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## SEXUAL BEHAVIOUR OF LEPHYPHANTES LEPROSUS (OHLERT) (ARANEIDA, LINYPHIIDAE), WITH NOTES ON THE FUNCTION OF THE GENITAL ORGANS

by

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With two plates and 19 text-figures

### INTRODUCTION

The Linyphiidae are builders of horizontal webs, on the underside of which the animals live. In most species the reproductive period is limited to a few weeks; after that time males are rarely met with. As in consequence all observations should be made in the course of a few weeks the species of this family are not very suited for the purpose of a lengthened and thorough investigation into the sexual behaviour. Tretzel (1954), however, observed the perennial occurrence of adult specimens of *Lepthyphantes leprosus* (Ohlert). Locket & Millidge (1953) and Wiehle (1956) likewise mentioned this phenomenon. The species moreover was known to occur in large quantities in the southern part of the Netherlands, viz., in the artificial marl-caves of the Kannerberg near Maastricht in the province of Limburg, particularly in the parts used by the local population for storing agricultural products. These qualities made *Lepthyphantes leprosus* an attractive test object.

Most test-animals were collected from the caves in the subadult stage, which enabled me to work with virginal specimens. All animals were kept individually in glass-cages or glass-tubes. For the purpose of observing the sexual behaviour a male was introduced into the cage of a female. Observations were facilitated by the use of a binocular microscope with low magnification.

The conditions, under which the animals were kept and observations were carried out, resembled those of the caves as nearly as possible: a temperature

of 10° C and a high relative humidity. Although the caves are dark, a small light was used to make observations possible.

Investigations were carried out during the winter 1962-1963.

#### COURTSHIP BEHAVIOUR

Courtship starts when a male is introduced into the web of a female or, under more natural conditions, when he climbs into the web himself. There are two different types of courtship, viz., without and with web-reduction, which will be described successively. Both types occur equally.

#### Courtship without web-reduction

Immediately after the animal has entered the web shaking<sup>1)</sup> and plucking<sup>2)</sup> may be observed. Plucking is the more common action. It is usually executed a number of times in succession. Shaking may occur once or twice and is not restricted to the beginning of courtship. These introductory movements soon are followed by vibrating<sup>3)</sup>, in the beginning at a very low intensity, but sustained for relatively long periods. It is always broken off when the female attacks the male by rushing in his direction. In a few cases many interruptions of this kind occurred, resulting in a very long period of "low intensity vibrating" as soon as the female retreated. Even a period of 577 seconds without a pause was observed once, but usually it goes on for a few minutes only. Gradually the periods become shorter, and at the end of each period the intensity suddenly changes from low to high. During the high intensity outbreaks the legs are moved, but the animal does not leave its place. Real walking is observed when the periods of vibrating have diminished to about 6 seconds, each period still commencing with low intensity vibrating. Walking goes very slowly at first, making an impression of caution, but becoming quicker each period. In the end, periods have diminished to 5 seconds, and consist of high intensity vibrating accompanied with walking for a short distance, and attaching of a thread to the web with the spinnerets. Low intensity vibrating is not to be seen anymore.

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1) Shaking: a very sudden contraction and immediate relaxation of the legs resulting in a very quick vertical movement of the body; shaking was observed in males only.

2) Plucking: the legs I alternately strongly pluck the threads of the web, occasionally both legs simultaneously, like plucking the strings of a guitar; observed in males only.

3) Vibrating: the palps are moved alternately up and down either slowly and with palps bent (low intensity), or very quickly with the palps stretched forward (high intensity); the movement is characteristic of the males and is a very striking component of the courtship.

Before long the male comes near the female, touches her with his fore-legs, moves away again, and turns a small circle in front of her. Approaching her again, he ends with drumming<sup>4)</sup> the web in front of the female, which makes slow inward swinging movements with the legs I. This sequence of actions (touching, moving away, turning a circle and drumming) may go on for some time but eventually the male moves in between the fore-legs of the female to start the pairing.

#### Courtship with web-reduction

The other type of courtship is characterized by the web-biting<sup>5)</sup> male. In these cases the male immediately starts to run about, attaching threads and vibrating his palps. The vibrating movement occurs in high intensity from the start. Soon the male touches the female, but turns away again and commences the web-biting. Sometimes the touching of the female does not come off and the web-biting starts immediately. Vibrating plays only a minor role from there on.

The biting either may be started at one place and be continued consistently from there, or several holes are fused into larger ones by biting away the intervening web. In either case this behaviour results in a reduction of the web-surface of 90-100 %, leaving only a small narrow strip of the original web in which the female is hanging. This remnant is usually situated against the substratum at the margin of the original web, and measures about 2 cm<sup>2</sup>. It is kept stretched by new threads attached by the male in the course of courtship. This situation attained, the male takes the mating position between the fore-legs of the female and the copulation starts.

Occasionally a movement may be observed which I have called clapping<sup>6)</sup>. It may be seen in both types of courtship. This action seems to take place after a relapse during which the male hangs quietly for a few minutes. Then suddenly clapping occurs and the normal behaviour is taken up again. However, relapses seldom interrupt courtship and clapping is but rarely seen.

A female, if willing to mate, does not show much activity during courtship. She may attack the male when he enters her web for the first time,

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4) Drumming: the legs of the first pair alternately make a number of quick beating movements against the surface of the web; the legs I are moderately stretched.

5) Web-biting: threads of the web are bitten through or torn loose with the chelicerae, which results in a circular hole in the web; owing to the tension of the threads in the web, even a few bites will produce a considerable effect.

6) Clapping: both palps are bent downwards, kept for a few seconds in this position and moved upwards very swiftly simultaneously; the movement is observed in males only.

but soon she will retreat and hang quite still unless she is touched by the male, in which case she will move away slowly for a small distance. If, however, she is not willing to receive a male in her web, she will attack him very tenaciously until he leaves. He may stand his ground in which case a typical way of drumming may be observed, viz., drumming with stretched legs 7). Charges in both cases consist of a sudden rush in the male's direction, often followed by threatening bites and striking movements with the fore-legs. I never noticed a real bite which wounded the male; in some cases she clearly bit the web instead of the male as could be deduced from the hole in the web afterwards.

As a rule an unwilling female soon starts web-pulling 8), at first with the palps only, but gradually the action becomes stronger with the aid of the fore-legs. It usually lasts for a considerable time. The action is sustained till the male leaves the web or stops courting. The effect of this movement on the male behaviour is very marked.

One of the effects of courtship is clearly visible in the abdomen of the female, where the genital area has become very markedly swollen. The epigyne now stands perpendicularly to the ventral surface of the abdomen.

Courtship is completed in about one hour. The shortest time observed was 26 minutes, the longest 133 minutes; the average time 66 minutes out of 18 cases. Courtship with web-reduction is shorter (average time 63 minutes) than courtship without this phenomenon (average time 72.5 minutes).

#### COPULATION

The copulation takes place on the underside of the female web or what is left of it. The male hangs between the fore-legs of the female (pl. 1-2), the ocular area just below the tips of the female chelicerae, his legs I drawn backwards. The female's attitude is normal, the legs I and II slightly spread. Their body-axes form an angle of  $30^{\circ}$  to  $45^{\circ}$  in the median plane, the abdomen of the male thrust into the web with the spinnerets. In this position the male is able to reach the epigyne of the female with his palps.

The copulation is interrupted a number of times, and the animals separate. During one of these interruptions the male spins the characteristic sperm-web, discharges a small drop of seminal fluid, and fills both palps. There

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7) Drumming with stretched legs: quick alternate beating movements against the surface of the web are executed with completely stretched legs I, which are kept closely parallel.

8) Web-pulling: both palps (low intensity) or palps and fore-legs (high intensity) are hooked into the web and make pulling movements at the web-texture; now and then a palp or leg comes loose and is hooked into the web again. Web-pulling is observed in females only.

is a remarkable difference in the mode of pairing before and after this important break. I shall therefore distinguish between phases A and B, phase A being the period from the first occurrence of the mating-position until the beginning of the characteristic break mentioned above, phase B the following period up to the final separation.

### Phase A

During copulation the palps are linked to the epigyne alternately. In order to bring about this connection, the male reaches forward his stretched palp, which is turned with the retro-lateral side to the epigyne, and fastens it to the protruding female organ. Then the component parts of the palp are pressed out of the normal position by the swelling of one of these parts, the haematodocha, to turn into functional contact with the epigyne. The haematodocha remains expanded briefly; when collapsing, the organs come loose again, and the elements return to their original positions. The palp just used is bent to the mouth-parts, which start nibbling<sup>9)</sup>. When this is finished, the other palp is linked to the epigyne.

At first the alternation of the palps goes irregularly due to difficulties with connecting the palp to the epigyne, and to not smoothly running contacts between elements of both organs. However, in the course of phase A the movements become quicker and more rhythmic. Once maximum speed attained, each palp is linked to the epigyne for 3 to 3.5 seconds only, and nibbling takes 5 to 5.5 seconds. When we consider that this alternate use of the palps may go on for hours (6 hours is the maximum observed duration of phase A), each palp must be hooked on to the epigyne from a few hundred up to a thousand times.

