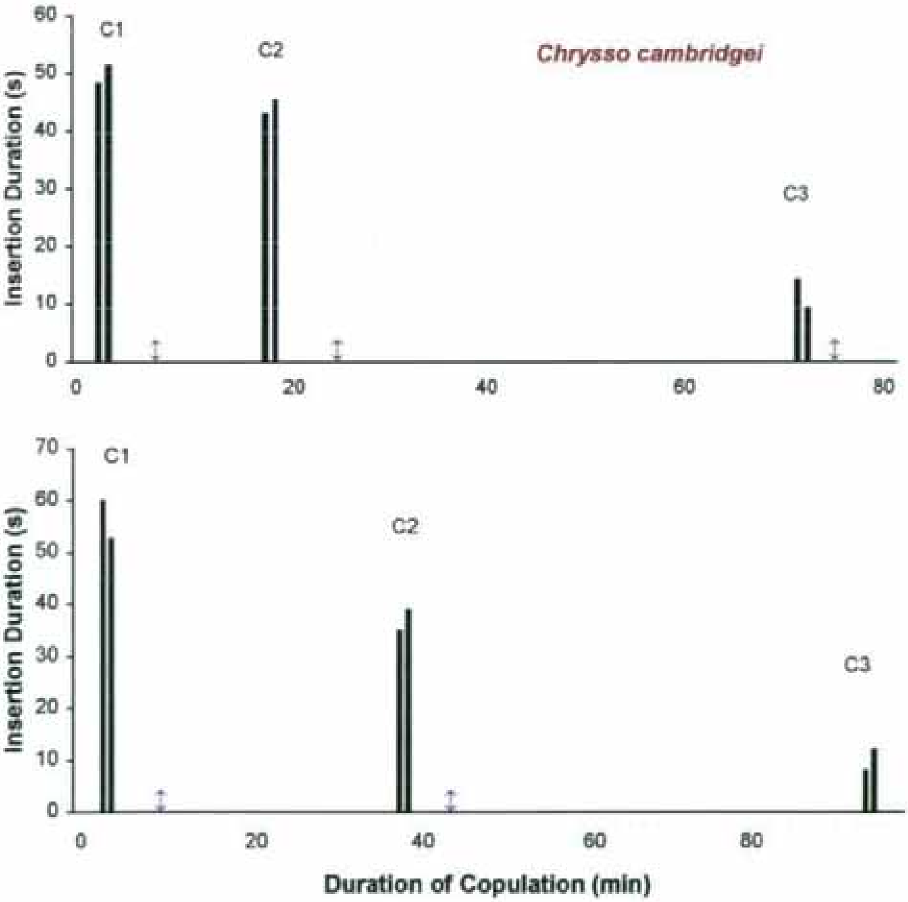


Fig. 30a, b: Copulation and insertion pattern in *Chrysso cambridgei*. Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates courtship. C1–3 = copulatory sequences.

quence insertions lasted only 7.7 s on average (range = 3.9–14.2, n = 10), the entire sequence took about 0.3–1 min. Apparently, a mating plug is transferred by the two short-time insertions. It is uncertain whether the male plug secretion originates from the male palp or genital tract. Remarkably, intervals between the last two copulatory sequences were much longer than those between the first two sequences (mean = 2.4 times, range = 1.6–3.6, n = 7), see Figure 30. The interval between first and second sequence lasted 23.1 min on average (range = 14.0–32.3; n=7), the interval between second and last sequence lasted 50.3 on average (range = 38–71 min, n = 7). After the third sperm induction which sometimes followed the final insertions, no further interactions of the partners were observed for 2–5 h.

Other observations: One female widely opened her chelicerae just before each insertion. One female started a prey attack on the male during sperm induction (not successful) and again shortly after copulation. Three mated females were allowed to copulate again. No further copulation occurred. In two pairings the female assumed the copulatory posture and the male tried to insert his palp 20 and 33 times for 1 and 4 min, but without success. One male left the web again after 2 min, the other remained motionless for half an hour. In a third pairing no interactions occurred during 1 h.

2 *Keijia kijabei* (BERLAND 1920) nov. comb. (Fig. 31a)

Theridion kijabei BERLAND 1920: 153, figs. 181–183, ♂♀, type locality Kijabe, Kenya.

Material: **Cape Verde Islands**, Santiago, São Jorge dos Orgãos, 15E03'N 23E37'W, 400 m, 15.12.1999–10.1.2000, leg. A. VAN HARTEN.

Taxonomy: This African representative unambiguously is a member of the former *Theridion tinctum*-group, which was recently separated from *Theridion* as a new genus (YOSHIDA 2001). Therefore, *T. kijabei* has to be transferred to *Keijia*. The type material of *K. kijabei* was examined (Muséum d'histoire naturelle Paris). This species has not been recorded again since its first description, but is present in recent collections from Yemen and the Cape Verde Islands (leg. A. VAN HARTEN).

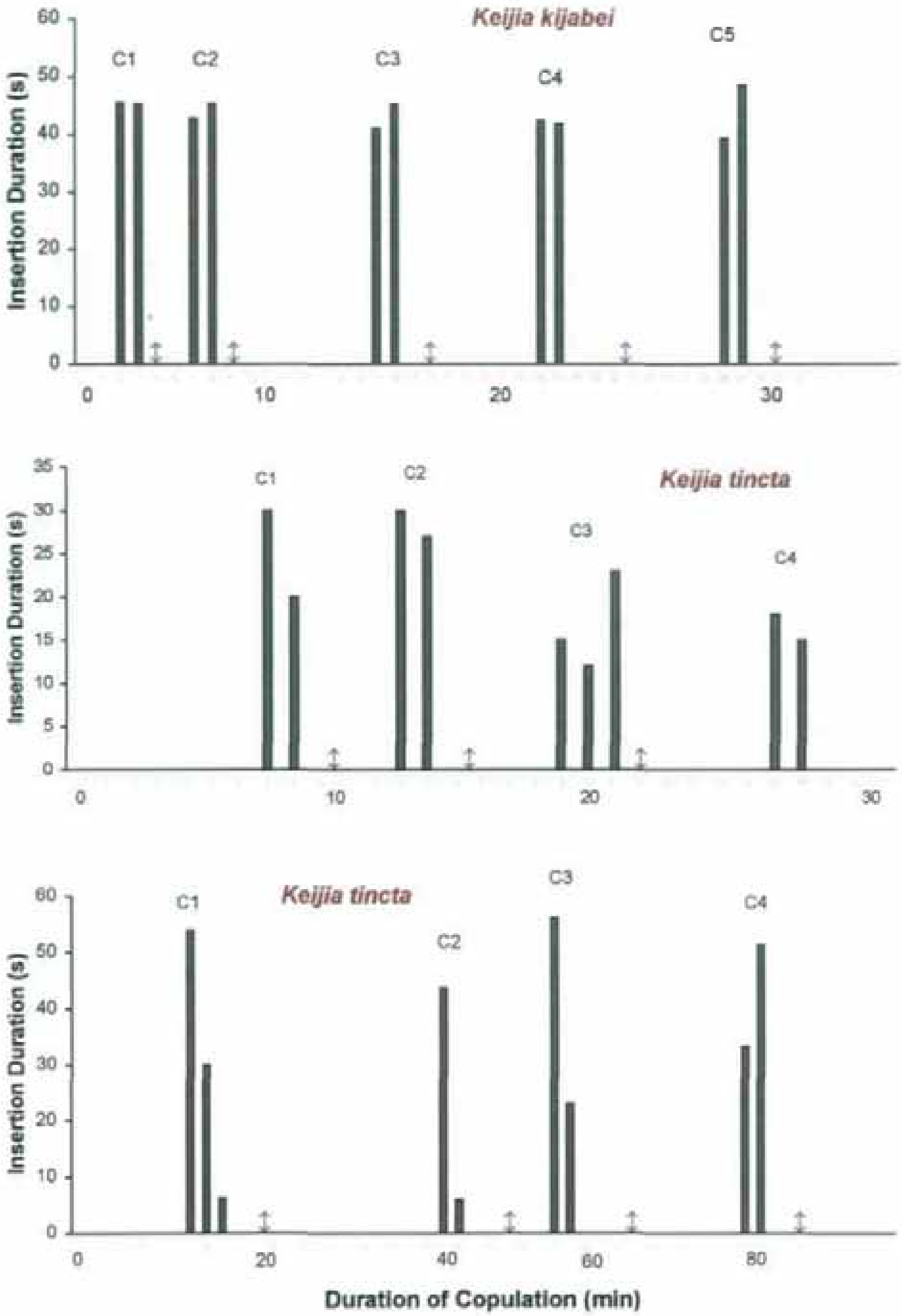


Fig. 31a–c: Copulation and insertion pattern in *Keijia kijabei* (a) and *K. tincta* (b, c). Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates courtship. C1–5 = copulatory sequences

Mating behaviour was observed from one pair only. Courtship and copulation is very similar to *K. tincta*. With the present number of observations it is hard to find a difference. Sperm induction is part of copulation. The male constructed five sperm webs, copulation also consisted of five copulatory sequences, each with two insertions (Fig. 31a). During insertion haematodochae pulsated rhythmically.

Courtship behaviour: During distant courtship the male made some walkabouts and frequently pulsated his abdomen before the first copulatory sequence and during in-

Fig. 32a–d: Different stages of copulation in *Keijia tincta*. **a**: Copulatory posture. **b**: Sperm induction, arrow points to sperm droplet. **c**, **d**: Insertion of left palp.

tervals. In later intervals body oscillations also occurred. Precopulatory courtship lasted only about 1 min. The female retained her inclined copulatory posture also during interruptions for sperm uptake up to the end of the last insertion.

Sperm induction: Spinning of the sperm web with induction took about 0.5 min on average (range = 0.5–0.6, n = 5), of which 0.1 min was used for construction of the sperm web. The male absorbed the sperm droplet within 0.4 min and by about 14 dipping movements (range = 10–18, n = 4).

Entire copulation duration 38 min. Total number of insertions 10. Total insertion time 7.3 min.

Copulatory pattern (Fig. 31a): similar to *K. tincta*. During each copulatory sequence two insertions were performed. Insertions lasted 43.7 s on average (range = 39.3–48.5, n = 10). Haematodochae inflated and deflated several times during an insertion, pulsating rhythmically. The copulatory sequences lasted about 1.6 min on average (range = 1.3–2.0, n = 5). During the last sequence the partners at first remained in copulatory posture for 3 min without being inserted, but with the male palp touching the epigynum several times. Then insertions took place. Intervals between two copulatory sequences lasted about 5 min on average (range = 2.0–7.5, n = 4). A mating plug was not discernible.

3 *Keijia tincta* (WALCKENAER 1802) (Fig. 31b, c, 32)

Material: **Austria**: N-Tyrol, Innsbruck-West, ♂♀, May 1998 and 2001. Ötztal Bahnhof, ♂♀, 4.6.1995; all leg. KNOFLACH.

Mating behaviour was observed from three pairs. Sperm induction is part of copulation. Males constructed three or four sperm webs, the first after the first copulatory sequence and the last either before or after the last sequence. Copulation consisted of 4 or 5 copulatory sequences, each usually with two insertions. During insertion haematodochae pulsated rhythmically. It is assumed that there is no pseudocopulation. According to duration of insertion, sperm transfer appears to start with the first copulatory sequence. A mating plug was not discernible.

Courtship behaviour: During distant courtship the male continuously pulsated his abdomen and performed some walkabouts. This was repeated after sperm induction and during the interval before the next copulatory sequence as well as after copulation. One male was observed to pluck alternately with his forelegs 39 times during precopulatory courtship (32 min long), but rarely during the interruptions for sperm uptake. Direct contact involved more female palpating, while the male still pulsated his abdomen when approaching her. Precopulatory courtship lasted 6, 8 and 32 min. Copulatory posture as typical of other *Theridion* species, see Fig. 32a, c, d. The female usually retained her inclined posture also during the interruptions for sperm uptake until end of copulation.

Sperm induction (Fig. 32b): Spinning of the sperm web with induction took about 1.1 min on average (range = 0.5–1.5, n = 6), 0.6 min of which was used for construction of the sperm web, the remaining half for absorption. The male absorbed the sperm droplet by about 12 dipping movements (range = 9–15, n = 4). The sperm droplet was rather small (Fig. 32b).

Entire copulation duration 18, 20 and 91 min. Total number of insertions 9, 8 and 11. Total insertion time 3.2, 4.9 and 6.4 min respectively.

Copulatory pattern (Fig. 31b, c): Most copulatory sequences involved two insertions, only in two sequences three insertions were performed. Sperm transfer is assumed to start with the first sequence. Insertions lasted 30.4 s on average (range = 6.0–56.2, n = 26). Remarkably, the haematodochae did not inflate once per insertion, but inflated and deflated several times, thus pulsating rhythmically (e.g. 19 times in a 33 s long insertion). The copulatory sequences lasted about 2 min on average (range = 1.2–4.2, n = 12). During the last sequences the partners occasionally maintained copulatory posture for 2–3 min without genitalia inserted. Intervals between two copulatory sequences lasted about 4 min in two pairs (range = 3.0–4.4, n = 6), but 20 min on average in the third pair (range = 10–30, n = 4). The latter male had his right legs I and II missing. A mating plug was not discernible.

Other observations: Another copulation of a virgin pair was observed superficially on account of photographic documentation. Again, four copulatory sequences were performed, each with two insertions. After the fourth sequence the female became restless and the male left her web.

4 *Nesticodes rufipes* (Lucas 1846) (Fig. 33, 34)

Material: Spain, Canary Islands, Tenerife: Puerto de la Cruz, ♂♀, 3.–10.1.2003, from house walls, leg. Knoflach & Thaler.

Identification according to Levi (1957) and Levy (1998).

Mating behaviour was observed from three pairs, one observation not in full detail on account of photographic documentation. Sperm induction is part of copulation. When copulating, males leave the female 8, 10 and 17 times for construction of sperm web and sperm induction. Thus, copulation is composed of 9, 11 and 18 copulatory sequences respectively. Whether the first copulatory sequence is a pseudocopulation still has to be investigated. At present, it is assumed to be a pseudocopulation owing to the large number of insertions. Insertions are all very short, about 1–2 s only. Male courtship is rather pronounced and regularly includes web-spinning behaviour. During the final sequences a mating plug is produced.

Courtship behaviour: During distant courtship, the male vibrated his abdomen and thereby stridulated distinctly. Remarkably, in this species male distant courtship comprised a long period of web-spinning behaviour. The male installed and attached numerous shorter threads in a region of about 2–5 cm, mainly in the upper zone of the female web, but also to the bottom and to the sides. In this part of the web he later constructed the sperm webs and performed further distant courtship. After this web-spinning the male took up a position oppo-

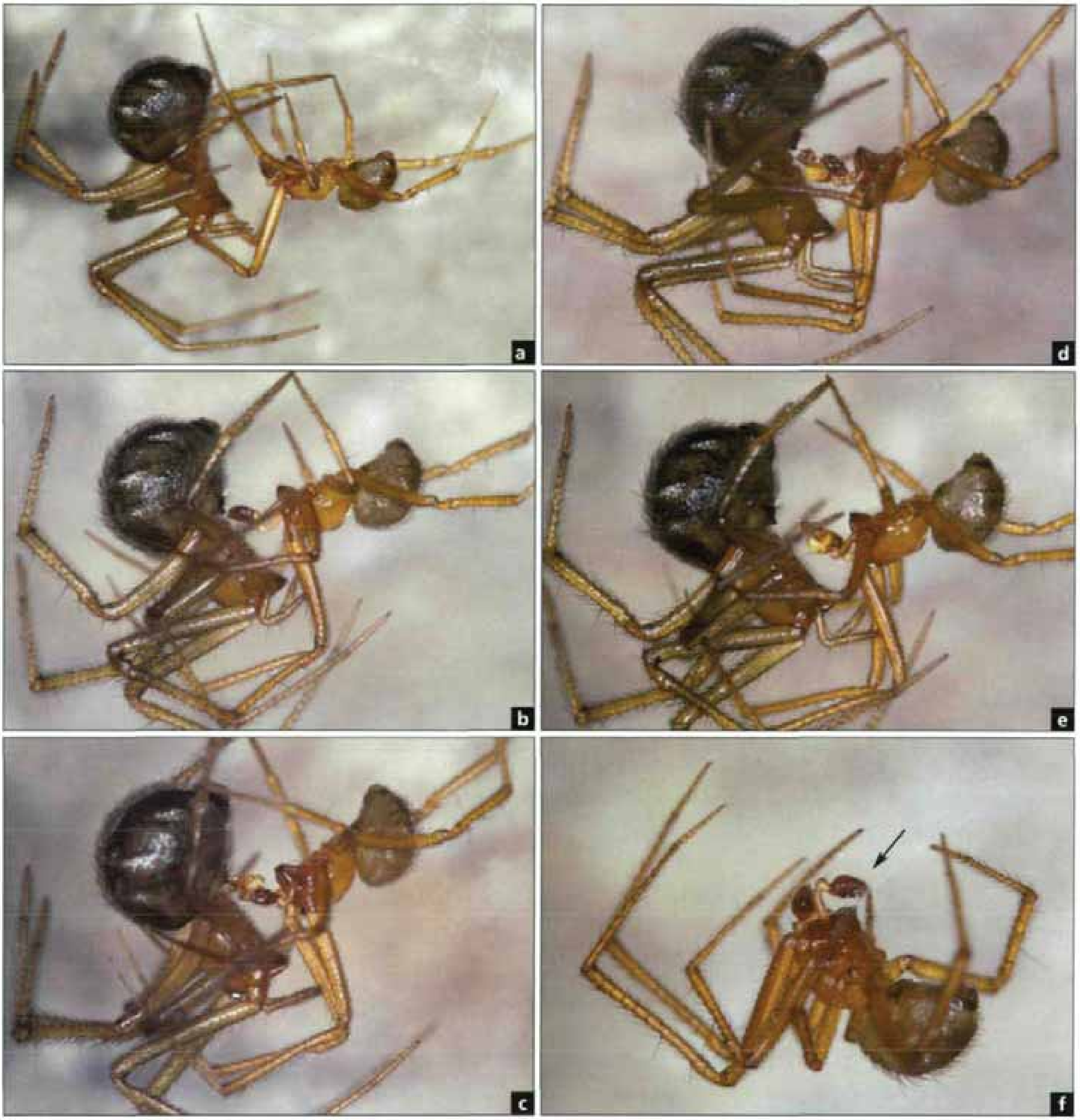


Fig. 33a–f: Copulation in *Nesticodes rufipes*. **a**: Male approach. **b**: Copulatory posture; forelegs of male grasping female's legs. **c**: Insertion of left palp. **d, e**: Withdrawal of palp in spite of haematodochal swelling. **f**: Sperm induction, arrow pointing to sperm droplet just being absorbed.

site the female, but still at a distance, and started to stridulate, to oscillate slightly and to pluck synchronously with his first legs. Thereby, his first legs remained half contracted, whereas the hind legs held the web. Plucking was intensive and frequent. Females were rather active and showed their willingness to pair by moving their first legs and palps up and down. They started these palpating movements when they recognised the male, and continued for a long time. In spite of the noticeable male web-spinning behaviour the female was not lured to him. Instead, the male approached the female, usually after plucking, with forelegs still contracted and spread sideways (Fig. 33a), stridulated, palpated the female and finally encompassed the female legs basally (Fig. 33b–e). This grip induced her to maintain copulatory posture. After each sperm induction and before the next copulatory sequence the males courted intensively as well.

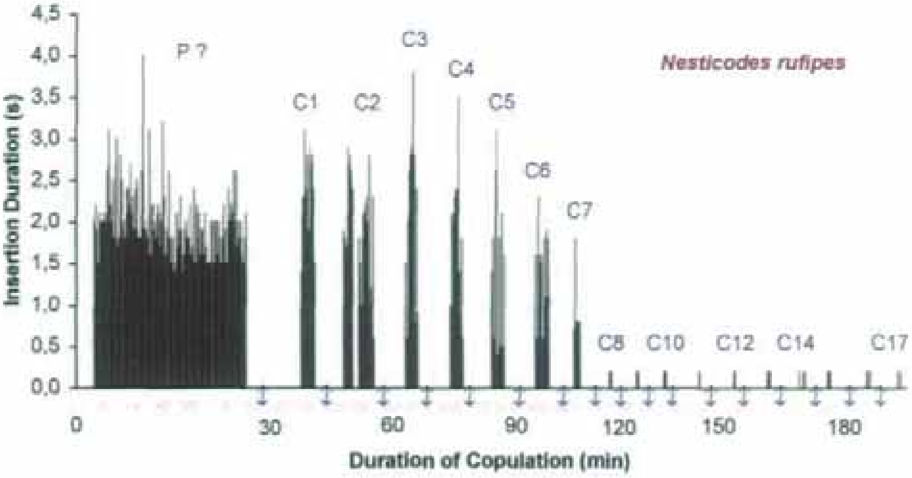


Fig. 34: Copulation and insertion pattern in *Nesticodes rufipes*. Each bar represents an insertion. Sperm induction indicated by double arrows. P? = probable pseudocopulation (not proved); C1–17 = copulatory sequences.

Thereby, they calmed the female, which appeared to become more aggressive as copulation advanced. Copulatory sequences, which followed after inconspicuous male courting without plucking, were sometimes interrupted by the female. Then the male escaped immediately and soon continued with web-spinning and further courtship in order to resume copulation. Number of pluckings increased with female aggressiveness. The number of sperm inductions/copulatory sequences performed by a male probably depends on the aggressiveness/willingness of the female. Precopulatory courtship lasted 5, 13 and 6 min. Intermediate courtship c. 5 min. Copulatory posture as typical of other theridiid species (Fig. 33c–f).

Sperm induction (Fig. 33f): Spinning of the sperm web with induction took about 1.0 min on average (mean = 62,4 s; range = 44–82, n = 26), 23 s of which were used for construction of the sperm web. The sperm droplet was absorbed within 40 s and by 11 dipping movements on average (range = 9–14).

Entire copulation duration 170, 140 and 198 min. Total number of insertions 181 and 203. Total insertion time 4.3 and 6.5 min (respectively).

Copulatory pattern (Fig. 34): Number of insertions during pseudocopulation 123 and 128 (respectively), with a mean duration of 1.3 and 2.0 s. Pseudocopulation lasted 30 (with interruptions), 20 and 10 min. In the following copulatory sequences each palp was inserted for a very short time as well (mean = 1.6 and 1.9 s), for about 13 times per sequence on average. The sequences lasted about 4 min (range = 2–7, n = 8). During the last 5, 5 and 10 sequences a mating plug secretion was transferred by short-time applications without haematodochal inflation. These plugging sequences were comparatively short, taking about 30–40 s, and involved about 30–40 palpal applications per sequence.

Females of *N. rufipes* were rather aggressive. Two males were pursued and devoured until the next day when not separated in time.

The copulatory behaviour of *N. rufipes* described by GONZALEZ (1989, sub *Theridion rufipes*, n = 27) differs profoundly from the present observation given above and probably may refer to another species. Copulation consisted of only 4–12 insertions, the first ones being shorter than the last ones, which then took 2–4 min. Construction of a sperm web is not mentioned.

5 *Paidiscura orotavensis* (SCHMIDT 1968) (Fig. 35a–d)

Material: **Spain**, Canary Islands, Tenerife: Buenavista, ♂♀, 19.2.2000 and 5.1.2003, leg. KNOFLACH & THALER.

Mating behaviour was observed from two pairs, one observation not in full detail on account of photographic documentation. *P. orotavensis* follows the *Theridion*-type of copulation, according to the time of sperm induction. Sperm induction is part of copulation. The male interrupted copulation two and three times for construction of sperm web and sperm induction. Copulation included three and four copulatory sequences respectively. Copulation proceeds via mating thread and female approach, which is exceptional among the representatives of the *Theridion*-type. Apparently, there is no pseudocopulation and no mating plug produced. Copulation is similar to *Paidiscura pallens*, but insertions obviously are shorter.

Courtship behaviour: Distant courtship was very distinct, predominant and was performed before each insertion. The male installed several times a mating thread, sometimes 1 cm long and sometimes even 6 cm. He intensively pulsated and vibrated his abdomen, oscillated his body and plucked alternately with his legs II (Fig. 35b). Once he pulled also with a single leg I. All these

Fig. 35a–d: Copulation in *Paidiscura orotavensis*. **a**: Sperm induction, arrow pointing to sperm droplet just being absorbed. **b**: Male plucking with legs III on the mating thread. **c**: Copulation via mating thread, male shortly before insertion. **d**: Insertion of left palp. Forelegs of male in contact with the female's legs.

movements were performed rhythmically, at constant intervals. In particular, alternate pluckings with legs II induced the female to approach him along the mating thread and to adopt the copulatory posture (Fig. 35c, d). Courtship lasted 14 min before the first insertion, later 2, 2.5 and 6 min. The female always approached the male for copulation.

Sperm induction (Fig. 35a): Spinning of the sperm web with induction took 1.2 min (n = 2), 14 s of which were used for construction of the sperm web. The sperm droplet was absorbed within 1 min and by 18–20 dipping movements.

Entire copulation duration 30 min. Total number of insertions 6 and 7. Total insertion time 21 s.

Copulatory pattern: Each palp was inserted once per sequence for a few seconds only (mean = 3.5, range = 2.4–4.6, n = 6). One male performed only one insertion in a final sequence. After each insertion the pair separated abruptly.

Other observations: Three further observations were negative. Females presumably were already mated and left their webs as soon as a male was introduced.

6 *Paidiscura pallens* (BLACKWALL 1834)

Material: **France**, Corsica, Calvi-surroundings, Forêt de Bonifatu, 750 m, ♂♀, 30.4.01, leg. KNOFLACH & THALER.

The single observation on the mating behaviour is incomplete, as the beginning is missing. *P. pallens* follows the overall pattern of *P. orotavensis*. Sperm induction is part of copulation and copulation is divided into copulatory sequences. Copulation proceeds via mating thread and female approach.

Courtship behaviour: Distant courtship was very intensive and predominant as in *P. orotavensis*. The male vibrated his abdomen and plucked with legs II alternately on the mating thread. Plucking and vibrating changed rhythmically. Courtship lasted 34 min after sperm induction and before the observed copulatory sequence.

Fig. 36a, b: Copulation in *Rugathodes bellicosus*. Insertion of left and right palp, leg contact present. Note widely opened chelicerae of male in (b).

Sperm induction: Spinning of the sperm web with induction took 2.6–2.7 min (n = 2). The sperm droplet was absorbed by 20–21 dipping movements.

Copulatory pattern: Only one copulatory sequence was fully observed. Each palp was inserted once per sequence for c. 40 and 47 s, longer than in *P. orotavensis*.

7 *Rugathodes bellicosus* (SIMON 1873) (Fig. 36, 37)

Material: Austria: Northern Tyrol, Obergurgl, Ötztal Alps, Gurgler Scharte, 2600 m, ♂♀, 6.7.1994, leg. THALER. Sellraintal, Kühtai, Haggen, 1650 m, 18.5.1996, leg. KNOFLACH.

Mating behaviour was observed four times in varying detail, with two copulations from one pair. Sperm induction is part of copulation. *R. bellicosus* males interrupted copulation 6, 9, 12 and 15 times for construction of sperm web and induction. Some males terminated copulation with a sperm induction, others with a sequence of insertions. Copulation consisted of 7, 10, 11 and 15 copulatory sequences. It has not been proved whether the first copulatory sequence is a pseudocopulation, but it appears unlikely. A mating plug was not discernible. Females apparently remate.

Courtship behaviour: During distant courtship, males pulsated their abdomen and sometimes jerked, once also body oscillations were performed. Courtship was very long and intensive in one male. This male also showed walkabouts and web-spinning behaviour. From time to time he approached the last exuvium of the female, which had remained in the web and which appeared to be more attractive than the nearby female. The male examined it thoroughly with his palps. The respective female usually remained motionless, only twice she was observed to jerk in response. Then the male contracted and released all legs synchronously and started direct contact, palpating the female several times. Precopulatory courtship lasted 5, 7 and 75 min. The male approached the female for copulation. Copulatory posture as typical of other *Theridion* species (Fig. 36a, b). During insertion the male's enlarged chelicerae sometimes were widely opened (Fig. 36a).

Sperm induction: Spinning of the sperm web with induction lasted 1.9 min on average (range = 1.5–2.5, n = 8), 1 min of which was used for construction of the sperm web. The sperm droplet was absorbed within 0.9 min and by about 13 dipping movements (range = 5–16). After induction the male often remained motionless for about one minute. In two males the pausing interval between last or penultimate sperm induction and last copulatory sequence took even 16 and 13 min (Fig. 37).

Fig. 37: Copulation and insertion pattern in *Rugathodes bellicosus*. Each bar represents an insertion. Sperm induction indicated by double arrows. C1–10 copulatory sequences.

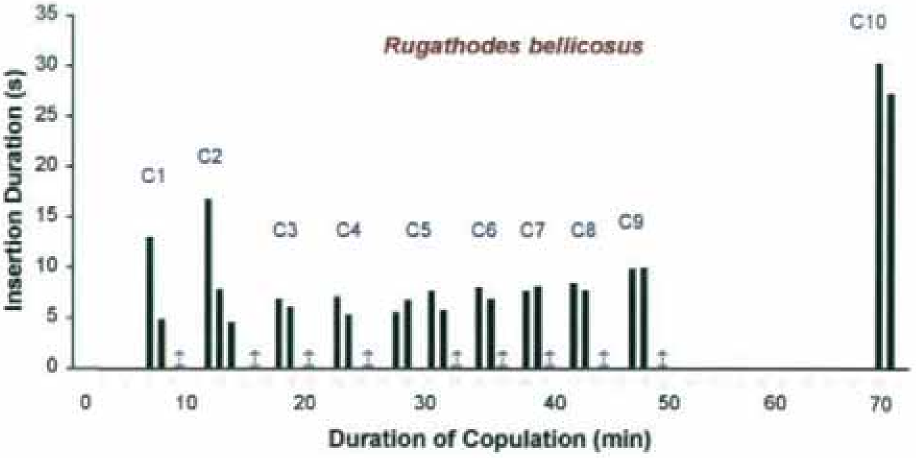


Fig. 38a–d: Copulation in *Simitidion lacuna*. **a, b**: Male approach, female moving her legs straightly apart. **c**: Insertion of left palp. **d**: Sperm induction, arrow pointing to sperm droplet just being absorbed.

Entire copulation duration averaged 61 min (range = 45–85, n = 4). Total number of insertions 20 on average (range = 14–23, n = 4). Total insertion time 1.0–3.7 min, rather low as compared with entire copulation time.

Copulatory pattern (Fig. 37): Each copulatory sequence usually involved two insertions (range = 1–4), which lasted in one pair 9.6 s on average (range = 4.5–30.2), in another even less (1–3 s). The male palp was pushed towards the epigynal region many times without successful insertion (=insertion attempts), 39 times in the first sequences and in the following about 6 times per sequence (given for one pair). A copulatory sequence took about one minute on average (range = 0.3–3.3, n = 22). In one pair the last two insertions were prolonged (Fig. 37).

8 *Simitidion lacuna* WUNDERLICH 1992 (Fig. 38, 39a)

Material: **Spain**, Canary Islands, above Orotava, Aguamansa, 1000 m, ♂♀, 17.2.–18.2.2000, leg. KNOFLACH & THALER.

Mating behaviour was observed from three pairs, two observations incomplete and not in full detail on account of photographic documentation or female aggression. Sperm induction is part of copulation. Males interrupted copulation 5, 6 and 7 times for construction of sperm web and sperm induction. Therefore, copulation consisted of 7, 8 and 9 copulatory sequences respectively. The first copulatory sequence is assumed to be a pseudocopulation, as in *S. simile*. Number and duration of insertions indicate that there is no sperm transferred during this sequence. In the course of the last sequence an inconspicuous mating plug is produced. Copulation follows the pattern of the *Theridion varians*-group and is very similar to that of *S.*

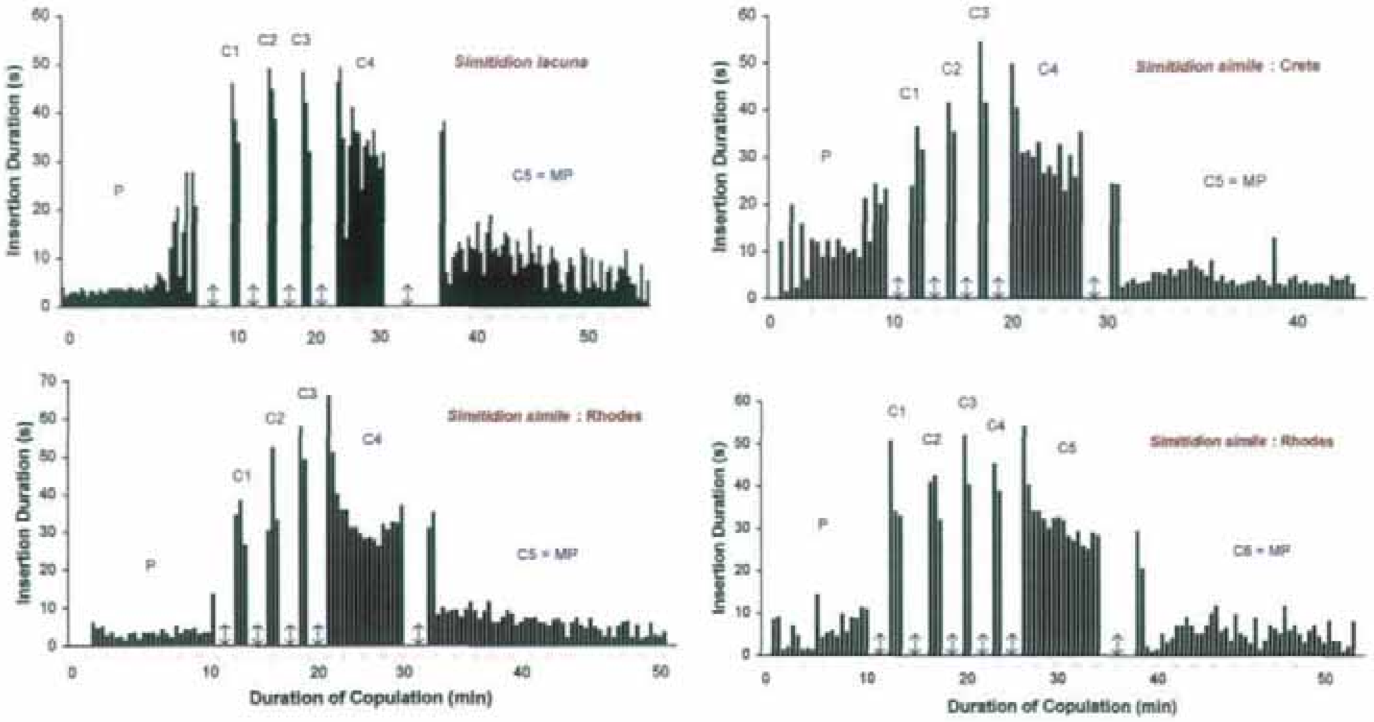


Fig. 39a–d: Copulation and insertion pattern in *Simitidion lacuna* (a) and *S. simile* (b–d) from Rhodes (b, d) and Crete (c). Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates duration of courtship. P = pseudocopulation; C1–16 = copulatory sequences; MP = Mating plug sequence.

simile. With the present data a separation from S. *simile* is not possible.

Courtship behaviour: Male courtship movements consisted of abdominal vibrations and alternate plucking with forelegs. Precopulatory courtship duration was variable, 0.5–15.0 min. The male approached the female for copulation. Copulatory posture as typical of other *Theridion* species, but female legs stretched straight sideways (Fig. 38a–c).

Sperm induction (Fig. 38d): Spinning of the sperm web with induction lasted only 44 s on average (range = 40–48, n = 9), 17 s of which were used for construction of the sperm web. The sperm droplet was absorbed within 27 s and by about 19 dipping movements (range = 15–24). As in the *Theridion varians*-group, the last sperm induction took relatively longer (61 s) with a larger number of palpal dips (32). The pause interval after this induction was also at least twice as long as after the previous ones (80 s). This final induction apparently produces the mating plug secretion, which is transferred from the male genital tract to the palps via the sperm web and then to the female epigynum. For sperm induction the male often returned to the same place in the web, not far away from the female, so that remnants of 5–6 sperm webs were found close together at the end.

Entire copulation duration 57 and 62 min. Total number of insertions 71. Total insertion time 31.4 min.

