

The female Genitalia of British Spiders of the Genus *Lepthyphantes* (Linyphiidae) II

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Introduction

In Wanless (1971), I presented photographs and line drawings of the epigynes of the British species of *Lepthyphantes* as an aid to identification. The present paper reports on a comparative study of the internal structure of the epigynes (vulvae).

A number of previous studies on the morphology and function of spider genitalia have been made, some of which have been valuable in understanding the interrelationships of species. Zorsch (1937), working on North American *Lepthyphantes*, described the morphology of the male palps and the complex nature of the epigyne. Wiehle (1956; 1963) illustrated vulvae of many British species in a taxonomic work on the German Linyphiidae. Other major works dealing with British *Lepthyphantes* but not containing detailed descriptions of the vulvae are those of Blackwall (1864), Pickard-Cambridge (1879), and Locket & Millidge (1953). The functional aspects of the *Lepthyphantes* genitalia were not understood until the work of van Helsdingen (1965), who described sexual behaviour of *Lepthyphantes leprosus* (Ohlert), and the interlocking mechanism of the male palp with the female epigyne. Similar studies include those of Gering (1953) on *Agelenopsis*, Cooke (1966) on *Dysdera* and Grasshoff (1968) on *Araneus diadematus* Clerck. The importance of these observations has been stressed by Locket (1968a), and van Helsdingen (1969; 1970) based his reclassification of the species of *Linyphia* Latreille principally on the functioning of the genitalia.

Part II - The Vulvae

Preparation of Epigynes

Cooke (1968) has given a synopsis of the main techniques for examining spider genitalia; all have disadvantages and there is no agreement on which is best. Locket (1968b) found that care was needed when comparing vulvae; for displacement, angle of

viewing and differing degrees of sclerotization combine to make precise interpretation difficult. To trace the ducts and distinguish detail within the scape it is necessary to examine the vulvae at high magnifications. This requires the use of a slide preparation and the removal of the soft non-chitinous elements. Techniques using clove oil or lactic acid clear the integument but do not remove the non-chitinous structures. Sodium hydroxide digests the softer structures and, if used at room temperature, distortion of the specimen is minimal. While it is inevitable that a slide preparation will produce some displacement, consistent results can be obtained if reasonable care is taken in preparing the vulvae.

The whole process is best carried out in a cavity block positioned on the stage of a stereoscopic microscope. When the epigyne and abdomen are left intact, details of the vulva are obscured by abdominal hairs. Each epigyne is therefore best removed from the abdomen while the spider is in 75% alcohol. The excised epigyne is passed through two changes of water before immersing in 10% sodium hydroxide at room temperature. It should be examined at 30 minute intervals, for the process of maceration is slow and depends on the size of the specimen and its degree of sclerotization. Maceration should be stopped when the integument is clear and the pigmented spermatheca can be seen in detail. Excess alkali is removed from the vulva by transferring to water for 5 minutes and immersing in 2% acetic acid for 10 minutes. During this stage the specimen is decalcified and changes in osmotic pressure may cause the scape partially to unfold and force any cell debris remaining in the organ to ooze out into the surrounding medium. After a further 5-minute soak in water, the specimen is dehydrated by grading through, 30, 50, 75, 90 to 100% alcohol. The specimen is transferred to fresh absolute alcohol for five minutes, cleared in xylol for two minutes and then placed in a drop of viscous canada balsam on a clean glass slide and orientated to give a dorsal or ventral view. A 7/8" square, number 1 cover glass is applied to the drop of mountant which should be of such a size that it is just covered by the cover glass. If the drop of balsam is too large, the vulva will float around and even rotate on its axis as the cover glass settles down. Too small a drop may result in serious

displacement by allowing excessive cover glass pressure to develop as the balsam hardens.

Interpretation of the structural elements in the vulva

The superficial anatomy of the vulva is clearly seen when viewed under the low power stereoscopic microscope. However, the magnification of this system is not high enough to resolve the fine structural detail. When the vulva is examined with a high power microscope there is no longer a three-dimensional image and the spatial relationship between the structural elements is partially lost. The morphology cannot be fully understood from an examination of only one specimen as detail within the organ is never clearly defined; furthermore, by looking at more than one preparation of each species from both dorsal and ventral aspects there is less likelihood of confusing morphological detail with optical artifacts. Such difficulties always occur when studying thick transparent specimens under the microscope (Barer, 1968).