Several breaks occur during phase A, usually caused by the necessity of mouth-cleaning<sup>10)</sup> in the male. The running away is attended with high intensity vibrating during 2 seconds approximately. The male remains in the neighbourhood and as soon as mouth-cleaning is completed, courtship-behaviour can be noticed. The components of this behaviour are again vibrating, walking, attaching of threads, and drumming. Web-biting does not occur, not even in males which show the type of courtship with web-reduction. Considerable time may be spent nibbling. Breaks during court-

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9) Nibbling: a palp is pressed against the chelicerae and gnathocoxae, which make munching and biting movements particularly at the embolus. Soon a white substance of unknown origin appears between the gnathocoxae, which substance is also visible at the embolus of the palp.

10) Mouth-cleaning (in the male): the drop of white substance mentioned above is removed from between the gnathocoxae with the aid of the legs III (pl. 2 fig. 2); the droplet is taken up with the tips of the tarsi III and put down into the web.

ship usually take from a few minutes to a quarter of an hour. In this way, long periods of actual copulation alternate with short intervals with mouth-cleaning and courtship.

An unexpected break without the necessity of mouth-cleaning, during which break a filling of the palps takes place, marks the transition of phase A to phase B.

Phase A takes from 102 minutes to 358 minutes; average time 209 minutes from 17 observed cases.

### Phase B

Phase B begins with a very important event, viz., the filling of the palps. The male starts web-biting and reinforcing the margin of the hole thus formed with new threads. If the web was reduced during courtship, biting and attaching of threads take place in the web made by the male during the courtship-period. In the hole, which measures 2 to 3 cm in diameter, a fork is constructed, the legs of the fork enclosing an angle of about  $60^\circ$ . The male now leaves its normal position on the underside of the web, climbs through the hole on the upperside, and stands up on the forked construction. The legs of the fork support the legs I and II of the animal, the stem supports the legs IV, the legs III remaining free. His spinnerets are now exactly above the angle of the fork. With sidelong swaying movements a minute triangular sperm-web (with sides measuring 1.5 mm) is constructed between the legs of the fork. Still in the same position on the upperside of the web the male rubs the genital area against the margin of the sperm-web and, quickly and rhythmically moving the legs III, he deposits a small white drop of sperm on the web near the margin. Immediately thereafter the male returns to the underside, revolving round the fork, and commences to dip the tips of his palps alternately with fast precise movements in the drop of sperm. During the absorption of the seminal fluid, the palps are curved around the margin of the sperm-web and thus are dipped directly into the fluid, not through the web. As soon as the whole drop is absorbed, the male leaves the sperm-web and, after some intensive plucking (often 10 to 15 times in quick succession) and a short courtship with vibrating and drumming, he returns to the female and resumes copulation. The male makes a very hurried impression during this break. The female has remained where the male left her.

The whole process of web-biting, construction of the sperm-web, absorption of the sperm, and courtship takes an average time of 4 minutes (shortest time observed 1.5 minute, longest 13 minutes). The actual absorption takes

33.5 seconds averagely (shortest time observed 19 seconds, longest 65 seconds), and the average number of dippings for each palp is 12 (smallest number observed 7, greatest 23).

Copulation is resumed for a moment only. After a few palp-connections, or even only one, the male leaves again and another filling of the palps takes place, which differs hardly from the preceding one. Usually the same hole in the web and often the same sperm-web are used. In that case the male uses the same fork but weaves a new sperm-web over the old one. Only once a male has been observed biting away the old sperm-web, and constructing a new fork with sperm-web in the old hole.

Again copulation is resumed and again the male leaves for a third filling of the palps. After this, copulation is not interrupted again till the end of phase B. The palps are linked again alternately to the epigyne, and nibbling occurs after each use of a palp. There is, however, an important difference with phase A becoming more and more pronounced as phase B goes on. While at first the time spent on functional contact of each palp is the same as during phase A, viz., 3 to 3.5 seconds, this period soon starts lengthening and in the end may even mount up to one minute. The maximum expansion of the haematodocha is attained as quickly as usual, but the collapsing is longer in coming every time. Shortly after the attainment of the expansion, the male starts pushing and even biting the haematodocha with the chelicerae and beating it with the free palp, until the volume of the haematodocha diminishes slowly and the other parts are set free. The female also becomes restless when a palp remains connected for a long time. The end of phase B is always caused by the running away of the female and not of the male as during phase A. With a short courtship the male sometimes induces the female into resuming the contact again but this seldom leads to successful linking of a palp, and the separation soon becomes final.

Phase B takes from 44 to 79 minutes. The average time is 59 minutes from 6 observed cases. Adding up the average times of the courtship-period, phase A, and phase B, we come to an average time of 334 minutes for one mating-period.

#### POST-COPULATORY BEHAVIOUR

The female, which has not shown much activity during courtship and pairing, now becomes very busy. Evading the courting male she starts cleaning the still swollen epigyne with the tips of the legs III. Special attention is paid to the epigyneal cavity and to the posterior side of the organ. The tips of the legs III are on their turn cleaned with the chelicerae and

gnathocoxae and this again brings on the necessity of mouth-cleaning<sup>11</sup>). When the male keeps courting her she starts web-pulling first with the palps only, later also with the legs. The movement is usually kept up for long periods without a pause, and clearly has a suppressing effect on the male's courtship, for he soon becomes less obtrusive and even sits still for considerable periods. He may either leave the web, or stay and keep very quiet. Nibbling still may be observed for some time. The epigyne of the female slowly returns to its normal state, and the web-pulling gradually diminishes.

When the next day a male is introduced into the web, the female will react with a rush in his direction accompanied by biting. When nevertheless the male persists in courting, the web-pulling can be observed again. In spite of numerous attempts I never observed a female pairing a second time, that is to say a female that had gone through a complete copulation. Males, on the other hand, have been observed pairing on three successive days with three different females.

However, it must be mentioned, that a female is willing to pair a second time, when the first copulation is interrupted before or at the end of phase A. If in such a case a male was brought into the web the next day, some aggressive behaviour might occur, but web-pulling was never observed. Courtship ran its normal course and the copulation that followed was indistinguishable from the first one. Only once I separated a female for the second time from her partner, again before the end of phase A; the next day a male was accepted for the third time, and again a normal, now uninterrupted copulation took place. After this complete copulation web-pulling was observed. During the following days her willingness to pair was investigated, but every courtship was met with aggression and web-pulling.

#### OTHER OBSERVATIONS

Observations on courtship and copulation were mainly made on material which had been collected in the subadult stage, the final moult always taking place in captivity. Thus the "age" of each animal, that is the number of days elapsed since the last moult, was known, and their virginal state was a certainty.

A female is not willing to tolerate a male in her web immediately when she has become adult. The first days she runs away or drops to the ground when a male enters the web. On the fifth day of her adult life a male may

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11) Mouth-cleaning (in the female): after intensive cleaning of the legs a small globule of dirt becomes visible between the gnathocoxae, which is removed with the aid of the tips of the palps and flicked off to the ground.



succeed for the first time. Males, on the other hand, have been observed courting on the second day of their adult lives; on the first day they keep still when brought into the web of a female. Willingness to mate seems to remain for a very long time. A female at an "age" of 88 days was observed to pair very normally, and the same can be said of a male of 70 days. Of course the limit may lie at a much higher age.

Eggs are laid 7 to 13 days after the pairing. They number 15 to 25 and are surrounded by some irregular threads and covered over by a small web. They hatch in 2 to 3 weeks. Each female lays three batches of eggs at intervals of one month approximately. The last time the number is usually smaller.

*Drosophilas*, brought into the cage for feeding purposes, were captured when falling on the web. They were usually caught and pulled through the web by the spider rushing to the spot before they were able to free themselves. Preys were sucked out without being wrapped up. The hole in the web caused by the capture of the insect was mended afterwards.

Once an observation on copulation was accidentally disturbed by a *Drosophila* which got entangled in the web. Pairing was interrupted at once and the male rushed to the fly and caught it. Interest in the female was surpassed by the appearance of food! Two hours later the male was observed courting the female again.

#### DISCUSSION OF COURTSHIP AND COPULATION

The occurrence of the two types of courtship mentioned above deserves special attention. Both types were observed about equally frequent; out of 29 cases 13 appeared to be accompanied by web-reduction. The difference is rather striking: either a nearly complete reduction of the web, or no web-biting at all. There are several possible causes for this dual behaviour, some of which, however, can be ruled out.

There are a number of observations on males performing the two types of courtship on different days (table 1); the sequence, in which the two types

TABLE I

#### Males showing both types of courtship

♂ No.	date	web-reduction
208	13. II.1963	none
208	20. II.1963	90—100 %
193	7.III.1963	none
193	8.III.1963	90—100 %
199	7.III.1963	60 %
199	8.III.1963	none

were executed by one male, was not constant. Therefore we may conclude that a male is not restricted by heredity to one type of courtship; that the two types are not caused by two different types of males; and that either type of courtship may be executed on a first mating-experience.

If we consider the "age" of the males, the type of courtship appears to be irrespective of the length of the adult life. The mean age of the web-reducing males was 32 days, of the non-web-reducing group 29 days. The difference cannot be considered significant.

Observations seem to point to the possibility that the female behaviour is a determining factor (table 2). The impression is created that an aggressive

TABLE 2

## Correlation of female behaviour to type of courtship

	with web-reduction	without web-reduction
female not aggressive	6 cases	3 cases
female aggressive	5 cases	10 cases

female, which executes many rushes in the male's direction after his entrance into the web, causes a courtship without web-reduction, while the web of a not or scarcely reacting female is bitten away. The number of cases observed is too small, while exact qualitative measurements of the female aggression have not been carried out. The supposition might, however, serve as a working-basis for further investigations.