Copulatory pattern (Fig. 39a): Number of insertions during pseudocopulation 44, with a mean duration of 6.2. Interestingly, the last insertions of this sequence were longer. Pseudocopulation lasted 7 and 8 min. Then three to five copulatory sequences followed with three long insertions (mean = 41.3, n = 9, and 49.4, n = 12). These insertions apparently reflect actual sperm transfer. These copulatory sequences lasted 2.6 min on average (range = 1.3–3.3). The penultimate copulatory sequence took much longer, 11 min (n = 2), and involved more insertions, 16 in one case, with a mean duration of 33.5 s. The mating plug sequence then lasted 17 and 22 min. During this last sequence of insertions haematodochal inflation gradually diminished. By these short-time applications a secretion is transferred which results in the formation of a mating plug, apparently as in the *T. varians*-group (KNOFLACH 1998), but inconspicuous.

Other observations: One female was allowed to copulate with a second male, but became aggressive and tried to capture him.

9 *Simitidion simile* (C. L. Koch 1836) (Fig. 39b–d)

Material: Greece: Rhodes, Petaloudes, 300 m, ♂♀, from shrub, 9.4.1996; Attaviros-surroundings, Agios Isidoros, 550 m, ♂♀, 10.4.1996; Rhodos NW, Paradisi, w Kremasti from *Cistus*, ♂♀, 11.4.1996; Profitis Ilias, footpath from Salakos, 400 m, ♂♀, 12.4.1996. Crete E, Lasithiou, near Kato Metohi, Monastery Vidianis, Ag. Georgios, ♂♀, 8.4.1998. Austria: N-Tyrol, Ötztal Bahnhof 21.4.1996; Innsbruck, Martinswand 25.5.1995; all leg. Knoflach & Thaler.

Mating behaviour was observed from six pairs, two observations incomplete. Sperm induction is part of copulation. Males interrupted copulation 5, 5, 6, 7 and 9 times for construction of sperm web and sperm induction. Therefore, copulation consisted of 6, 6, 7, 8 and 10 copulatory sequences respectively (see also Knoflach 1996). The first copulatory sequence is assumed to be a pseudocopulation, but has not been proved. Number and duration of insertions indicate that there is no sperm transferred during this sequence. In the course of the last sequence an inconspicuous mating plug is produced. Copulation follows the pattern of the *Theridion varians*-group and is very similar to that of *Simitidion lacuna*.

Courtship behaviour: Male courtship movements were intensive and consisted of long-lasting abdominal vibrations and strong alternate plucking with forelegs (present in all males observed). The male performed these distant courtship movements also during the intervals between copulatory sequences, in particular after sperm induction. Precopulatory courtship duration varied from 2 to 20 min. During contact courtship the male continued vibrating his abdomen and palpated the female with forelegs and palps. The male approached the female for copulation. Copulatory posture as typical of other *Theridion* species. Copulatory courtship: during insertion the male also intensively vibrated his abdomen.

Sperm induction: Spinning of the sperm web with induction lasted only 44 s on average (range = 30–56, n = 17), 18 s of which were used for construction of the sperm web. The sperm droplet was absorbed within 26 s and by about 18 dipping movements (range = 10–26). As in the *Theridion varians*-group, the last sperm induction took relatively longer (52 s, range = 40–75, n = 4) with a slightly larger number of palpal dips (mean = 26, range = 17–42, n = 4) and a comparatively larger sperm droplet. The pause interval after this induction was almost twice as long as after the previous ones; duration of entire interval including sperm induction 2.5 min on average for the last induction (n = 6), and 1.3 min on average for the previous ones (n = 16). This final induction apparently produces the mating plug secretion, which is transferred from the male genital tract to the palps via the sperm web and then to the female epigynum. The final mating plug sequence started with two normal insertions with haematodochal swelling, but then genitalia contact changed. Haematodochal inflation was diminished with each further insertion and sometimes the palp was applied to the epigynum without much rotation. Altogether about 60 palpal applications (47–105, n = 4) took place in this phase, which lasted 15 min on average (range = 10–20, n = 5).

Entire copulation duration averaged 57 min (range = 42–92, n = 5). Total number of insertions 51 on average (range = 44–60, n = 5). Total insertion time 18.8 min on average (range = 16.9–20.8, n = 4).

Copulatory pattern (Fig. 39b–d): Number of insertions during pseudocopulation 21–28, with a mean duration of 7.0 ± 0.5 s (mean ± s.e, range = 1.1–24.2, n = 96). Pseudocopulation lasted 4.5 to 9 min (mean = 8, n = 4). Then three to five, or even seven copulatory sequences followed with two to three longer insertions (mean ± s.e = 42.9 ± 1.4 s, range = 23.7–61.8, n = 50). These insertions apparently reflect actual sperm transfer. These copulatory sequences lasted 2.1 min on average (range = 1.7–2.7, n = 24). The penultimate copulatory sequence took much longer, 11.0 min (range = 7.5–14.0, n = 6), and involved more insertions, 14–28 (mean = 19, n = 5), with a mean duration of 29.2 ± 1.0 s (mean ± s.e., range = 4.0–65.9, n = 96). The mating plug sequence then lasted 10.0–20.2 min (mean = 15.2, n = 5). During this last sequence of insertions haematodochal inflation gradually diminished. By short-time applications a secretion was transferred which resulted in the formation of a mating plug, apparently as in the *T. varians*-group (see KNOFLACH 1998), but inconspicuous. Pairs from Crete, Rhodes and northern Tyrol show similar copulatory patterns (Fig. 39b–d).

Other observations: A female from Rhodes was allowed to copulate with a male from Austria, and vice versa, also a female from Austria with a male from Rhodes. Both copulations proceeded typically. The females produced fertile egg-sacs. Unsuccessful observations: Twice a male from Rhodes courted for more than 2 h, vibrating and plucking alternately throughout, but without success. Apparently, the rather freshly moulted female (also from Rhodes) was not willing to mate at that time. Two further unsuccessful copulations involved females which were collected when already adult and therefore might have been already mated. The males tried to insert their palps, but insertions were not fully accomplished and then copulation was interrupted by the female.

10–15 *Theridion melanurum*-group

The first copulatory sequence does not represent a pseudocopulation (contra KNOFLACH 1998). Thus, sperm transfer is assumed to start with the first insertion. Males interrupt copulation several times for sperm uptake, which therefore is part of copulation. In *T. ochreolum* only 3–5 copulatory sequences took place, in the others 5–11. During most copulatory sequences each palp is inserted once. Insertions last less or about one minute in *T. betteni*, *T. mystaceum* and *Theridion* sp. Remarkably, these species show an obligatory resting period after each copulatory sequence, which takes about 20 min in *T. betteni*, 29 min in *T. mystaceum* and even 2.3 h in *Theridion* sp. (including time for sperm uptake). In the other species insertions last longer, 1.6 min on average and up to 3.4 min in *T. musivivum*, 3 min on average and up to 7.6 min in *T. ochreolum*, 4 min on average and up to 7.6 min in *T. melanurum*. This group of species does not show such long pause intervals. Furthermore, they perform one or more final copulatory sequence(s) differing considerably from the previous ones by numerous short insertions: 2 sequences in *T. melanurum*, 2–4 in *T. musivivum* and usually 1 in *T. ochreolum*. There is no mating plug discernible. In many observations the last male copulatory action was another sperm induction, apparently preparing for the next mate.

10 *Theridion betteni* WIEHLE 1960 (Fig. 40, 41a)

Material: Austria, N-Tyrol, Ötztal, Längenfeld, 1300–1400 m, ♂♀, 23.4.1994, leg. KNOFLACH & THALER.

Mating behaviour of *T. betteni* was observed from three pairs, but with low accuracy as regards number and duration of insertions. Sperm induction is part of copulation. The males constructed 10 and 11 sperm webs during and at the end of copulation. Copulation included 11 copulatory sequences, which were followed by a regular resting period of about 20 min (including time for sperm uptake). In one pair, each palp was inserted once per sequence (the other not recorded in detail). It is unlikely that the first copulatory sequence is a pseudocopulation. Thus, sperm transfer is assumed to start with the first insertion. Apparently there is no mating plug.

Courtship behaviour: During distant courtship males intensively pulsated their abdomen and also oscillated their body. Abdominal vibrations sometimes were performed also in the intervals after sperm induction beween two copulatory sequences. During direct contact the male palpated the female with his forelegs and palps and vice versa. Precopulatory courtship lasted 0.5, 1 and 4 min. The male approached the female for copulation (Fig. 40a). Copulatory posture similar to other *Theridion* species, with leg contact (Fig. 40d–f).

Sperm induction (Fig. 40a, b): Spinning of the sperm web with induction took on average about 1.0–1.5 min. The sperm droplet was absorbed by 12 dipping movements (only once recorded).

The entire copulation duration occupied 3, 3.8 and 4 h, total number of insertions about 20, total insertion time about 6.5, 8 and 13 min.

Copulatory pattern (Fig. 41a; roughly estimated). After each sperm induction a long, regular resting period followed, see also *T. mystaceum*. After about 20 min on average in two pairs and 14 min in the third pair, the male returned to the female for the next in-

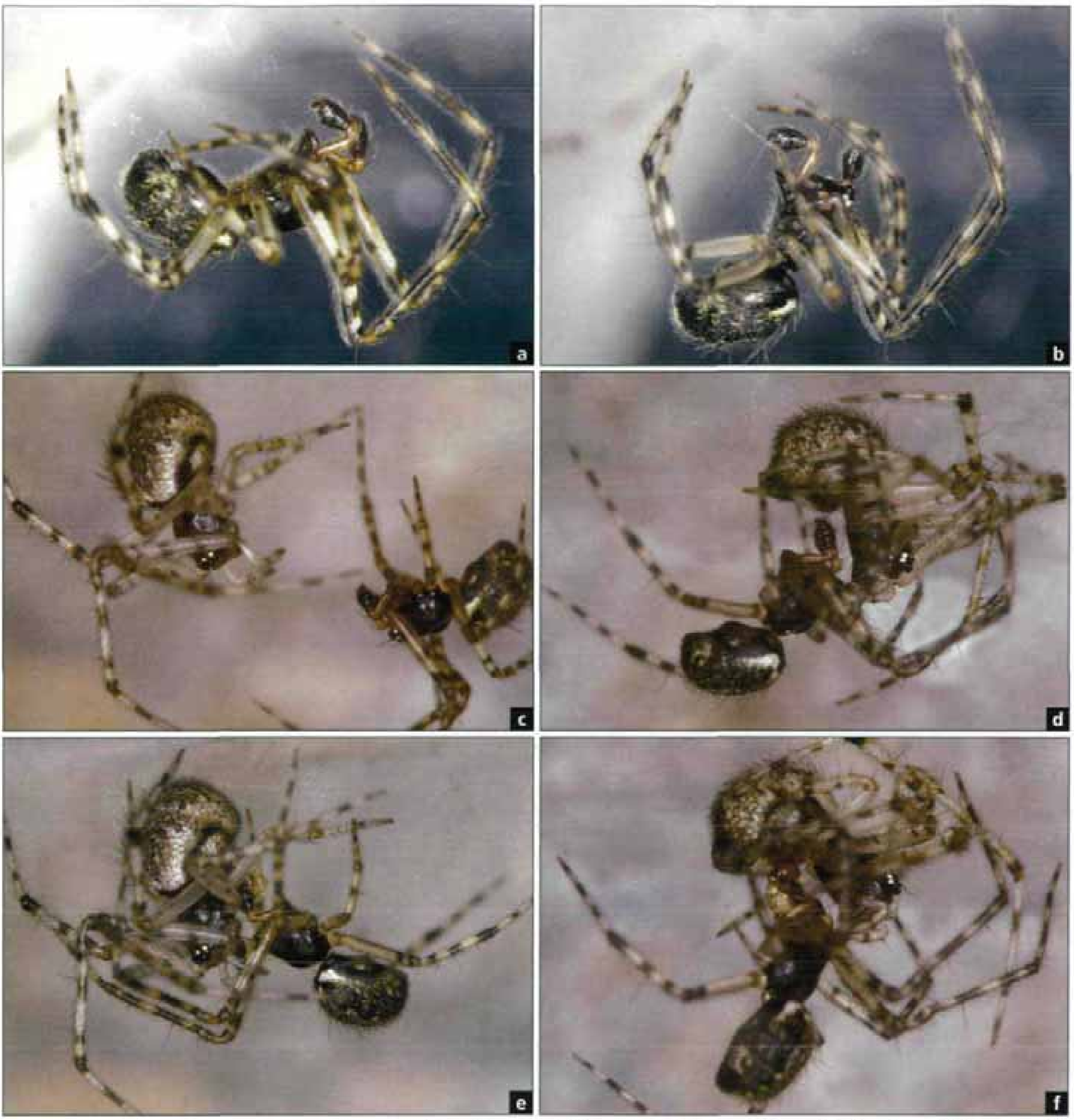


Fig. 40a–f: Copulation in *Theridion betteni*. **a**: Construction of sperm web. **b**: Sperm induction, tiny sperm droplet just being absorbed. **c**: Male approach. **d**: Copulatory posture; forelegs of male in contact with female's legs. **e, f**: Insertion of right and left palp.

sertions (overall mean = 17.7, range = 3–35, n = 30). In all pairs the last 2–3 resting periods were shorter than the previous ones (3–7 min). During a copulatory sequence each palp was inserted only once for about 30–50 s (only recorded in one pair). The sequences lasted about 2 min (n = 23), except for the final 2–3 sequences, which took longer, about 8 min (n = 7). Insertion attempts occurred regularly. No mating plug could be found.

BRAUN (1964) observed the mating behaviour of *T. betteni* from specimens from N-Tyrol, Innsbruck surroundings, collected by K. THALER on 4.6.1963. Only 2–4 copulatory sequences were performed, with 4–18 inserations per sequence. Insertions lasted only 0.5–3 s. Sperm inductions took place 3–4 times and lasted 0.5–1.0 min. These observations appear to reflect rematings rather than copulations of virgins. Copulations then differ considerably, see also *T. melanurum*.

11 *Theridion melanurum* HAHN 1831 (Fig. 42a, b)

Material: Germany, Sachsen-Anhalt, Halle/Saale, from house walls, ♂ ♀, 9.4.2003, leg. KNOFLACH & THALER.

Mating behaviour of *T. melanurum* was observed from two pairs. Sperm induction is part of copulation. The males constructed 7 and 9 sperm webs during copulation, one male also at the end of copulation. Copulation included 8 and 9 copulatory sequences. It is assumed that there is no pseudocopulation. Insertion duration indicates that insemination starts with the very first insertions. In the course of copulation there is a clear change from long-time to shorter insertions. A mating plug was not discernible.

Courtship behaviour: During distant courtship both males intensively pulsated their abdomen and plucked with their forelegs. One male also performed web-spinning and oscillated his body. During the direct contact phase of courtship the male palpated the female with forelegs and palps and vice versa. Precopulatory courtship lasted 6 and 8 min. The male approached the female for copulation. Copulatory posture as typical of other *Theridion* species.

Sperm induction: Spinning of the sperm web with induction took on average 1.8 min (range = 1.6–2.2, n = 16), 0.7 min of which wase used for construction of the sperm web. The sperm droplet was absorbed within 1.4 min and by 25 dipping movements on average (range = 21–33, n = 16).

Entire copulation duration occupied 150 and 210 min, total number of insertions 37 and 137, total insertion time 91.3 and 129.3 min (respectively).

Copulatory pattern (Fig. 42a, b): During the first copulatory sequences each palp was inserted only once for about 4 min (mean ± s.e. = 4.0 ± 0.4, range = 0.6–7.6, n = 24) without resting period. Haematodochae were highly inflated. These sequences lasted 9.4 min on average (range = 4.3–13.5, n = 12). In the following 1–3 intermediate sequences some additional shorter insertions took place (mean duration 1.3 min ± 0.2 s.e., range = 0.1–6.4). The final copulatory sequence involved numerous shorter insertions (in one case 99 insertions with a mean duration of 36.0 ± 2.3 s, mean ± s.e, range = 2.2–65.8, n = 99). In the first pair this last sequence may be missing (Fig. 42a). The female suddenly became aggressive, interrupted copulation and started attacking the male, so that he left the web. The last observed sequence of this pair is interpreted as a penultimate one. The penultimate sequence lasted 22 and 24 min. Haematodochal inflation diminished in the insertions of the penultimate and final se-

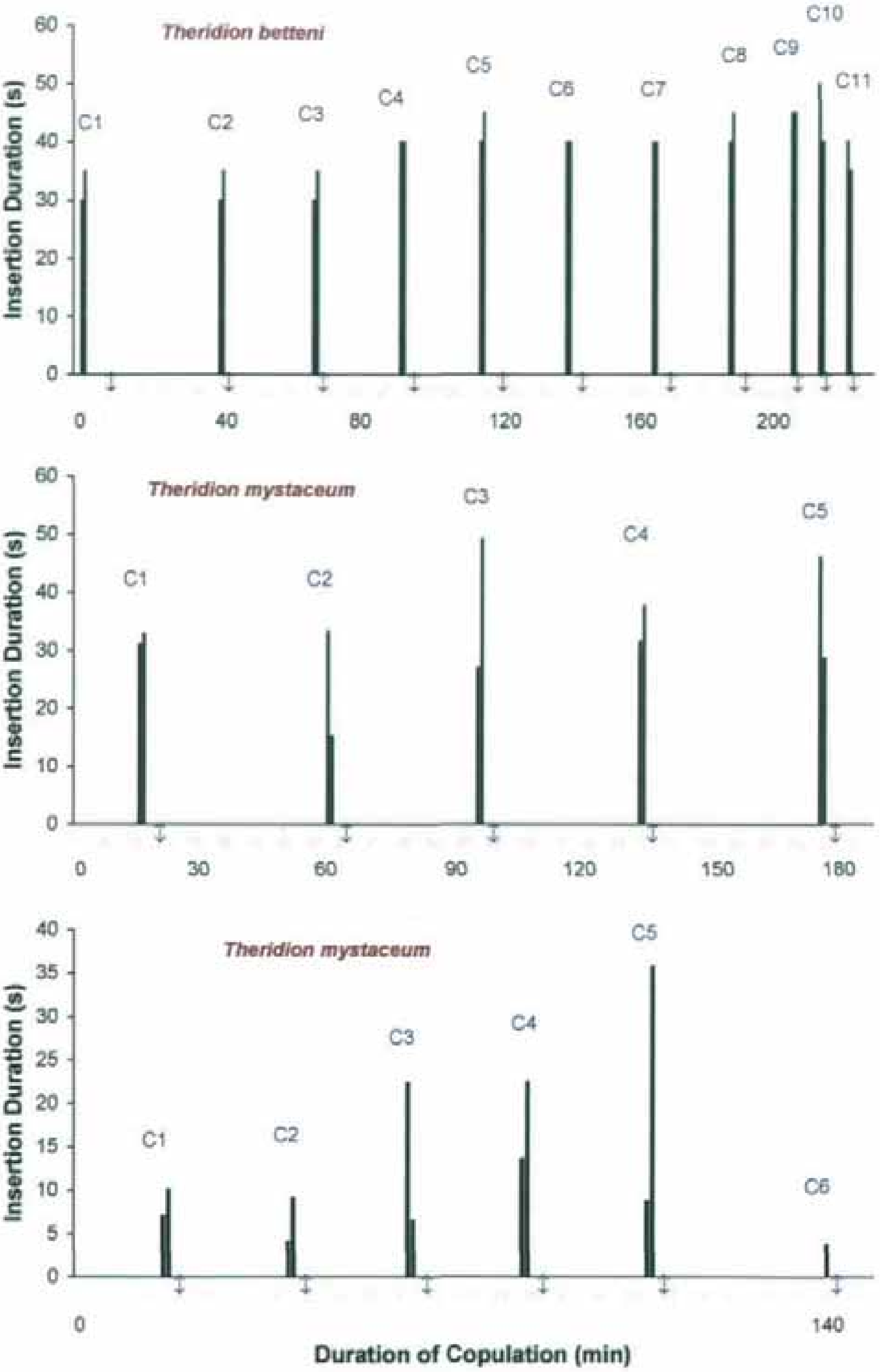


Fig. 41a–c: Copulation and insertion pattern in *Theridion betteni* (a) and *T. mystaceum* (b, c). Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates duration of courtship. C1–11 = copulatory sequences.

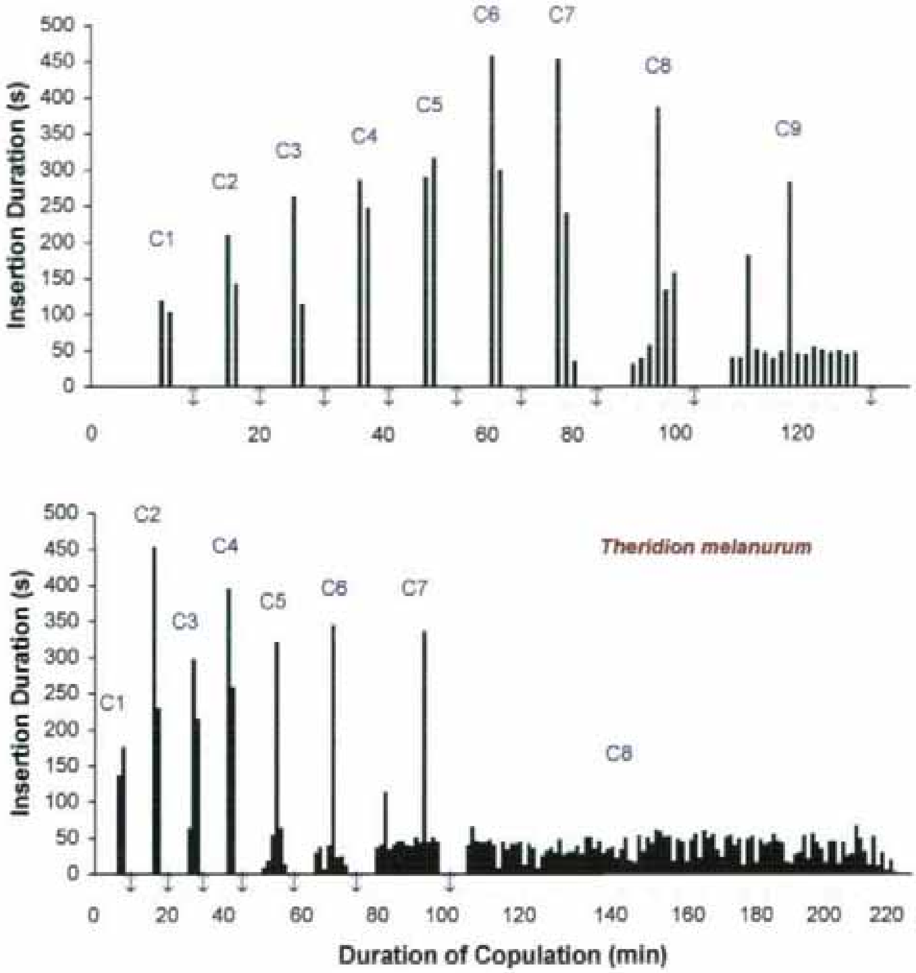


Fig. 42a, b: Copulation and insertion pattern in *Theridion melanurum*. Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates duration of courtship. C1–9 = copulatory sequences.

quence. Only a few insertions were accompanied by full haematodochal expansion. The final sequence was comparatively long, lasting 111 min, including short resting periods. In the first sequences insertions usually succeeded at once, insertion attempts occurred at a low rate or not at all (mean = 1.7 attempts, range = 0–7, n = 13). In the penultimate and last sequence numbers of insertion attempts increased considerably, 16–19 in the penultimate sequence and 267 in the last one. The male palp frequently touched the epigynum for a short time (1–2 s) without being rotated and without haematodochal swelling. A mating plug was not discernible.

GERHARDT (1927; sub *Theridium denticulatum*) observed five copulations of *T. melanurum* from specimens from Halle (same locality as in the present paper). Number of sperm inductions (7, n = 2 and 9, n = 1) correspond well with the present observations. Entire copulation apparently lasted longer, about 6 h, and insertions took up to 12–15 min. Shorter insertions in the last sequences were not mentioned. Apparently, in rematings the copulatory pattern differs considerably. GERHARDT (1926) observed a copulation which consisted of only two insertions of about 1 min duration. Sperm induction did not occur. This incomplete copulation indicates that the female was already mated (GERHARDT 1926).

12 *Theridion musivivum* SCHMIDT 1956 (Fig. 43, 44)

Material: **Spain**, Canary Islands, Tenerife: Puerto de la Cruz, ♂♀, 16.–23.2.2000 and 3.–10.1.2003, from house walls. Orotava, Aguamansa, ♂♀, 9.1.2003; above Orotava, Aguamansa, 1100 m, ♂, 18.2.2000. Orotava, Barroso, c. 900 m, ♀, 22.2.2000; Teno, Erjos, ♀, 6.1.2003; all leg. KNOFLACH & THALER.

Mating behaviour of *T. musivivum* was observed from 10 pairs, one of them not in full detail on account of photographic documentation. Sperm induction is part of copulation. The male constructed 5–10 sperm webs (mean = 7) during copulation, but also at the end. Copulation included an equal number of sequences. There is no pseudocopulation. Apparently, insemination starts with the very first insertions. One female, which was separated after the first copulatory sequence, built a cocoon with about 100 eggs within a period of two weeks. Sperm transfer is also reflected by the long lasting insertions. A mating plug was not discernible.

Courtship behaviour: Courtship was rather inconspicuous. Distant precopulatory courtship, if present at all (n = 5), consisted of male abdominal pulsations and plucking with forelegs (n = 4). These movements were sometimes also performed after sperm induction and during interruptions caused by the female. During the direct contact phase of courtship the male palpated the female with his forelegs and palps, and vice versa. Usually the female appeared active only in this phase of courtship. Duration of precopulatory courtship was short, 0.3–6.0 min. The male approached the female for copulation (Fig. 43a, b). During insertion the male regularly pulsated his abdomen, presumably displaying copulatory courtship. Copulatory posture as typical of other *Theridion* species, but leg contact comparatively loose (Fig. 43c, d).

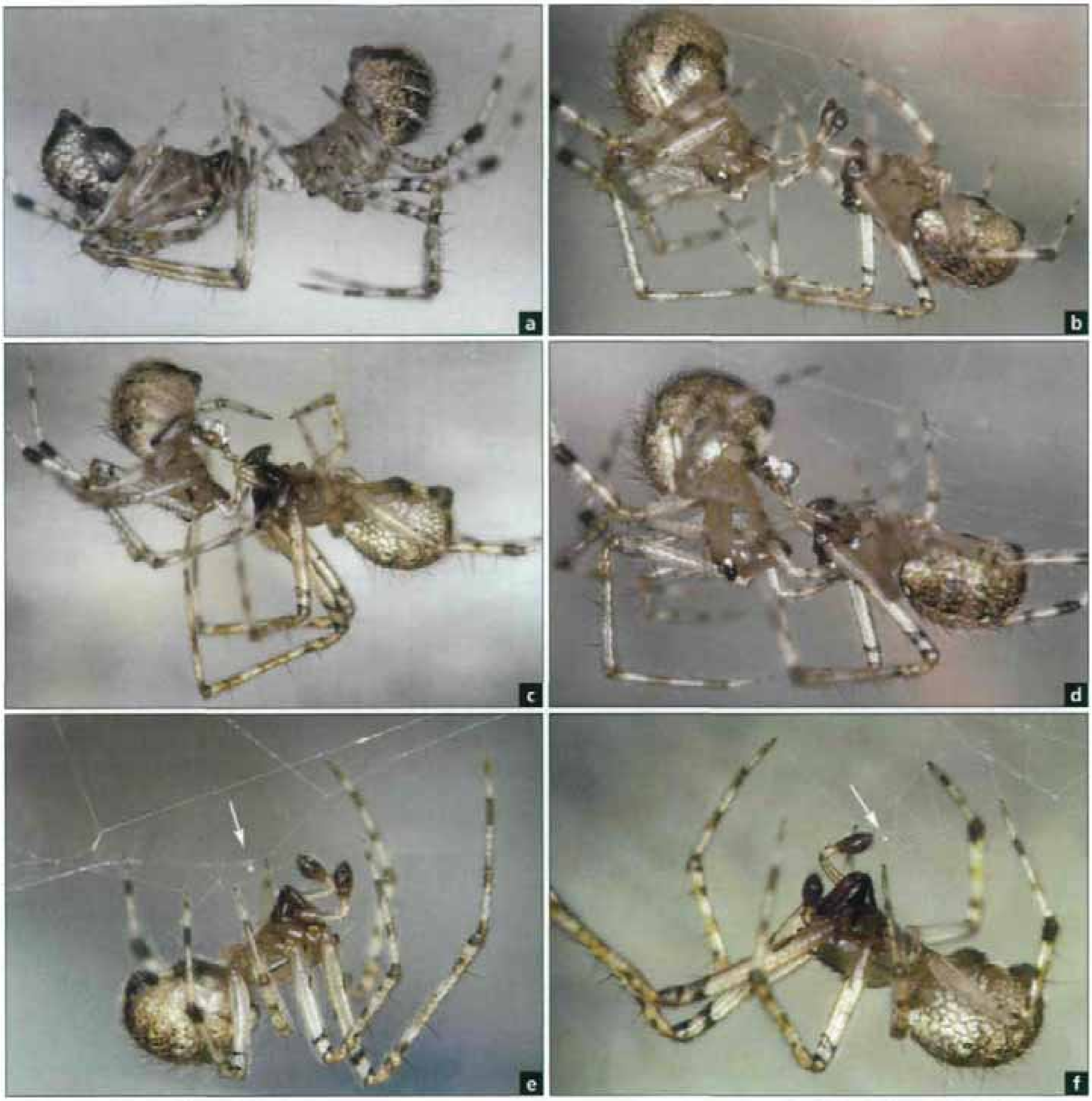


Fig. 43a–f: Copulation in *Theridion musivivum*. (a, b) Male approach. (c, d) Insertion of left and right palp. (e, f) Construction of sperm web completed, tiny sperm droplet (arrow) deposited (e) and just before absorption (f).

Sperm induction (Fig. 43e, f): Spinning of the sperm web with induction took on average 46.0 ± 0.9 s (mean ± s.e., range = 32–65, n = 64), 11 s of which were used for construction of the sperm web. The sperm droplet was absorbed within 37 s and by 16.3 ± 0.5 dipping movements on average (mean ± s.e., range = 9–24, n = 59). The bridge of the sperm web consisted of a few transverse threads only, and the sperm droplet was rather small. After sperm uptake the male immediately returned to the female for the next sperm transfer without much of a pause.

Entire copulation duration averaged 50 min (range = 35–65), total number of insertions on average 91 (range = 32–132), total insertion time 36 min on average (range = 17–48).

Copulatory pattern (Fig. 44a–f): During the first 3–6 copulatory sequences each palp was inserted only once for about 1.6 min (mean ± s.e. = 98.8 ± 5.1 s, range = 1.2–203.9, n = 76) without pause interval.

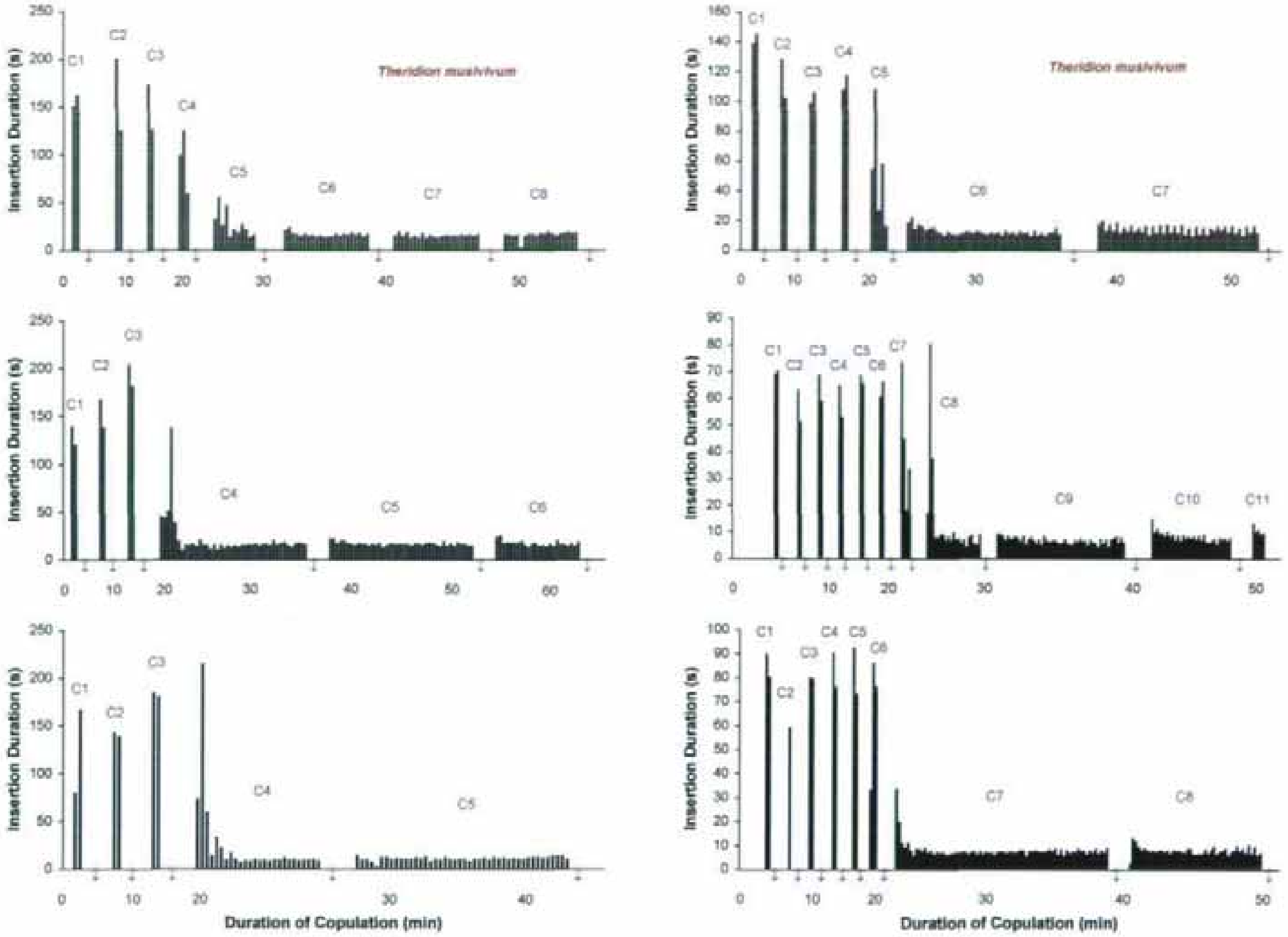


Fig. 44a–f: Copulation and insertion pattern in six pairs of *Theridion musivivum* from Tenerife. Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates duration of courtship. C1–11 = copulatory sequences.

Haematodochae were highly inflated (Fig. 43d). These sequences lasted 3.6 min on average (range = 1.5–6.5, n = 37). After an intermediate sequence, several copulatory sequences followed during which each palp was inserted numerous times (28 times on average, range = 4–74, n = 26), but for a shorter time (mean ± s.e. = 12.3 ± 0.4 s, range = 0.5–214, n = 727). Accordingly, haematodochal inflation diminished in these insertions. These final sequences were comparatively long, lasting 8.2 min on average (range = 3.7–17.2, n = 25), including some pauses. Insertion attempts occurred at a low rate, insertions usually succeeded at once. A mating plug was not seen.

Other observations: One virgin male at first built a sperm web when introduced into a web of a virgin female. This is another confirmation of the absence of pseudocopulation. One copulated female became aggressive when encountering a second male (two weeks after copulation). She intensively jerked and pulsated her abdomen so that the male left her web. One female started a sudden attack during the short-time insertions of her first copulation and threw viscous threads towards the male. In spite of this the male courted and resumed copulation until her next attack. Number of insertions was rather low in this pair. Three further copulations were interrupted once by the female, again during the short insertions, but were continued then in a normal way.

13 *Theridion mystaceum* L. Koch 1870 (Fig. 41b, c)

Material: **Austria**, N-Tyrol, Innsbruck, from house wall, ♂♀, 18.4.2003; Kranebitten ♂♀, 13.5.1995, leg. Knoflach & Thaler.

Mating behaviour was observed from two pairs, which were collected as adults. Therefore, it is not known for certain whether they were virgin. One pairing is assumed to be virgin, the other perhaps was already mated. Sperm induction is part of copulation. Males constructed 5 and 6 sperm webs during and at the end of copulation. Copulation included 5 and 6 copulatory sequences, which were followed by a regular resting period of 29 min (including time for sperm uptake). Each palp was inserted once per sequence. Again, it is assumed that there is no pseudocopulation, see also e.g. *T. musivum*. A mating plug was not discernible.