The generalised structure of the *Lepthyphantes* vulva

The structure of the vulva is fundamentally similar in all *Lepthyphantes* species, structural variations falling within a framework that appears consistent for the genus.

The scape projects in a posterior direction from the epigynal cavity that is bounded and shaped by four sclerites: an anterior genital sclerite, two lateral genital sclerites and a subgenital sclerite. As the scape usually has an S-shaped or sigmoid configuration it can be conveniently divided into three parts or regions.

The anterior part of the scape originates from its fixed base beneath the anterior genital sclerite. From its knob-shaped turning point it continues as the median part of the scape that in turn folds over to give rise to the posterior part of the scape, the free end of which is modified to form the stretcher. On either side of the base of the stretcher are the lateral lobes. Within the scape are two sperm ducts that open externally in the bursa copulatrix on the interior surface of the posterior part of the scape. Each sperm duct joins a darkly pigmented body, the spermatheca, which is supported by an apodeme. Associated with the apodeme of each spermatheca is a short fertilization canal that opens into the epigynal cavity and is limited in some species by an arched plate.

Terminology

This is based mainly on that used by van Helsdingen (1965), but a number of new terms and changes have been introduced in order to describe certain parts in greater detail.

The relationship between the four sclerites which support and protect the scape is perhaps most easily seen in *L. nebulosus* (Sundevall) but can be made out in all *Lepthyphantes* vulvae.

The *anterior genital sclerite* (Pl. VII; Fig. 10: *ag*) forms the roof of the epigynal cavity. It is usually seen as a fine membrane that extends as an arch over the scapoid base. The relationship between these two structures is of particular interest, for in many vulvae they are both well developed (Pl. IV; 3), and together form the orifice of the epigynal cavity. In other vulvae, only the anterior genital sclerite is sufficiently well developed to form the orifice, the scapoid base being reduced to a fine membrane (Pl. IV; 4).

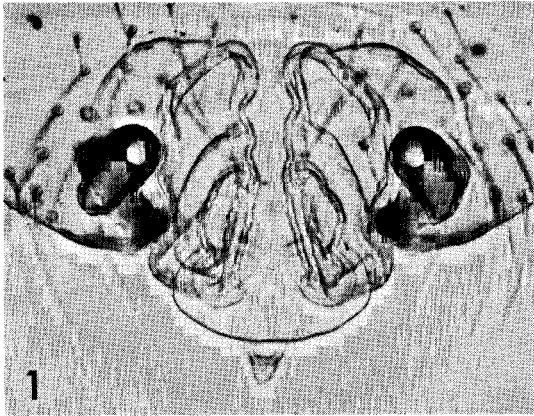
The *lateral genital sclerites* (*lg*) form the lateral walls of the epigynal cavity. In some species the sclerites are bifurcated, one part fusing with the apodeme, the other appearing to fuse with the subgenital sclerite. Both the lateral and anterior genital sclerites are derived from the abdominal integument and are characterised by cuticular hairs on their outer surface. Together they form the lateral plates described by van Helsdingen.

The *subgenital sclerite* (*sg*), described by van Helsdingen as the median plate, forms the floor of the epigynal cavity. Its lateral margins are often drawn out into lobe-like structures, one part of which fuses with the apodeme, the other extending anteriorly into the epigynal cavity. Although it is derived from the integument its outer surface is free of cuticular hairs; its base (not shown in the diagrams) originates from the epigastric fold.

The sclerites of the epigynal cavity frequently bear teeth or lobes. A distinction is made between these terms as applied to the *Lepthyphantes* vulvae.

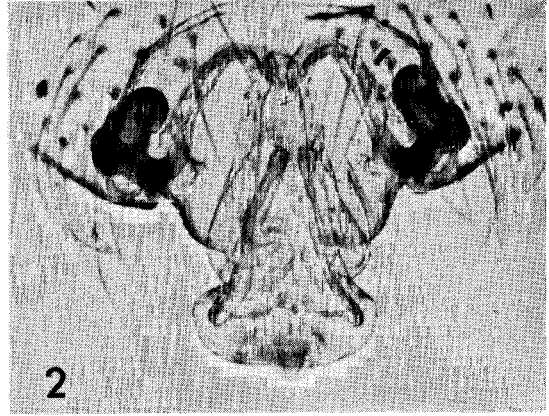
A tooth may be defined as a small projection from the free margin of a sclerite (Fig. 7: *agt*) whereas a lobe is a large tongue-like extension which may project backwards into the epigynal cavity when its distal extremity may be obscured (Fig. 15: *lgl*).