Similar behaviour has not yet been recorded of other species in this or other families. Well known, however, is the phenomenon of the "Hochzeitsgewebe" of the Theridiidae, a rather closely related family (Gerhardt, 1923), and of one species of the Linyphiidae (Braun, 1961). This "Hochzeitsgewebe" is a small web constructed by the male in the course of courtship in the immediate neighbourhood of, and in contact with, the female's web. The female is enticed to this web where the animals pair. The web of the female remains intact. Moreover, in the Argiopidae the male generally constructs a few threads near the web of the female, and copulation takes place on these threads. Thus in both Theridiidae and Argiopidae we observe some constructing activity of the male before or during courtship. Linyphiidae attach numerous threads to the female web during courtship but this does not result in a separate construction. It may be possible, however, that we are dealing here with two processes which lead to the same result, viz., the restriction of the female's freedom of movement to a small area. This process then is not obligatory in *Lepthyphantes leprosus*.

According to Kaestner (1956), Linyphiidae are deprived of sight, which

certainly does apply to *Lepthyphantes leprosus* living in dark caves. Sensitiveness to vibrations in the web must be the main sense in these animals. It is thus not surprising that many of the actions executed by the male in the female's web during courtship are focused on this property. Clapping, shaking, plucking, and vibrating, all will be conveyed to the female through the web, which is well suited to this task in consequence of its structure. Web-pulling, on the other hand, must be perceived by the male.

Vibrating, and possibly clapping, may be related to the stridulatory apparatus occurring in this family. This organ consists of a number of parallel ridges or grooves on the retro-lateral surface of the chelicerae, and a small tooth on the innerside of the femur of each palp near its base. When vibrating the male executes the movements needed for a proper functioning of this mechanism. The surface of the web is not touched with the palps during the vibrating-periods, and drumming on the web consequently must be ruled out in this case (Braun, 1961).

Plucking is markedly intensive when the male leaves the sperm-web after absorbing the seminal fluid. It is executed some 10 to 15 times in very quick succession. When observed at the start of courtship it is always limited to five times at the utmost, and the intervals are longer. It is conspicuous that in both cases this movement is made only when the male enters the web. We may conclude plucking to be a typical introductory movement, which is restricted to the two moments mentioned. Shaking and clapping are not limited to a special phase, but may occur at any time during courtship. Both movements are not commonly observed.

The web-pulling executed by the female will be conveyed to the male through the web. The effect of this movement on the male behaviour is very conspicuous. The vibrating-periods become more spaced and gradually disappear altogether, the male hanging absolutely still or leaving the web.

Nibbling has been observed and described many times, and all authors agree as to its occurrence after the palp comes loose from the epigyne. Several suppositions, such as moistening, rearranging, and stimulating of the palp, have been made with regard to the function of this behaviour. Kullmann (1964) is inclined to look upon it as moistening, and he presumes a special function. He suggests that the saliva dissolves the membrane by which the cleistospermia (Bertkau, 1875) are enveloped when ejaculated by the male. However that may be, in *Lepthyphantes leprosus* soon after the commencement of the copulation a white secretion becomes visible on the palp of the male, on the epigyne of the female, and between the gnathocoxae of the male. In the course of pairing the production of the secretion outruns the consumption, the amount of substance between the gnathocoxae increases, and

mouth-cleaning becomes necessary. With the tips of the legs III a small globule is removed and put into the web. Pairing terminated, a number of these globules is visible in the web, but they are very small and barely perceptible to the naked eye.

If we assume the secretion to originate from the mouth-opening of the male, we might compare the phenomenon with the "Stomatäre Exkretion" described by Braun (1956) as occurring in *Teutana triangulosa* (Walckenaer) and (1961) in *Ostearius melanopygius* (Cambridge). He described it, however, as small sausage-like bodies appearing from the mouth when the male is excited during courtship. The small oval corpuscles reminding of blood cells, described by Braun (1956) as occurring in the sausage-like bodies, also have been observed in the white secretion of *Lepthyphantes leprosus*, where they are oval to bean-shaped.

As mentioned, mouth-cleaning is executed in the male with the aid of the legs III, in the female by the palps instead. Evidently the palps of the male have lost this function when becoming adapted to the special function of sperm-transfer.

The transfer of the seminal fluid from the genital orifice to the palps has been described at length by many authors. In *Lepthyphantes leprosus* the very characteristic triangular sperm-web is build either in a hole in the female web, or in case of web-reduction between threads made by the male outside the remnants of the female web. The change of position is very marked: the fork is constructed from below (normal position), the web itself from above, the drop of seminal fluid is also discharged from above, but the animal returns to the underside again in order to take up the sperm. The palps are curved around the margin of the web alternately and the emboli are dipped directly into the drop.

The change of position seems to be characteristic of the Linyphiidae. In *Drapetisca socialis* (Sundevall), however, the whole chain of actions takes place at one side of the web (Kullmann, 1964), which should be considered an adaptation to its peculiar way of life. The species builds a small web on vertical substrata, such as treetrunks, walls, rocks, etc., which makes change of position impossible.

Another exception is *Ostearius melanopygius* (Cambridge), in which species all movements are performed from below (Braun, 1961). This is considered to be characteristic of the Micryphantidae (Gerhardt, 1923) and Braun therefore suggested, sustained by this and other ethological considerations, to consider the Donacochareae (to which group of genera *Ostearius* belongs) a separate taxon between the Linyphiidae and Micryphantidae. However, up till present the behaviour of one or more species of only eight genera

of the Linyphiidae has been observed more or less accurately, while the family comprises about 70 genera. Braun's conclusion therefore seems a little premature.

It must have been a mistake when Kullmann (1964), observing in *Cresmatoneta mutinensis* (Canestrini) the normal change of position described above, considered it to be an exception; this is in contradiction to what is observed by all other authors.

Irregularities may occur within the species. Once a male of *Lepthyphantes leprosus* constructed a nearly perpendicular sperm-web between a few threads, which connected the main web to the bottom of the cage. Consequently all actions had to be executed in a vertical attitude. First the fork was constructed from one side, then the normal change of position took place, the sperm-web was completed and the seminal fluid ejaculated from the other side. After that the animal started to return to the original side to absorb the sperm. However, he did not succeed in doing so and filled his palps without a second change of position curving his palps around the web-margin and dipping them into the drop of sperm through the web (!). The drop thereupon disappeared as quickly as usual.

At the start of phase B, *Lepthyphantes leprosus* three times ejaculates a drop of sperm and takes it up with the palps. During the intervening periods the mating position is resumed, and the palps connect a few times with the epigyne. Sometimes the same sperm-web is used three times, but equally frequent two or three sperm-webs are constructed. A hole in the web may be used for two different sperm-webs, but as a rule a new hole is bitten each time. When a sperm-web is employed a second time, much weaving occurs over the old web but no attention is paid to the fork. Once I observed a male biting away his first sperm-web and constructing a new one on the same spot. We may conclude this behaviour not to be very fixed. Three fillings have been observed without exception in this species. Records of other species of the Linyphiidae all mention one or two fillings of the palps. For *Lepthyphantes nebulosus* (Sundevall) two fillings were reported by Gerhardt (1923). Apparently there are differences at this point within the genus and even within the species-group. Gerhardt did not mention any reduction of the web, but his data were based on two observations only.

The description of the copulation given above agrees fairly well with the scanty data available from literature. The strikingly swollen genital area of the female was mentioned by Locket (1926) for *Lepthyphantes leprosus*, but his account of the pairing is incomplete and only deals with the filling of the palps and the second phase. The difference in times needed for connecting the palp to the epigyne during phases A and B was mentioned by Gerhardt

(1923). He stated that the male fills his palps some time after the last moult and empties them during the first copulation (my phase A). Then refilling takes place and copulation may go on (my phase B). The lengthening of the connection-times he ascribed to fatigue.

This course of events, which seems to be the rule in some other families and which was recently mentioned again for Lycosidae by Vlijm et al. (1963), was doubted to hold true in the Linyphiidae by Kullmann (1964). Filling of the palps after the last moult has never been observed by him when investigating the behaviour of *Cresmatoneta mutinensis* (Canestrini), which agrees with my finds in the case of *Lepthyphantes leprosus*. There are three other phenomena which point in the same direction, the last one being decisive in my opinion.

- a. The female behaviour changes at the end of phase B with the occurrence of web-pulling; this change in the female behaviour is never observed when copulation is interrupted before or at the end of phase A.
- b. The willingness of the female to pair disappears at the end of a normal copulation; when a pairing is interrupted at the end of phase A a female is willing to pair a second time.
- c. Eggs are only laid after a normal copulation; in interrupted cases eggs never are produced.

The conclusion can be drawn that in *Lepthyphantes leprosus* transfer of sperm does not take place during phase A but only after the filling of the palps at the beginning of phase B. It is too early yet to generalize and to consider it to be the rule in the whole family, though until now the opposite never has been observed. The long connection-times during phase B must be caused by the functional change. Changes in the female behaviour and disappearance of willingness to pair are clearly correlated. Possibly the filled receptacula cause the female to switch to web-pulling, which has a marked checking influence on the male courtship.