Courtship behaviour: During distant courtship both males intensively pulsated their abdomen. One male also plucked alternately with his forelegs I and II (in the assumed mated pairing). Periods of activity alternated rhythmically with periods of quiescence. These distant courtship movements were performed also in the intervals beween two copulatory sequences. During the direct contact phase of courtship the male palpated the female with his forelegs and palps, and vice versa. Precopulatory courtship lasted 4 and 12 min. The male approached the female for copulation. Copulatory posture as typical of other *Theridion* species.

Sperm induction: Spinning of the sperm web with induction took on average 1.9 min (range = 1.7–2.2, n = 11), 0.4 min of which was used for construction of the sperm web. The sperm droplet was absorbed within 1.5 min and by 24 dipping movements on average (range = 17–27, n = 10).

Entire copulation duration occupied 128 and 166 min, total number of insertions 10 and 11, total insertion time 2.4 and 5.5 min (respectively).

Copulatory pattern (Fig. 41b, c): After each sperm induction a long, regular resting period followed, during which one male remained more or less motionless at about 2 cm distance from the female, the other one also courted. After about 26 min on average (range = 16–37, n = 9) he returned to the female for the next insertions. During a copulatory sequence each palp was inserted only once for 33.3 s on average (range 15.3–49.2, n=10) in one pair, but only 14 s on average in the other pair (range = 6.5–35.8, n = 10). This second pairing perhaps involved a female which might have been already mated. The sequences lasted 2 min on average (range = 1.5–2.7, n = 9). About 3 insertion attempts occurred per sequence (range = 0–6). A mating plug was not present.

Fig. 45: Copulation in *Theridion ochreolum*. Insertion of left palp.

The mating behaviour of *T. mystaceum* is summarised in BRAUN (1964, sub *T. neglectum*), based on observations of G. PETER (1961, thesis at University of Mainz; not seen). Three copulatory sequences were observed, each with two insertions of 30–45 s. Sperm induction lasted 1.0–1.5 min. WIEHLE (1952, sub *T. neglectum*) records only two copulatory sequences and a mean insertion duration of 68 s. Thus, numbers of copulatory sequences and sperm inductions given in the literature are lower than in the present paper.

14 *Theridion ochreolum* LEVY & AMITAI 1982 (Fig. 45–47)

Material: **Cyprus**, Paphos, from house walls, ♂♀, April 1995, leg. KNOFLACH & THALER.

Identification according to LEVY (1998).

Mating behaviour of *T. ochreolum* was observed from 8 pairs. Sperm induction is part of copulation. Four males constructed two sperm webs during copulation, three males also a third sperm web at the end of copulation. One male even performed 4 sperm inductions during copulation and concluded copulation with a fifth sperm uptake. Copulation consisted of three (n = 7) and five (n = 1) copulatory sequences. There is no pseudocopulation. Apparently, insemination starts with the very first insertions. When interrupted after the first copulatory sequence one female built a cocoon within a period of two weeks (contra KNOFLACH 1998). Sperm transfer is also reflected by the long-lasting insertions. A mating plug was not discernible.

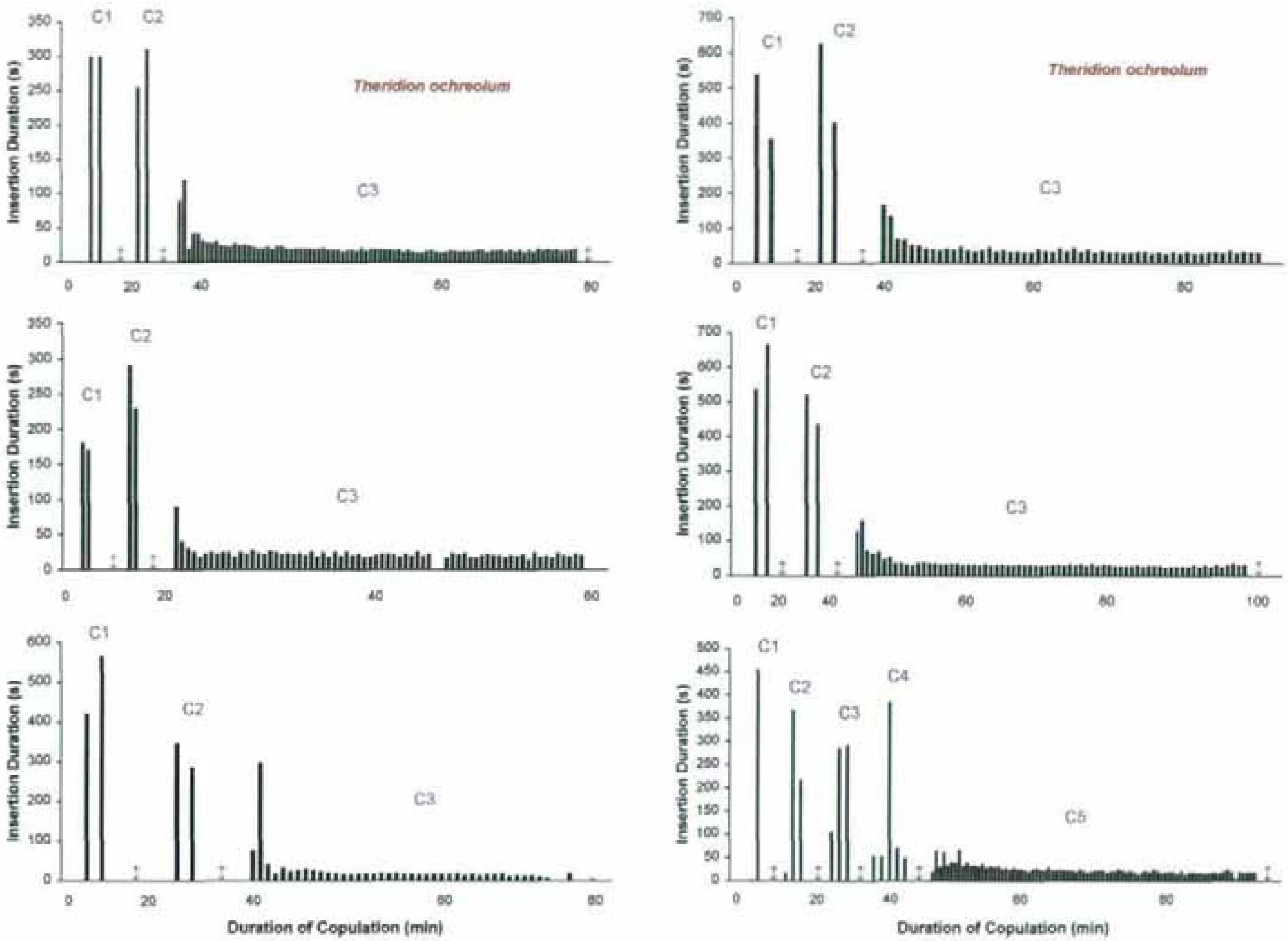


Fig. 46a–f: Copulation and insertion pattern in six pairs of *Theridion ochreolum* from Cyprus. Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates duration of courtship. C1–5 = copulatory sequences.

Courtship behaviour: During distant courtship the male regularly and intensively pulsated his abdomen and jerked. Some males also oscillated their body. These movements were sometimes also performed after sperm induction. Direct contact involved mutual palpating with male and female forelegs and palps. Usually the female was active only in this phase of courtship. Precopulatory courtship lasted 6 min on average (range = 1–30, n = 6). The male approached the female for copulation. During insertion the male regularly pulsated his abdomen, presumably displaying copulatory courtship (44 pulsations in a 9 min insertion, 66 in a 10.4 min insertion, but only 2 in short insertions), see also Figure 47. Copulatory posture as typical of other *Theridion* species (Fig. 45), but often without leg contact between the partners.

Sperm induction: Spinning of the sperm web with induction took on average 1.5 min (range = 1.3–1.9, n = 11), 0.5 min of which was used for construction of the sperm web. The sperm droplet was absorbed within 1.1 min and by 17 dipping movements on average (range = 14–24, n = 11).

Entire copulation duration occupied 78.8 min on average (range = 60–101), total number of insertions on average 69 (range = 42–97), total insertion time 54.4 min on average (range = 40.5–76.5).

Copulatory pattern (Fig. 46a–f): During the first two copulatory sequences each palp was inserted only once for about 6 min (mean ± s.e. = 6.2 ± 0.5, range = 2.8–11.1, n = 28) without pause interval. Haematodochae were highly inflated, especially the basal haematodocha. Both insertion duration and haematodochal inflation indicate actual sperm transfer. These sequences lasted 11.6 min on average (range = 6.0–20.5, n = 18). In one pairing even four such sequences were performed, also with more insertions (Fig. 46f) and with a mean insertion duration of 3.0 ± 0.7 min (range = 2–455 s, n = 13). This pairing was not definitely virgin, as the female was collected as adult. In the last copulatory sequence each palp was inserted frequently (63 times on average, range = 42–86, n=8), but for a shorter time (mean 27.4 ± 0.5 s, range = 3–295, n = 503). Accordingly, haematodochal inflation diminished in these insertions. This final sequence was comparatively long, lasting 41.5 min on average (range = 18.5–53.5, n = 8), including some pauses. Insertion attempts occurred at a rather low rate, insertions often succeeded at once. A mating plug was not present, the epigynal atrium appeared to be unplugged.

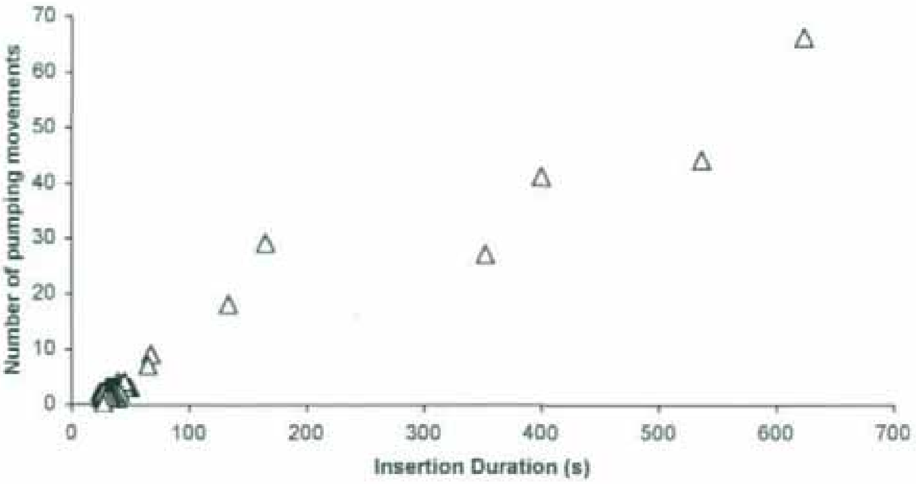


Fig. 47: Relationship between number of pumping movements during insertion and insertion duration in a copulation of *Theridion ochreolum*. Each symbol represents one insertion.

15 *Theridion* sp. (close to *T. melanurum*) (Fig. 48)

Material: Cyprus, Paphos, from house walls, ♂♀, February 1995 (same locality as *T. ochreolum*). **Greece**: Crete, Stalida, from house walls, 4.4.–10.4.1998. Kefallonia, Lassi, 19.9.1999 (♂♀ matured in Nov./Dec. 1999); Aenos, 1050 m, beated from *Abies cephalonica*, ♂♀, 16.5.2002. Rhodes, above Salakos, way to Prof. Ilias, 400 m, ♂♀, 12.4.1996; Attaviros-surroundings, Agios Isidoros, 550 m, 4♀, 10.4.1996; all leg. Knoflach & Thaler.

Taxonomy: This species is close to *T. melanurum*, but differs by genital structures and even much more by copulatory behaviour.

Mating behaviour was never observed completely owing to long duration of resting periods. The most complete observation covered a period from 16.00 h until 01.00 h and from 07.00 h until 14.00 h, when the last sperm web was built (observation was continued until 19.00 h). Also another pair started copulation at midday and were still occupied the next day at 14.00 h. Thus, in two pairs copulation continued for almost two days. The missing intermediate part was extrapolated. A further nine copulations were partially observed. Sperm induction is part of copulation. The males constructed at least 4, 5 and 7 sperm webs (presumably up to 9 or 10) during and at the end of copulation. Copulation included an equal number of copulatory sequences, which were followed by a regular resting period of more than 2 h (including time for sperm uptake). Most frequently, each palp was inserted once per sequence. Again, it is assumed that there is no pseudocopulation, see also e.g. *T. musivivum*. A mating plug was not discernible.

Courtship behaviour: Distant courtship was not very conspicuous. The male often remained motionless and then suddenly approached the female. If the male was more active, he intensively pulsated his abdomen. Some males also oscillated their body, jerked slightly, plucked with forelegs and performed web-spinning and also web-biting behaviour. These distant courtship movements were sometimes present also in the intervals between two copulatory sequences. Direct contact involved mutual palpating with male and female forelegs and palps. Precopulatory courtship lasted 4.6 min on average (range = 1–12, n = 11). The male approached the female for copulation. Copulatory posture as typical of other *Theridion* species.

Sperm induction: Spinning of the sperm web with induction took on average 2.3

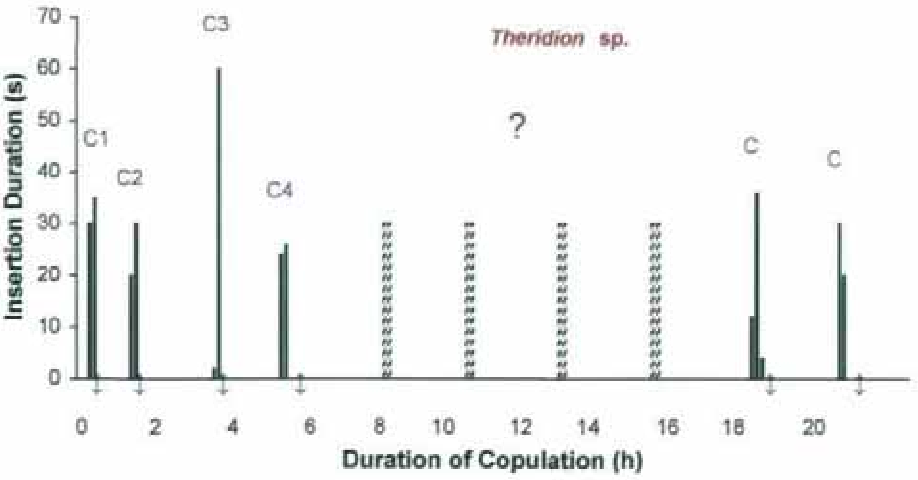


Fig. 48: Incomplete copulation and insertion pattern in *Theridion* sp. of the *T. melanurum*-group from Cyprus. Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates duration of courtship. C1–4 = copulatory sequences, dotted bars assumed.

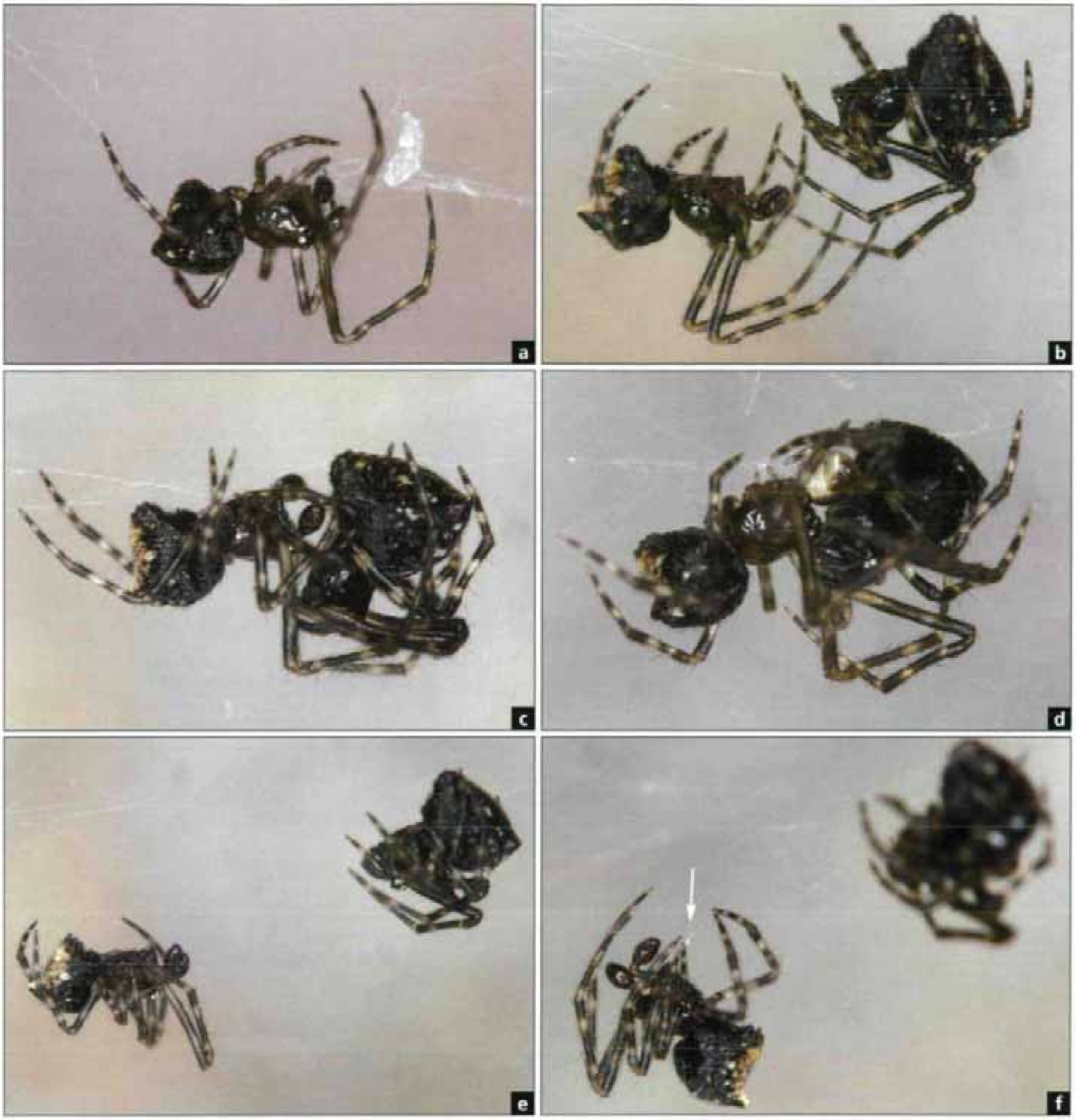


Fig. 49a–f: Copulation in *Theridion conigerum*. **a**: Male occupied with web reduction. **b**: Male approach. **c**: Copulatory posture, forelegs of male in contact with the female's legs. **d**: Insertion. **e, f**: Construction of sperm web close to the female. **e**: Tiny sperm droplet just before absorption (f, arrow).

min (range = 1.7–3.2, n = 12), about 1 min of which was used for construction of the sperm web. The sperm droplet was absorbed within 1.8 min and by 32 dipping movements on average (range = 22–42, n = 12).

Entire copulation duration occupied 21 h in a pairing from Cyprus and at least 26 h in a pairing from Crete, total number of insertions estimated at about 20, total insertion time about 8–10 min (roughly estimated).

Copulatory pattern (Fig. 48; incomplete): After each sperm induction a long, regular resting period followed, during which the male remained more or less motionless at about 1–2 cm distance from the female. After 2.3 h on average (range = 1.2–3.5, n = 17) he returned to the female for the next insertions. During a copulatory sequence each palp often was inserted only once for 54 s on average (mean ± s.e. = 54.4 ± 10.4, range = 2–267, n = 24). Sometimes only one, sometimes three insertions occurred per sequence. Haematodochae were highly inflated and reached an enormous volume. The sequences lasted about 3 min on average (range = 1–7, n = 17). A mating plug was not discernible.

Further *Theridion* species

16 *Theridion conigerum* SIMON 1914 (Fig. 49a–f)

Material: **Austria:** Northern Tyrol, Ötztal, Längenfeld, 1300–1400 m, 23.4.1994, leg. KNOFLACH & THALER.

Mating behaviour of *T. conigerum* was observed from two pairs, but with less accuracy as regards number and duration of insertions. Sperm induction is part of copulation. *T. conigerum* showed a high number of sperm uptakes. Males interrupted copulation 19 and 20 times for construction of sperm web and sperm induction. Copulation consisted of 19 and 21 copulatory sequences respectively, since the first male terminated copulation with a sperm induction while the second one terminated with two insertions. It is unlikely that the first copulatory sequence is a pseudocopulation. Thus, sperm transfer is assumed to start with the first insertion. Apparently there is no mating plug.

Courtship behaviour: Distant courtship movements were not very distinct, neither abdominal vibrations nor pluckings were observed. One male cut off parts of the female web and inserted threads of his own (Fig. 49a). In the second pairing web-reduction was not present. Direct contact was more obvious, involving mutual palpating with male and female forelegs and palps. The male also palpated the female's sternum and abdomen. Palpating usually occurred at the beginning of a copulatory sequence, but also before and after the next insertion or insertion attempt. Precopulatory courtship lasted 1 and 14 min respectively. The male approached the female for copulation (Fig. 49b). Copulatory posture as typical of other *Theridion* species (Fig. 49c, d).

Sperm induction (Fig. 49e, f): Sperm induction took place in close vicinity of the female. Spinning of the sperm web with induction lasted a little less than one minute (roughly estimated) and involved 20–24 dipping movements.

Entire copulation duration 162 and 120 min. Total number of insertions about 30. Total insertion time about 10 min (low estimate).

Copulatory pattern: During each of the c. 20 copulatory sequences one or two insertions proceeded, some of them lasting around 20–30 s (roughly estimated), others perhaps longer. Insertion attempts were also present. The entire copulatory sequences lasted 2.5 min on average (range = 0.5–10.5, n = 41). In the final sequences haematodochal swelling was as large as in the previous sequences.

Other observations: One pair was allowed to copulate once again one day after the first copulation. Remating occurred, again with about 20 copulatory sequences or sperm inductions.

17 *Theridion grancanariense* WUNDERLICH 1987 (Fig. 50, 51)

Material: Spain, Canary Islands, Gran Canaria: Pico de los Nieves, 1600 m, pine wood, ♂♀, 14.2.2001; Barranco del Mulato NE Mogan, ♀, 15.2.2001, 350 m; pass NE Mogan, Montana de Tauro, 900 m, ♂ sad, 15.2.2001; all leg. THALER & KNOFLACH.

Taxonomy: The female of *T. grancanariense* illustrated by WUNDERLICH (1987) does not belong to the holotype male, but apparently represents a female of *T. musivivum*.

Mating behaviour of *T. grancanariense* was observed from three pairs, one observation not in full detail on account of photographic documentation. Sperm induction is part of copulation. When copulating, males left the females 4, 5 and 6 times for construction of sperm web and sperm induction. Thus, copulation was composed of 5, 6 and 7 copulatory sequences respectively. Again, the first copulatory sequence is assumed to be a pseudocopulation. Also here number and duration of insertions indicate that there is no sperm transferred during this sequence. In the course of the last sequence an inconspicuous mating plug is produced. According to the presence of a presumed pseudocopulation and of a final mating plug sequence, as well as the prolonged penultimate copulatory sequence, copulation resembles that of the *T. varians*-group.

Courtship behaviour: During distant courtship, males pulsated their abdomen

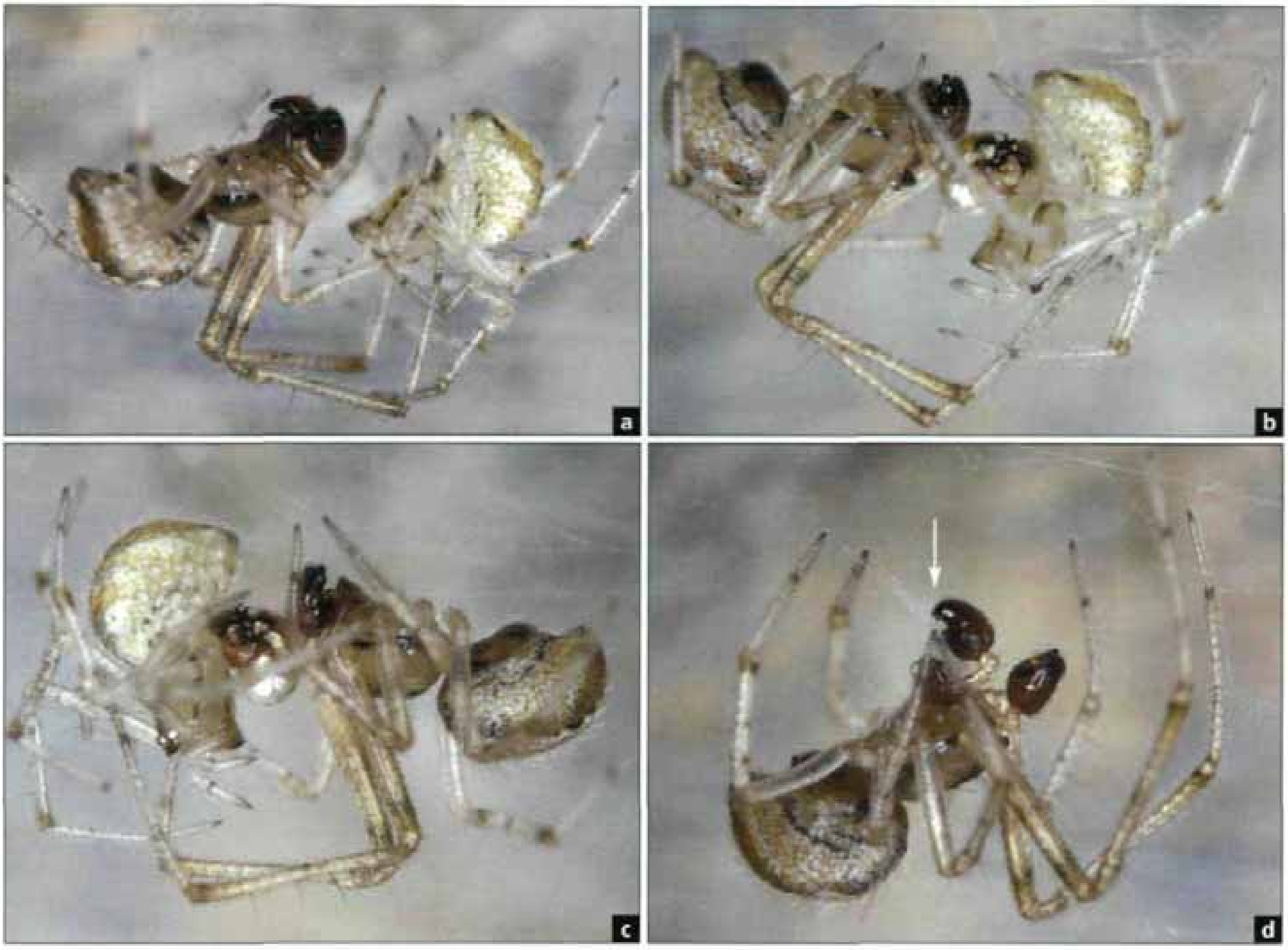


Fig. 50a–d: Copulation in *Theridion grancanariense*. **a**: Copulatory posture, male chewing his right palp preparing insertion. Forelegs of male in contact with female's legs. **b, c**: Insertion of right and left palp. **d**: Sperm induction, sperm droplet just being absorbed (arrow).

and plucked alternately with their forelegs. Plucking was very intensive and frequent in one male (n = c. 20). This male also showed walkabouts and irregular web-spinning behaviour. During direct contact males intensively palpated female legs and body with their forelegs and palps. In this phase the females were active and palpated in response when they were willing to mate. Otherwise they turned away from the males and males then continued with courtship. When approaching the females for copulation, males again intensively palpated the female and thereby induced her to adopt the copulatory posture. Courtship duration was variable, 35, 11 and 16 min. Copulatory posture as typical of other *Theridion* species (Fig. 50a–c).

Sperm induction (Fig. 50d): Spinning of the sperm web with induction took about 2.2 min on average (range = 99–165 s, n = 9), 44 s of which were used for construction of the sperm web. The sperm droplet was absorbed within 83 s on average and by 17 dipping movements on average (range = 9–20).

Entire copulation duration 180, 238 and 222 min. Total number of insertions (-), 140 and 152. Total insertion time 119.6 and 139.6 min (respectively).

Copulatory pattern (Fig. 51a, b): Number of insertions during pseudocopulation 41, 62 and 36, with mean duration of 10.9 and 10.3 min. Pseudocopulation lasted 24, 56 and 25 min. Then several copulatory sequences followed, during which each palp was inserted for about 10 min (mean = 10.6 and 10.9) and with enormous haematodochal swelling (Fig. 50b, c). These insertions apparently reflect actual sperm transfer. Intermediate copulatory sequences lasted 21.5 min on average (range = 18.2–28.0, n = 9), but the penultimate sequence was much longer, 44.5, 27.8 and 33.0 min in the three pairs respectively. One male was attacked by the female during an intermediate sperm induction, so that he had to escape and his palps remained uncharged. Nevertheless, he then returned to the female, courted and continued with the next long insertions as usual. During the last two sequences the number of insertions was increased, while insertion duration decreased. In the very last copulatory sequence haematodochal inflation gradually disappeared. It is assumed that by these short-time applications a mating plug secretion is transferred, apparently as in the *T. varians*-group (Knoflach 1998), but less conspicuous as only the copulatory orifices are sealed and not the entire epigynal groove. Also much less time was invested for formation of this plug, 45–46 min.

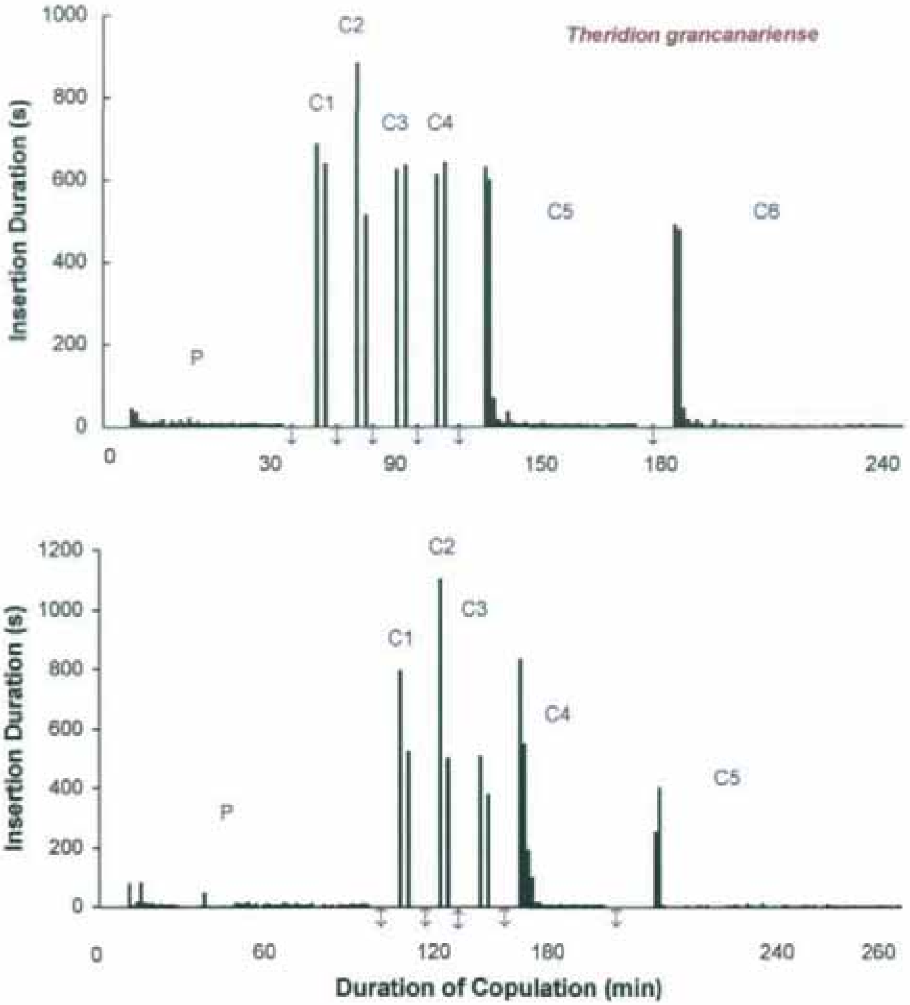


Fig. 51a, b: Copulation and insertion pattern in two pairs of *Theridion grancanariense* from Gran Canaria. Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates duration of courtship. P = pseudocopulation (not proved); C1–6 = copulatory sequences.

18 *Theridion incanescens* Simon 1890 (Fig. 52, 53)

Material: Yemen, Sana'a, ♂♀, July 1998, leg. A. van Harten.

Taxonomy: This species was first described by Simon (1890) from Yemen and since then has not been mentioned any more. The recent material from Yemen corresponds well to the type material (Muséum d'histoire naturelle Paris, AR 2329, examined).

Mating behaviour of *T. incanescens* was observed from one pair only. Sperm induction is part of copulation. Males interrupted copulation 4 times for construction of sperm web and sperm induction. Copulation consisted of 5 sequences. The first copulatory sequence is assumed to be a pseudocopulation. Duration of insertions indicates that no sperm is transferred during this sequence. In the course of the last sequence a conspicuous mating plug is produced. Copulation follows the pattern of the *T. varians*-group.

Courtship behaviour: During distant courtship the male performed some rapid walkabouts with web-spinning, abdominal pulsations and intensive pluckings with forelegs. When approaching the female, direct contact with mutual palpating took place. Precopulatory courtship lasted 3 min. Male plucking and palpating occurred before each copulatory sequence, and especially after the second sperm induction, when the female became aggressive and tried to prey on the male. This intermediate courtship lasted 20 min. Copulatory posture as typical of other *Theridion* species (Fig. 53).

Sperm induction: Spinning of the sperm web with induction took about 1 min (51, 58 and 63 s, n = 3). The sperm droplet was absorbed by 22–26 dipping movements. As in the *T. varians*-group, the last sperm induction took relatively long (95 s) with a larger number of palpal dips (36) and a huge sperm droplet (more than 3 times larger than previous ones). The final sperm induction apparently produces the mating plug secretion, which is transferred from the male genital tract to the palps via the sperm web and then to the female epigynum (see also Knoflach 1998).

Entire copulation duration 96 min. Total number of insertions 85. Total insertion time 21.2 min.

Copulatory pattern (Fig. 52): Number of insertions during pseudocopulation 11, with a mean duration of 3.7 min (range =

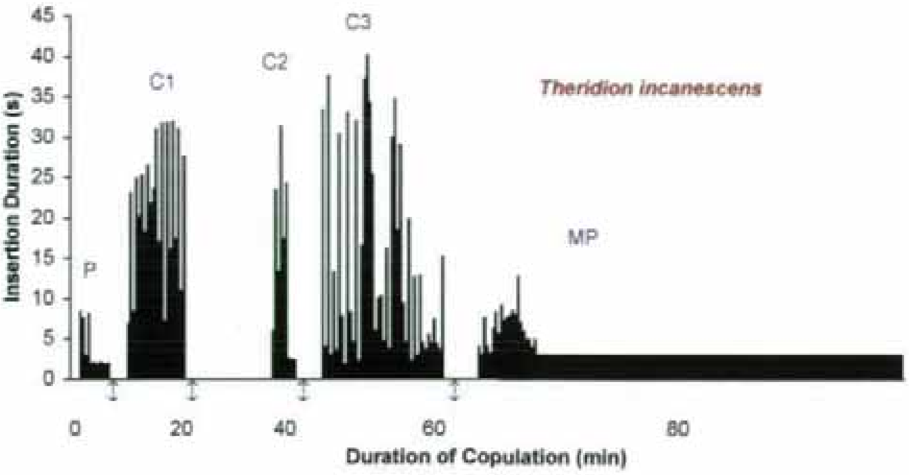


Fig. 52: Copulation and insertion pattern in *Theridion incanescens* from Yemen. Each bar represents an insertion. Sperm induction indicated by double arrows. Gap before pseudocopulation indicates duration of courtship. P = pseudocopulation (not proved); C1–3 = copulatory sequences; MP = mating plug sequence.

1.8–8.4). Pseudocopulation lasted 2 min. Then three intermediate copulatory sequences followed with numerous insertions (21, 9 and 44) and longer insertions (mean = 21.6, range = 6.9–31.8 for C1; mean = 14.7, range = 2.4–31.4 for C2; mean = 14.7, range = 2.2–40.3 for C3). These insertions apparently reflect actual sperm transfer. Intermediate copulatory sequences lasted 10.4, 3.0 and 14.3 (respectively). During the last sequence haematodochal inflation disappeared already after the second insertion. By about 130 palpal applications a secretion is transferred which results in the formation of the mating plug (Fig. 53), apparently as in the *T. varians*-group (KNOFLACH 1998). The mating plug sequence lasted 32 min.