Therefore we may render the pairing of *Lepthyphantes leprosus* schematically:

courtship — copulation A — sperm-absorption — copulation B.

Sperm-absorption during the actual mating-period of one pair has been recorded by Braun (1964) for the Theridiidae, where some short copulations alternate with sperm-absorptions. Nothing is mentioned about a first filling of the palps after the last moult and there seems to be no difference between the first copulation-series and the next with regard to connection-times. In the Argiopidae sperm-absorption does not occur during the pairing but some time after the last palp-connection (Gerhardt mentions 30 to 50 minutes). Pairing may, however, be resumed later on. This family thus should answer

fully to Gerhardt's rule concerning the pairing of spiders. Observations during the period between last moult and first pairing are wanted both in Theridiidae and Argiopidae.

The absence of a filling of the palps between last moult and copulation therefore seems to be a particularity of some Linyphiidae (and Micryphantidae ?) as far as we know now. The question arises how this situation has developed. Has the first absorption disappeared altogether? Is the sperm-absorption in *Lepthyphantes leprosus* comparable to the refilling of the palps some time after copulation as occurring in the Argiopidae? Or has the original first absorption shifted from between last moult and courtship to the courtship-period, and possibly even to the copulation, necessitating an interruption during copulation?

In my opinion there is a very slight indication which supports the last possibility. Sperm-absorption in *Lepthyphantes leprosus* is always preceded by the construction of a sperm-web, and this again by the biting of a hole in the web. Web-biting therefore is clearly connected with the process of sperm-absorption. As mentioned, web-biting also occurred very strikingly in roughly half of the courtships observed. It is possible that we are dealing here with a remnant of a sperm-absorption, which once has occurred during courtship. I was strengthened in this opinion by an observation on *Prolinyphia emphana* (Walckenaer). In this species the pairing proceeds in the same way as in *Lepthyphantes leprosus* with two sperm-absorptions between phases A and B. Web-reduction during courtship does not occur in this species. In one instance, which seemed exceptional being the only one out of ten observations, web-reduction did occur. Not during courtship, however, but preceding the construction of the first sperm-web. Instead of biting a hole in the web, which action usually takes about one minute, the male went on web-biting for 10 minutes achieving a reduction of nearly 50 %. As the measurements of the web were originally about 10 by 12 cm and a hole normally measures about 2 cm across, the reduction clearly was a multiple of the normal web-biting. What caused the continuation of the biting in this case could not be explained. It shows, however, the possibility to consider web-reduction a continuation of the first action of the sperm-absorbing process. If this is the case, we might look upon web-biting during the courtship-period in *Lepthyphantes leprosus* as a rudimentary start to a filling of the palps, while the actual absorption does not occur. Whether the absorption concerned has disappeared or has shifted to the copulation still remains unexplained.

This interpretation is irrespective of a possible influence of aggressiveness by the female or another factor, which then should determine whether or not web-biting will occur during courtship.

## FUNCTIONAL ASPECTS OF THE GENITAL ORGANS

In the course of the many copulations observed, an attempt was made to investigate the functioning of the genital organs. In spite of long observations, for which the prolonged copulations gave ample opportunity, visual perception only disclosed the complexity of the contact. It is very difficult to determine the movements exactly, as the connecting of the palp with the epigyne and the expansion of the palp proceed very quickly, and the elements are very small. Photographing this small object was experienced to be very difficult. Killing the animals during copulation, as indicated by Osterloh (1922), appeared to be the only way to study the genital organs in functional contact. A superficial study of the morphology and anatomy of the epigyne and male palp in their non-functioning positions was necessary, in order to be able to compare these with the functional situation.

## The epigyne

The complicated structure of the female's genital organ is only partly understandable from a ventral view (fig. 3). In this way it is usually figured to serve the purpose of identification of the species. A cavity is partly covered by a "scape" (*ss*), which runs from its base at the anterior side in posterior direction, a small rounded object appearing from below (*s*). The lateral wall of the cavity bears two lateral teeth (*lt*), one at each side. Two lateral lobes (*ll*) are visible at the sides of the scape. A lateral view (fig. 2) shows the scape to be folded at the tip and to run in anterior direction again. The small rounded object (*s*) visible at the tip of the scape in ventral view appears to be attached to the lateral lobe (*ll*) and median lobe (*ml*) which are situated dorsally of the scape. The lateral wall of the cavity bears two lateral plates (*lp*) at the postero-lateral corners.

At the end of courtship the epigyne sticks out perpendicularly to the ventral surface. In this situation, which can be brought about artificially by heating a specimen in lactic acid for about one hour, the structure of the organ is easily understood. The lateral view (fig. 1) again shows the lateral tooth (*lt*) and lateral plate (*lp*) on the wall surrounding the epigyneal cavity. The scape consists of a straight part (*ss*), from the base at the anterior side of the chitinous wall to the turning-point, and an arched part (*as*) from the turning-point onwards. The tip consists of a median lobe (*ml*) on the interior surface of the arched part of the scape and a lateral lobe (*ll*) at each side. A posterior view (fig. 4) shows the stretcher (*s*), reminding of the trunk of an elephant, to be attached to the posterior side of the median lobe. Two sperm-ducts run



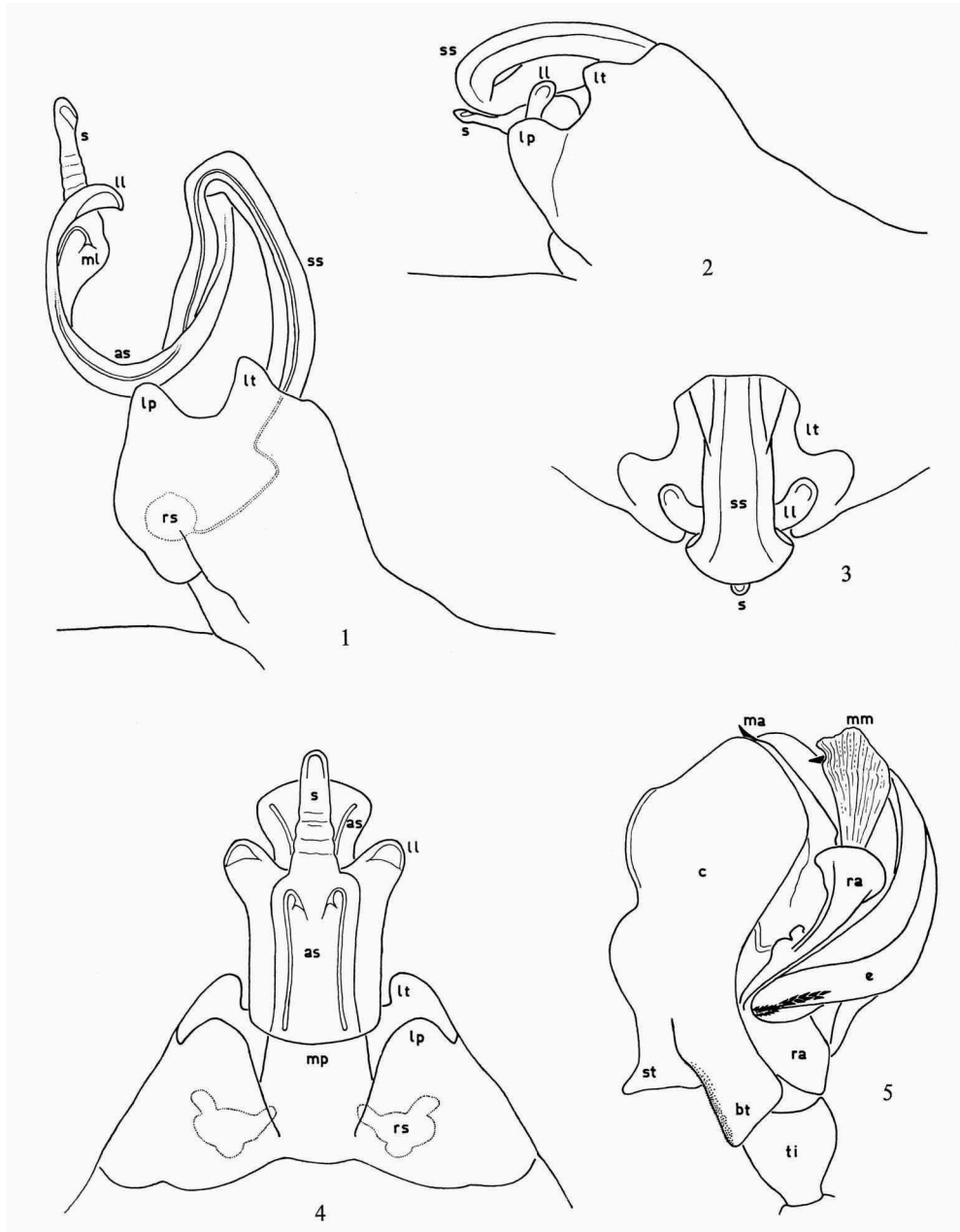


Fig. 1-5. *Lepthyphantes leprosus* (Ohlert). 1, epigyne, functional situation, lateral view; 2, epigyne, non-functional situation, lateral view; 3, epigyne, non-functional situation, ventral view; 4, epigyne, functional situation, posterior view; 5, left palp of male, pro-lateral view. 1-5, X 80.

parallel through the whole length of the scape, from a small aperture at each side of the median lobe on the interior surface of the arched part (fig. 1) to the base of the scape, then they turn sideways and run through the wall of the epigyneal cavity, one at each side, to the receptacula seminis (*rs*) at the posterior side of the cavity underneath the lateral plates. The posterior wall of the cavity has two deep incisions at each side of the median plate (*mp*). The scape is broad and knob-shaped at the turning-point.