Fig. 53: Copulation in *Theridion incanescens*. Formation of mating plug (arrow).

19 *Theridion ohlerti* (THORELL 1870) (Fig. 54a–f)

Material: **Austria**: Northern Tyrol, Brenner region, Obernberg, ♂♀, 1800–1900 m, 23.4.1994, leg. KNOFLACH & THALER.

Mating behaviour was observed twice from one pair, but one observation not in full detail and with less accuracy as regards duration of sperm induction and insertion. Sperm induction is part of copulation. *T. ohlerti* showed the highest number of sperm inductions observed up to now among comb-footed spiders. Males interrupted copulation 25 times for construction of sperm web and induction. Copulation consisted of 26 sequences. It has not been proved whether the first copulatory sequence is a pseudocopulation. A mating plug was not discernible. Females apparently remate.

Courtship behaviour: Male distant courtship comprised a long period of web-spinning. The male installed numerous threads, approached the female (Fig. 54a, b), palpated her gently, left her again, and continued with web-spinning. The female was relatively active and jerked 30 times before the first insertion, and 2–20 times before each insertion throughout copulation (altogether about 250 times when virgin and at least 150 times when copulated once). During precopulatory courtship once the male neither showed abdominal vibrations nor pluckings, but from the second insertion onwards he vibrated his abdomen intensively before most insertions. Male abdominal vibrations and female jerks then alternated. Palpating usually occurred at the beginning of an insertion. Precopulatory courtship lasted 31 min in one case. The male approached the female for copulation. Not only the copulatory sequence, but each insertion was preceded by an intensive courtship period. Copulatory posture as typical of other *Theridion* species, with leg contact (Fig. 54d–f).

Sperm induction: Spinning of the sperm web with induction was very fast, taking only 20–25 s and involving 14–18 dipping movements. The sperm droplet was rather small.

Entire copulation duration 374 and 200 min. Total number of insertions c. 90 and 74. Total insertion time c. 2 and 3 min,

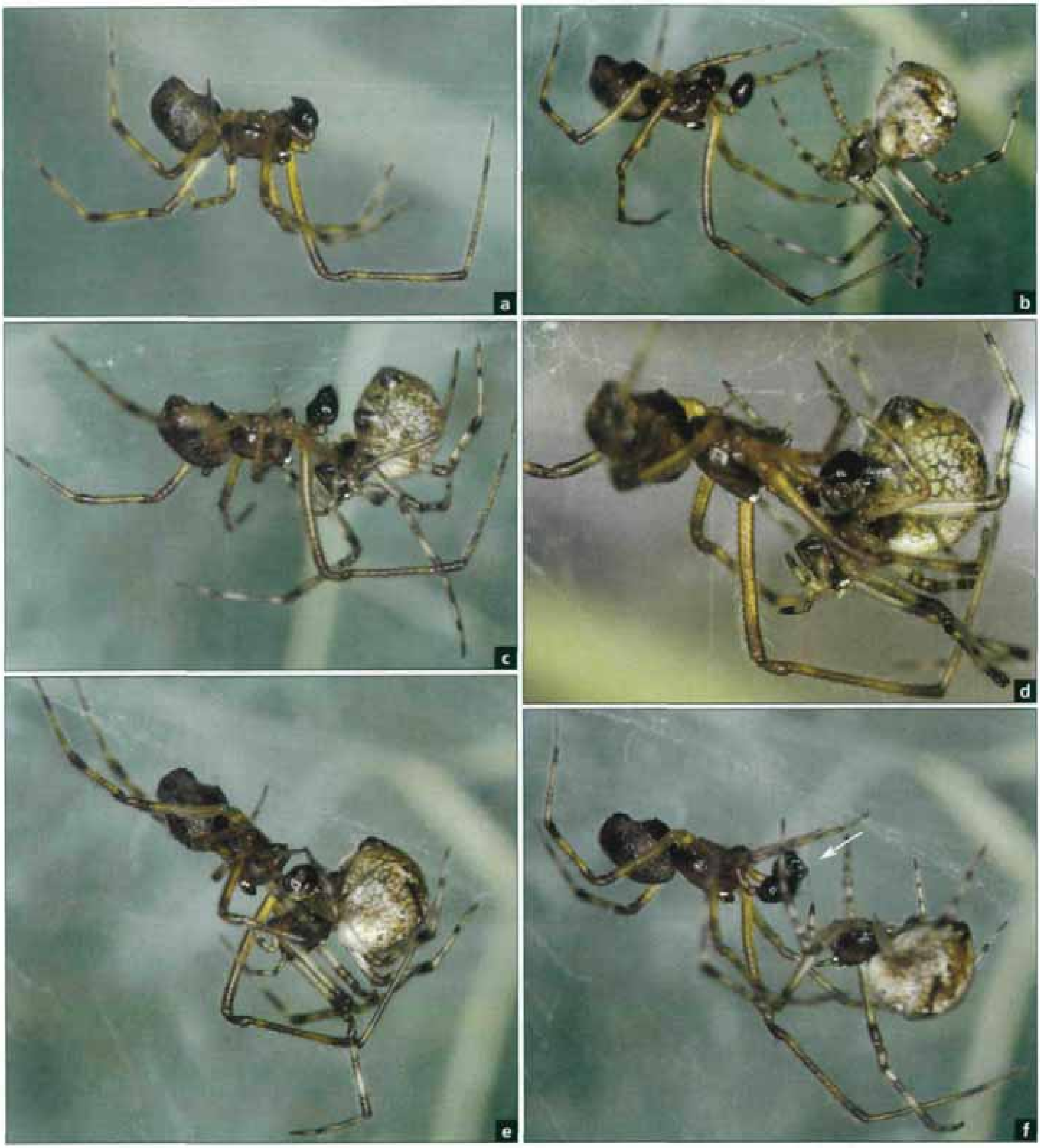


Fig. 54a–f: Copulation in *Theridion ohlerti*. **a, b**: Male approach. Male chewing his left palp preparing insertion (b). **c**: Copulatory posture, forelegs of male in contact with female's legs. **d, e**: Insertion. **f**: Withdrawal of palp, haematodochae collapse after removal and sclerites and embolus are thereby twisted back to their original position (arrow).

very low as compared with entire copulation time. Most of the time is invested in courting activities and sperm induction.

Copulatory pattern: The first copulatory sequence involved 23 insertions and lasted 53 min in one pair. During each of the following 25 copulatory sequences three insertions on average occurred (range = 1–7), all of them lasting only 1–3 s. Insertion attempts were also present. The entire copulatory sequences lasted 2 min on average (range = 0.5–7.0), depending on the insertion number.

Generic placement: *Theridion ohlerti* has been transferred to the genus *Achaearanea* by HEIMER & NENTWIG (1991), as it had

Fig. 55: Copulation in *Theridion pinicola* from Corsica. Insertion of left palp.

been placed by SIMON (1914) and WIEHLE (1937), both sub *T. umbraticum*, in a *Theridion*-subgroup together with species now placed into *Achaearanea*. However, in genital morphology, e.g. two tegular apophyses are present in the male palp, and especially in copulatory behaviour, it clearly resembles *Theridion* sensu lato. Therefore, its placement in *Theridion* is strongly supported here. Nevertheless, the copulatory pattern of *T. ohlerti* differs considerably from that of the *T. varians*-group, which includes the type species of the genus.

20 *Theridion pinicola* SIMON 1873 (Fig. 55, 56)

Material: France, Corsica: Calvi, Forêt de Bonifatu, Bocca di l'Erbaghiolu, 1200 m, ♂♀, 30.4.2001 and 2.5.2001. Haute Asco, 1400–1440 m, ♀ and juv, 12.9.2001; all leg. KNOFLACH & THALER.

Mating behaviour of *T. pinicola* was observed from three pairs. Sperm induction is part of copulation. Males interrupted copulation 6, 7 and 8 times for construction of sperm web and sperm induction. Therefore, copulation consisted of 7, 8 and 9 sequences respectively. The first copulatory sequence is assumed to be a pseudocopulation. Number and duration of insertions indicate that there is no sperm transferred during this sequence. In the course of the last sequence a mating plug is produced. Copulation follows the pattern of the *T. varians*-group.

Courtship behaviour: During distant courtship, if performed at all, one male pulsated his abdomen and plucked with his forelegs. Direct contact involved mutual palpating with male and female legs and palps. Courtship duration was variable, 0.5–50.0 min. The male approached the female for copulation. Copulatory posture as typical of other *Theridion* species (Fig. 55).

Sperm induction: Spinning of the sperm web with induction took 1.2 min on average (range = 59–82 s, n = 21), 16 s of which were used for construction of the sperm web. The sperm droplet was absorbed within 58 s and by only 7 dipping movements on average (range = 5–8). During the last dip the male palp remained on the droplet for a rather long time.

Entire copulation duration 56, 64, 72 min. Total number of insertions 92, 72, 58. Total insertion time 18, 23, 20 min respectively.

Copulatory pattern (Fig. 56a, b): Number of insertions during pseudocopulation 47, 27 and 21, with a mean duration of 1.5, 1.6 and 2.3 min. Pseudocopulation lasted 8.7, c. 5 and 9.3 min respectively. Then several copulatory sequences followed during which each palp is inserted for a longer time (mean = 35.2, 55.6 and 49.4 respectively). These in-

Fig. 56a, b: Copulation and insertion pattern in two pairs of *Theridion pinicola* from Corsica. Each bar represents an insertion. Sperm induction indicated by double arrows. P = pseudocopulation (not proved), C1–8 = copulatory sequences, MP = mating plug sequence.

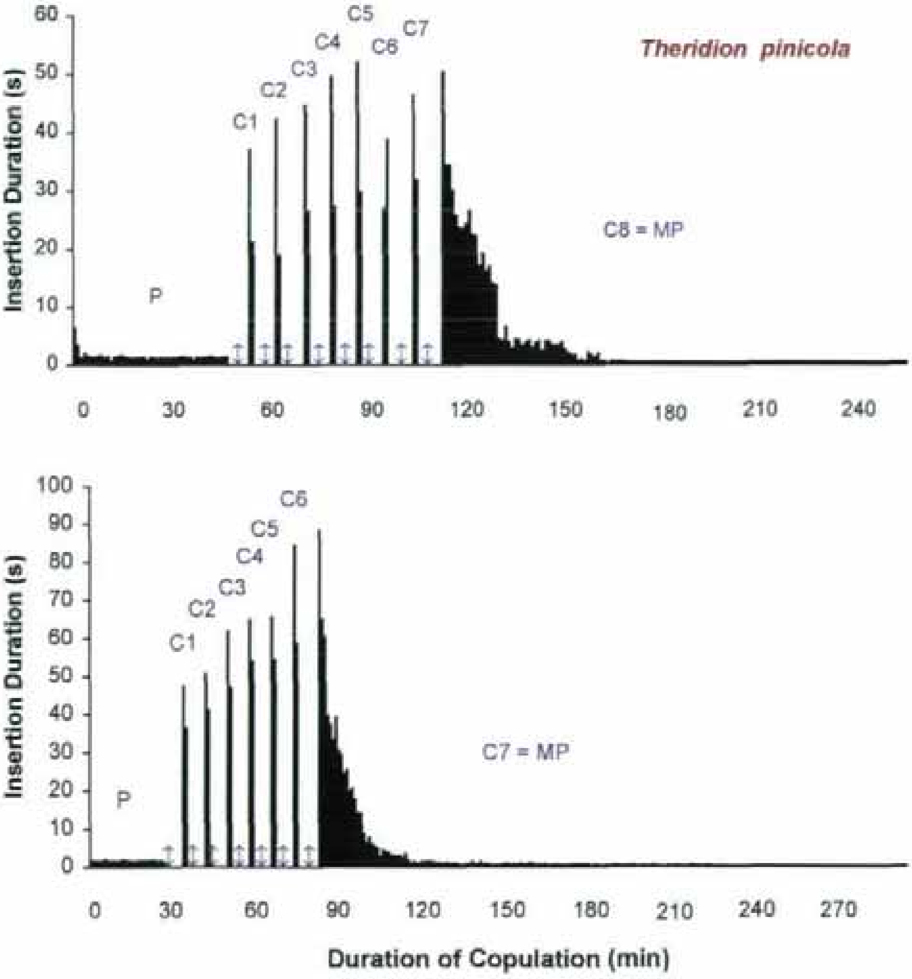


Fig. 57a–d: Copulation in *Theridion impressum*. **a**: Male approach with contracted forelegs. **b, c**: Insertion of right and left palp. Forelegs of male contracted and not in contact with female's legs. **c**: Haematodochae of right palp still expanded, although opposite palp already inserted. **d**: Sperm induction, sperm droplet just before absorption (arrow).

sertions apparently reflect actual sperm transfer. Such intermediate copulatory sequences lasted 1.8 min on average (range = 1.2–2.7, n = 18). During the last sequence of insertions haematodochal inflation gradually disappeared. By numerous short-time applications a secretion was transferred which resulted in the formation of a mating plug, apparently as in the *T. varians*-group (KNOFLACH 1998). The mating plug sequence lasted 36.8, 41.0 and 25.3 min.

21, 22 *Theridion sisyphium*-group

21 *Theridion impressum* L. KOCH 1881 (Fig. 57, 58)

Material: **Italy**, Sardinia E, Baunei-Dorgali, Urzulei-surroundings, 600 m, ♂♀, 5.6.2003, leg. KNOFLACH & THALER.

Mating behaviour of *T. impressum* was observed from three pairs, but one observation not in full detail, on account of photographic documentation. Sperm induction is part of copulation. The male constructed 3, 4 and 6 sperm webs during copulation. Copulation included 4 and 5 copulatory sequences, which were followed by a regular resting period of 9 min (including time for sperm uptake). In most sequences each palp was inserted once. It is assumed that there is no pseudocopulation. A mating plug was not discernible.

Courtship behaviour: Similar to *T. sisyphium*. Male distant courtship consisted of abdominal vibrations and cautious palpating with first legs. In response, the female jerked and striked her forelegs towards the male. He then gradually approached her with forward-extended palps and started direct contact. As in *T. sisyphium* and in contrast to other *Theridion* species, the male drummed his palps against the female's genital region and sternum. All these male and

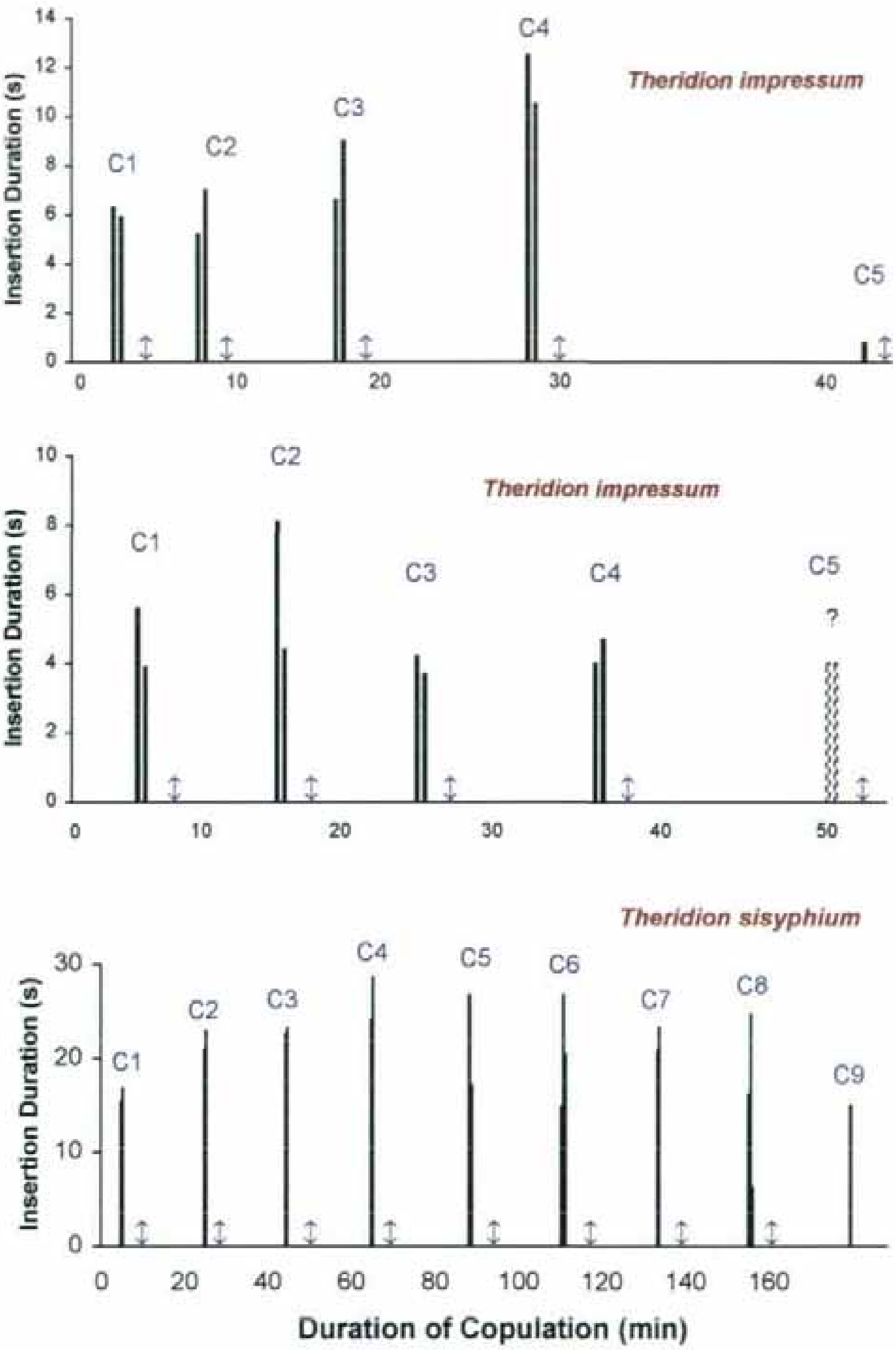


Fig. 58a–c: Copulation and insertion pattern in two pairs of *Theridion impressum* from Sardinia (a, b) and in *Theridion sisyphium* from Northern Tyrol (c). Each bar represents an insertion. Sperm induction indicated by double arrows. C1–9 = copulatory sequences.

female movements were repeated before each copulatory sequence. After sperm induction the male sometimes oscillated his body. Precopulatory courtship lasted 2.5–4.0 min. Copulatory posture as in other *Theridion* species (Fig. 57a–c), but the male's legs remained half contracted during insertion and did not touch the female's legs (Fig. 57a–c).

Sperm induction (Fig. 57d): Spinning of the sperm web with induction took a relatively long time, about 1.8 min on average (range = 1.2–2.2, n = 7), 0.5 min of which was used for construction of the sperm web. The sperm droplet was absorbed within 1.3 min and by 11 dipping movements on average (range = 4–16, n = 7).

The entire copulation duration occupied 25, 41 and 66 min, total number of insertions 7–10, total insertion time about 1 min only.

Copulatory pattern (Fig. 58a, b): The regular pause interval between two copulatory sequences was shorter than in *T. sisyphium*, lasting about 9 min on average (range = 4.8–11.3). As in *T. sisyphium* usually two insertions took place per sequence, sometimes only one. Insertions were shorter than in *T. sisyphium*, mean duration only 6 s (range = 1–12, n = 19). After insertions the partners remained motionless for about half a minute. Then the male moved away for sperm uptake. The sequences lasted 1.4 min on average (range = 0.5–2.2, n = 8). A mating plug was not discernible.

Copulatory behaviour of *T. impressum* has been described already by Braun (1963). Unlike in the present pairings, Braun (1963) recorded 1–2 copulatory sequences and 1 sperm induction only. Furthermore, the resting period between two sequences took about 34 min in one pair (n = 1, Braun 1963). Only insertion duration fully agrees with the present observations. The females of Braun (1963) were collected as adult specimens. Therefore, it is uncertain whether these females were virgin. Copulations of virgin or previously mated females may differ considerably.

22 *Theridion sisyphium* (Clerck 1757)
(Fig. 58, 59)

Material: Austria, N-Tyrol, Innsbruck, Kranebitten, ♂♀, 13.5.1995, leg. Knoflach & Thaler.

Mating behaviour of *T. sisyphium* was observed from two pairs, but only once completely. Contact courtship involved conspicuous male drumming. Sperm induction is part of copulation. The male constructed 8 sperm webs during copulation. Copulation included 9 copulatory sequences, which were followed by a regular resting period of 20 min (including time for sperm uptake). In most sequences each palp was inserted once. It is assumed that there is no pseudocopulation, see also e.g. *T. musivivum*. A mating plug was not observed.

Courtship behaviour: During distant courtship the male vibrated his abdomen and carefully palpated with his first legs towards the female and again retracted his legs. He then cautiously approached the female with half contracted forelegs, palps extended forwards, and started direct contact. In contrast to other *Theridion* species, the male intensively and alternately drummed his palps against the female's epigynum, sternum and mouthparts, while the female remained more or less motionless. Drumming was performed before most insertions for 27 s on average (range = 2–100, n = 17), with about 28 contacts on average (range = 3–100, n = 20). Only once no drummings occurred. After sperm induction the male sometimes oscillated his body and then became motionless again. Distant courtship was performed shortly before each copulatory sequence. Precopulatory courtship lasted 3 min. Copulatory posture as in other *Theridion* species (Fig. 59). The male's legs remained half contracted during insertion and did not touch the female's legs. As the copulatory sequence advanced the female changed her inclined posture to a more horizontal one.

Sperm induction: Each construction of a sperm web was preceded by 'irregular' web-spinning. Actual spinning of the sperm web with induction took a relatively long time, about 2.8 min on average (range = 2.0–3.9, n = 10), 1.2 min of which were used for construction of the sperm web. The sperm droplet was absorbed within 1.5 min and by only 8 dipping movements on average (range = 1–12, n = 10). Once the male dipped only one palp into the droplet for a long time. Sometimes he continued his dipping movements without touching the sperm web any more.

The entire copulation duration occupied 189 min, total number of insertions 17, total insertion time 6.5 min.

Fig. 59: Copulation in *Theridion sisyphium*, male approaching for insertion.

Copulatory pattern (Fig. 58c): After each sperm induction a long, regular resting period followed, during which the male remained more or less motionless and courted only shortly before the next sequence. After about 20 min on average (range = 19–22, n = 8) he returned to the female for the next insertions. During a copulatory sequence each palp was inserted only once for 20.6 s on average (range 7.2–28.5, n=19). The sequences lasted 2 min on average (range = 1.3–2.3, n = 8). A mating plug was not obvious.

Copulatory behaviour of *T. sisyphium* has been described previously by LOCKET (1926) and BRAUN (1963). The present observation corresponds well with regard to overall copulatory pattern, number of copulatory sequences, sperm inductions and insertions. BRAUN (1963) recorded 4–7 copulatory sequences, LOCKET (1926) at least 6, each with two insertions. Also the resting period between two sequences lasted 19 min on average in one pair (BRAUN 1963). The present virgin female remained rather passive, while the females described in the literature participated much more actively in courtship. A pre-stage of a mating thread, as reported by BRAUN, was not observed in the present pairing. The male performed only some walkabouts and irregular web-spinning. Insertions lasted about twice as long as those documented in LOCKET (1926) and BRAUN (1963).

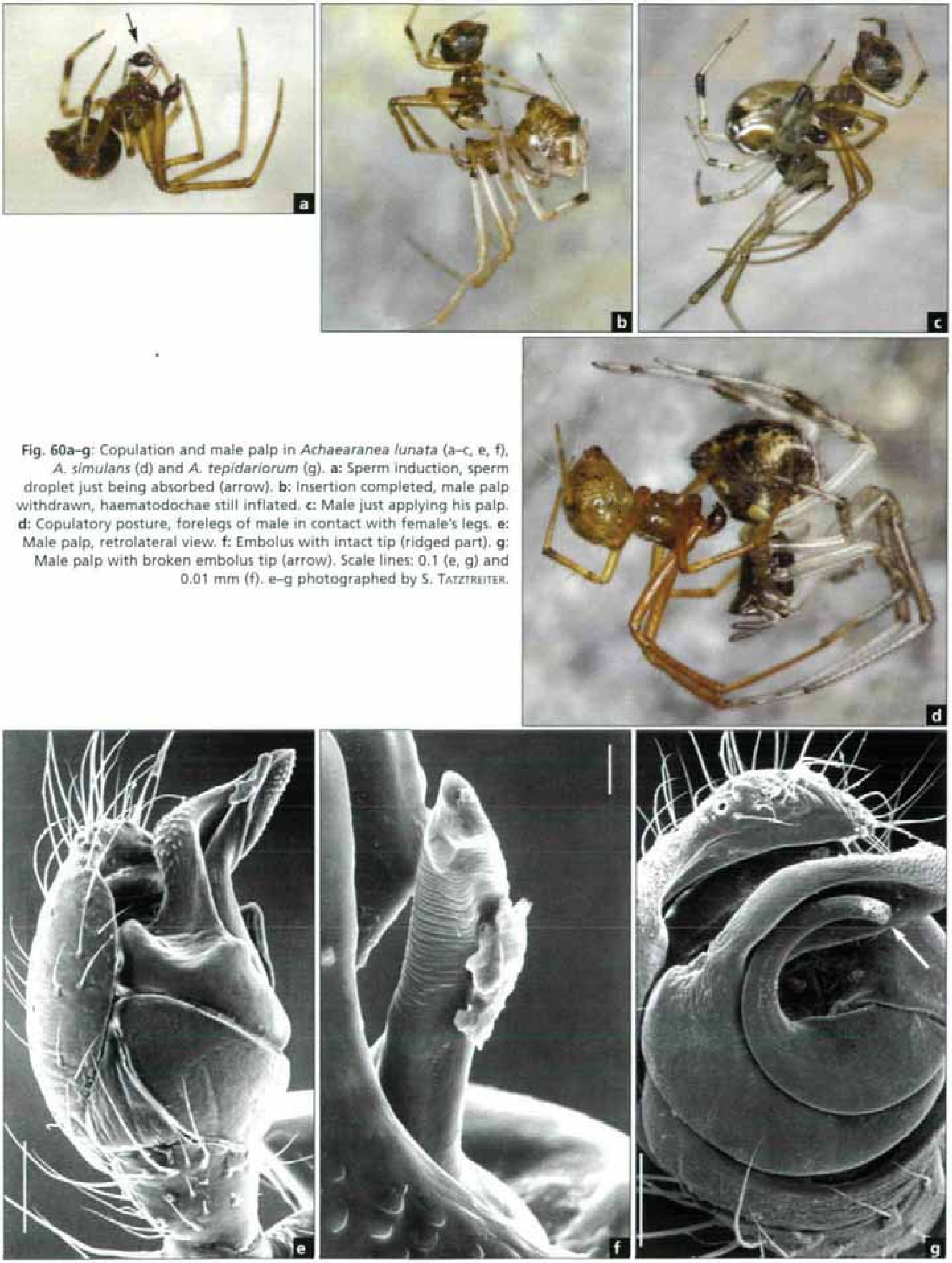


Fig. 60a–g: Copulation and male palp in *Achaearanea lunata* (a–c, e, f), *A. simulans* (d) and *A. tepidariorum* (g). **a:** Sperm induction, sperm droplet just being absorbed (arrow). **b:** Insertion completed, male palp withdrawn, haematodochae still inflated. **c:** Male just applying his palp. **d:** Copulatory posture, forelegs of male in contact with female's legs. **e:** Male palp, retrolateral view. **f:** Embolus with intact tip (ridged part). **g:** Male palp with broken embolus tip (arrow). Scale lines: 0.1 (e, g) and 0.01 mm (f). e–g photographed by S. TATZTREITER.

Steatoda-type

23–25 *Achaearanea*

Representatives of the genus *Achaearanea* perform the shortest insertions among Theridiidae, lasting only 1–5 s. Courtship proceeds without construction of a mating web. The following behavioural elements support its placement among the *Steatoda*-type: Sperm induction takes place independently of copulation and is a long process; number of insertions is low. In the field 2–3 males can be found on the periphery of a female web. Sometimes also heterospecific males were among them.

23 *Achaearanea lunata* (CLERCK 1757) (Fig. 60a–f)

Material: Austria, Innsbruck, Kranebitten, ♂♀, 6.6.1994, leg. KNOFLACH.

Mating behaviour was observed from two pairs. No mating threads were constructed. Copulation involved 4–6 insertions of a few seconds duration only. Apparently there is no mating plug.

Courtship behaviour: During distant courtship, the male pulsated his abdomen and plucked synchronously with all legs. Precopulatory courtship lasted 1.0–1.5 min, intermediate courtship before the following insertion 0.5–6.5 min (mean = 2.4, n = 7). Copulatory posture as typical of other theridiid species (Fig. 60b, c).

Sperm induction (Fig. 60a): Once, sperm induction took place 50 min after copulation. The entire procedure with construction of the sperm web and induction lasted about 10 min. During palpal dippings drop contact was maintained for a long time.

Entire copulation duration occupied 10 and 16 min. Total number of insertions 4 and 6. Total insertion time only 5–8 s. The pair quickly separated after insertion. A few insertion attempts were observed.

GERHARDT (1923) observed one copulation of A. *lunata* (sub *Theridium formosum*) with a single insertion of a few seconds duration. Afterwards the male was sucked out by the female.

24 *Achaearanea simulans* (THORELL 1875) (Fig. 60d)

Material: Austria, Innsbruck, Kranebitten, ♂♀, 6.6. 1994 and 16.6.1994, leg. KNOFLACH.

Mating behaviour was observed from five pairs. Courtship and copulation was similar to that in A. *lunata* and A. *tepidariorum*. Copulation involved 1–4 insertions of a few seconds duration only. Precopulatory courtship lasted 0.5–15 min. Insertions often followed in succession. Copulatory posture as typical of other theridiid species (Fig. 60d). Sperm induction took place independently of copulation and was not observed. Entire copulation duration occupied only 1–2 min, total number of insertions mostly 2, once only 1 and once 4; total insertion time a few seconds only.

25 *Achaearanea tepidariorum* (C. L. KOCH 1841) (Fig. 60g)

Material: Austria, Innsbruck W, ♂♀, May and June 1994, leg. KNOFLACH. Innsbruck, from inside house, ♂♀, Jan. 2002, leg. VOGEL.

Mating behaviour was observed from three pairs. No mating threads were constructed. Copulation involves two insertions of a few seconds duration only. Apparently there is no mating plug.

Courtship behaviour: During distant courtship, the male pulsated his abdomen, jerked intensively, and plucked with forelegs. Also web-spinning activities were observed, but not in the ritualised form of a mating web. During his walkabouts through the female web, the male attached threads and thereby courted. The female was remarkably active, often changed her position within the web, palpated, and one female also plucked with forelegs. Shortly before insertion the male often performed strong body oscillations by synchronous contraction and relaxation of all legs 1–40 times, so that the female was passively moved. Then both partners approach for copulation. Insertion was succeeded by another courtship period, preparing the next insertion. Precopulatory courtship lasted 6–25 min, intermediate courtship before the following insertion 1–72 min. Copulatory posture as typical of other theridiid species.

Sperm induction: Once, sperm induction took place 35 min after copulation. Spinning of the sperm web with induction lasted 16 min, 8 min of which were used for construction of the sperm web. The male absorbed the sperm droplet within 8 min and by 20 dipping movements.

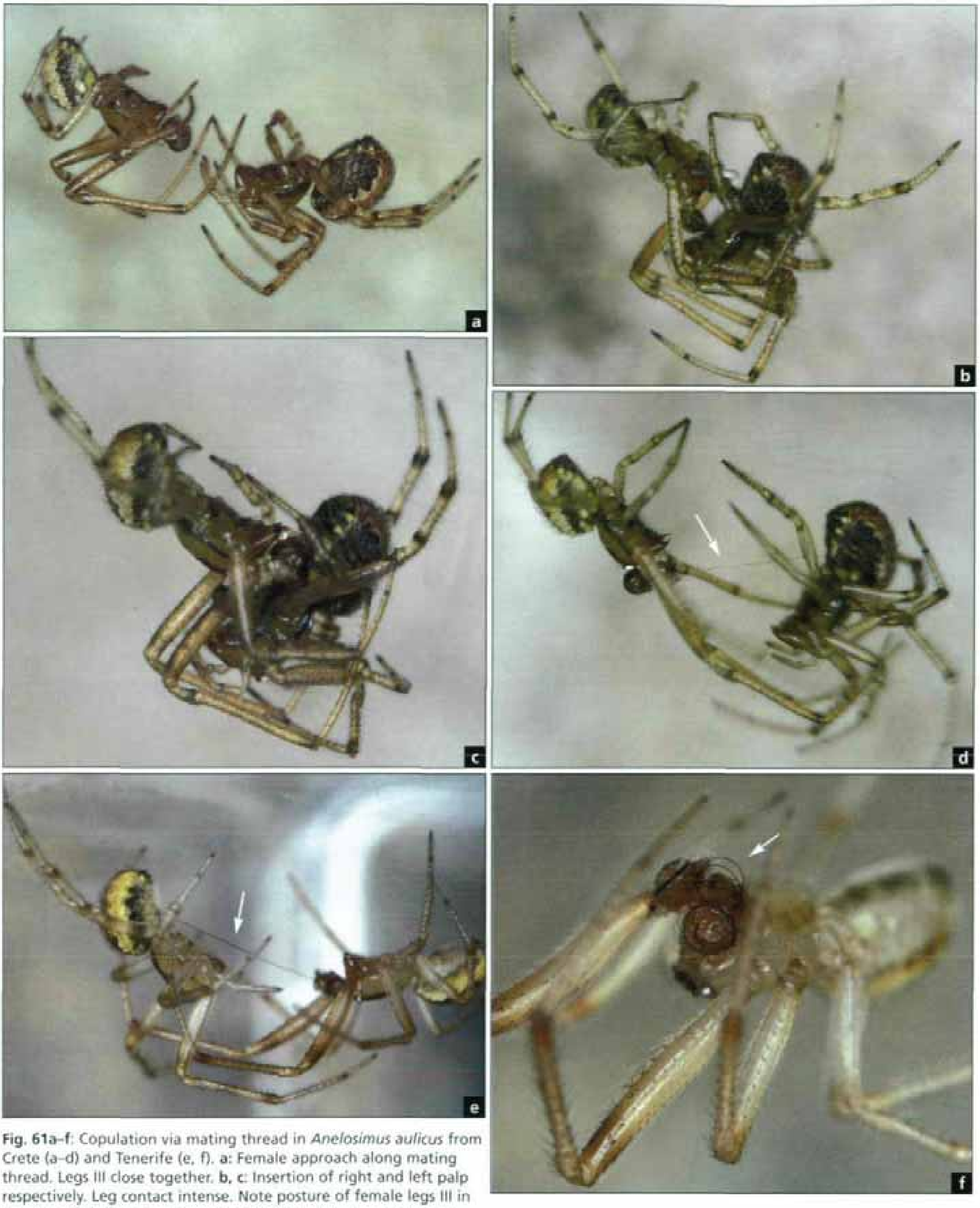


Fig. 61a–f: Copulation via mating thread in *Anelosimus aulicus* from Crete (a–d) and Tenerife (e, f). **a**: Female approach along mating thread. Legs III close together. **b, c**: Insertion of right and left palp respectively. Leg contact intense. Note posture of female legs III in (b). **d, e**: Withdrawal of palp, thread-like embolus torn out from female duct (arrows). **f**: Restoration of disarranged embolus (arrow).

Entire copulation duration occupied 3, 8 and 80 min, depending on the duration of intermediate courtship. Total number of insertions 2. Total insertion time 2–5 s. The pair quickly separated after insertion.

Overall course of copulation as described by Gerhardt (1923, sub *Theridium tepidariorum*) and Bonnet (1935). The unusually active role of the female during courtship was outlined by Bonnet. Courtship for virgin females was shorter than for mated females (Bonnet 1935). Gerhardt (1923) observed ipsilateral insertion and numerous unsuccessful insertions. Insertions lasted up to 5 s (Gerhardt 1923) and 5–7 s (Bonnet 1935). Sometimes also the same palp was inserted twice. Rematings took place, but females guarding an egg-sac refused copulation (Bonnet 1935). Sperm induction was observed once about 40 min after copulation (Gerhardt 1923). The whole procedure lasted 15 min, of which 7 min were used for construction of sperm web, 8 min for actual induction. During insertion the tip of the embolus breaks off (Abalos & Baez 1963; Locket & Luczak 1974), which is known especially for *Latrodectus*. However, the small embolus piece found left in the female receptacle (Abalos & Baez 1963) appears to be an ineffective mating plug. The breaking point is at the ridged distal part (Fig. 60g versus 60f; intact embolus shown here for A. *lunata* for comparison).

26 *Anelosimus aulicus* (C. L. Koch 1838) (Fig. 61, 62)

Material: **Cyprus**, Akamas peninsula, Fontana Amorosa, 16.2.1995, ♂♀ reared from an egg-sac, leg. Knoflach & Thaler. **Greece**, W-Crete, Georgioupolis-surroundings, ♂♀, 31.3.–1.4.1999. Kefallonia, Karavados-surroundings, ♂♀, 12.–13.5.2002, leg. Knoflach & Thaler. Yemen, Sana'a Juni 1998, leg. van Harten.

Mating behaviour was observed from six pairs, two of them not in full detail on account of photographic documentation. A. *aulicus* clearly follows the *Steatoda*-type of copulation. Sperm induction takes place independently of copulation. Copulation proceeds via mating thread and female approach and involves 4–10 insertions. A. *aulicus* has a remarkably long embolus, which is three times longer than the male's body and which is fully inserted into the corresponding female copulatory duct. During withdrawal of the palp the thread-like embolus is torn out from the female's duct and thereby stretched (Fig. 61d, e, 62) and disarranged. After withdrawal follow c. 5 min of restoration, during which the male brings its embolus into the original spiral resting condition. Apparently no mating plug is produced.

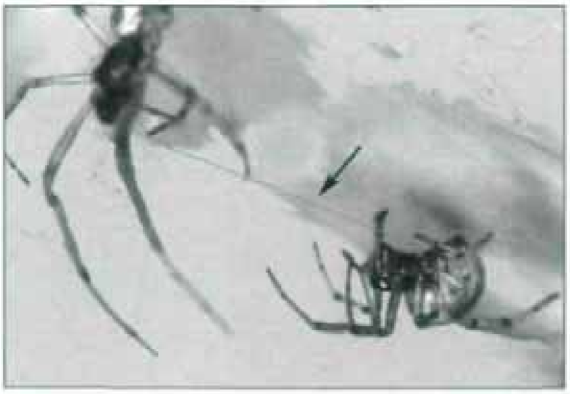


Fig. 62: Copulation in *Anelosimus aulicus* from Yemen. Withdrawal of thread-like embolus (arrow), which is three times longer than the male's body. Ultimate disengagement accomplished by female turning around.

Courtship behaviour: When in contact with the female web, the male pulsated his abdomen and and then started to remove a part of the female web for construction of the mating thread. Sometimes he briefly approached the female before this and palpated her. During his walkabouts the male regularly pulsated his abdomen and jerked. Before installing the mating thread the male cut away threads of the female, thereby forming a hole in the densely spun female web. The mating thread was usually spun only to and from the female, but sometimes was reinforced or even replaced. On the mating thread he intensively vibrated his abdomen and thereafter plucked alternately with legs. Abdominal vibrations were rather slow and low frequent, but intense. They consisted of rubbing movements of the abdomen against the posterior rim of the prosoma. The abdomen was moved up and down, but also swivelled sidewards. Plucking was mainly performed by legs II in a high frequency sequence. Legs I and III were used less frequently and also with low speed. Legs I-III were in contact with the mating thread, with legs II and III being flexed and forming a circle, while legs IV were anchored in the scaffold web. Vibrations and pluckings took place successively. Upon plucking, the female approached him along the mating thread and assumed the copulatory posture just opposite him (Fig. 61a). Then the palp

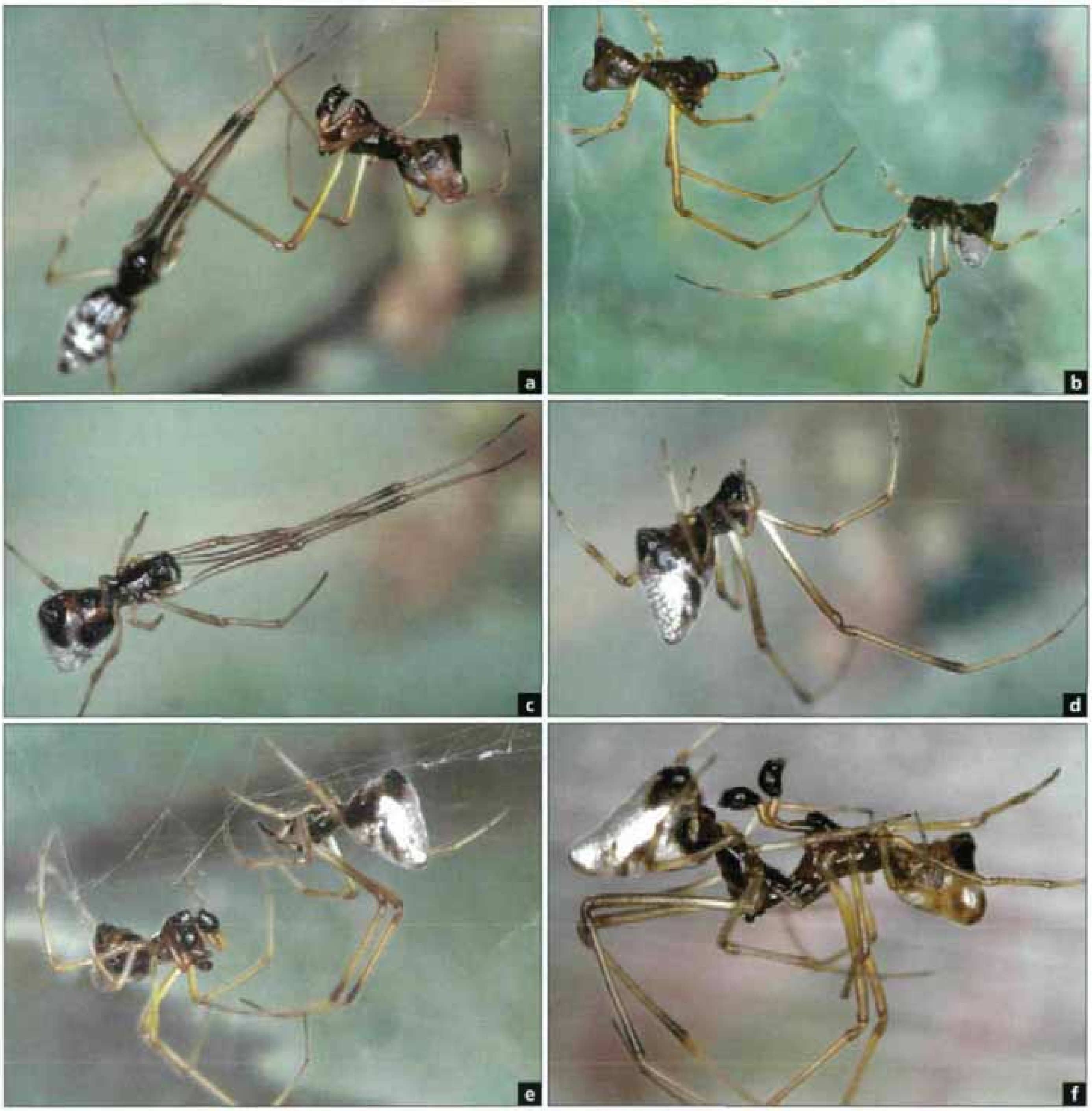


Fig. 63a–f: Courtship and approach in *Argyrodes argyrodes*. **a, c**: Inert posture of female with forelegs stretched and close together. **b, d**: Alert acceptance posture of female with widely opened forelegs. **e**: Male approach. **f**: Copulatory posture, female in contact with male clypeal organ, male shortly before insertion. Note enlarged patella of the male palp. Pairs from Cape Verde Isl. (a, c–e), Kefallonia (b) and Tenerife (f).

was inserted cautiously. During copulation both male and female legs III remained in contact with the mating thread (Fig. 61b, c). The male performed such courtship before each insertion, often using the same mating thread, sometimes also a newly inserted one. Courtship lasted 15 min on average before the first insertion (range = 7–30, n = 5), but only 1.8 min on average before the following insertions (range = 0.3–7.7, n = 18). One female quickly retreated shortly before insertion and thereby avoided copulation several times. Copulatory courtship: During insertion the male intensely vibrated and swivelled his abdomen in a similar way as during precopulatory courtship. This movement accompanied haematodochal inflation and disappeared with haematodochal collapse. Shortly before withdrawal slight abdominal vibrations were again visible.

Sperm induction: Sperm induction is not part of copulation and has never been observed.

Entire copulation duration averaged about 85 min (range = 23–139, n = 4). Total number of insertions 4–8 (mean = 6, n = 4). Total insertion time 9.4 min on average (range = 6.9–11.0, n = 4).

Copulatory pattern: Up to 8 insertions occurred, which lasted 1.6 min on average (range = 0.1–4.0, n = 25), the first two taking longer than the last ones (first: 2.7 min on average, range = 1–4, n = 12 versus last: 0.6 min on average, range = 0.1–2.0, n = 13). During withdrawal of the palp male and female had their chelicerae widely opened (Fig. 61d). When separating the female turned around and moved away. Withdrawal of the palp at first proceeded abruptly, but then the thread-like embolus was torn out cautiously from the female's duct. As a result, the embolus was stretched (Fig. 61d, e, 62) and completely disarranged. In the following c. 5 min long phase of regeneration (range = 1.5–10.0, n = 14) the male restored the embolus to the original spiral condition (Fig. 61f). The palp was continuously rubbed by leg III of the same side, sometimes also by leg II and by the other palp. A mating plug was not discernible.

Other observations: One male had his palp extremely disarranged after insertion and took 50 and 38 min for its restoration (after the first two insertions). As well as the embolar torsion, haematodochae were overinflated and hardly collapsed. In the last insertions the embolus was not inserted into the female duct, but instead twisted around the inflated palp outside the vulva. Nevertheless, palpal grip and haemaetodochal inflation were successful.

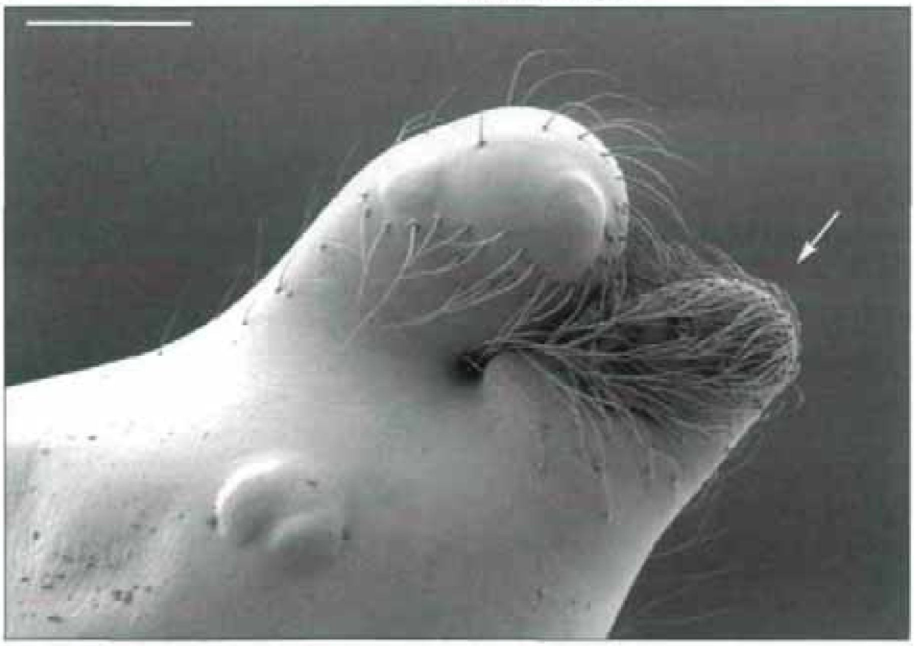
27 *Argyrodes argyrodes* (Walckenaer 1842) (Fig. 63–71)

Material: **Greece**, Kefallonia, Lassi, ♂♀, 19.9.1999, leg. Knoflach & Thaler. **Spain**, Canary Islands, Tenerife, Buenavista, ♂♀, 19.2.2000 and 5.1.2003; Punta del Hidalgo, ♂♀, 7.1.2003, leg. Knoflach & Thaler. **Cape Verde Islands**, Santiago, São Jorge dos Orgãos, 15°03'N 23°37'W, 400 m, ♂♀, 15.12.1999–10.1.2000, leg. A. van Harten. All specimens were collected from webs of *Cyrtophora citricola* (Forskål 1775). *Argyrodes argyrodes* lives as a kleptoparasite in the webs of other spiders, frequently those of *Cyrtophora citricola* (see Kullmann 1959).

Mating behaviour was observed from seven pairs, two of them not in full detail on account of photographic documentation. Sperm induction takes place independently of copulation. Courtship and copulation proceed without construction of a mating thread and with male approach. Copulation involves numerous insertions, which took place intermittently. During copulation the female locks her chelicerae onto the male clypeal organ, where a fluid secretion appears. At the end of copulation a conspicuous mating plug is produced. Interestingly, ipsilateral insertion takes place.

Courtship behaviour: Distant courtship was very intensive. The male vibrated his abdomen, plucked with his forelegs and then oscillated his body. Oscillations became more intensive toward the end of a moving sequence up to a few final maximal amplitudes. The female, usually not facing the male, had her legs close together and stretched out forward (Fig. 63a, c). She was passively moved and oscillated by the male's courting. When she was willing to mate she turned to the male and widely opened her forelegs (Fig. 63b, d). Then direct contact followed with mutual palpating until the female grasped the male's clypeal protuberance with her chelicerae. Thereby, the copulatory posture was achieved (Fig. 63f, 65a–f). When grasping the male's secretory organ she had to incline her body. Precopulatory courtship lasted 0.5–62.0 min (mean = 14.3, n = 6). Once a male also removed parts of the female web and installed threads

Fig. 64: Male clypeal organ of *Argyrodes argyrodes*. Anterior lobe (arrow) with numerous glandular hairs and pores, posterior lobe with two pairs of eyes, clypeal notch interposed. Scale line 0.2 mm. Photo: K. Pfaller.



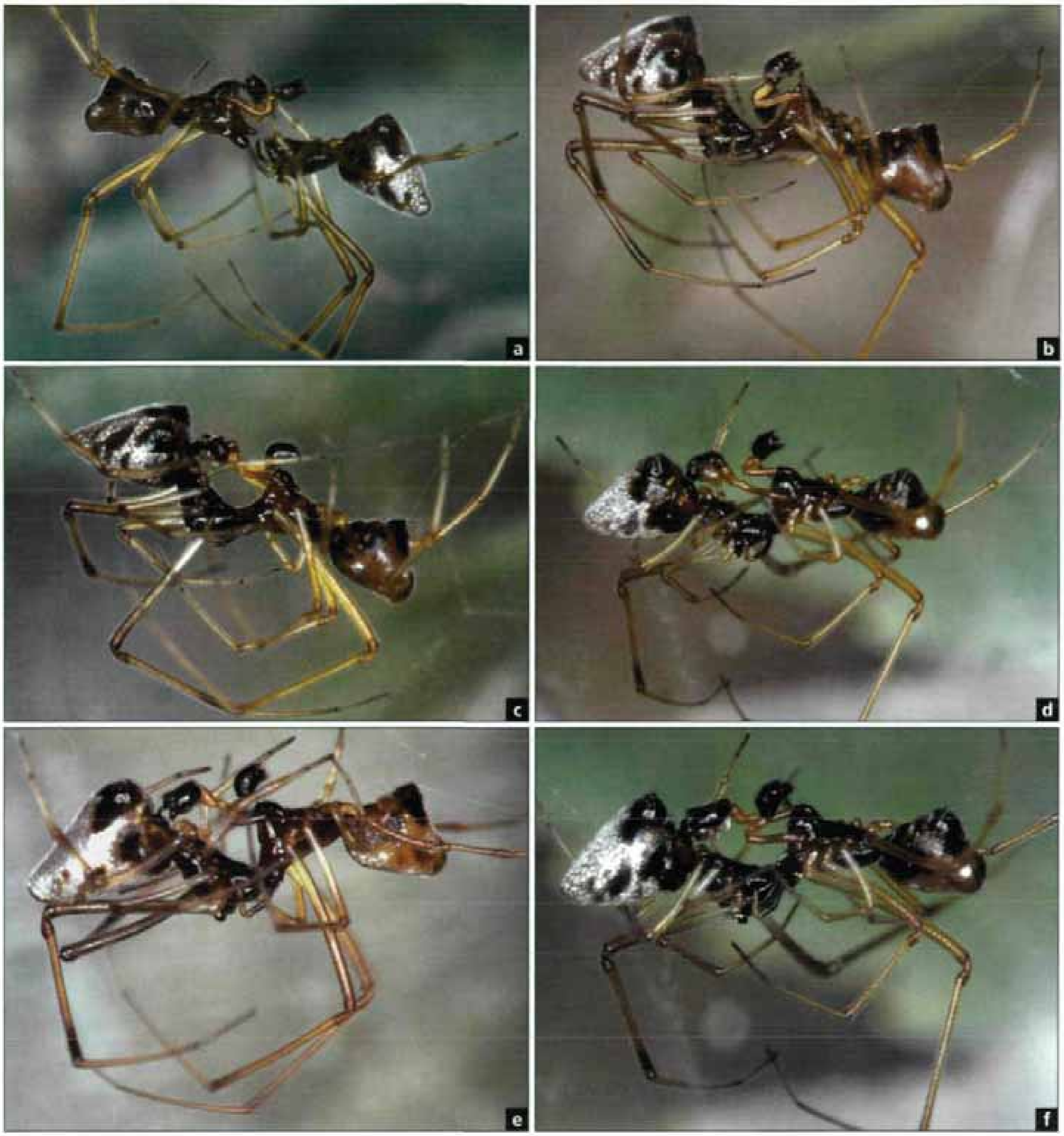


Fig. 65a–f: Copulation in *Argyrodes argyrodes*. **a:** Female shortly before grasping male clypeal organ, with her chelicerae opened; male moving palp forwards for insertion. **b:** Copulatory posture, female in contact with clypeal organ. **c, d:** Insertion of right palp. **e:** Insertion attempt without haematodochal inflation. **f:** Insertion of left palp. Leg contact loose. Pairs from Cape Verde Isl. (a–d, f) and Tenerife (f).

of his own. Male courtship was performed throughout copulation, as copulation was interrupted several times. After separation the female again adopted her resting position with her legs close together. Only after intensive courting did she resume the copulatory posture. The more interruptions took place the more time was invested in courtship.

Sperm induction: Once a male was observed occupied with sperm induction one day after copulation.

Entire copulation duration averaged 176.7 min (range = 60–369, n = 7). Total number of insertions 112 on average (range = 37–198, n = 6). Total insertion time 18.7 min on average (range = 13.2–25.9, n = 5).

Copulatory pattern (Fig. 67a–d): Copulation was frequently interrupted, 36 times on average (range = 5–79, n = 6). The male approached the female several times in order to resume copulation (Fig. 63e). Palps usually were inserted alternately about 112 times, for 11.0 ± 0.5 s on average (mean ± s.e., range = 0.4–97.7, n = 510). Insertion duration increased as copulation advanced. Maxima of insertions generally took place shortly before the mating plug was produced (Fig. 67a–d). During a sequence of insertions the female was continuously in contact with the male's secretory organ (Fig. 65b–f). Secretory fluid was visible in the groove between the two cephalothoracic projections (clypeal organ see Fig. 64), where the female placed her chelicerae and performed vigorous rhythmical sucking movements. Numerous insertion attempts occurred, 137 in a copulation with 37 insertions, but only 57 attempts in a copulation with 198 insertions. In another copulation, number of successful and unsuccessful insertions was equal (at least for 3 h observed). On a few occasions, the male actively inflated his bulbus without contact with the epigynum. Owing to the large number of interruptions and insertion attempts copulations appeared rather agitated. Remarkably, in *A. argyrodes* the male palp was inserted ipsilaterally, the left male palp inserts into the left female copulatory duct and vice versa (Fig. 66). Among Theridiidae ipsilateral insertion was known previously only in *Tidarren*, where it occurs facultatively (KNOFLACH & VAN HARTEN 2000a), and in *Steatoda castanea* (GERHARDT 1926).

Mating plug: At the end of copulation a conspicuous mating plug is produced (Fig. 70, 71). In contrast to hitherto known mating plugs of Theridiidae (KNOFLACH 1998), the plug secretion comes from the male palpal organ. The male alternately stretches out his palps, and lets the basal haematodochae inflate. Such haematodochal swelling of the unlocked palp is unusual. Palpal stretching and haematodochal inflation was performed 8–54 times sequentially (mean = 25, n = 17), until a large secretion droplet appeared on the distal end of the palp (Fig. 68, 69d–i). Then the male approached the female and transferred the secretion by a few palpal applications (5.6 on average, range =

Fig. 66: Copulation in *Argyrodes argyrodes*. Ipsilateral insertion, left male palp is applied to left female copulatory orifice (arrow). Right copulatory orifice unengaged.

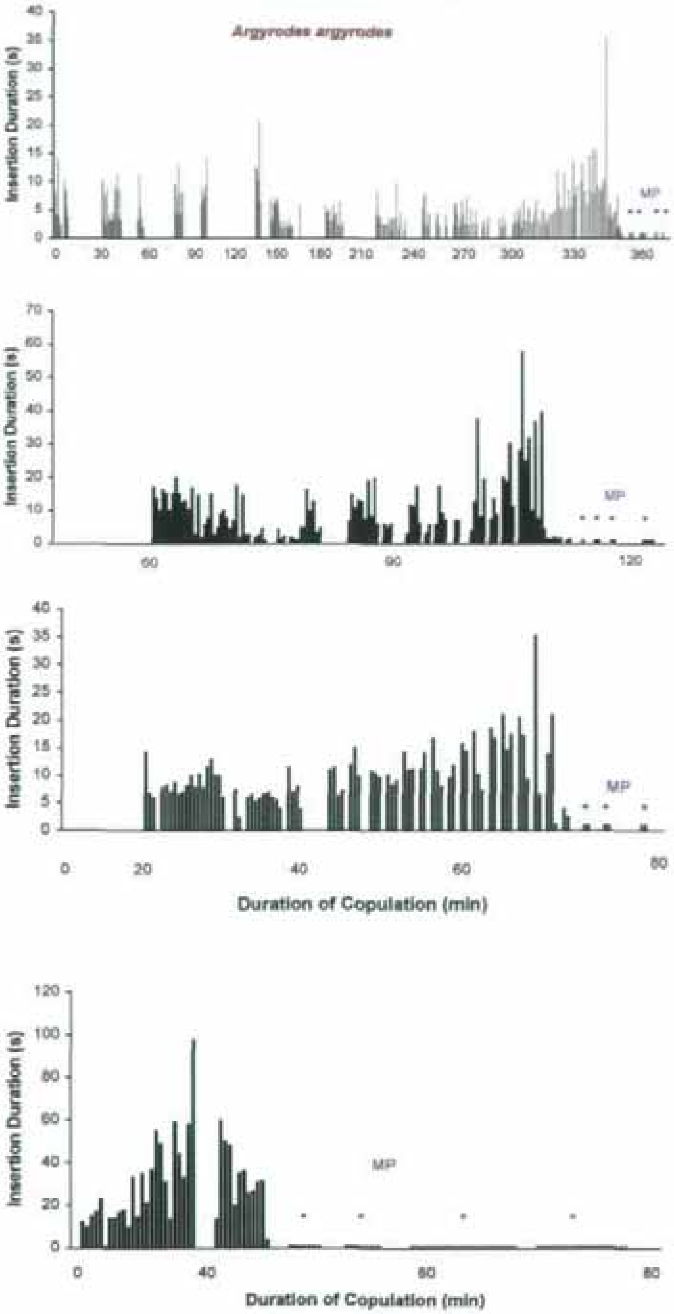


Fig. 67a–d: Copulation and insertion pattern in four pairs of *Argyrodes argyrodes* from Tenerife. Each bar represents an insertion. MP = transfer of mating plug by short palpal applications marked with an asterisk.

Fig. 68a–c: Production of mating plug in *Argyrodes argyrodes*. The plug secretion comes from a gland of the male palp. It is discharged upon the male's stretching and swinging his palps forwards numerous times. **a**: Onset; **b**, **c**: end of palpal swinging. Arrows point to plug secretion. Male from Tenerife (a) and from Cape Verde Isl. (b, c).

1–24, n = 24), without inserting palpal sclerites. Altogether 3–5 such plugging secretions were formed and subsequently transferred. The mating plug secretion is apparently released at the distal end of the palp, where the embolus and conductor are close together (see Fig. 69a–c versus 69d–i). There the droplet is held by the membrane of the conductor and finally transferred. Apparently, the mating plug secretion originates from a gland within the palpal organ as in *Amaurobius* (Amaurobiidae, see SUHM et al. 1996). Discharge of the secretion is assumed to be associated with haematodochal swelling, i.e. haemolymph pressure. This mode of mating plug production has not been observed in any of the other c. 60 theridiid species studied. The secretion finally hardens and becomes a solid, brownish plug. The shape of the plug is irregular (Fig. 71b). Sometimes the secretion mass is deformed by the final palpal contacts.

Multiple mating: Four females, which had copulated once, were allowed to remate. They rejected the courting males at least for the 3–4 h of observation. Usually, the male was separated from its mate after copulation. Only one pair was kept together after copulation and was observed to remate five days after their first copulation. The male was able to dislodge the mating plug, apparently by numerous palpal applications. Then typical copulation proceeded and ended in the formation of another huge mating plug. Thus, the mating plug does not necessarily impede a further copulation.

The mating plug largely protrudes from the female epigynum (Fig. 70b, c). GERHARDT (1928, fig. 17a) obviously observed a plugged female of *A. argyrodes* and misinterpreted the mating plug as an epigynal structure. The epigynum of a virgin female does not protrude (Fig. 63f, 65a, b, 71a). GERHARDT (1928) observed only two short insertions, which apparently represented only an attempt to mate. Also in an *Argyrodes* from the Cape Verde Islands described as a new species, *A. scapulatus* SCHMIDT, GEISTHARDT & PIEPHO 1994, the specific epithet refers to

Fig. 69a–i: Male palp of *Argyrodes argyrodes*, ventral view. **a–c**: Virgin male without glandular secretion on embolus-conductor complex. **d–i**: Male fixed at the end of mating plug production. Arrow points to mating plug secretion on membrane of conductor. (a-f) left, (g-i) right palp. C = Conductor; E = Embolus. Scale lines: 0.2 mm (a, b, d, e, g-h), 0.05 mm (c, f, i). Photos: K. PFALLER.

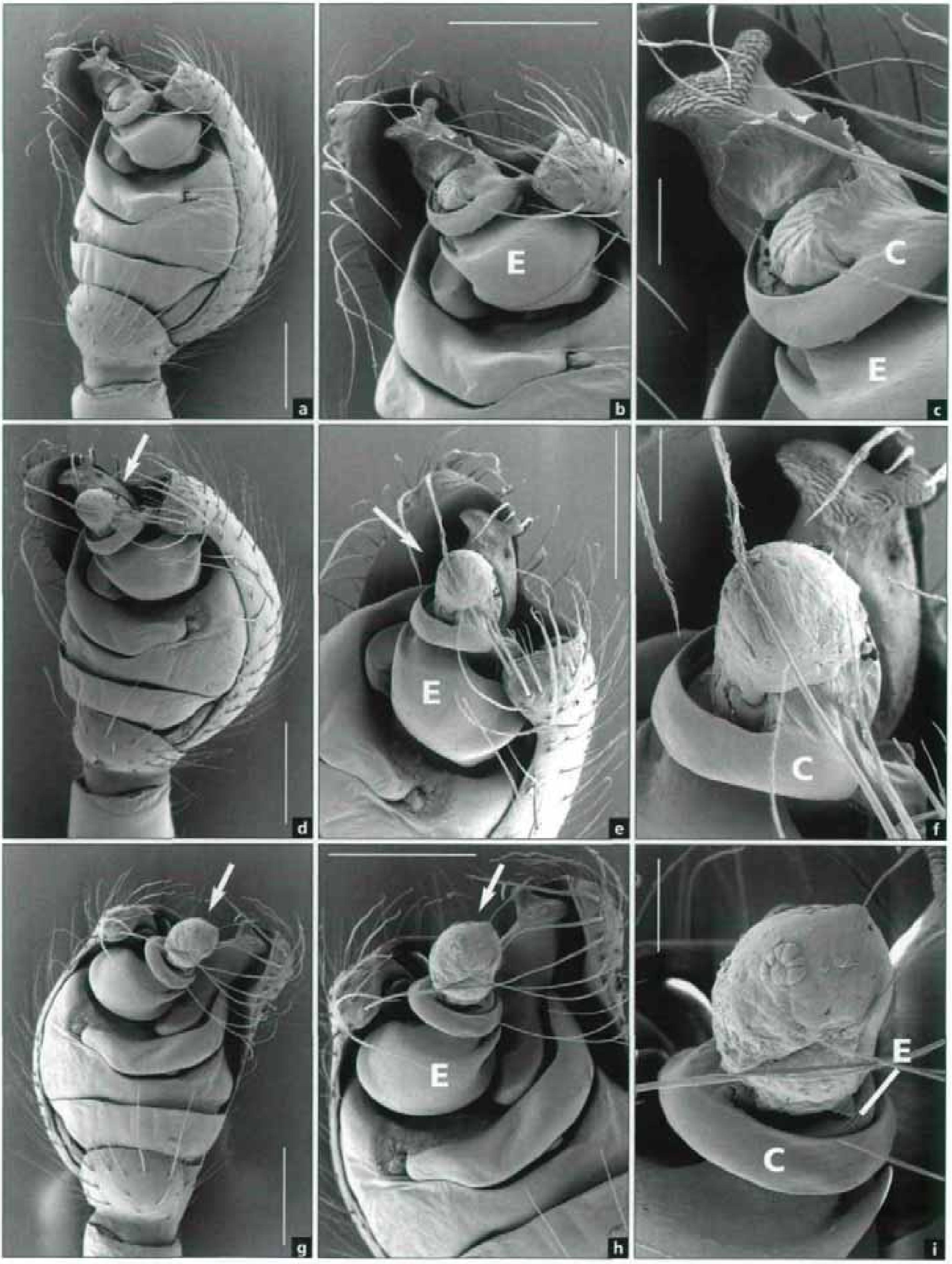

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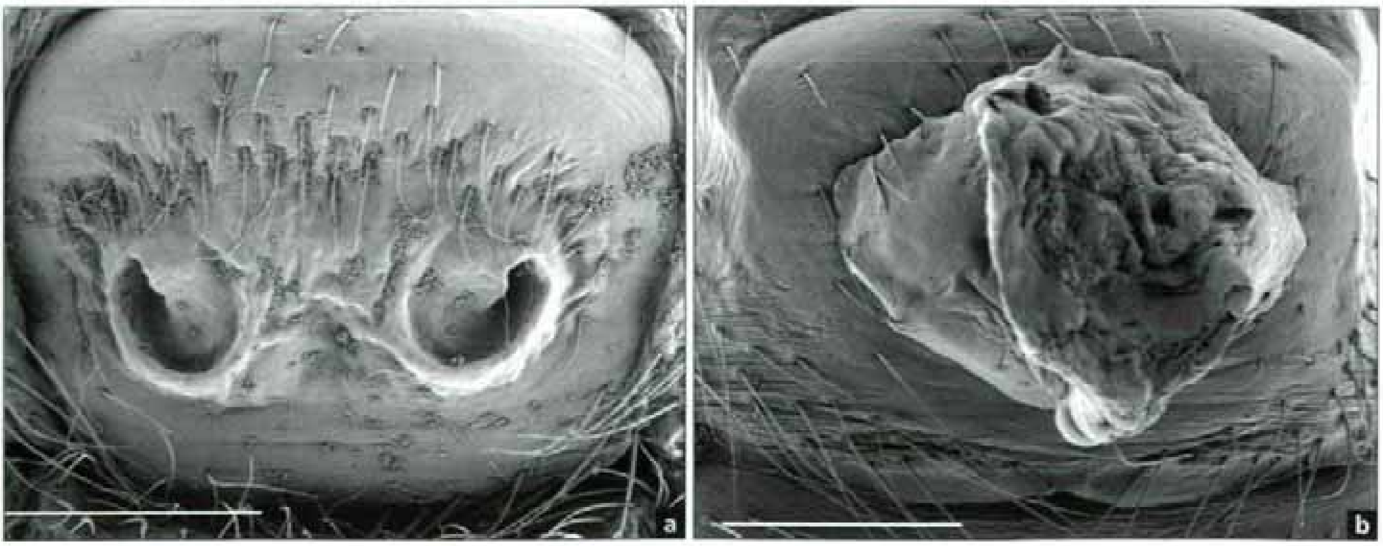
Fig. 70a–c: Copulated females of *Argyrodes argyrodes*. **a**: First portion of mating plug secretion just transferred, secretion still transparent. **b, c**: Secretion hardened to solid, brownish plug, largely protruding from epigynum (arrows). Female from Kefallonia (a), Tenerife (b) and Gran Canaria (c).

the alleged projecting epigynum, which most probably is a mating plug.

The male clypeal organ of the genus *Argyrodes* has been the subject of numerous studies (LEGENDRE & LOPEZ 1974, LOPEZ & EMERIT 1979 and 1981, etc.). The exact effect of the glandular secretion on the female was discussed by WHITEHOUSE (1987), who suggested that a stimulating effect was more likely than a calming one. WHITEHOUSE (1987) rejected a nutritive function of the secretion, as the females did not appear to move their mouthparts. However, in the present females sucking movements were observed. Apparently, the female is brought into copulatory posture by this gustatory component. Mating has been observed in *A. antipodianus* O. P.-CAMBRIDGE 1880 from New Zealand, with special emphasis on courtship movements (WHITEHOUSE & JACKSON 1994). SCHMIDT (1999) briefly described a 50 min long copulation of an undetermined *Argyrodes* species from the Cape Verde Islands. To my knowledge, the formation of the mating plug in *Argyrodes* has not previously been reported.

Fig. 71a, b: Epigynum of *Argyrodes argyrodes*. **a**: Virgin female, copulatory orifices free. **b**: Copulated female, amorphous plug covers epigynum. Scale lines: 0.2 mm. Photos: K. PFALLER.



28–31 *Enoplognatha ovata*-group

The *E. ovata*-group clearly follows the *Steatoda*-type of copulation. Sperm induction takes place independently of copulation, sometimes after copulation. At the beginning the male spins a layer of silk to and from the female, which represents the mating web. Courtship and copulation proceed via the mating web, to which the female is lured by continuous plucking. Thus, the female approaches for copulation. Then palps are inserted alternately in rapid succession. During insertion haematodochae inflate only once. Copulations are comparatively short, lasting 9–70 min. A mating plug was not found. Following species were observed: *E. afrodite*, *E. latimana*, *E. ovata* and *E. penelope*. Ethological differentiation at present is not possible owing to small sample size. It appears that *E. latimana*, *E. ovata* and *E. penelope* are rather close, whereas *E. afrodite* differs clearly by increase of insertion duration with advance of copulation and longer copulation duration. Also in morphology *E. afrodite* is the most distinctive representative of the *E. ovata*-group. It is the only species which has the trichobothrium on metatarsus I submedian instead of subapical; the male chelicerae are comparatively short and genital morphology is markedly different. In the cladogram it is the most basic species (HIPPA & OKSALA 1983).

28 *Enoplognatha afrodite* HIPPA & OKSALA 1983 (Fig. 72, 73)

Material: Greece, Rhodos, Attaviros surroundings, Ag. Isidoros, 550 m, ♂♀, 10.4.1996. Profitis Ilias, footpath above Salakos, 550–600 m, ♂♀, 12.4.–13.4.1996; all leg. KNOFLACH & THALER.

Fig. 72a–c: Copulation in *Enoplognatha afrodite*. **a:** Male has completed construction of mating web, which is outlined by arrows. His plucking with legs II induces the female to approach him. **b:** Insertion of left palp. Leg contact present. **c:** Construction of sperm web.