### The male palp

This secondary genital organ of the male is a very complex structure. It is usually pictured from the outside for the purpose of distinguishing the species. The organ is composed of a number of elements, which normally lie folded together but come out of their non-functioning positions during copulation. Most parts have been given names (Osterloh, 1922; Merrett, 1963). The paper by Merrett in particular has facilitated my work considerably. However, Merrett did not discuss the functional aspects of the elements.

In retro-lateral view (fig. 8) the paracymbium and the lamella are conspicuous. The paracymbium (*pc*) is a tub-shaped element with three offshoots, viz., a large flat internal one by which the element is attached to the cymbium (*c*), a relatively small proximal crest, and a distal one which is slender and tapers to a point. The internal offshoot bears a number of short hairs on the external surface. The lamella (*l*) is a dark element coming from the ventral side, broadening out and narrowing again distally where it is toothed and

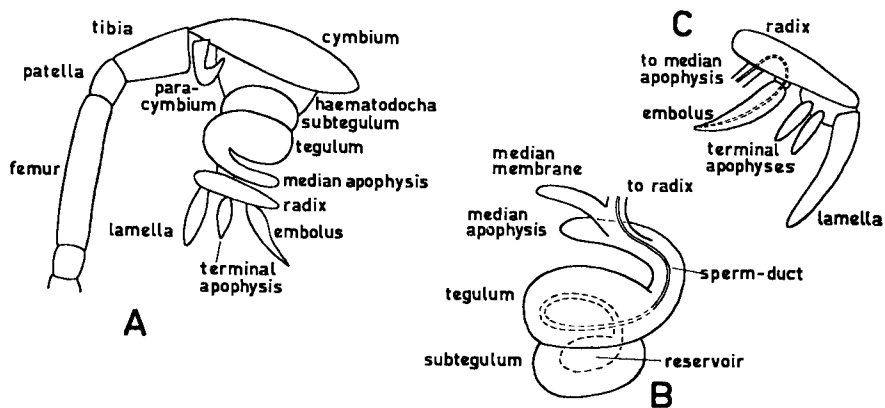


Fig. 6. Generalized palp of the Linyphiidae. A, entire appendage; B-C, details of elements. Modified after Merrett, 1963.

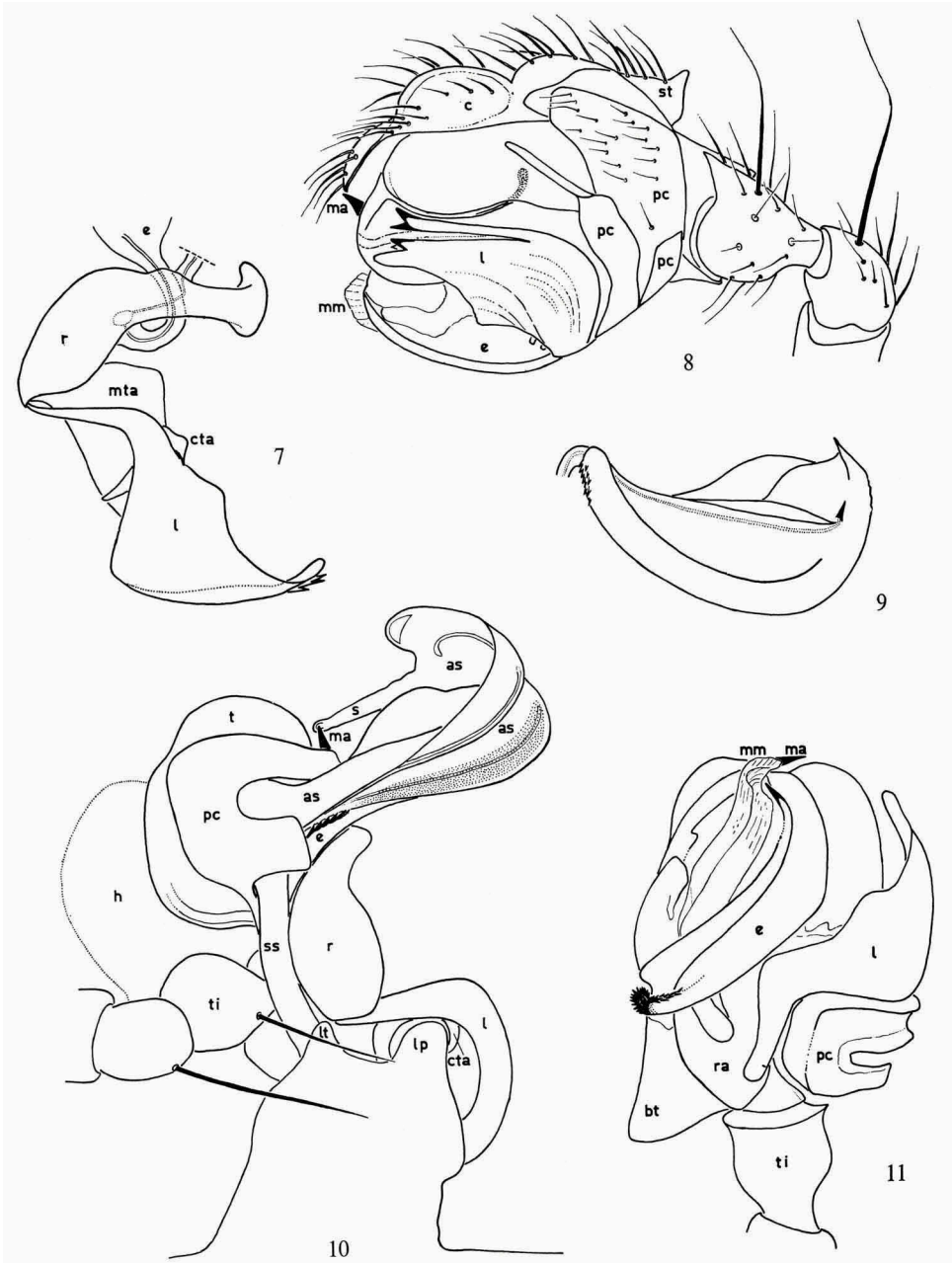


Fig. 7-11. *Lepthyphantes leprosus* (Ohlert). 7, radix, lamella, and terminal apophyses of male palp; 8, left palp of male, retro-lateral view; 9, embolus of male palp; 10, male palp and epigyne in functional contact, non-functioning view; 11, left palp of male, ventral view. 7-11,  $\times 80$ .

incised. The cymbium (*c*), which is the transformed hairy tarsus, bears a small tubercle (*st*) near the base at the posterior side. At the tip of the palp the median apophysis (*ma*) and median membrane (*mm*) are clearly visible, the embolus (*e*) can be seen only partly at the ventral side.

Viewed from the ventral side (fig. 11) the tub-shaped part of the paracymbium (*pc*) is visible with the proximal crest and the base of the slender distal appendage. The lamella (*l*) can be followed to its point of attachment to the radix (*r*), which for the greater part is concealed. The embolus (*e*) is also attached to the radix and bears many small teeth near the base. The tip is concealed by the median membrane (*mm*). The median apophysis (*ma*) is again visible at the tip of the palp. The cymbium bears a big tubercle (*bt*) near its base at the anterior margin.

In internal or pro-lateral view (fig. 5) the same elements are recognizable, viz., the embolus (*e*) accompanied by the median membrane (*mm*), the median apophysis (*ma*) sticking out at the tip of the palp, the radix (*r*), of which element both ends are visible, and the cymbium (*c*) with the hairless small tubercle (*st*) and the big tubercle (*bt*). The latter has the dorsal surface covered with numerous small warts (fig. 15).

The structure of the palp and the connections of the elements cannot be understood from the unexpanded palp. A treatment with lactic acid causes expansion of the haematodocha and thus the situation as occurring during copulation can be imitated. Merrett (1963) gave a generalized scheme of the male palps of the Linyphiidae (fig. 6), which scheme I have followed as to the names of the elements.

The paracymbium is fixed to the cymbium on the retro-lateral side near the base (fig. 8). In the expanded palp the haematodocha has unfolded completely (fig. 19, *h*). It is a large bladder-like element, which unrolls clockwise in the left palp, anti-clockwise in the right one as seen from the dorsal side. The swelling of the element seems to be brought about by pressure of the body-fluid (Gerhardt & Kaestner, 1938). There is an open connection with the body cavity through the segments of the palp and the alveolus (*a*). The tegulum (fig. 16, *t*), to which the other elements of the palp are attached, forms the other extremity of the haematodocha. The element is situated on the retro-lateral surface in the expanded palp. As opposed to Merrett no distinction has been drawn between subtegulum and tegulum. The sperm-duct arises from a reservoir in the tegulum and can be observed in places. The median apophysis (fig. 16, *ma*) bends round the tegulum from the base to the sharp tip. It is the sharp tip which is conspicuous at the extremity of the unexpanded palp. The sperm-duct runs through the basal half and then branches off to the radix surrounded by a membrane. The median membrane

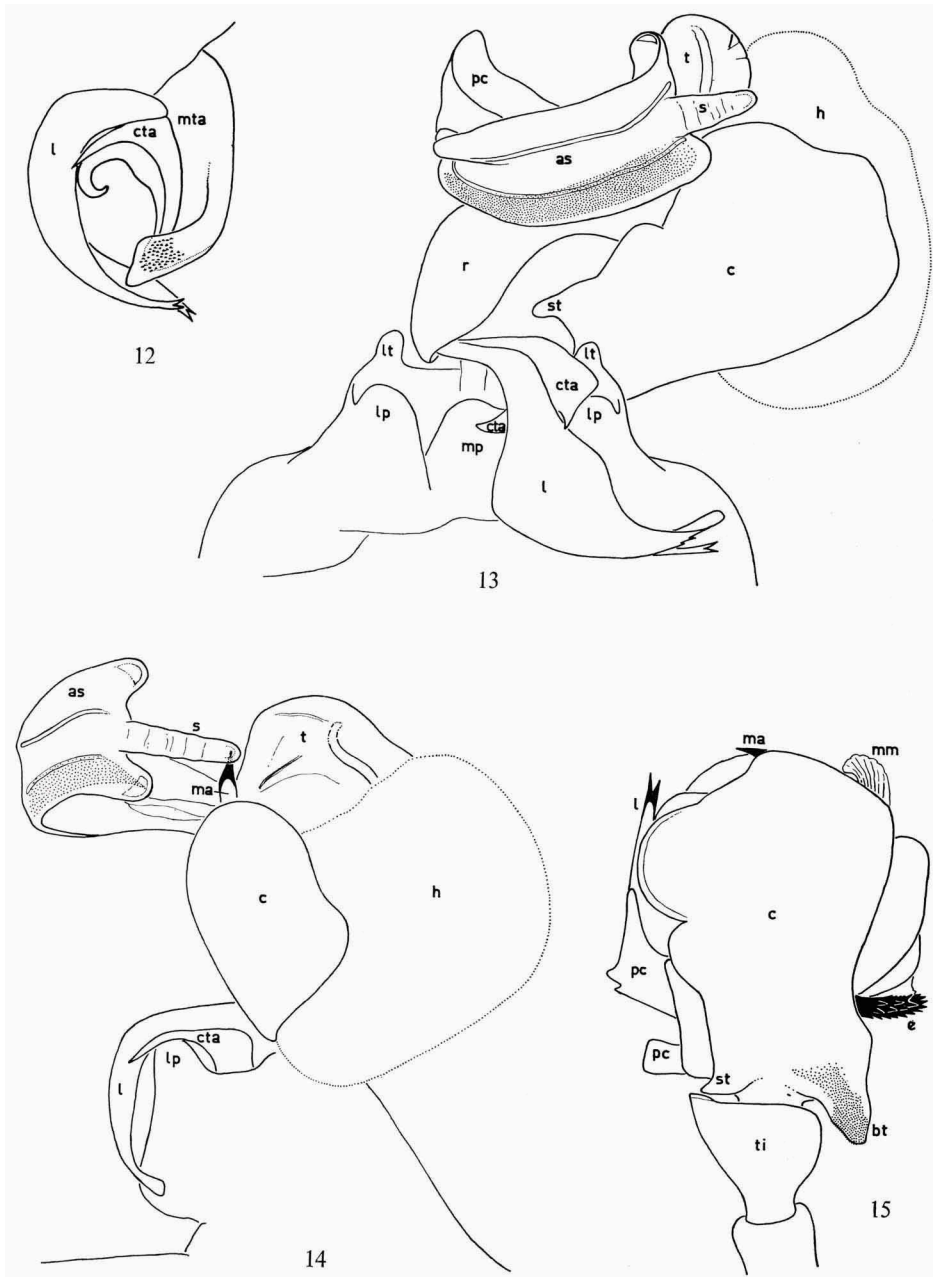


Fig. 12-15. *Lephyphantes leprosus* (Ohlert). 12, lamella, membranous and chitinous terminal apophyses of male palp; 13, male palp and epigyne in functional contact, posterior view; 14, male palp and epigyne in functional contact, functioning view; 15, left palp of male, dorsal view. 12-15,  $\times 80$ .

(*mm*) is a flat appendage arising from the membrane surrounding the sperm-duct; it is visible at the prolateral side of the unexpanded palp where it covers the tip of the embolus.

On its way to the embolus the sperm-duct runs through the radix (fig. 7, *r*). It is a curved element, which is half flattened with a terminal knob, half more cylindrical and broader. The sperm-duct enters the flattened half, runs to the middle of the element, then leaves for the embolus. Just before it leaves the radix it forms a spherical thickening called "Fickertsche Drüse", which is supposed to be a gland. The sperm-duct is surrounded again by a membrane between radix and embolus. The cylindrical half of the radix supports the lamella (fig. 7, *l*) and the membranous terminal apophysis (*mta*). The connections are membranous and versatile. The lamella, membranous terminal apophysis and chitinous terminal apophysis (*cta*) are also versatilely connected with each other. It is difficult to describe the shape of these elements intelligibly and clearly. The lamella is the strongly chitinous element visible in retro-lateral view of the non-functioning palp. One branch of the chitinous terminal apophysis tapers to a dark curving tooth, supporting a small tooth, which curves round the margin of the lamella (fig. 7). The other branch is attached to the membranous terminal apophysis (fig. 12), which element ends in a thin curved blade bearing many small teeth on the outer surface.

The embolus (fig. 9) is more or less disk-shaped with a thick outer margin and a thin membranous inner part. The margin is strongly toothed near the base and tapers to a point distally. The sperm-duct runs from the base of the element through the inner part to a sharply pointed sperm-duct-tooth near the base of which the duct ends. The sperm-duct-tooth is situated at the inside of the thickened outer margin not far from the tip of the element.

#### Functional contact during copulation

By killing the animals during copulation on the moment of maximum expansion of the haematodocha, the copulatory organs can be fixed in the functioning attitude and in functional contact. In this way it becomes possible to understand the functional aspects of the elements of palp and epigyne. The functional situation has been pictured (fig. 10, 13, 14, 17, 18) in five different aspects of the epigyne, viz., a ventral, anterior, posterior, functioning and non-functioning view, the left palp being connected. The rule that the left palp connects with the left side of the epigyne and the right palp with the right side holds true for *Lepthyphantes leprosus*. Thus the functioning side in the figures stands for the left side. In the case of the

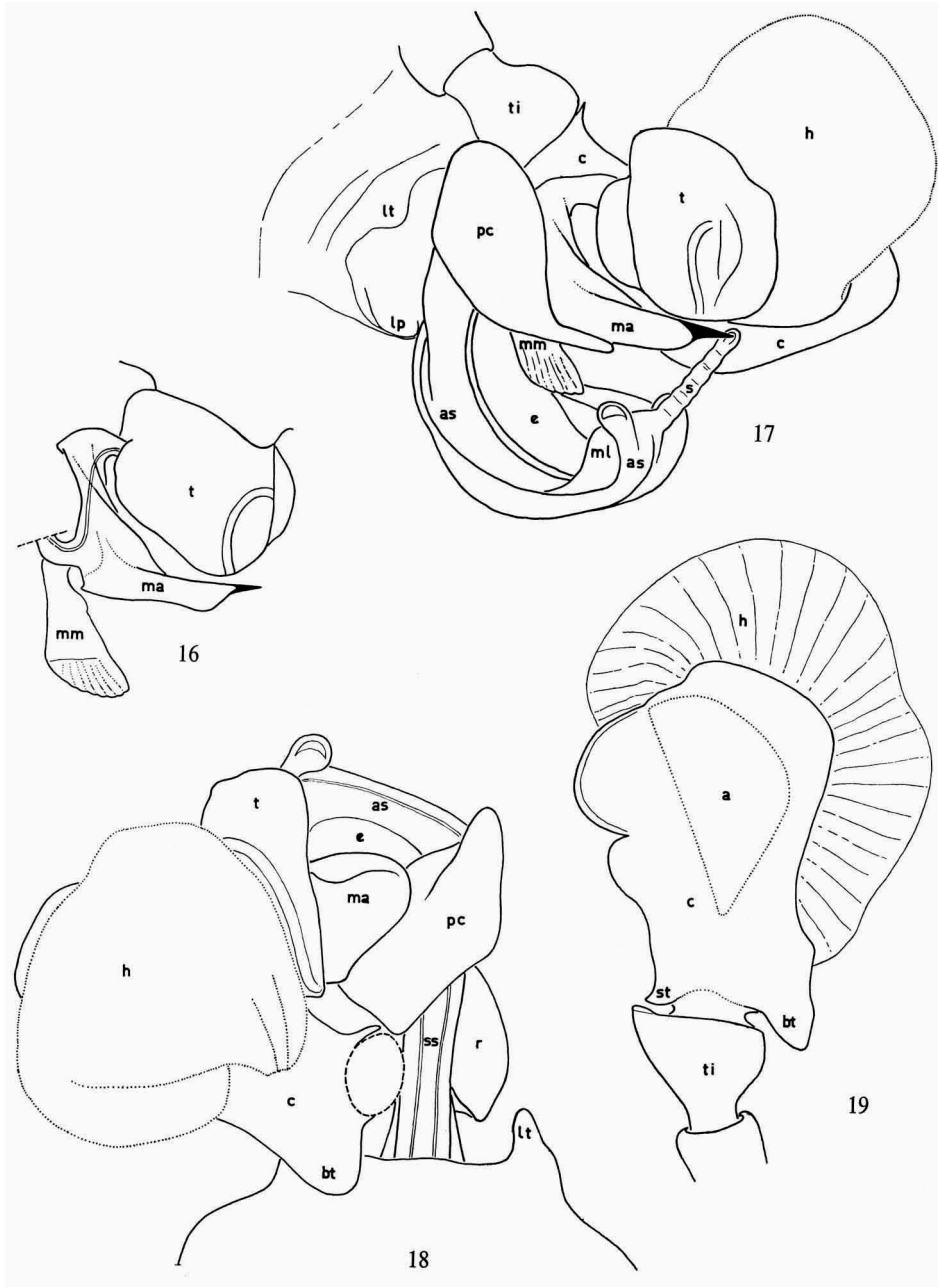


Fig. 16-19. *Leptyphantes leprosus* (Ohlert). 16, tegulum, median apophysis and median membrane of male palp; 17, male palp and epigyne in functional contact, ventral view; 18, male palp and epigyne in functional contact, anterior view; 19, male palp with expanded haematodocha, dorsal view. 16-19,  $\times 80$ .