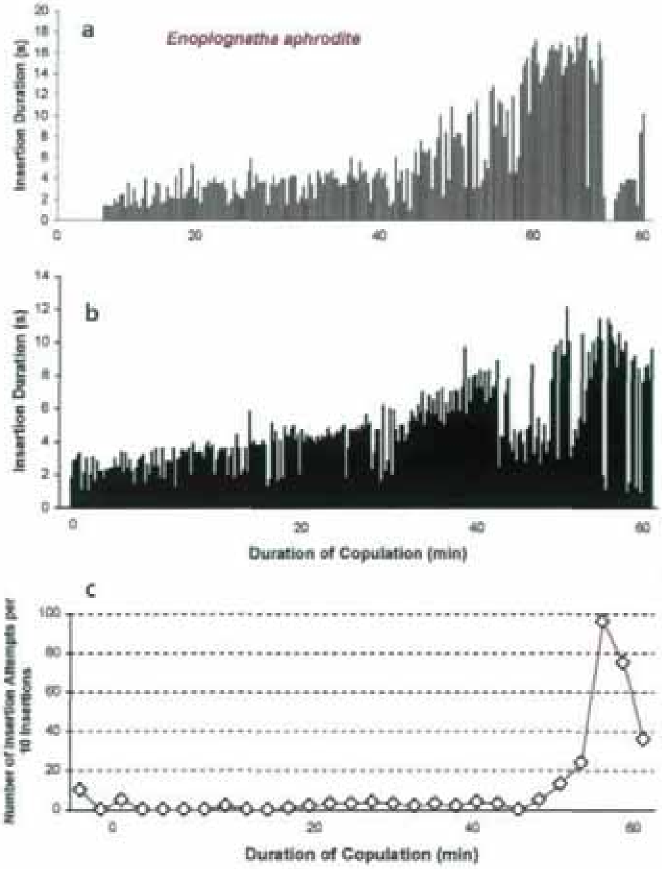


Fig. 73a–c: Copulation and insertion pattern in two pairs of *Enoplognatha afrodite* from Rhodes. Each bar represents an insertion. **c:** Frequency of insertion attempts during copulation of (b).

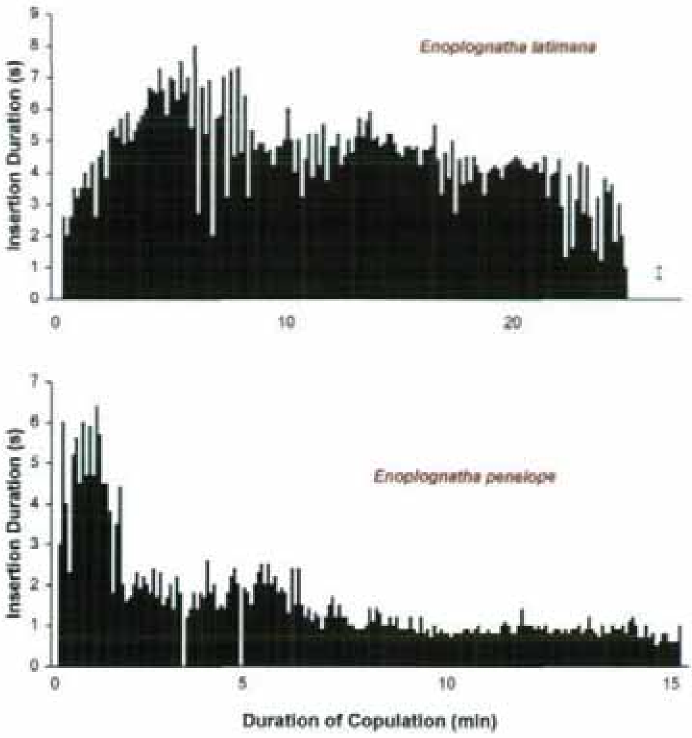


Fig. 74a, b: Copulation and insertion pattern in *Enoplognatha latimana* (a) from Sardinia and *E. penelope* (b) from Corfu. Each bar represents an insertion.

Mating behaviour was observed from four pairs, two of them not in full detail. Sperm induction takes place independently of copulation. The male starts with construction of a layer of silk to and from the female, which represents the mating web. Copulation proceeds via mating thread and female approach and involves numerous short insertions. A mating plug was not found.

Courtship behaviour: When in contact with the female web, the male vibrated his abdomen, approached the female immediately, palpated her and then started to construct the mating web. The male installed numerous threads in an area of 2–4 cm to and from the female, so that a considerable silk layer was produced (Fig. 72a). Spinning of the mating web lasted 16 min on average (range = 8–33, n = 4). On the silk layer he intensively vibrated his abdomen and thereafter plucked alternately with his legs III (but with legs II when legs III were lacking, see Fig. 72a). After about 5 min of such courting (range = 3–11, n = 4) the female approached him and assumed the copulatory posture opposite him. Copulatory posture as typical of other Theridiidae (Fig. 72b). Precopulatory courtship, comprising construction of the mating web and plucking, lasted 31 min on average (range = 5–44, n = 4). Copulatory courtship: The male often vibrated his abdomen with different amplitudes during a sequence of insertions, especially before/after insertion.

Sperm induction: Once a male was seen constructing a sperm web just after copulation (Fig. 72c), but the observation was incomplete. In all other cases the male left the female web a few minutes after copulation, when the female jerked and started web-spinning.

Entire copulation duration averaged 56 min (range = 34–70, n = 4). Total number of insertions 192 and 267. Total insertion time 19 and 21 min.

Copulatory pattern (Fig. 73a–c): Copulation consisted of a sequence of rapidly alternating insertions, which lasted altogether 45 min on average (range = 32–60, n = 4). Insertions were rather short, lasting 4.9 ± 0.2 s on average (mean ± s.e., range = 0.8–17.8, n = 524). With advance of copulation insertion duration increased (Fig. 73a, b), but also the number of unsuccessful insertions (Fig. 73c). For a rather long time these insertion attempts occurred at low rate (0–10 per 10 insertions), but then accelerated towards the end of copulation (up to 96 attempts per 10 insertions). Moreover, haematodochal swelling declined noticeably with the final successful insertions. In two pairings the insertion sequence was interrupted by the female 2–3 times. The male then retreated and briefly installed a few new threads and plucked, until the female approached once again for the next insertions.

29 *Enoplognatha latimana* Hippa & Oksala 1982 (Fig. 74a)

Material: **Italy**, Sardinia, above Lanusei, 900 m, ♂♀, 6.6.2003, leg. Knoflach & Thaler.

Mating behaviour was observed from one pair only. Sperm induction takes place after copulation. Copulation proceeds via mating thread and female approach and involves numerous short insertions. A mating plug was not found.

Courtship behaviour: When in contact with the female web, the male pulsated his abdomen, briefly approached the female, palpated her and started to construct the mating web. As in *E. afrodite* the male installed numerous threads in an area of 3–4 cm to and from the female. After 2 min, he intensively vibrated his abdomen and thereafter plucked alternately with his legs II on the mating web. After only 0.5 min of such courting the female approached him and assumed the copulatory posture. Copulatory posture as typical of other Theridiidae. Precopulatory courtship altogether lasted 2.5 min, including construction of the mating web.

Sperm induction: Sperm induction took place 2 min after copulation. Spinning of the sperm web with induction lasted 16.3 min, 7 min of which were used for construction of the sperm web. The male absorbed the sperm droplet within 9.3 min and by about 35 dipping movements. No further attempt to mate was observed.

Entire copulation duration occupied 23 min. Total number of insertions 159. Total insertion time 12 min.

Copulatory pattern (Fig. 74a): Copulation consisted of a sequence of rapidly alternating insertions. Insertions were rather short, lasting 4.5 s on average (range = 1–8, n = 159). With advance of copulation insertion duration slightly decreased. At the end the palp was applied five times without haematodochal swelling, which were assessed as insertion attempts. Thus, number of insertion attempts was very low.

30 *Enoplognatha ovata* (CLERCK 1757) (Fig. 75)

Material: Austria, Innsbruck, Martinswand, ♂♀, 17.6.1994, leg. KNOFLACH & THALER.

Mating behaviour was observed from five pairs, all of them not in full detail as regards number and exact duration of insertions. Sperm induction takes place independently of copulation. As in *E. afrodite*, the male starts with construction of a mating web. Copulation proceeds via mating thread and female approach and involves numerous short insertions.

Courtship behaviour: When in contact with the female web, the male intensively vibrated his abdomen, approached the female, palpated her and started to construct the mating web. Further courting, see also *E. afrodite*. The female sometimes jerked in response to the male's movements and finally approached him and assumed the copulatory posture (Fig. 75a). Copulatory posture as typical of other Theridiidae (Fig. 75b, c). Precopulatory courtship, comprising construction of the mating web and plucking, lasted 13.2 min on average (range = 1–26, n = 5). Copulatory courtship: The male often vibrated his abdomen during a sequence of insertions.

Sperm induction: Not observed. In most observations the male left the female web a few minutes after copulation, when the female jerked and started web-spinning or even prey attack.

Entire copulation duration averaged 23.6 min (range = 17–43, n = 5). Total number of insertions not recorded, but estimated at about 100–200.

Copulatory pattern: Copulation consisted of a sequence of rapidly alternating insertions, which lasted a few seconds only (3–6 s). Insertion duration decreased with advance of copulation and then lasted only 1 s. Accordingly, haematodochal swelling declined as well. Number of unsuccessful insertions was higher at the end. None of the five copulations was interrupted by the female.

Other observations: A female was allowed to remate nine days after the first copulation. In spite of long and intensive male courtship no copulation took place. Instead, the male was preyed upon and sucked out by the female. Another female of uncertain state (presumably mated) was aggressive at the very beginning, but was calmed by the male's courting. After only 2 min of insertions she also attacked and devoured the male.

The reports of GERHARDT (1921, 1923), LOCKET (1926) and BRISTOWE (1929) on the copulation of *E. ovata* (sub *Theridium lineatum*, *Phyllonethis lineata* and *Theridion ovatum* respectively) leave only a little doubt on the identity of the species, as its sibling *E. latimana* is much less common than *E. ovata*. Copulations lasted 13–45 min (GERHARDT 1921, 1923), 12–15 min (LOCKET 1926) and 15 min (BRISTOWE 1929), and proceeded in a similar way as in the present pairings, with numerous short insertions up to 10 s. LOCKET (1926) recorded 107 insertions in one observation, which

Fig. 75a–c: Copulation in *Enoplognatha ovata*. **a:** Female approach. **b, c:** Insertion of right and left palp. Leg contact present. Note light colour and exuvium (upper left) of freshly moulted female.

lasted at first 10–12 s, but mostly 5–7 s. Sperm induction took place 20–30 min and once even 3.7 h after copulation (GERHARDT 1921, 1923), whereas BRISTOWE (1929) observed it soon after copulation. The whole process of construction of the sperm web and induction lasted 17 min (BRISTOWE 1929), according to GERHARDT 5 and 10 min, of which 2 and 6 min respectively were used for construction of the sperm web. The male absorbed the sperm droplet within 3 and 4 min (GERHARDT 1921, 1923) and by 26 dipping movements (BRISTOWE 1929). In two observations the female finally became aggressive and started to attack the male (LOCKET 1926).

31 *Enoplognatha penelope* HIPPA & OKSALA 1982 (Fig. 74b)

Material: Greece, Corfu, Dasia, Kato Korakiana, 100 m, olive grove, ♂♀, 27.5.1996 and 30.5.1996, leg. KNOFLACH & THALER.

Mating behaviour was observed from two pairs. Sperm induction takes place independently of copulation. Overall procedure of copulation is similar to *E. afrodite*, but courtship was brief and a mating web was missing. *E. penelope* is the largest representative of the *E. ovata*-group. Perhaps the comparatively small size of the observation jars did not allow construction of a mating web, as typical of the other members of this group.

Courtship behaviour: Courtship was very brief. When in contact with the female web, the male remained motionless for a few minutes and then slightly vibrated his abdomen. In both observations the female approached the male immediately so that he did not construct a mating web, nor did he pluck. Copulatory posture as in the other species of this group. Precopulatory courtship lasted only half a minute. Copulatory courtship: With each insertion the male seized the female so that both were shaking. Such vigorous pulling movements were not observed in the other species of the *E. ovata*-group.

Sperm induction: In one observation the male left the female web a few minutes after copulation, when she became aggressive, in the other observation the female left her web. 20 and 40 min later the males started construction of sperm web and induction. Interestingly, one male built two sperm webs in succession. Only one sperm uptake was recorded completely. The whole procedure lasted 13.2 min, 9 min of which were used for construction of the sperm web. The male absorbed the sperm droplet within 4.2 min and by 26 dipping movements. Afterwards the male was again introduced into the female web but showed no further attempt to mate.

Entire copulation duration occupied 9 and 15 min. Total number of insertions rather variable, 31 and 182. Total insertion time 2.7 and 4.9 min.

Copulatory pattern (Fig. 74b): Copulation consisted of a sequence of rapidly alternating insertions. Insertions were rather short, lasting only 1.6 ± 0.09 s on average (mean ± s.e., range = 0.5–6.4, n = 182) in one pair and 5.3 s ± 0.26 on average in the other pair (range = 3.0–11.2, n = 31). During each insertion the male seized the female with the palp just in use. Insertion duration decreased with advance of copulation (Fig. 74b), whereas numbers of unsuccessful insertions increased. In the observation with a high number of insertions haematodochal swelling declined noticeably halfway through copulation. Palps were then inserted with minimal expansion. In both pairings insertion sequence was interrupted by the female 1–2 times. The male then vibrated his abdomen and gently plucked, until the female approached again for the next sequence of insertions.

32 *Enoplognatha verae* BOSMANS & VAN KEER, 1999 (Fig. 76)

Material: **Tunisia**, Hammamet, ♂, 21.–28.2.1997, under stone. Cap Bon, Korba, ♀, 23.2.1997, under stone, leg. KNOFLACH & THALER.

According to BOSMANS & VAN KEER (1999) *E. verae* is a member of the *E. ovata*-group, based on cheliceral dentation and leg length. However, coloration and pattern differ considerably from all other representatives of the *E. ovata*-group (Fig. 76). Specimens have a brown to greyish ground colour and a dorsal abdominal folium instead of being more or less uniformly yellow. Legs are conspicuously speckled. Copulatory behaviour differs from the *E. ovata*-group by the insertion pattern (two long insertions at the beginning), long copulation duration, haematodochal pulsations and by presence of a mating plug.

Mating behaviour was observed from one pair, but unfortunately not complete. Beginning of courtship and parts of the advanced phase of copulation were not recorded. Therefore, further observations are needed to confirm the moment of sperm induction. Copulation involves a few long and numerous short insertions. During insertion haematodochae pulsate rhythmically. Copulation ends with formation of a mating plug.

Fig. 76: Male of *Enoplognatha verae*. Note coloration as compared with the *E. ovata*-group.

Courtship behaviour: Beginning of courtship escaped observation. Thus, it was not observed whether a mating web was built. The male was found to vibrate his abdomen and to pluck with his legs I and II until the female approached. Copulatory posture as in the other species of this group.

Sperm induction: not observed.

Entire copulation duration occupied 3.7 h. Total number of insertions not observed; in the first hour of copulation exactly 100 insertions took place. Another 35 min sequence of insertions was not recorded in detail, but would have involved c. 80 insertions if the final insertion time was maintained. Total insertion time about 1 h (44 min in the fully recorded hour plus estimated 15 min in the missing 35 min).

Copulatory pattern: Copulation comprised a sequence of insertions of varied duration (mean ± s.e. = 26.2 ± 8.3 s, range = 6.5–775.0, n = 100). At the beginning two long insertions took place, lasting 13 and 6 min. Then insertion duration decreased rapidly and numerous shorter insertions followed, which took about 14.7 ± 0.6 s on average (mean ± s.e., range = 6.5–39.0, n = 97). Remarkably, haematodochae were not inflated once during insertions, but pulsated rhythmically, see also 35 *E. sattleri*. In the long-time insertions haematodochae inflated for 7–9 s until they collapsed again. Dur-

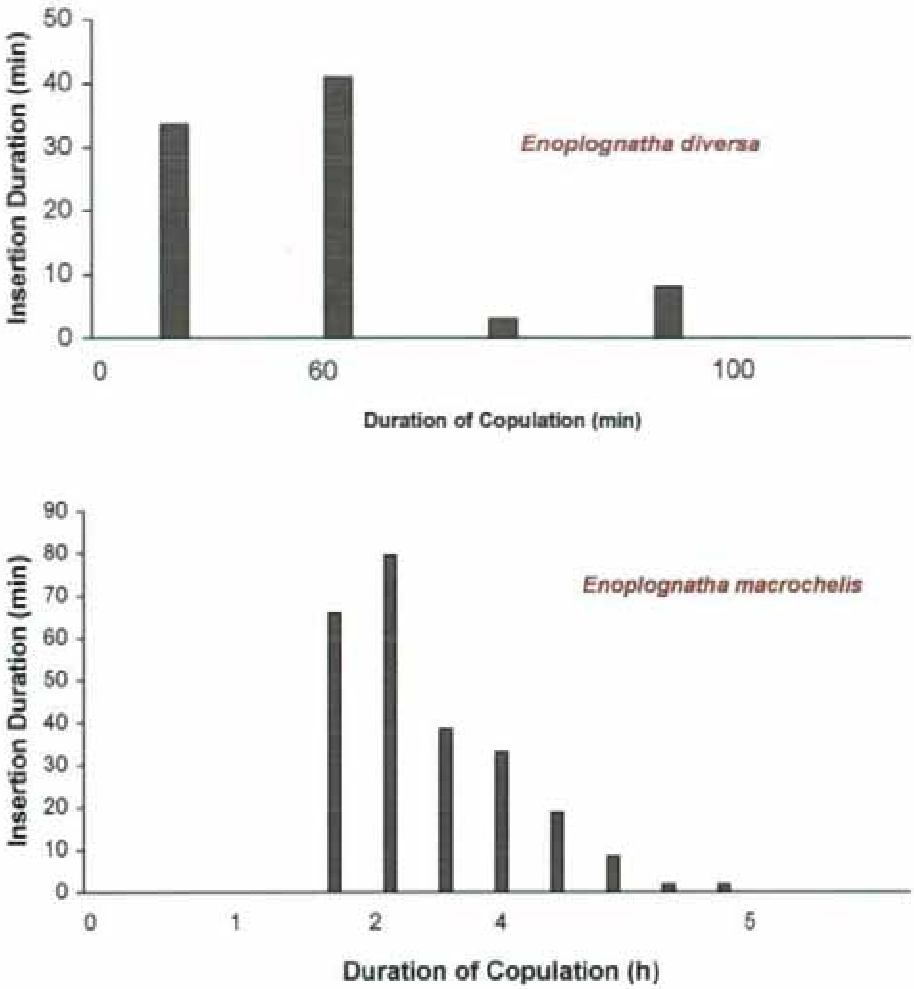


Fig. 77a, b: Copulation and insertion pattern in *Enoplognatha diversa* from Tunisia (a) and *Enoplognatha macrochelis* from Cyprus (b). Each bar represents an insertion.

ing a shorter insertion 2–3 such swellings were performed. After the first hour of insertions the pair maintained copulatory posture, but were motionless for a long period (at least 20 min) and then again resumed insertions. Twice copulation was interrupted for production of the mating plug secretion (duration 10–20 min). The male was found with a secretion droplet on his palps. This behaviour needs further confirmation, as the process itself was not observed. The secretion clearly represents a mating plug, but its origin is uncertain. It may come from glands of the male palp or from the mouthparts. The secretion was transferred to the epigynum by very short applications without haematodochal swelling for about 10 min. Finally, a marked, whitish secretion droplet protruded from the epigynum, which was still visible 1 h later. The mating plug apparently was not very solid, as it was easily removed by needles.

33–35 *Enoplognatha diversa*-group

Sperm induction takes place independently of copulation. Courtship, see *E. ovata*-group. Copulation proceeds via mating thread and starts with a few long insertions, lasting longer than 10 and up to 80 min. During insertion haematodochae pulsate rhythmically. Entire copulation duration usually occupied more than 1 and up to 4 h. It appeared that no mating plug was formed. Following species were observed: *E. diversa*, *E. macrochelis*, and *E. sattleri*. Again, small sample size makes comparison difficult. It appears that *E. sattleri* exceeds the other species in large number of insertions. *E. macrochelis* is apparently notable for comparatively long insertion duration.

33 *Enoplognatha diversa* (BLACKWALL 1859) (Fig. 77a)

Material: **Tunisia**, Hammamet, ♂, 21.–28.2.1997. Cap Bon, Korba, ♂♀, 23.2.1997, leg. KNOFLACH & THALER.

Mating behaviour was observed from two pairs. A third observation was incomplete. Sperm induction takes place independently of copulation. Copulation proceeds via mating thread and involves a few long insertions. During insertion haematodochae pulsate rhythmically. Apparently no mating plug is produced.

Courtship behaviour: Courtship corresponds with other *Enoplognatha* species. The male vibrated his abdomen, approached the female and constructed a mating web. Upon his continuous vibrating and plucking with legs II the female approached and assumed copulatory posture. Construction of mating web and plucking was repeated for most insertions. Precopulatory courtship lasted 2, 10 and 12 min, courtship before later insertions 0.5, 9 and even 30 min. Copulatory posture typical of other theridiid species.

Sperm induction: One male built a dense sperm web half an hour after copulation and remained for 15 min motionless on the web, by which time induction was completed. The other male left the female web 6 min after copulation.

Entire copulation duration occupied 100 and 104 min. Total number of insertions 3 and 4. Total insertion time 70 and 86 min.

Copulatory pattern (Fig. 77a): Copulation comprised only a few long insertions, with a mean duration of 23.2 min (range = 3–41, n = 8). Insertions mostly did not take place in immediate succession, but were preceded by another courting period. Remarkably, haematodochae were not inflated once during insertion, but pulsated rhythmically. A mating plug was not discernible.

34 *Enoplognatha macrochelis* LEVY & AMITAI 1981 (Fig. 77, 78)

Material: **Cyprus**, Paphos surroundings, Coral Bay, ♂ ♀, 12.2.1995; Akamas peninsula southern coast, Ag. Georgios surroundings, ♂ ♀, 17.2.1995; Polis, Akamas peninsula, Fontana Amorosa, ♂, 16.2.1995; all leg. KNOFLACH & THALER.

Mating behaviour was observed from five pairs. Sperm induction takes place independently of copulation. Copulation proceeds via mating thread and involves several long insertions, sometimes also a few shorter ones. During insertion haematodochae pulsate rhythmically. Apparently no mating plug is produced.

Courtship behaviour: Courtship similar to *E. diversa*. Abdominal vibrations and plucking with legs II were very intensive in all observations. Construction of mating web, vibrating and plucking sometimes also occurred when copulation was interrupted (in three pairs recorded). Precopulatory courtship lasted 6–43 min (mean = 26, n = 5), courtship before later insertions 1, 2, 9 and 17 min. Copulatory posture typical of other theridiid species, with leg contact (Fig. 78b, c). Copulatory courtship: Towards the end of an insertion the male intensively vibrated his abdomen. Haematodochal pulsations, see copulatory pattern.

Sperm induction: Sperm induction was not observed. Two males left the female web shortly after copulation.

Fig. 78a–c: Copulation in *Enoplognatha macrochelis*. **a**: Male during courtship. **b**, **c**: Insertion. Forelegs of male in contact with female's legs.

Entire copulation duration occupied 2.5 h on average (range = 0.9–4.4, n = 5). Total number of insertions averaged 8 (range = 2–12, n = 5). Total insertion time 2.2 h on average (range = 0.9–4.1).

Copulatory pattern (Fig. 77b): Copulation comprised 2–12 insertions, with a mean duration of 17.2 ± 3.4 min (range = 1.0–79.5, n = 38). At the beginning 2–4 long insertions took place, lasting 42 min on average (range = 14.5–79.5, n = 14). Then insertion duration decreased gradually. In two pairings 5–10 palp-epigynum contacts occurred, which took no longer than one second and sometimes were accompanied by short haematodochal inflation. They were not assessed as successful insertions. Copulation was interrupted once in two pairs and twice in another pair. Haematodochae pulsated rhythmically for 2–5 s during insertion. Shortly before a pulsation, the male's chelicerae were stretched and his abdomen moved in slight jerks, according to the rhythmical increase of hydraulic pressure. A mating plug was not discernible on the tiny epigynal atrium.

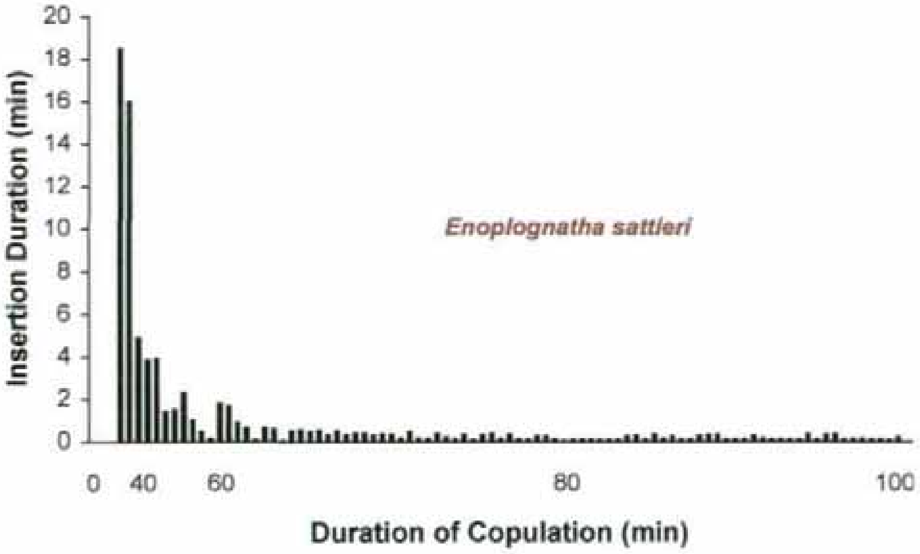


Fig. 79: Copulation and insertion pattern in *Enoplognatha sattleri* from Tenerife. Each bar represents an insertion.

35 *Enoplognatha sattleri* BÖSENBERG 1895 (Fig. 79)

Material: **Spain**, Canary Islands, Tenerife, Teno Alto, c. 600 m, ♂ ♀, 21.2.2000, leg. KNOFLACH & THALER. Adult male guarded the subadult female shortly before her maturation.

Mating behaviour was observed from one pair. Sperm induction takes place independently of copulation. Overall procedure of copulation similar to *E. diversa*. Copulation involves a few long and numerous short insertions. During a long insertion haematodochae pulsate rhythmically. Apparently no mating plug is produced.

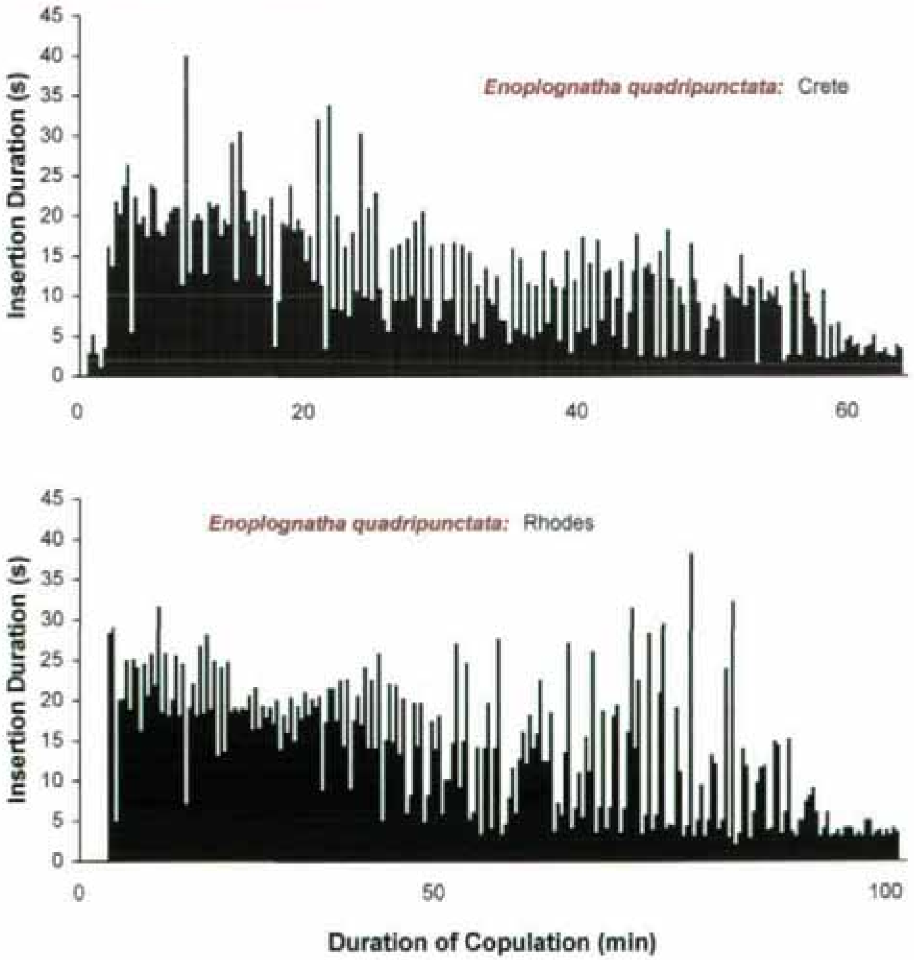
Courtship behaviour: Courtship was very brief, but escaped observation. Precopulatory courtship lasted at most only 2–3 min. Copulatory posture as in the other species of this group. Copulatory courtship: From time to time the male intensively vibrated his abdomen, usually when the female became restless. During long-time insertions rhythmical haematodochal pulsations took place. With each pulsation, his chelicerae were slightly moved as well as his abdomen, according to the rhythmic increase of hydraulic pressure.

Sperm induction: Not observed. The male left the female web 0.5 min after copulation, when she became aggressive.

Entire copulation duration occupied 95 min. Total number of insertions 87. Total insertion time 76.2 min.

Copulatory pattern (Fig. 79): Copulation comprised a sequence of insertions of varied duration (mean ± s.e. = 52.6 ± 17.1 s, range = 2.6–1110, n = 87). At the beginning two long insertions took place, lasting 16 and 18.5 min. Then insertion duration decreased gradually and numerous short insertions followed, which took about 15 s on average (range = 2.6–39, n = 73). Remarkably, haematodochae were not inflated once during the long-time insertions, but pulsated rhythmically, see also courtship. When separating, a small secretion droplet protruded from the epigynum, which probably was sperm. Dissection of the female epigynum revealed that the tiny epigynal atrium was unplugged.

Fig. 80a, b: Copulation and insertion pattern in two pairs of *Enoplognatha quadripunctata* from Crete and Rhodes. Each bar represents an insertion.



36, 37 *Enoplognatha thoracica*-group

36 *Enoplognatha quadripunctata* SIMON 1884 (Fig. 80a, b)

Material: Greece, Rhodos, Profitis Ilias, above Salakos, 550–600 m, ♂♀, 12.4.–13.4.1996; E-Crete, Kera, s. Mohos. c. 700 m, ♂, 8.4.1998; Pefkos, ♀, 5.4.1998, olive grove; all leg. KNOFLACH & THALER.

E. quadripunctata is a member of the *E. thoracica*-group and close to *E. thoracica*. Identification according to BOSMANS & VAN KEER (1999). In the present observations *E. quadrimaculata* differs from *E. thoracica* by long copulation time, high number of insertions and comparatively short insertion duration.

Mating behaviour was observed from two pairs. Sperm induction takes place independently of copulation. The male starts with construction of a mating web. Copulation proceeds via female approach and involves numerous short insertions. A mating plug was not found.

Courtship behaviour: When in contact with the female web, the male vibrated his abdomen, approached the female and installed the mating threads to and from the female. After 1.5 and 5 min of such spinning he intensively and continuously vibrated his abdomen and plucked alternately with legs II for half a minute, until the female approached him and assumed the copulatory posture. Copulatory posture as in other *Enoplognatha* species. Precopulatory courtship, comprising construction of the mating web and plucking, lasted only 2.5 and 5.5 min. Copulatory courtship: The male often vibrated his abdomen intensively during an insertion, which is a typical stridulatory movement.

Sperm induction: Not observed. One male was pursued and attacked by the female soon after copulation and had to be removed from her web.

Entire copulation duration occupied 65 and 92 min. Total number of insertions 210 and 228. Total insertion time 41.2 and 49.6 min.

Copulatory pattern (Fig. 80a, b): Copulation consisted of a sequence of rapidly alternating insertions, lasting 13.2 ± 0.4 s on average (mean ± s.e., range = 1.0–39.9, n = 413). With advance of copulation insertion duration decreased (Fig. 80a, b) and number of unsuccessful insertions increased. For a long time insertion attempts occurred at low rate (mean = 1.2; range = 0–4 per 10 insertions), but then accelerated near the end of copulation (up to 16 attempts per 10 insertions). Also haematodochal swelling gradually declined towards end of copulation. Copulation was not interrupted by the female.

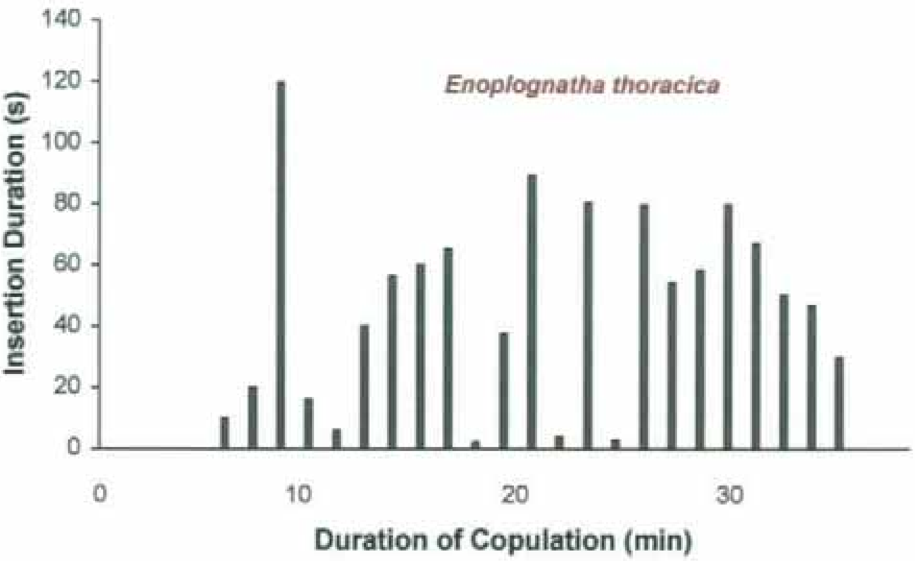


Fig. 81: Copulation and insertion pattern in *Enoplognatha thoracica* from Northern Tyrol. Each bar represents an insertion.

37 *Enoplognatha thoracica* (HAHN 1833) (Fig. 81)

Material: Austria, N-Tyrol, E Landeck, Starkenbach 800 m, ♂♀, May 1996, leg. KNOFLACH & THALER.

Mating behaviour was observed from one pair only. Overall pattern as in *E. quadripunctata*. Number of insertions was lower than in *E. quadripunctata*, whereas insertions lasted longer. However, further observations are needed to confirm these differences. A mating plug was not found. Precopulatory courtship lasted only 2.5 min. Sperm induction was not observed.

Entire copulation duration occupied 32 min. Total number of insertions 25. Total insertion time 19.5 min.

Copulatory pattern (Fig. 81): Copulation consisted of a sequence of 25 alternating insertions, lasting 46.9 ± 6.7 s on average (mean ± s.e., range = 2.3–120.0, n = 25). The female suddenly became aggressive and terminated copulation. Thereupon the male left her web.

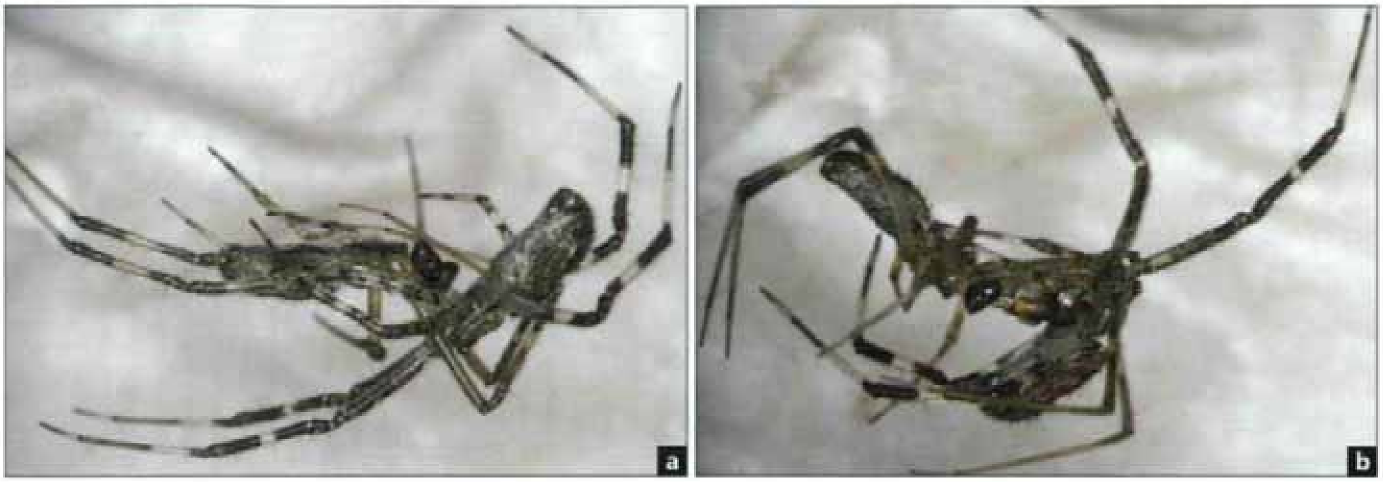


Fig. 82a, b: Copulation in *Episinus maculipes* from Sardinia. **a:** Couple just before insertion. **b:** Insertion of left palp, female has turned 180° around, male faces venter of female. Forelegs of male in contact with female's legs.