right palp being used, mirror-images must be made of all figures with respect to the median plane of the epigyne; the right side then becomes the functioning one, ventral, anterior and posterior sides remain unaltered. The small size of the haematodocha in the figures is due to the shrinking of the element during the preservation in alcohol.

In the posterior aspect (fig. 13) the lateral plate (*lp*) and lateral tooth (*lt*) of the epigyne are clearly visible at the non-functioning side. At the functioning side the lateral plate is concealed behind the lamella (*l*), which reaches with its toothed tip to the end of a groove below the lateral plate. One branch of the chitinous terminal apophysis (*cta*) is pressed against the median plate (*mp*). Of the scape of the epigyne only the outside of the arched part (*as*) is visible in this view, the straight part being concealed behind the radix (*r*). At the dorsal half (the left half) of the arched part the embolus (*e*) glimmers through. The free end of the arched part points in anterior direction at the functioning side, the stretcher (*s*) pointing aside. The cymbium (*c*) of the palp leans on the chitinous wall of the epigyne at the functioning side.

From the non-functioning side (fig. 10) nearly the whole scape can be observed. The straight part (*ss*) disappears into the tub-shaped paracymbium (*pc*) between the internal offshoot and the proximal crest. The arched part of the scape (*as*) comes out between the crest and the distal offshoot. The arched part is clearly distorted at the base, then turns off to the functioning side. The stretcher (*s*), the trunk-like element situated on the median lobe at the tip of the scape, is visible in the background, kept stretched by the black tip of the median apophysis (*ma*). The embolus (*e*) lies inside the arched part of the scape in the dorsal half while the sperm-duct in the ventral half can be followed to its aperture near the tip. The radix (*r*) is pressed against the straight part of the scape, the lamella (*l*) runs from the tip of the radix in posterior direction and turns to the posterior side of the epigyne.

From the functioning side (fig. 14) the tip of the scape (*as*) with the embolus inside and the stretcher (*s*) are clearly visible. The latter is kept tight by the black median apophysis (*ma*). The lamella (*l*) and chitinous terminal apophysis (*cta*) are in contact with the posterior side of the epigyne. The cymbium (*c*) is seen from the tip with the shrunken haematodocha (*h*) at the anterior side.

In the ventral view (fig. 17) the distal offshoot of the paracymbium (*pc*) can be observed. It is pressed against the median membrane (*mm*), which on its turn lies against the embolus (*e*). The scape (*as*) can be followed from its emergence from the paracymbium to the tip, where the stretcher (*s*) is kept tight by the median apophysis (*ma*). This element together with the



tegulum (*t*) is best recognized in this view. The cymbium (*c*), tibia (*ti*), and shrunken haematodocha (*h*) are situated at the anterior side. Of the epigyne the lateral tooth (*lt*) and lateral plate (*lp*) are visible at the non-functioning side.

From the anterior side (fig. 18) the straight part of the scape (*ss*) can be seen disappearing into the paracymbium (*pc*), of which element the internal side of the internal offshoot is visible. It is attached to the cymbium (*c*), which is seen here from the ventral side with the big tubercle (*bt*) pressed against the wall of the epigyne at the functioning side. The tegulum (*t*) is attached to the haematodocha (*h*), which at the moment of maximum expansion is about twice as large as figured here. The median apophysis (*ma*) disappears behind the tegulum, the arched part of the scape (*as*) can be observed in the background. The radix (*r*), pressed against the posterior side of the straight part of the scape (*ss*), sticks out at the non-functioning side.

#### DISCUSSION OF THE GENITAL ORGANS

The figures together with the observations on pairing animals make it possible to understand some functional aspects of the elements. A palp, which is to be connected with the epigyne, is stretched forward and turned with its retro-lateral side (the outside) to the epigyne. The tub-shaped paracymbium then is pushed over the broad knob formed by the end of the straight part and the base of the arched part of the scape. The haematodocha starts to expand pressing all elements of the palp out of their non-functioning positions and swinging them in a distal direction. While expanding, the haematodocha unrolls spirally, causing the median apophysis to grip into the depression at the tip of the stretcher, and lifts up the arched part of the scape. Meanwhile the lamella comes into contact with the lateral plate at the functioning side of the epigyne, and in co-operation with the two terminal apophyses fastens the palp at the posterior wall of the epigyne. The chitinous terminal apophysis with its strongly chitinous tooth is pressed against the median plate, the membraneous terminal apophysis disappears into the epigyneal cavity and gives an extra point of support by means of its rough outer surface, which presumably is pressed against the wall of the epigyneal cavity. When becoming fixed to the posterior wall of the epigyne the lamella and the two terminal apophyses press the radix in anterior direction against the straight part of the scape. In the mean time the still expanding and unrolling haematodocha causes the tegulum to turn and consequently the median apophysis, being attached to the tegulum, pulls the stretcher and the arched part of the scape aside to the functioning side. The pointed end of the embolus is shoved into the depression of the lateral lobe of the scape while its base is

pressed against the arched part of the scape by the radix, which at the same time is pressed against the posterior side of the straight part of the scape. The embolus is held there by the distal offshoot of the paracymbium. The sperm-duct-tooth of the embolus thus fits into the aperture of the epigyneal sperm-duct on the functioning side. The sharply toothed base of the embolus probably keeps it from slipping out of the arched part of the scape. The median membrane lies between this offshoot and the embolus. The cymbium is pressed with the big tubercle against the outer wall of the epigyne at the anterior side of the functioning half; the rough dorsal surface of this tubercle probably serves to keep the element from slipping away, while it is supported by the lateral tooth of the epigyne at the functional side. The continuing expansion of the haematodocha must provide the pressure by which the sperm is pressed through the sperm duct.

The complicated structure of the paracymbium with the strong distal offshoot and striking proximal crest very clearly serves the purpose of fixing the palp to the scape. The tub-shaped part corresponds with the knob of the scape, the proximal crest grips around the straight part, the base of the distal offshoot holds the base of the arched part. Together with the cymbium, which in its turn finds a point of support against the anterior wall and lateral tooth of the epigyne, the paracymbium fastens the palp firmly to the epigyne. All other elements, however, are attached to the tegulum, which is situated on the haematodocha. The lamella together with the two terminal apophyses give a solid basis to these elements. With respect to the median membrane, the question arises whether this element has a clear-cut function during copulation. It is pressed between the embolus and the distal offshoot of the paracymbium. Probably its function should be sought in the non-functioning palp, where it could serve the purpose of protecting the sperm-duct-tooth at the pro-lateral side of the palp (fig. 5, 11).

The folded and partly arched scape is characteristic of many genera of the Linyphiidae, e.g., *Lepthyphantes*, *Centromerus*, *Agyneta*, *Microneta*. It is not surprising that in these genera the male palp bears a well developed and specialized paracymbium. A strong black median apophysis is always sticking out at the tip of the palp, a lamella is visible at the retro-lateral or ventral side. On the other hand there are a number of genera, e.g., *Linyphia*, *Porrhomma*, *Bathyphantes*, where no scape of this type is found. The male palp in these genera bears a paracymbium of simple structure, the median apophysis does not project at the tip. Still other genera take intermediate positions between the two types.

For a full understanding of the systematics and relationships in this family a comparative study of the functioning of the genital organs should

be very helpful. Merrett (1963) took an important step with his comparative study of the male palps. This paper is meant to be a further contribution.

### SUMMARY

1. Two types of courtship occur in *Lepthyphantes leprosus*, with and without web-reduction respectively. There is a slight indication that the female behaviour determines which type of courtship will occur.

2. The greater part of the movements during courtship seem to be focused on the creation of vibrations, which can be conveyed by means of the web. This in particular applies to the action which has been called "vibrating" and which probably has some connection with the stridulating apparatus occurring in these animals.

3. The copulation consists of two phases; at the start of the second phase the palps are three times filled with sperm. It can be demonstrated experimentally that the palps have not been filled before. Consequently during the first phase of the copulation no transfer of sperm takes place.

4. Possibly the occurrence of web-biting during courtship can be interpreted as a remnant of an earlier construction of a sperm-web. In that case this behaviour might be a clue to the evolutionary development of this type of sexual behaviour.

5. There is a marked change in the female behaviour at the end of the copulation. Attempts to induce a female to pair a second time failed. Possibly the filled receptacula seminis form the stimulus to change the behaviour and to react negatively upon the male courtship.

6. The elements of the epigyne and male palp are described and figured. Some functions of the various elements of the genital organs can be understood by means of pairs of animals killed in copula.

### LIST OF ABBREVIATIONS USED IN THE FIGURES

<i>a</i> , alveolus	<i>ml</i> , median lobe
<i>as</i> , arched part of scape	<i>mm</i> , median membrane
<i>bt</i> , big tubercle	<i>mp</i> , median plate
<i>c</i> , cymbium	<i>mia</i> , membranous terminal apophysis
<i>cta</i> , chitinous terminal apophysis	<i>pc</i> , paracymbium
<i>e</i> , embolus	<i>r</i> , radix
<i>h</i> , haematodocha	<i>rs</i> , receptaculum seminis
<i>l</i> , lamella	<i>s</i> , stretcher
<i>ll</i> , lateral lobe	<i>ss</i> , straight part of scape
<i>lp</i> , lateral plate	<i>st</i> , small tubercle
<i>lt</i> , lateral tooth	<i>t</i> , tegulum
<i>ma</i> , median apophysis	<i>ti</i> , tibia

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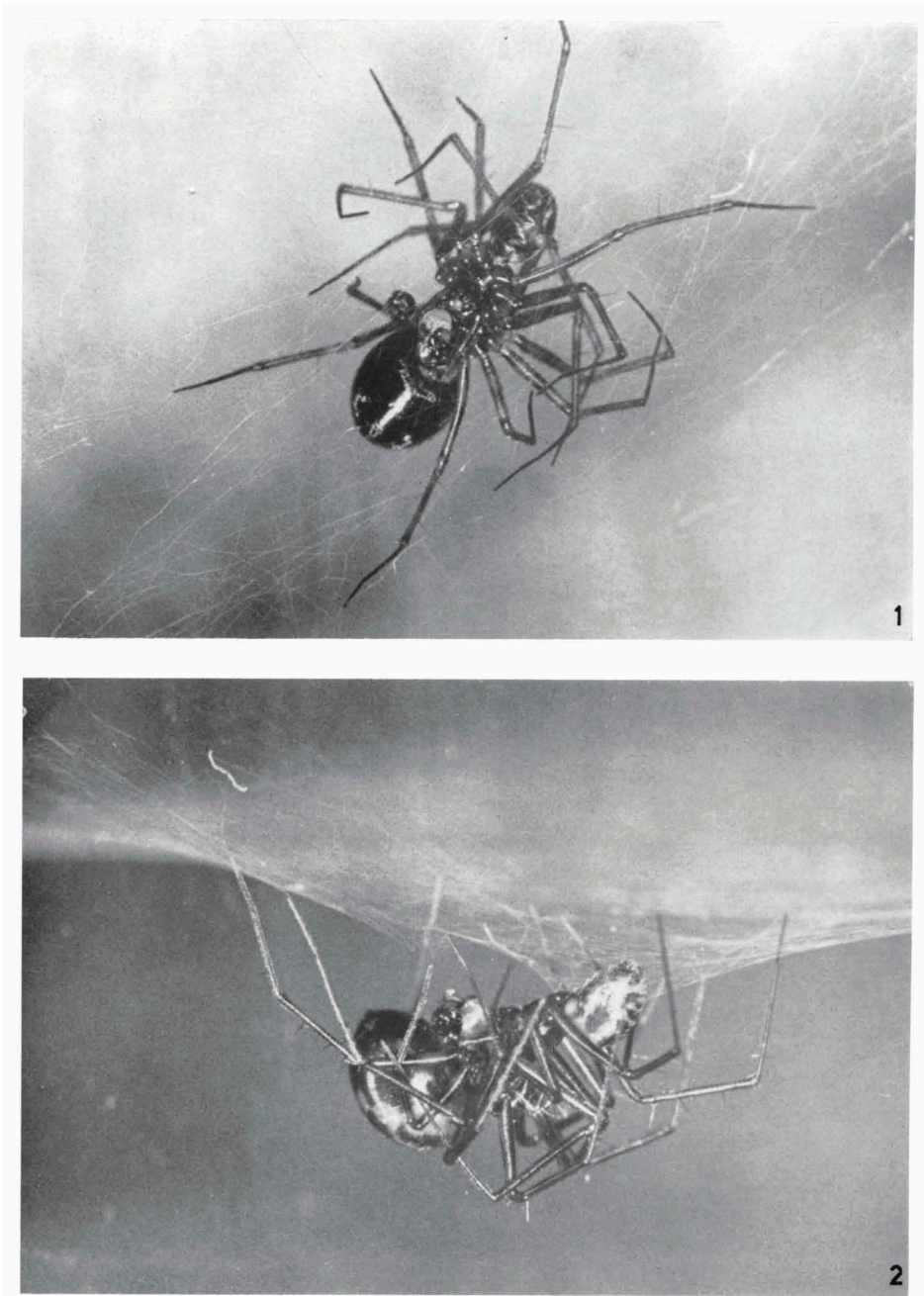


Fig. 1-2. *Lepthyphantes leprosus* (Ohlert), copulation attitude. 1, ventral view, male above with right palp in function; 2, lateral view, male on right with left palp in function. 1-2,  $\times 9$ .

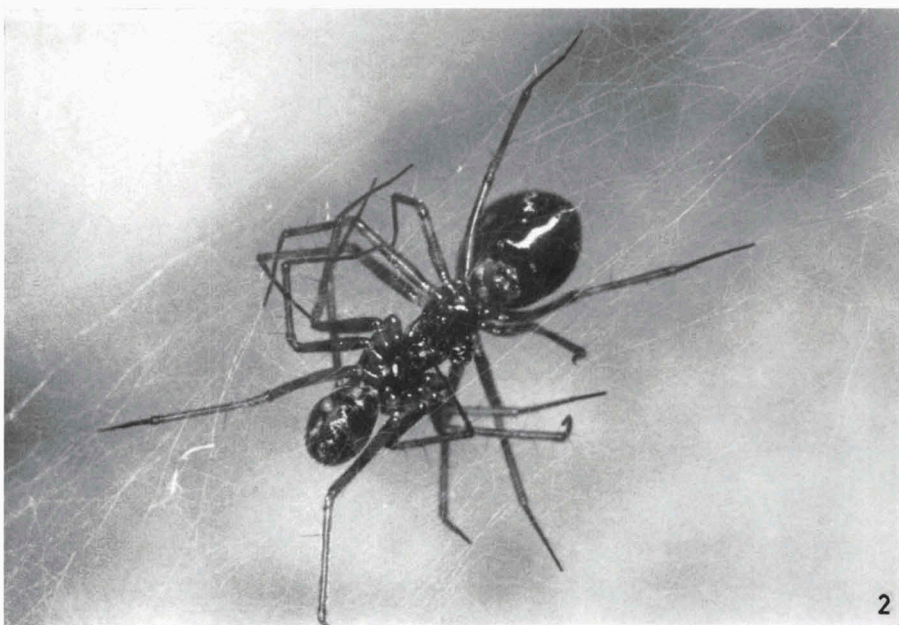
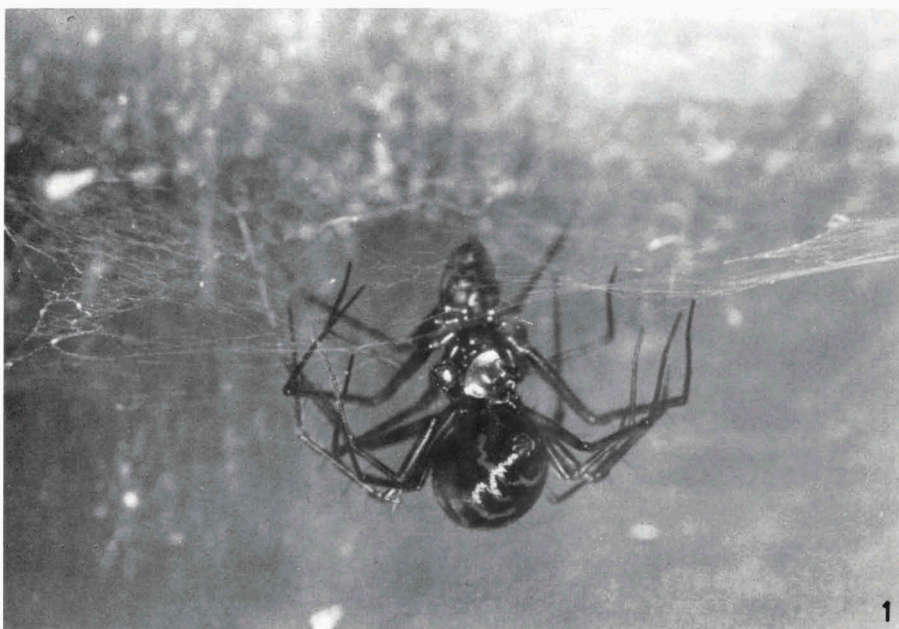


Fig. 1-2. *Lepthyphantes leprosus* (Ohlert). 1, copulation attitude, posterior view of female, male in background, right palp in function; 2, male interrupting phase A of copulation, removing a droplet of white substance from gnathocoxae with left leg III.  
1-2,  $\times 9$ .