38 *Episinus maculipes* CAVANNA 1876 (Fig. 82, 83)

Material: Italy, Sardinia, above Lanusei, 900 m, ♂♀, 6.6.2003, leg. KNOFLACH & THALER.

Representatives of the genus *Episinus* differ from most other comb-footed spiders by their elongate body shape and by web-reduction. Their snare is reduced to 2–3 threads.

Twenty times virgin males were introduced into the cages of virgin females and observed for 3–8 h, but without success. The spiders remained motionless for hours. Only one pair suddenly copulated 14 min after they were put together. The exact beginning escaped notice, but it appeared that courtship was either very short or even absent. Construction of a mating thread can be excluded. Each palp was inserted once for c. 1.5 min. During the first insertion the female rotated a little and thereby changed her position. As a result, both partners faced the same direction (Fig. 82a versus 82b). After the first insertion the male swiftly applied the opposite palp without courting. Then the pair quickly separated. A mating plug was not discernible. Sperm induction takes place independently of copulation.

Sperm induction (Fig. 83a, b): One hour after copulation the male started construction of the sperm web and induction. The whole procedure lasted 7 min, 2.4 min of which were used for construction of the sperm web, the remaining time for induction. The male absorbed the large sperm droplet by only 6 dipping movements. The palps remained on the droplet for a long time (Fig. 83b) and the sperm droplet quickly disappeared.

LOCKET (1927) once observed a copulation of *Episinus truncatus* LATREILLE 1809. No male courting movements were discerned. The female suddenly approached the male for copulation, which involved two insertions of 2.4 and 3.7 min duration. Thus, the overall procedure appears to be similar to *E. maculipes*.

39 *Euryopis episinoides* (WALCKENAER 1847) (Fig. 84a, b)

Material: Greece mainland, ♂, Chalkidiki, Olympiada, 16.9.1996, ♀, Ioannina, camp site, 12.9.1996, leg. KNOFLACH & THALER.

Representatives of the genus *Euryopis* are specialized in feeding on ants (HIRSCH-

Fig. 83a, b: Sperm induction in *Episinus maculipes*. **a:** Construction of sperm web completed, sperm droplet just released (arrow). **b:** Absorption almost completed.

Fig. 84a, b: Copulation in *Euryopis episinoides* from Chalkidiki. Owing to web-reduction copulation takes place on the ground. Female's body propped up and legs stretched aside.

BERG 1969). They are considered to be wandering spiders and do not build webs for prey capture but still use silk for immobilisation of the prey (CARICO 1978).

Mating behaviour was observed from one pair only. No mating threads were constructed. The male hectically pursued the female for about 5 min, without obvious courtship movements. Then female and male briefly threw silk towards each other with their legs IV, thereby facing in opposite directions. This activity otherwise is part of prey capture, but apparently caused no harm. Afterwards insertion followed in the next 1.5 min. Then the pair quickly separated. Again the male pursued the female for 5 min, and after another silk-wrapping activity, the second copulation proceeded (duration c. 1 min). As the spiders were not hanging in a web, the copulatory posture was reversed compared with other theridiid spiders (Fig. 84a, b). The female became propped up from the ground. Apparently there is no mating plug. Sperm induction takes place independently of copulation and was not observed.

Entire copulation duration occupied c. 15 min. Total number of insertions 2. Total insertion time c. 2 min.

HIRSCHBERG (1969) describes a copulation of *Euryopis flavomaculata* (C.L. KOCH 1836), which apparently runs off in a similar way. The female threw silk when the male approached her. Each palp was inserted for 40 s.

40 *Steatoda bipunctata* (LINNAEUS 1758) (Fig. 85, 86)

Material: **Austria**: Innsbruck, Kranebitten, from house walls, ♂♀, March 1997, leg. KNOFLACH; Innsbruck surroundings, from waste container, ♂♀, Sept. 2003, leg. VOGEL.

Mating behaviour was observed from three pairs, but never in full detail. Sperm induction takes place independently of copulation. Copulation proceeds via mating web and involves one or two insertions of 1–2 h duration. The male palp is inserted ipsilaterally. Two different phases were present during insertion. Haematodochae pulsate rhythmically in the first phase, but remain constantly inflated in the second phase. It is assumed that during this second phase of insertion a mating plug is produced (Fig. 86b), which apparently originates from the male palp. Remarkably, females were never aggressive. *S. bipunctata* is markedly distinct from the following *Steatoda* species in morphology and also in behaviour. It differs by long insertion duration, long courtship duration, by a different way of mating plug production and apparently by lack of female aggression.

Courtship behaviour: Not recorded in full length. One male courted for 9 h. One male soon started with construction of the mating web. Another male at first approached the female, encompassed her body, in particular her abdomen, with his forelegs and remained in contact with her body or sometimes close to her for the next half hour (Fig. 85c, d). Then he gradually disengaged

Fig. 85a–d: Copulation in *Steatoda bipunctata*. **a, b**: Insertion of left palp. Couple hanging upon the mating web. Leg contact present. **c, d**: Mate guarding with intense body contact. Male underneath female.

body contact and started to construct a dense mating web as typical of other *Steatoda* species, which took about 1 h. Apart from spinning, the male also removed threads, vibrated his abdomen and regularly approached the female for a short contact phase. He palpated her, encompassed her body with his forelegs and once threw strands of silk onto her. Finally, he displayed ritualised distant courtship on the mating web, while the female faced the opposite direction. At the beginning, his courting movements were slow and weak, abdominal pulsations were of low frequency and alternate plucking with legs III not very intensive. These movements became more and more intensive with advance of courtship. From time to time he turned around 180° and plucked alternately with legs I and II. After a few seconds he again returned to the original posture and continued plucking with legs III, which thereby were strongly flexed. For copulation the female has to be induced to turn around (the moment of female approach was not observed). Copulatory posture at the beginning as typical of other Theridiidae (Fig. 85a, b), but then became changed by female rotation and varied greatly. Copulatory courtship: During insertion the male regularly stridulated. His chelicerae were opened from time to time. In the first phase of insertion haematodochal pulsations occurred rhythmically, in the second phase jerks, see also copulatory pattern. One day after copulation one of the males appeared to guard the well-nourished female by close body contact, sometimes encompassing her body with his forelegs (Fig. 85c, d).

Sperm induction: Not observed.

Entire copulation duration: not completely recorded, several hours to days. Total number of insertions 1–2. Total insertion time about 2.2–2.5 h (when only one insertion took place).

Copulatory pattern: Insertions lasted 2.2 h (n = 2) and 2.5 h (n = 1). Before a successful insertion numerous insertion attempts took place. Thereby, the male stretched out his palps and pushed one

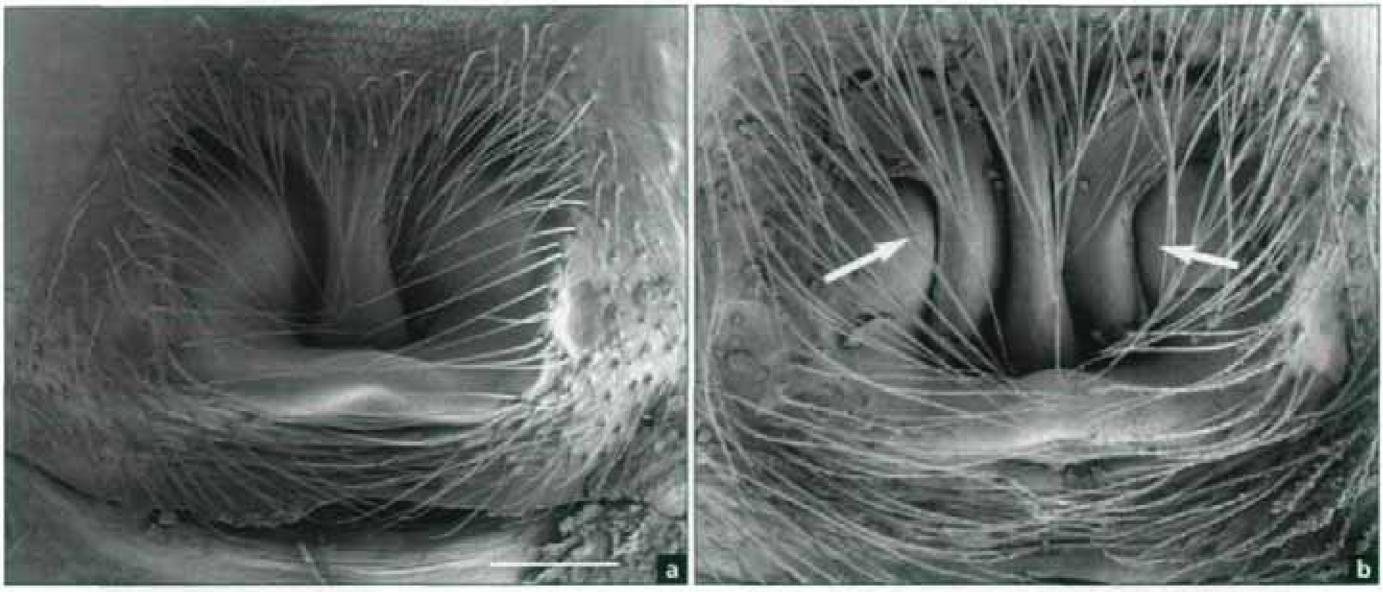


Fig. 86a, b: Epigynum of *Steatoda bipunctata*. **a:** Virgin female, copulatory slits unconcealed. **b:** Copulated female, mating plug covers and fits to copulatory slits (arrows). Scale lines 0.2 mm. Photos: K. Pfaller.

against the epigynum, in one case 38 times until the palp was locked. Two phases were distinguishable during insertion. During the first phase haematodochae pulsated rhythmically for about 50 min (n = 2), 28–40 times per minute. Then pulsations disappeared and instead haematodochae remained inflated throughout. The male now showed slight rhythmical jerks (50–55 times per minute) and synchronous contraction of legs (in particular leg III), by which the female was passively pulled. From time to time he also stridulated (at most once per minute). This second phase lasted 74 and 101 min. Each insertion was terminated by the female. She finally became restless, tried in vain to push off the palp with her hindlegs, and then turned around 90–180°. Genital contact is rather tight. The male did not withdraw his palp, but continued jerking. This sometimes calmed the female for a while and caused her to assume the original posture again. One female changed her posture 9 times in the last hour of insertion and interestingly, palp-epigynum contact was not affected. Rotations of 180° usually caused the male to unlock his palp. Haematodochal pulsations in the first phase of insertion appear to reflect sperm transfer. The second phase of insertion perhaps serves to produce the mating plug. After copulation an elongate, whitish, compact mass filled the entrance around the copulatory orifice which had just been occupied (Fig. 86b versus 86a). The mating plug is assumed to originate from the male palp, since transfer from the mouthparts and from the genital tract via the sperm web can definitely be excluded. Moreover, the male's mouthparts remained clean throughout copulation. Of course, it is possible that a female product also forms part of the secretion mass. Ipsilateral insertion was confirmed by the presence of a mating plug. After insertions of the right palp the right side of the female epigynum was plugged and vice versa. Females never became aggressive towards end of insertion. None of the males was attacked.

The present observations on *S. bipunctata* correspond well with Gerhardt (1923, 1924, 1925), Gwinner-Hanke (1970), Menge (1869; sub *Eucharia bipunctata* p. 261) and Bristowe (1958): construction of a mating web regularly occurred; courtship took an extremely long time, several hours to days, usually 6–8 h, and once even one week (Gwinner-Hanke 1970); insertions lasted 1.2–1.9 h (Gerhardt 1923, 1924), 0.8–2.5 h (Gwinner-Hanke 1970) and 2.5 h (Menge 1869); Gerhardt (1923) already outlined that there are different phases during insertion; copulation consisted of 1 or 2 insertions, the second one being shorter (Gwinner-Hanke 1970); cessation of genital contact was always initiated by the female. Gwinner-Hanke (1970) illustrated different mating postures of *S. bipunctata*, which are the result of female rotation. Lack of female aggression was noted by Bristowe (1958). A mating plug is not mentioned in the literature (Menge 1869; Gerhardt 1923, 1924, 1925; Gwin-

Fig. 87a–d: Copulation in *Steatoda castanea*. **a**: Insertion of left palp. **b**: Production of mating plug secretion (arrow), presumably originating from the mouthparts. **c**: Transfer of plug secretion upon insertion. Note both male palps stretched out. Leg contact loose. **d**: Epigynum filled with secretion (arrow), which later hardens.

NER-HANKE 1970). Sperm induction was observed once by GERHARDT (1924) and lasted 24 min, of which 2.7 min were used for construction of the sperm web, the rest for actual induction. According to GWINNER-HANKE (1970) *S. bipunctata* produced a clicking, metallic stridulatory sound of 700–1400 Hz and 23 ms duration, which was not audible to the human ear.

41 *Steatoda castanea* (CLERCK 1757) (Fig. 87a–d)

Material: **Austria**: Innsbruck, inside house, ♂♀, March 1997, leg. KNOFLACH.

Mating behaviour was observed from only one pair and not in detail on account of photographic documentation. Sperm induction takes place independently of copulation. Copulation proceeded via mating web and involved 9 short insertions of 0.5–1 min duration. During insertions haematodochae pulsate rhythmically. At the end, a mating plug is produced, apparently as in *S. triangulosa* originating from the mouthparts (Fig. 87d).

Courtship behaviour: not analysed in detail. The male constructed a mating web as typical of other *Steatoda* species. The female soon approached him for copulation. Copulatory posture as in *S. triangulosa*, but both palps stretched straight (Fig. 87a, c).

Sperm induction: was observed in the female web 1 h after copulation, but not recorded in detail.

Entire copulation duration occupied 36 min on average. Total number of insertions 9. Total insertion time about 5 min. During insertion haematodochae pulsated rhythmically. Towards the end of copulation a large whitish secretion droplet protruded from the epigynum (Fig. 87d). The mating plug presumably originates from the mouthparts as in *S. triangulosa* and is transferred via insertion (Fig. 87b, c).

This observation on *S. castanea* agrees with those of GERHARDT (1926): construction of a mating web regularly occurred; insertions lasted 1–5 min; one copulation consisted of 9 insertions. According to GER-

HARDT (1926) ipsilateral insertion took place. The whitish to bluish mating plug secretion was once observed on the male palp after palpal chewing, which strengthens the assumption that it originates from glands of the mouthparts. Apparently the mating plug does not impede a further copulation as remating was observed (GERHARDT 1926).

42 *Steatoda grossa* (C. L. KOCH 1838) (Fig. 88a–d)

Material: Austria: Innsbruck, inside house, ♂♀, Jan.–Dec. 2001 and Dec. 2003, leg. VOGEL. **Spain,** Canary Islands, Gran Canaria, Embalse de la Soria, ♂, 12.3.2001, 500 m, leg. KNOFLACH & THALER.

Mating behaviour was observed from four pairs. Sperm induction takes place independently of copulation. Precopulatory courtship may proceed with or without mating web and may involve silk throwing onto the female web. Copulation involves 1–5 insertions lasting about 10 min. During insertions haematodochae pulsate rhythmically. Apparently no mating plug is produced.

Courtship behaviour: Precopulatory courtship proceeded in two different ways, as in *S. paykulliana*. Two males constructed a mating web as typical of other *Steatoda* species (Fig. 88d). The silk layer was spun with a length of 2–5 cm and a height of 2–3 cm. On the mating web the male plucked with legs III in a rapid alternating sequence and performed spasmodic body jerks at the end of a plucking sequence (Fig. 88b, c), his legs II and III being strongly flexed. He also vibrated his abdomen. One of these males briefly threw strands of silk onto the female web and then started web spinning activities. In two other cases the male immediately threw strands of silk unto the female web (Fig. 88a) and started insertion after palpating the female 2 or 3 times, without spinning a mating web. This alternative precopulatory courtship lasted 3 and 5 min, precopulatory courtship with mating web 10.5 and 21 min. Both males which performed silk throwing only at the beginning, started construction of a mating web after the first insertion. The male usually courted before each insertion or insertion attempt, only once did another insertion follow immediately after the first. Silk throwing occurred also in the interval before the next inser-

Fig. 88a–d: Copulation in *Steatoda grossa*. **a:** Male throws strands of silk onto female web, which probably serves to reduce her web. **b:** Male plucking with legs III on the mating web. **c:** Female approach. **d:** Insertion of left palp on the mating web.

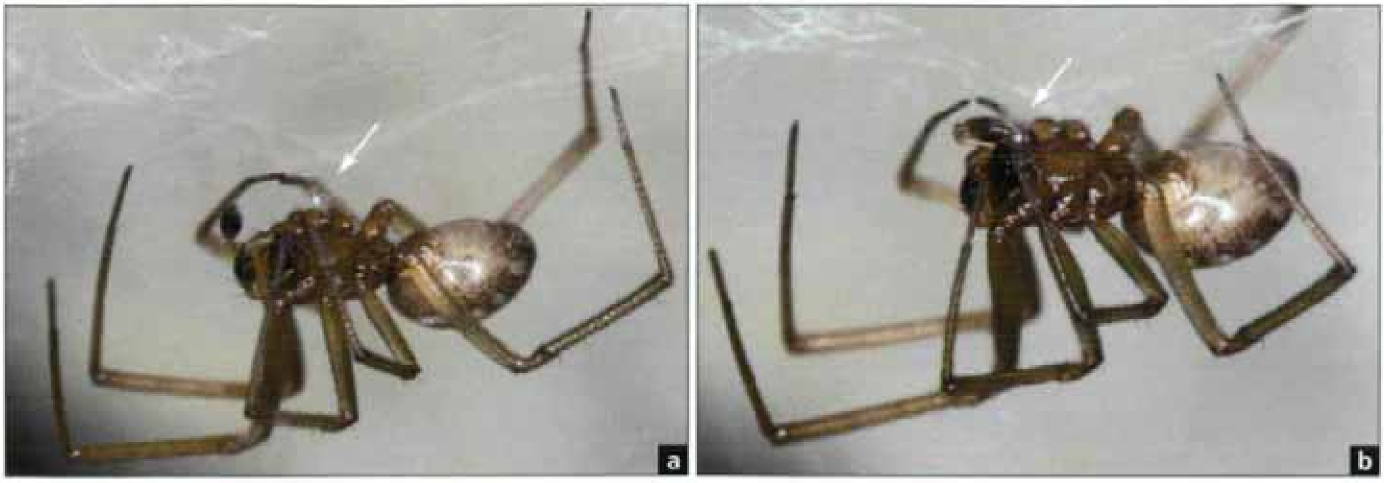


Fig. 89a, b: Sperm induction in *Steatoda grossa*. **a**: Construction of sperm web completed, sperm droplet just released (arrow) and male moved backwards. **b**: Left palp dipping into sperm droplet.

tion. This intermediate courtship lasted 1.7–5.0 min. Copulation proceeded by female approach and finally the male inserted his palp, which was directed straight forward. Copulatory posture typical of other Theridiidae (Fig. 88d), but inserted male palp kept straight. Copulatory courtship: During insertion rhythmical haematodochal pulsations took place, so that the female was passively moved, see also copulatory pattern.

Sperm induction: was observed once in the female web 1 h after copulation. Overall procedure lasted about 10 min, but probably was disturbed by the female. Another male was found terminating sperm induction outside the female web 1.5 h after copulation.

Entire copulation duration occupied 68.6 min on average (range = 40–123, n = 4). Total number of insertions 1, 2, 3 and 5. Total insertion time averaged 28.2 min (range = 19.5–38.0, n = 4).

Copulatory pattern: Copulation comprised 1–5 insertions, lasting 10.2 min on average (range = 0.3–19.5, n = 11). Insertion attempts in form of palpal jabs regularly occurred, in one copulation at an extraordinarily high rate of c. 150. During insertion haematodochae did not inflate once, but pulsated rhythmically. For a 17 min long insertion 378 haematodochal swellings were recorded. Number of haematodochal swellings was higher in the first part of insertion and gradually decreased. In the first 9 min of this insertion 23–29 swellings per minute took place (mean = 26, n = 9), in the second half 15–22 (mean = 18, n = 8). A male from Austria copulated with a female from Gran Canaria in a typical way. Three females became more restless and more aggressive towards the end of copulation.

Mating behaviour of *S. grossa* was investigated by GERHARDT (1925, 1926) and GWINNER-HANKE (1970), sub *Teutana grossa*. Both described regular construction of a mating web, but no silk throwing behaviour. Copulation was considered to involve only one insertion (GERHARDT 1925). Anyway, one pair was separated after the first insertion and placed together again after about 15 min and then continued with the second insertion (GERHARDT 1925). This second insertion was treated as a separate copulatory observation, although probably copulation was continued. A further three observations appear to refer always to the same pair and therefore are rematings. Could this have been the reason that males performed only one insertion? In GWINNER-HANKE (1970) males were allowed to remate and then performed only one insertion, and also a more dissociated courtship behaviour and longer stridulation. Among numerous insertion attempts five successful insertions with rhythmical haematodochal swellings were recorded by GERHARDT (1925), lasting 12 min on average (range = 5–20, n = 5). GWINNER-HANKE (1970) reported an insertion duration of mostly 10–30 min, once even 112 min, while insertions of 2–7 min duration were regarded as failed. A mating plug was not mentioned and rematings apparently were possible. Thus, most of the behavioural traits agree with the present observations, with the exception of insertion number, which appears

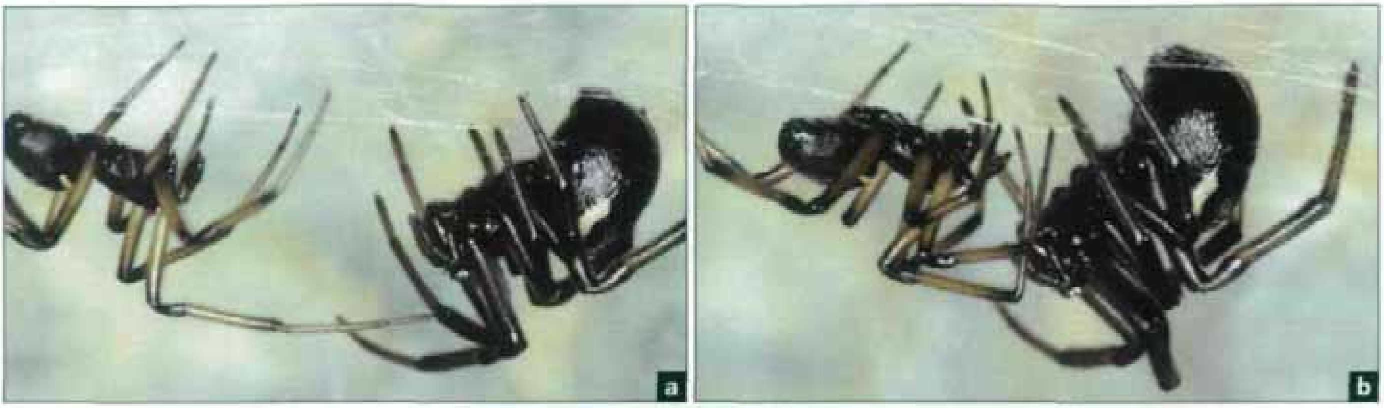


Fig. 90a–c: Copulation in *Steatoda paykulliana*. **a:** Female approach upon male plucking. **b:** Couple shortly before insertion. **c:** Insertion of left palp.

to be higher in virgin pairings. According to GWINNER-HANKE (1970) *S. grossa* produced a scraping stridulatory sound, which was audible to the human ear.

43 *Steatoda paykulliana* (WALCKENAER 1805) (Fig. 90, 91)

Material: **Cyprus**, Paphos surroundings, Coral Bay, ♂♀, 12.2.1995; Polis, Akamas peninsula, Fontana Amorosa, ♂♀, 16.2.1995; Akamas peninsula southern coast, Ag. Georgios surroundings, ♂♀, 17.2.1995; all leg. KNOFLACH & THALER. Adult males were frequently found guarding the subadult female shortly before her maturation.

Mating behaviour was observed from three pairs. Sperm induction takes place independently of copulation. Courtship may proceed with or without mating web. Copulation involves a few insertions lasting 1–6 min. During these insertions haematodochae pulsate rhythmically. Apparently no mating plug is produced.

Courtship behaviour: Abdominal vibrations were the basic male movements when in contact with the female web. Females, although freshly moulted virgins, appeared to be rather aggressive. They rushed out from their retreat and sometimes threw viscous silk, but were soon calmed by the male's movements. Courtship proceeded in two different ways. One male constructed a mating web as typical of other *Steatoda* species (Fig. 91). Precopulatory courtship lasted 109 min, including long resting periods. In two cases the male immediately threw strands of silk onto the female but also onto her web. A similar, but more distinct phenomenon regularly occurs in the genus *Latrodectus* as leg-binding. This alternative mode of courtship in *Steatoda paykulliana* lasted only a few seconds up to 2 min. After plucking with legs II in a rapid alternating sequence the female approached him within seconds and assumed the copulatory posture. Abdominal vibrations and plucking were sometimes repeated before the next insertions. Copulatory posture typical of other Theridiidae (Fig. 90b, c, 91).

Fig. 91: Copulation in *Steatoda paykulliana* from Cyprus. Insertion of right palp. Note dense mating web. Leg contact present.

Fig. 92a, b: Copulation in *Steatoda triangulosa* from Tenerife. (a, b) Insertion of right and left palp. Note stretched out male palp and loose leg contact.

Sperm induction: not observed. One male left the female web 10 min after the second insertion, another one 20 min after the final insertion.

Entire copulation duration occupied 7, 17 and 19 min. Total number of insertions 2, 3 and 18 (two longer and 16 short ones). Total insertion time averaged 4.5, 6 and 11 min.

Copulatory pattern: Copulation comprised 2–3 insertions, lasting 1–6 min (mean = 2.9, n = 7). In one pair, a further 16 short insertions (5–20 s duration) followed after two longer ones. Before successful insertion the male sometimes pushed his palp against the epigynum. During insertions haematodochae pulsated rhythmically. The volume of haematodochae was rather small when inflated (Fig. 90c, 91). With the end of copulation two females became aggressive and tried to prey on the males. Both males performed silk throwing during courtship instead of web spinning.

Mating behaviour of S. *paykulliana* has been observed previously by BRISTOWE (1931), GERHARDT (1933) and KULLMANN (1964), all sub *Lithyphantes paykullianus*, and corresponds to the present observations: two insertions of about 5–6 min duration, sometimes followed by some shorter, irregular ones; insertions with haematodochal pulsation (GERHARDT 1933). A mating plug was not mentioned. Construction of a mating web took place in all observations, but no hint of the male's silk throwing behaviour could be found, as recorded for the present pairings. Sperm induction once took place 45 min after copulation, lasting altogether 17 min, of which 2 min were used for construction of the sperm web and 15 min for induction (GERHARDT 1933). KULLMANN (1964) observed male cohabitation in the web of a subadult female for 8 days until her maturation.

44 *Steatoda triangulosa* (WALCKENAER 1802) (Fig. 92–94)

Material: Greece: E Crete, near Ierapetra, Sarakinas gorge, above Mithi, 150–200 m, ♂, 28.9.1998. E-Crete, Ierapetra – Sitia, dried up brooklet near Lastros, ♀, 29.9.1998. Kefallonia, Lassi, from house walls, ♂♀, 19.9.1999. Karpathos, above Volada, c. 600 m, ♀, 20.9.2000, under stone. **Corsica**: Cargèse, ♂, 21.11.2000. **Spain**, Canary Islands, Tenerife: Puerto de la Cruz, ♂♀, 3.–10.1.2003, from house walls, leg. KNOFLACH & THALER. **Yemen**, Sana'a, ♂♀, 18.6.1998, leg. VAN HARTEN.

Mating behaviour was observed from four pairs. Sperm induction takes place independently of copulation. Copulation proceeds via mating threads and involves 2–3 insertions lasting about 1.5 min. During these insertions haematodochae pulsate rhythmically. At the end, a mating plug is transferred from the mouthparts to the epigynum by several short palpal applications.

Courtship behaviour: When in contact with the female web, the male vibrated his abdomen at high frequency for a rather long time (12–20 s in one male). The female was rather active and vibrated her body in response, but more vigorously, at lower frequency and usually for a shorter time (3 s in one female). Usually, the male approached the female immediately, palpated her and then started to construct the mating web. In two cases the male briefly threw strands of

Fig. 93a–e: Copulation in *Steatoda triangulosa* from Tenerife. **a, b**: Production of mating plug secretion (arrows), originating from mouthparts. **c, d**: Transfer of plug secretion upon insertion. Note stretched out male palp. **e**: Epigynum covered with secretion (arrow).

silk onto the female with his hindlegs, which is known as leg-binding in *Latrodectus*, and then started web spinning activities. He removed threads and installed numerous new ones while moving to and from the female at a range of 2–4 cm. At a distance from the female he paused for a while and performed slight, but continuous abdominal vibrations. When approaching and palpating her again, she vibrated her body. Finally, apart from abdominal vibrations, he started plucking with legs II in a rapid alternating sequence on the silk layer. One male also used leg I. This movement caused the female to approach him within seconds and to assume the copulatory posture. Before each insertion or sequence of insertion attempts the same courting procedure took place. Copulatory posture was variable, sometimes typical of other Theridiidae (Fig. 92a, b), but sometimes the female turned around at the beginning of insertion, so that the partners faced the same direction. This posture resembles that of *Crustulina*. After insertion the female returned to her retreat. Precopulatory courtship lasted 12 min on average (range = 2–20, n = 4), but only 1–3 min be-

Fig. 94: Copulation in *Steatoda triangulosa* from Yemen. Transfer of mating plug secretion via male palp from mouthparts to epigynum. Arrows point to secretion.

fore the next insertion. Copulatory courtship: During insertions strong, rhythmical haematodochal pulsations took place, so that the female was passively moved.

Sperm induction: was observed once in the female web 15 min after copulation and once outside the female web 1.2 h after copulation. Spinning of the sperm web with induction lasted 11.6 min, 2.6 min of which were used for construction of the sperm web. The sperm droplet was absorbed within 9 min and by 66 dipping movements (n = 1). In the second observation sperm induction took 13.5 min.

Entire copulation duration occupied 16 min on average (range = 9–23, n = 4). Total number of insertions 2 (n = 2) and 3 (n = 2). Total insertion time averaged 3.5 min (range = 2.2–4.2, n = 4).

Copulatory pattern: Copulation comprised 2–3 insertions (Fig. 92a, b), the first two of which lasted 1.7 min on average (range = 0.7–2.1, n = 8). Insertions were regularly preceded by a number of insertion attempts or palpal jabs (mean = 9 per insertion, range = 1–21, n = 7). Haematodochae did not inflate once during insertions, but pulsated rhythmically. A third insertion, if performed at all, lasted only 18 and 26 s and formed part of the mating plug transfer. After the second insertion, the male produced the mating plug secretion in his mouthparts and transferred it to the palps by palpal chewing (Fig. 93a, b). The secretion was discharged between labium and chelicerae, which were widely opened, the palps being dipped in between. The secretion was finally transferred to the epigynum by numerous short palp-epigynum contacts without haematodochal swelling (Fig. 93c, d, 94). In two cases 61 contacts were recorded. They were vigorous palpal jabs against the epigynum, which did not proceed in continuous succession, but in 6 and 9 sequences were interrupted by courtship. The female then assumed a more horizontal copulatory posture (Fig. 93c, d). When separating, a large secretion droplet protruded from the epigynum (Fig. 93e, 94). After copulation the male intensively chewed and cleaned his palps. Towards the end of copulation females became more and more aggressive and tried to attack the males. One old virgin female from Karpathos was paired with a male from Corsica. Courtship and insertions proceeded normally, but before formation of the mating plug, the female preyed upon the male and sucked him out.

These observations agree well with GERHARDT (1933) and BRAUN (1956), both sub *Teutana triangulosa*: construction of a mating web, 2–3 insertions of about 1.5 min duration (once even 6 min, BRAUN 1956) and 3 insertions of 2, 3 and 1.5 min duration (GERHARDT 1933). Also formation of the mating plug has already been described (BRAUN 1956). Sperm induction took place 1.5 h after copulation, lasting altogether 13 min, of which 5 min were used for construction of the sperm web and 8 min for induction (n = 4) (BRAUN 1956). GERHARDT (1933) observed sperm induction 20 min after copulation and recorded 5–6 min for actual sperm induction (without spinning).

45 *Theridion* (?) *nigrovariegatum* SIMON 1873 (Fig. 95a, b)

Material: **Italy**, Venezia Giulia, Trieste, ♂, 4.5.1994, leg. BERTRANDI. **Austria**: Northern Tyrol, Innsbruck, Kranebitten, ♀, 6.6.1994, leg. KNOFLACH. Innsbruck, Martinswand, ♂♀, 17.6.1994 and 25.5.1995, leg. KNOFLACH & THALER.

Mating behaviour was observed from five pairs, among them one female and one male were allowed to remate. Courtship

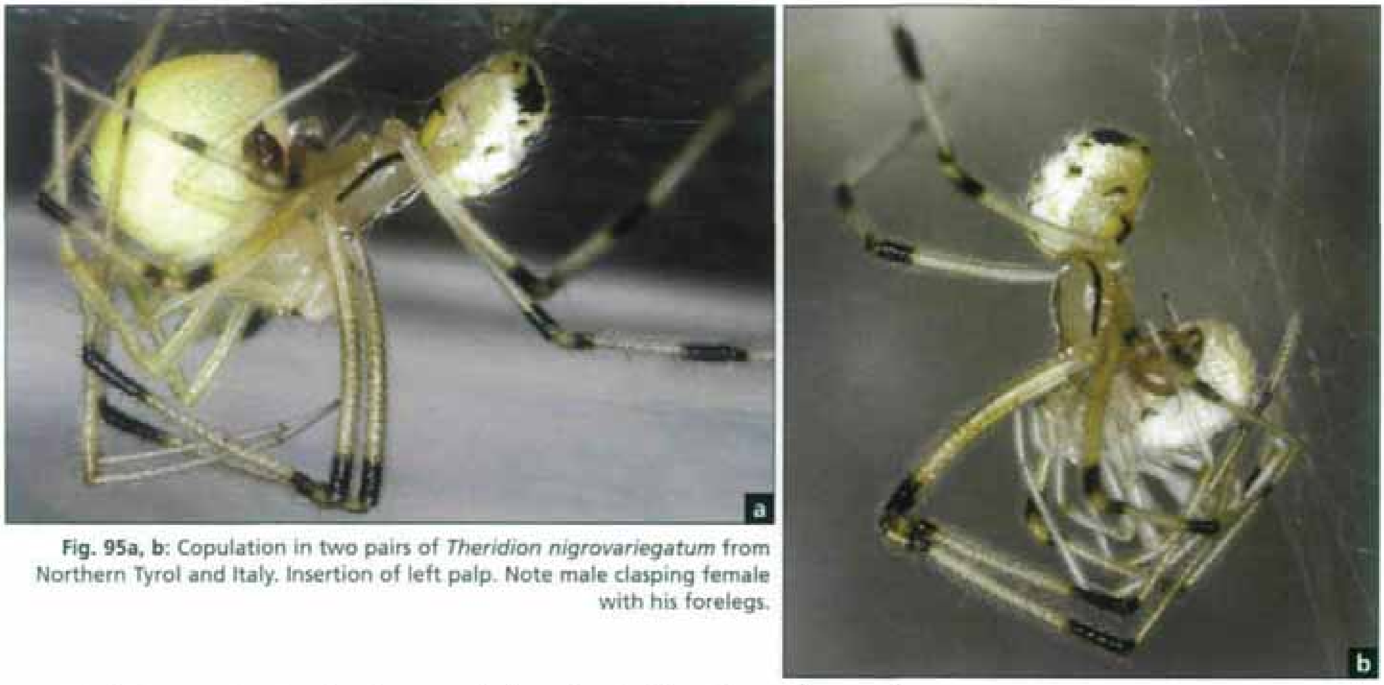


Fig. 95a, b: Copulation in two pairs of *Theridion nigrovariegatum* from Northern Tyrol and Italy. Insertion of left palp. Note male clasping female with his forelegs.

proceeds without a mating thread and copulation by male approach. Sperm induction takes place independently of copulation. Copulation usually consisted of two insertions only. A mating plug was not discernible. Females apparently remate.

Courtship behaviour: During distant courtship, males pulsated their abdomen and jerked, once also plucking with forelegs was performed. There was no web-spinning behaviour. During the direct contact phase of courtship the male palpated the female's abdomen with his palps and forelegs and thereby induced her to assume the inclined copulatory posture. Also her epigynal region was palpated. Precopulatory courtship lasted 1–17 min. The male approached the female for copulation with bent forelegs. Copulatory posture as typical of other theridiid species, with intense leg contact (Fig. 95a, b). The male tightly clinched the female with his long forelegs. Once a pair remained for 8 min in this posture before the actual insertion started. Interestingly, during insertion the inflated male palpal organ is kept at right-angles to the basal limbs of the palp. Copulatory courtship: At the beginning of insertion the male regularly showed pumping movements of the entire body, by which maximal haematodochal expansion was achieved. Then a period of complete motionlessness followed. Some males intensively vibrated their abdomen by bouncing it sidewards, usually towards the end of insertion. As the abdomen is rotated against the prosoma, these movements appear to reflect stridulation. Postcopulatory courtship: After copulation the females usually became active, males often vibrated their abdomen. One male regularly performed abdominal vibrations for a period of 45 min, but only until sperm induction. Afterwards he remained motionless for more than 6 h.

Sperm induction: Sperm induction has been observed only once, 45 min after copulation. The whole procedure of spinning of the sperm web with induction lasted 16 min. For absorption of the sperm droplet the male dipped his palps into the droplet for a rather long time, 20–30 s at the beginning and later more than 1 min. The sperm droplet was very large and after induction there was still a large portion left on the web. For the next half hour the male remained motionless, holding the sperm web with his legs.

Entire copulation duration averaged 21 min (range = 7–37, n = 5). Total number of insertions 2 (n=4) or 3 (n=1). Total insertion time 8.7 min on average (range = 4.1–16.0).

Copulatory pattern: Each insertion lasted 4.4 min on average (range = 3.0–5.5). During insertion haematodochae were highly inflated, reaching an enormous volume (Fig. 95b). The opposite male palp is spread sideways. No further insertions were observed in a period of 7.5 and 2 h. Once a female expelled her mate from the web 1.2 h after copulation.

Generic placement: *T.* (?) *nigrovariegatum* does not follow the *Theridion*-type of copulation according to the time and duration of sperm induction and number of insertions. Also morphology of the male palp differs from *Theridion* by the presence of only one tegular apophysis. Its generic placement therefore has to be reconsidered.

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Zusammenfassung

Diversität im Fortpflanzungsverhalten von Kugelspinnen (Araneae, Theridiidae). Kugelspinnen zeigen eine große Vielfalt in Morphologie und Lebensweise. Diese Diversität spiegelt sich auch im Fortpflanzungsverhalten wieder. Dieser Übersicht zum Fortpflanzungsverhalten der Kugelspinnen liegen Beobachtungen an etwa 70 Arten zugrunde. Davon werden 45 Arten im Detail und 30 zum ersten Mal beschrieben. In einem allgemeinen ersten Abschnitt werden die hauptsächlichen Elemente der Kopula vorgestellt und verglichen. Die Spermaaufnahme umfasst den Bau des Spermanetzes und die eigentliche Tasterfüllung, die Aufnahme des Spermatropfens. Entsprechend dem Zeitpunkt der Spermaaufnahme bestehen zwei Typen. Beim plesiomorphen *Steatoda*-Typ findet die Spermaaufnahme unabhängig von der Kopula, irgendwann zwischen Reifehäutung und Kopula statt, beziehungsweise zwischen den Kopulationen. Die Zeitspanne zwischen Samenaufnahme und Kopula ist verhältnismäßig groß, das Sperma wird demnach für längere Zeit in den Tastern gespeichert. Beim abgeleiteten *Theridion*-Typ bildet die Spermaaufnahme einen festen Bestandteil der Kopula. Die Männchen unterbrechen die Kopula mehrmals zur Tasterfüllung, sodass Kopulationsserien (Sequenzen von Insertionen) und Spermaaufnahmen alternieren. Hier verbleibt das Sperma nur kurzfristig in den Tastern, da die Spermaübertragung unmittelbar anschließt. Die Spermaaufnahme findet in unmittelbarer Nachbarschaft zum Weibchen statt und läuft wesentlich rascher ab als beim *Steatoda*-Typ. In der Zahl der Spermanetze übertreffen die *Theridion*-Arten alle bisher bekannten Spinnen.

Bei einigen Vertretern des *Steatoda*-Typs ist das Werbeverhalten stark ritualisiert. Das Männchen spinnt einen Hochzeitsfaden oder ein Hochzeitsgespinst im Netz des Weibchens, an dem es solange wirbt, bis das Weibchen sich zur Kopula annähert. Die Kopula findet am Hochzeitsgespinst statt. Bei den Arten des *Theridion*-Typs ist die Werbung hingegen plastisch, ein Hochzeitsgespinst fehlt, das Männchen nähert sich dem Weibchen zur Kopulation.

Das Kopulationsmuster, das sich aus der Zahl und der Dauer der Insertionen und deren zeitlichem Auftreten ergibt, ist bei den Vertretern des *Theridion*-Typs spezifisch. Manche *Theridion*-Arten, z.B. der *T. melanurum*-Gruppe, weisen gleichartige Kopulationsserien auf. In der *T. varians*-Gruppe sind die Kopulationsserien differenziert, wie schon die verschiedene Dauer der Insertionen zeigt. Die Kopula beginnt mit einer Pseudokopula, einer einleitenden Sequenz von Insertionen, bei der kein Sperma übertragen wird. Die Insemination beginnt erst nach der ersten Spermaaufnahme. Bei diesen Arten wird in der letzten Kopulationserie ein Begattungszeichen gebildet.

Insgesamt wechseln die Männchen des *Theridion*-Typs ihre Taster häufiger, die Gesamtzahl der Insertionen ist durchschnittlich höher als beim *Steatoda*-Typ. Die Insertionsdauer ist beim *Theridion*-Typ vergleichsweise niedrig, die eigentliche Spermaübertragung benötigt bei vielen Arten nur einen Bruchteil der gesamten Kopulationsdauer. Beim *Steatoda*-Typ decken sich Dauer von Spermatransfer und gesamter Kopula weitgehend. Die Arten des *Theridion*-Typs investieren einen großen Anteil der Kopulationszeit in andere Funktionen wie Pseudokopula, Bau der Spermanetze, Partnerbewachung und Begattungszeichen. Die Eingliederung der Spermaaufnahme in das Kopulationsverhalten dürfte durch rasche Wiederholung der Kopulation entstanden sein. Dies scheint eine Möglichkeit, den Befruchtungserfolg zu erhöhen. Durch die wiederholten Kopulationen wird das Weibchen lange anderen Männchen vorenthalten.

Die Genitalstrukturen entelegyner Spinnen korrelieren sehr streng, sodaß ein Taster nur auf eine Seite des weiblichen Genitalorgans passt. Als Charakteristikum für entelegyne Spinnen galt bis vor kurzem ipsilaterale Insertion: der Embolus des rechten Tasters inseriert in den rechten Einführungsgang der Epigyne und vice versa. Kugelspinnen verhalten sich jedoch auch in dieser Hinsicht heterogen. Bei *Argyrodes argyrodes* und *Steatoda bipunctata* wurde eindeutig ipsilaterale Insertion beobachtet. Im Gegensatz dazu inserieren die Männchen der *Theridion varians*-Gruppe kontralateral, der rechte Taster inseriert in den linken Einführungsgang und umgekehrt. Die Männchen der Eintasterspinnen können einhergehend mit dem sexuellen Schocktod nur ein Receptaculum der polyandrischen Weibchen inseminieren. Sie sind jedoch in der Lage, die noch virginelle Seite der Vulva auszuwählen und fakultativ ipsi- oder kontralateral zu inserieren.

Bei einigen Kugelspinnen dient die letzte Phase der Kopula der Bildung eines Begattungszeichens. Dieses versiegelt die weibliche Genitalöffnung temporär oder permanent, und verzögert oder verhindert damit eine weitere Kopula. Begattungszeichen sind bei Kugelspinnen mehrfach und auf verschiedene Weise entstanden. Bei *Steatoda triangulosa* stammt es von Drüsen der Mundregion, bei *Argyrodes argyrodes* und *Steatoda bipunctata* von Drüsen des männlichen Tasters. Bei der *Theridion varians*-Gruppe wird das Begattungszeichen von Sekreten des männlichen und weiblichen Genitaltraktes gebildet. Das männliche Sekret wird über das letzte Spermanetz auf die Taster und schließlich auf die Epigyne übertragen.

Taxonomie: Für zwei Arten wird eine neue Gattungskombination vorgeschlagen: *Keijia kijabei* (BERLAND 1920) nov. comb. (aus *Theridion*), *Theridion ohlerti* THORELL 1870 (nec *Achaearanea o.*).

References

ABALOS J.W. & E.C. BAEZ (1963): On spermatic transmission in spiders. — Psyche **70**: 197–207.

ABALOS J.W. & E.C. BAEZ (1967): The spider genus *Latrodectus* in Santiago dell Estero, Argentina. — In: RUSSELL F.E. & P.R. SAUNDERS (Eds.): Animal Toxins. Pergamon Press, Oxford, New York: 59–74.

AGNARSSON I. (in press): Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). — Zool. J. Linnean Soc.

ANDRADE M.C.B. (1996): Sexual selection for male sacrifice in the Australian redback spider. — Science **271**: 70–72.

ANDRADE M.C.B. & E.M. BANTA (2002): Value of remating and functional sterility in redback spiders. — Animal Behaviour **63**: 857–870.

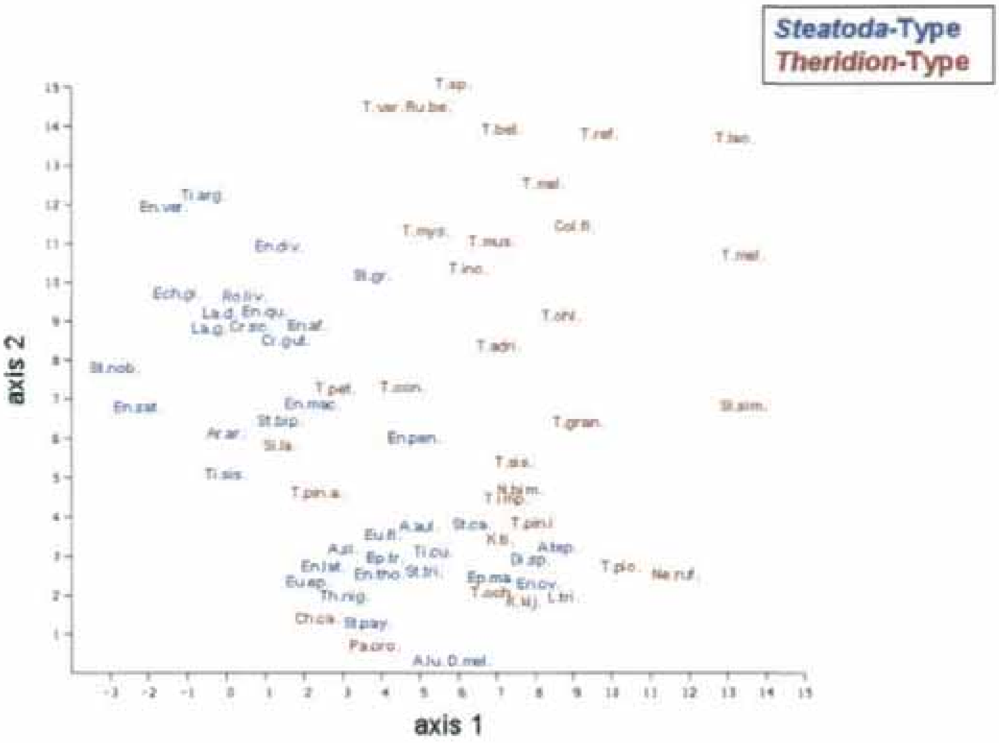
BERENDONCK B. & H. GREVEN (2002): Morphology of female and male genitalia of *Latrodectus revivensis* SHULOV, 1948 (Araneae, Theridiidae) with regard to sperm priority patterns. — Proc. 19th Europ. Coll. Arachnol. (Aarhus 2000): 157–167.

BERLAND L. (1920): Araneae (2^{e} partie). — Voyage de Ch. ALLUAUD et R. JEANNEL en Afrique Orientale (1911–1912). Résultats scientifiques, Arachnides **4**: 95–180.

BHATNAGAR R.D.S. & J.G. REMPEL (1962): The structure, function, and postembryonic development of the male and female copulatory organs of the black widow spider *Latrodectus curacaviensis* (MÜLLER). — Can. J. Zool. **40**: 465–510.

BONNET P. (1935): *Theridion tepidariorum* C.L.KOCH, araignée cosmopolite: répartition, cycle vital, moeurs. — Bull. Soc. hist. nat. Toulouse **68**: 335–385.

BOSMANS R. & J. VAN KEER (1999): The genus *Enoplognatha* PAVESI, 1880 in the Mediterranean region (Araneae: Theridiidae). — Bull. Br. arachnol. Soc. **11**: 209–241.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K.sij.
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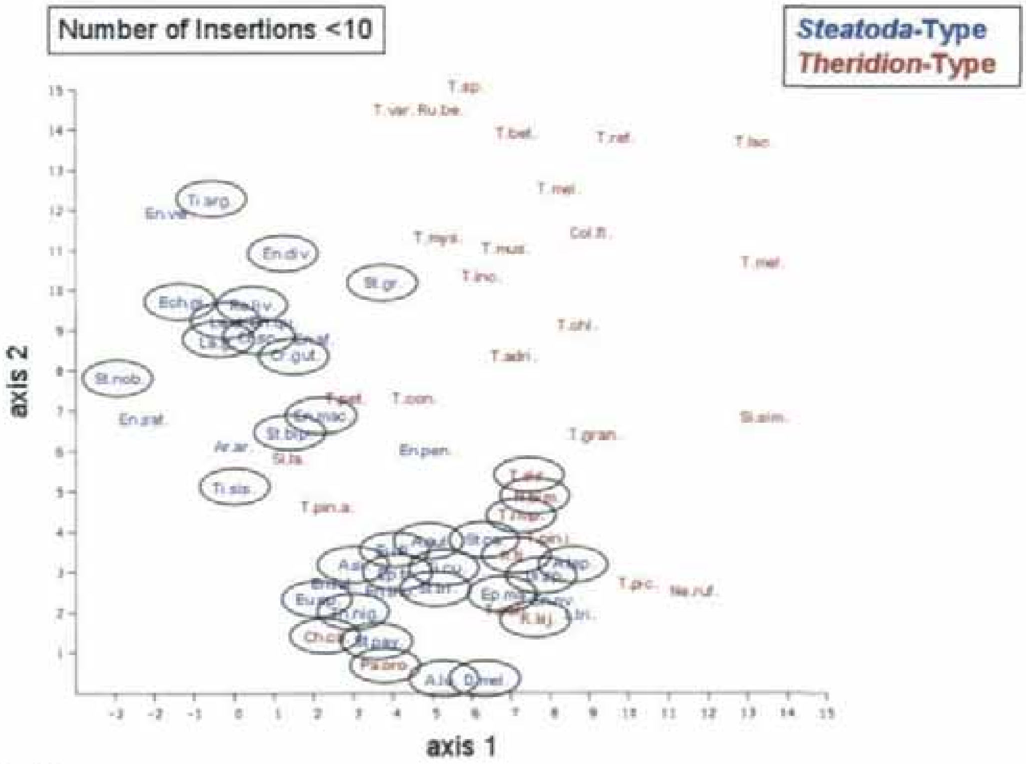
Fig. I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Theridion-Type
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Fig. II

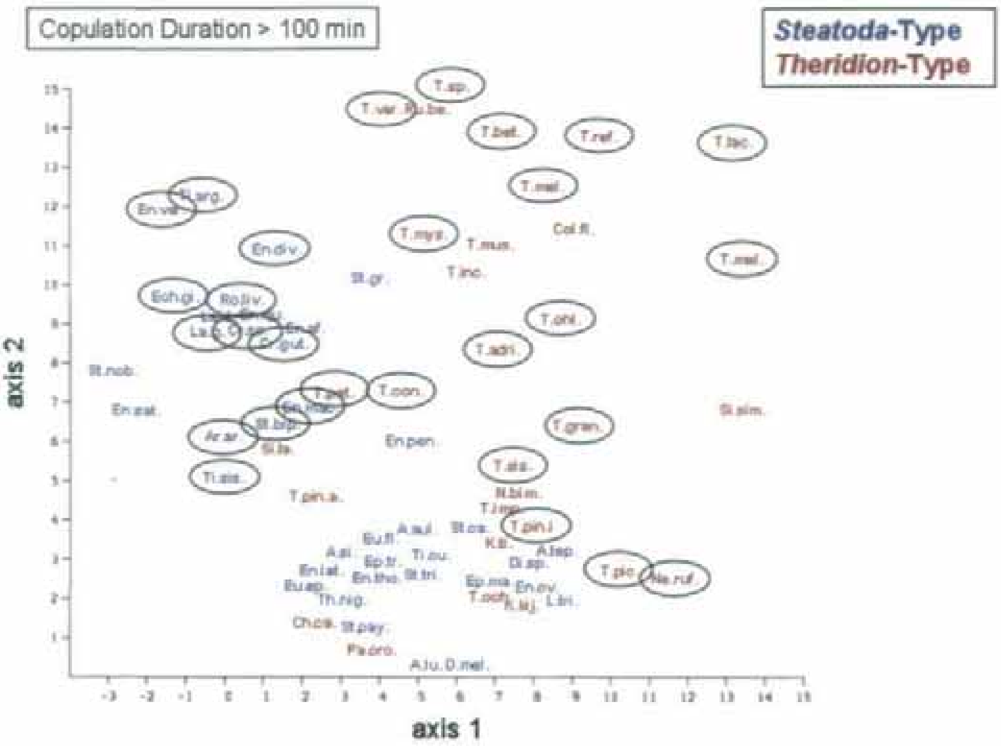

Fig. III

Appendix, **Fig. I–III**: Principal coordinate analysis based on 29 variables of copulatory behaviour, male and female body size, web and stratum (see DIGBY & KEMPTON 1987). Data were dichotomised and assessed as Euklidian quadratic distance matrix. Procedure computed in MATLAB; two negative singular values eliminated. Plot program in Erlgraph. Axis 1 roughly reflects number of insertions, axis 2 duration of copulation. In (II) species with low number of insertions are outlined, in (III) species with long copulation duration. Variables: **1** Duration of courtship. **2** Copulation duration. **3** Time of actual sperm transfer. **4** Number of insertions. **5** Number of sperm inductions during copulation. **6** Male body length. **7** Female body length. **8** Ratio of male/female body size. **9** Mating plug absent or present. **10** Duration of formation of mating plug. **11** Pseudocopulation absent or present. **12** Duration of pseudocopulation. **13** Moment of sperm induction. **14** Duration of sperm induction. **15** Courtship via mating web or by male approach. **16** Haematodochae inflate only once per insertion or pulsate. **17** Type of mating plug (oral, palpal, epigastric; parts of palp). **18** Sexual cannibalism (not observed, facultative or obligatory). **19** Sexual size dimorphism less pronounced or pronounced. **20** Male chelicerae normal, slightly enlarged or enlarged. **21** Stratum: ground or above ground (low vegetation, canopy, bark and walls). **22** Web-building or web reduced. **23** Male palpal tibia short or long and slender. **24** Embolus short and stout, intermediate or long, thread-like. **25** Length of female copulatory duct normal or long and convoluted. **26** Degree of sclerotisation (less sclerotised, sclerotised). **27** Course of sperm duct normal or convoluted. **28** Paracymbium hook-like or hood-like. **29** Maternal care (normal brood care or periodically social).

Braun R. (1956): Zur Biologie von *Teutana triangulosa* (Walck.) (Araneae: Theridiidae, Asageneae). — Z. wiss. Zool. **159**: 255–318.

Braun R. (1963): Zur Sexualbiologie der *Theridion sisyphium*-Gruppe (Arach., Aran., Theridiidae). — Zool. Anz. **170**: 91–107.

Braun R. (1964): Die Sexualbiologie von *Theridion betteni* Wiehle 1960, ein Beitrag zur systematischen Differenzierung der *Theridion melanurum*-Gruppe (Arach., Aran., Theridiidae). — Zool. Anz. **173**: 379–387.

Breene R.G. & M.H. Sweet (1985): Evidence of insemination of multiple females by the male black widow spider, *Latrodectus mactans* (Araneae, Theridiidae). — J. Arachnol. **13**: 331–335.

Bristowe W.S. (1929): The mating habits of spiders, with special reference to the problems surrounding sex dimorphism. — Proc. Zool. Soc. London **1929**: 309–358.

Bristowe W.S. (1931): The mating habits of spiders: a second supplement with the description of a new thomisid from Krakatau. — Proc. Zool. Soc. London **1931**: 1401–1412.

Bristowe W.S. (1958): The World of Spiders. — Collins, London, Glasgow: 1–304.

Carico J.E. (1978): Predatory behaviour in *Euryopis funebris* (Hentz) (Araneae: Theridiidae) and the evolutionary significance of web reduction. — Symp. Zool. Soc. London **42**: 51–58.

Dahl F. (1902): Abgebrochene Copulationsorgane männlicher Spinnen im Körper der Weibchen. — Sber. Ges. naturf. Freunde Berlin **1902**: 36–47.

Digby P.G.N. & R.A. Kempton (1987): Multivariate analysis of ecological communities. — Chapmann & Hall Ltd., New York: 1–206.

Eberhard W.G. (1985): Sexual selection and animal genitalia. — Harvard University Press, Cambridge: 1–244.

Eberhard W.G. (1996): Female control: Sexual selection by cryptic female choice. — Princeton University Press, Princeton, New Jersey: 1–501.

Elgar M.A. (1995): The duration of copulation in spiders: comparative patterns. — Rec. Western Austral. Mus., Suppl. **52**: 1–11.

Elgar M.A. (1998): Sperm competition and sexual selection in spiders and other arachnids. — In: Birkhead T.R. & A.P. Moller (Eds.): Sperm Competition and Sexual Selection. Academic Press, San Diego... Toronto: 307–339.

Forster L.M. (1992): The stereotyped behaviour of sexual cannibalism in *Latrodectus hasselti* Thorell (Araneae: Theridiidae): the Australian redback spider. — Austral. J. Zool. **40**: 1–11.

Forster R.R., Platnick N.I., & J. Coddington (1990): A proposal and review of the spider family Synotaxidae (Araneae, Araneoidea), with notes on theridiid interrelationships. — Bull. Am. Mus. Nat. Hist. **193**: 1–116.

Gerhardt U. (1921): Vergleichende Studien über die Morphologie des männlichen Tasters und die Biologie der Kopulation der Spinnen. — Arch. Naturgesch. **(A) 87**: 78–247, 3pl.

Gerhardt U. (1923): Weitere sexualbiologische Untersuchungen an Spinnen. — Arch. Naturgesch. **(A) 89**: 1–225, 3 pl.

Gerhardt U. (1924): Weitere Studien über die Biologie der Spinnen. — Arch. Naturgesch. **(A) 90**: 85–192.

Gerhardt U. (1925): Neue sexual-biologische Spinnenstudien. — Z. Morph. Ökol. Tiere **3**: 567–816.

Gerhardt U. (1926): Weitere Untersuchungen zur Biologie der Spinnen. — Z. Morph. Ökol. Tiere **6**: 1–77.

Gerhardt U. (1927): Neue biologische Untersuchungen an einheimischen und ausländischen Spinnen. — Z. Morph. Ökol. Tiere **8**: 96–186.

Gerhardt U. (1928): Biologische Studien an griechischen, corsischen und deutschen Spinnen. — Z. Morph. Ökol. Tiere **10**: 576–675.

Gerhardt U. (1933): Neue Untersuchungen zur Sexualbiologie der Spinnen, insbesondere an Arten der Mittelmeerländer und der Tropen. — Z. Morph. Ökol. Tiere **27**: 1–75.

Gonzalez A. (1989): Analisis del compartomiento sexual y production de ootecas de *Theridion rufipes* (Araneae, Theridiidae). — J. Arachnol. **17**: 129–136.

Gwinner-Hanke H. (1970): Zum Verhalten zweier stridulierender Spinnen *Steatoda bipunctata* Linné und *Teutana grossa* Koch (Theridiidae, Araneae), unter besonderer Berücksichtigung des Fortpflanzungsverhaltens. — Z. Tierpsychol. **27**: 649–678.

Heimer S. & W. Nentwig (1991): Spinnen Mitteleuropas. Ein Bestimmungsbuch. — Paul Parey Verl., Berlin, Hamburg: 1–543.

Helsdingen P.J. van (1965): Sexual behaviour of *Lepthyphantes leprosus* (Ohlert) (Araneida, Linyphiidae) with notes on the function of the genital organs. — Zool. Meded. **41**: 15–42.

Helsdingen P.J. van (1983): Mating sequence and transfer of sperm as a taxonomic character in Linyphiidae (Arachnida: Araneae). — Verh. Naturwiss. Vereins Hamburg (NF) **26**: 227–240.

Helversen O. von (1976): Gedanken zur Evolution der Paarungsstellung bei den Spinnen (Arachnida: Araneae). — Entomol. Germ. **3**: 13–28.

Hippa H. & I. Oksala (1983): Cladogenesis of the *Enoplognatha ovata* group (Araneae, Theridiidae). — Annales Entomol. Fennici **49**: 71–74.

Hirschberg D. (1969): Beiträge zur Biologie, insbesondere der Brutpflege einiger Theridiidae. — Z. wiss. Zool. **179**: 189–252.

Huber B.A. (1995): The retrolateral tibial apophysis in spiders — shaped by sexual selection? — Zool. J. Linnean Soc. **113**: 151–163.

Huber B.A. (1998): Spider reproductive behaviour: a review of Gerhardt's work from 1911–1933, with implications for sexual selection. — Bull. Br. arachnol. Soc. **11**: 81–91.

Huber B.A. & A. Senglet (1997): Copulation with contralateral insertion in entelegyne spiders (Araneae: Entelegynae: Tetragnathidae). — Netherlands J. Zool. **47**: 99–102.

Knoflach B. (1994): Zur Genitalmorphologie und Biologie der *Crustulina*-Arten Europas (Arachnida: Araneae, Theridiidae). — Mitt. schweiz. entomol. Ges. **67**: 327–346.

Knoflach B. (1996): Das Männchen von *Simitidion agaricographum* (Levy & Amitai) (Arachnida: Araneae, Theridiidae). — Ber. naturwiss.-med. Vereins Innsbruck **83**: 149–156.

Knoflach B. (1997): Zur Taxonomie, Verbreitung und Sexualbiologie von *Theridion adrianopoli* Drensky (Arachnida: Araneae, Theridiidae). — Ber. naturwiss.-med. Vereins Innsbruck **84**: 133–148.

Knoflach B. (1998): Mating in *Theridion varians* Hahn and related species (Araneae: Theridiidae). — J. nat. Hist. **32**: 545–604.

Knoflach B. (1999): The comb-footed spider genera *Neottiura* and *Coleosoma* in Europe (Araneae, Theridiidae). — Mitt. schweiz. entomol. Ges. **72**: 341–371.

Knoflach B. (2000): Acrobatic copulation in the theridiid spider *Dipoena melanogaster* (C.L. Koch, 1837). — Newsl. Br. arachnol. Soc. **89**: 8–10.

Knoflach B. (2002a): Copulation and emasculation in *Echinotheridion gibberosum* (Kulczynski, 1899) (Araneae, Theridiidae). — Proc. 19th Europ. Coll. Arachnol. (Aarhus 2000): 139–144.

Knoflach B. (2002b): Zum Fortpflanzungsverhalten der Kugelspinnen. Gefährlicher Sex. — Biol. uns. Zeit **3**: 166–173.

Knoflach, B. & S.P. Benjamin (2003): Mating without sexual cannibalism in *Tidarren sisyphoides* (Araneae, Theridiidae). — J. Arachnol. **31**: 445–448.

Knoflach, B. & A. van Harten (2000a): Palpal loss, single palp copulation and obligatory mate consumption in *Tidarren cuneolatum* (Tullgren, 1910) (Araneae, Theridiidae). — J. nat. Hist. **34**: 1639–1659.

Knoflach, B. & A. van Harten (2000b): Redescription of *Theridion lacticolor* Berland (Araneae, Theridiidae) with notes on mating behaviour. — Cimbebasia **16**: 215–222.

Knoflach B. & A. van Harten (2001a): *Tidarren argo* n.sp. (Araneae, Theridiidae) and its exceptional copulatory behaviour: emasculation, male palpal organ as a mating plug and sexual cannibalism. — J. Zool. **254**: 449–459.

Knoflach B. & A. van Harten (2001b): The genus *Latrodectus* (Araneae: Theridiidae) from mainland Yemen, the Socotra Archipelago and adjacent countries. — Fauna of Arabia **19**: 321–361.

Knoflach B. & K. Thaler (1998): Kugelspinnen und verwandte Familien von Österreich: Ökofaunistische Übersicht (Araneae: Theridiidae, Anapidae, Mysmenidae, Nesticidae). — Stapfia **55**: 667–712.

Knoflach B. & K. Thaler (2000): Notes on Mediterranean Theridiidae (Araneae) - I. — Memorie Soc. Entomol. ital. **78**: 411–442.

Kullmann E. (1959): Beobachtungen und Betrachtungen zum Verhalten der Theridiide *Conopistha argyrodes* Walckenaer (Araneae). — Mitt. zool. Mus. Berlin **35**: 275–292, Abb. 1–8.

Kullmann E. (1964): Neue Ergebnisse über den Netzbau und das Sexualverhalten einiger Spinnenarten. — Z. zool. Syst. Evolutionsforschung **2**: 41–122.

Legendre R. & A. Lopez (1974): Étude histologique de quelques formations glandulaires chez les araignées du genre *Argyrodes* (Theridiidae) et description d'un nouveau type de glande: la glande clypéale des males. — Bull. Soc. Zool. France **99**: 453–460.

Levi H.W. (1957): The spider genera *Enoplognatha, Theridion* and *Paidisca* in America north of Mexico (Araneae, Theridiidae). — Bull. Amer. Mus. Nat. Hist. **112**: 1–123.

Levi H.W. & L.R. Levi (1962): The genera of the spider family Theridiidae. — Bull. Mus. Comp. Zool. **127**: 1–71, Fig. 1–334.

Levy G. (1998): Fauna Palaestina. Arachnida III. Araneae: Theridiidae. — The Israel Acad. Sci. Humanities Jerusalem: 1–227.

Locket G. H. (1926): Observations on the mating habits of some web-spinning spiders. — Proc. Zool. Soc. London **1926**: 1125–1146.

Locket G. H. (1927): On the mating habits of some spiders of the family Theridiidae. — Annals Mag. Nat. Hist. (London) **(9) 20**: 91–99.

Locket G. H. (1979): Some notes on the life history of *Steatoda nobilis* (Thorell). — Newsl. Br. arachnol. Soc. **25**: 8–10.

Locket G.H. & J. Luczak (1974): *Achaearanea simulans* (Thorell) and its relationship to *Achaearanea tepidariorum* (C.L. Koch) (Araneae, Theridiidae). — Bull. entomol. Pologne **44**: 267–285.

Lopez A. & M. Emerit (1979): Données complementaires sur la glande clypéale des *Argyrodes* (Araneae, Theridiidae). Utilisation du microscope électronique à balayage. — Revue Arachnologique **2**: 143–153.

Lopez A. & M. Emerit (1981): The clypeal gland of *Argyrodes fissifrontella* Saaristo, 1978 (Araneae, Theridiidae). — Bull. Br. arachnol. Soc. **5**: 166–168.

Lubin Y.D. (1986): Courtship and alternative mating tactics in a social spider. — J. Arachnol. **14**: 239–257.

Matsumoto T. (1993): The effect of the copulatory plug in the funnel-web spider, *Agelena limbata* (Araneae: Agelenidae). — J. Arachnol. **21**: 55–59.

MENGE A. (1869): Preußische Spinnen. III. Abtheilung. — Schr. naturforsch. Ges. Danzig (NF) 2: 219–264.

MÜLLER G.H. (1985): Abgebrochene Emboli in der Vulva der „Schwarzen Witwe" *Latrodectus geometricus* C.L.KOCH 1841 (Arachnida: Araneae: Theridiidae). — Entomol. Z. **95**: 27–30.

PEASLEE J.E. & W.B. PECK (1983): The biology of *Octonoba octonarius* (MUMA) (Araneae, Uloboridae). — J. Arachnol. **11**: 51–67.

PLATNICK N. (1971): The evolution of courtship behaviour in spiders. — Bull. Br. arachnol. Soc. **2**: 40–47.

PLATNICK N.I. (2003): The world spider catalog, version 4.0. — American Museum of Natural History, New York, online at http://research.amnh.org/entomology/spiders/catalog81–87/index.html.

ROBINSON M.H. & B. ROBINSON (1980): Comparative studies of the courtship and mating behavior of tropical araneid spiders. — Pacific Insects Monogr. **36**: 1–218.

ROVNER J.S. (1967): Copulation and sperm induction by normal and palpless male linyphiid spiders. — Science **157** (3790): 835.

SCHMIDT G. (1999): Spinnen von den kapverdischen Inseln Boavista, Ilheu do Sal Rei und Maio (Araneae). — Arachnol. Magazin **7**: 1–15.

SIMON E. (1890): Études arachnologiques, 22e memoire. Étude sur les arachnides de l'Yemen. — Annales Soc. entomol. France (6)**10**: 77–124.

SIMON E. (1914): Les Arachnides de France 6 (1). — Roret, Paris: 1–308.

STUMPF H. (1990): Observations on the copulation behaviour of the sheet-web spiders *Linyphia hortensis* SUNDEVALL and *Linyphia triangularis* (CLERCK) (Araneae: Linyphiidae). — Bull. Soc. europ. Arachnol. No. h.s.: 340–345.

SUHM M., THALER K. & G. ALBERTI (1996): Glands in the male palpal organ and the origin of the mating plug in *Amaurobius* species (Araneae, Amaurobiidae). — Zool. Anz. **234**: 191–199.

THORNHILL R. & J. ALCOCK J. (1983): The evolution of insect mating systems. — Harvard University Press, Cambridge, Massachusetts, London: 1–547.

WHITEHOUSE M.E.A. (1987): The external structure of the protrusions on the cephalothorax of male *Argyrodes antipodiana* (Theridiidae). — Bull. Br. arachnol. Soc. **7**: 142–144.

WHITEHOUSE M.E.A. & R.R. JACKSON (1994): Intraspecific interactions of *Argyrodes antipodiana*, a kleptoparasitic spider from New Zealand. — New Zeal. J. Zool. **21**: 253.268.

WIEHLE H. (1937): Spinnentiere oder Arachnoidea, VIII. 26. Familie, Theridiidae oder Haubennetzspinnen (Kugelspinnen). — Tierwelt Deutschlands **33**: 119–222.

WIEHLE H. (1952): Eine übersehene deutsche *Theridion*-Art. — Zool. Anz. **149**: 226–235.

WIEHLE H. (1961): Der Embolus des männlichen Spinnentasters. — Verh. dt. zool. Ges. (Bonn) **1960**: 457–480.

WIEHLE H. (1967): Steckengebliebene Emboli in den Vulven von Spinnen (Arach., Araneae). — Senckenbergiana biologica **48**: 197–202.

WUNDERLICH J. (1987): Die Spinnen der Kanarischen Inseln und Madeiras. — Taxonomy & Ecology (Triops-Verlag, Langen) **1**: 1–435.

YOSHIDA H. (2001). A revision of the Japanese genera and species of the subfamily Theridiinae (Araneae: Theridiidae). — Acta Arachnologica, Tokyo **50**: 157–181.

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