The terms are prefixed by the name of the sclerite from which they originate.



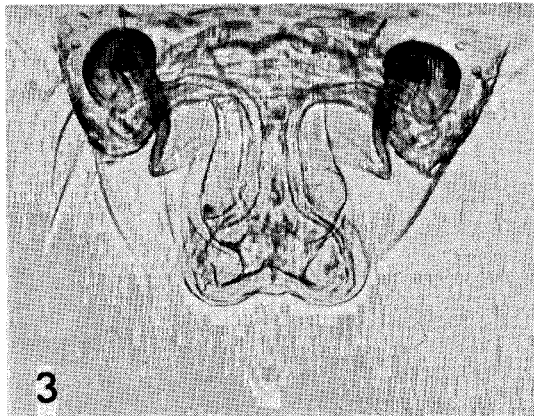
1 *L. tenuis*

x 140



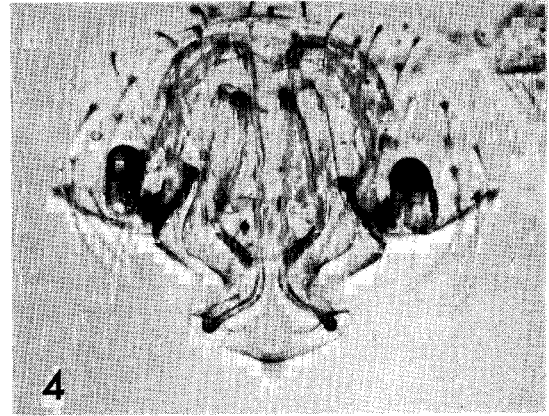
2 *L. tenebricola*

x 125



3 *L. cristatus*

x 125



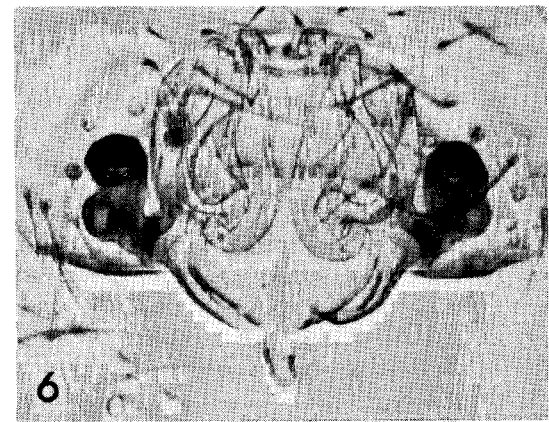
4 *L. zimmermanni*

x 140



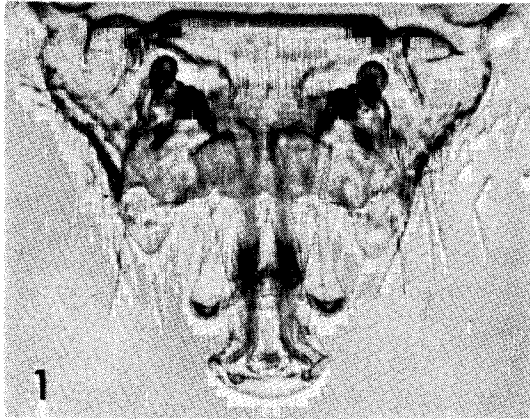
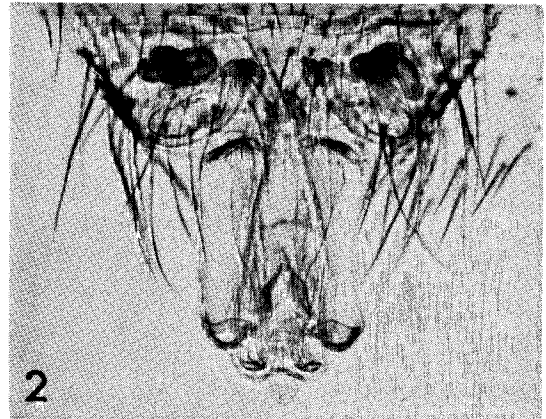
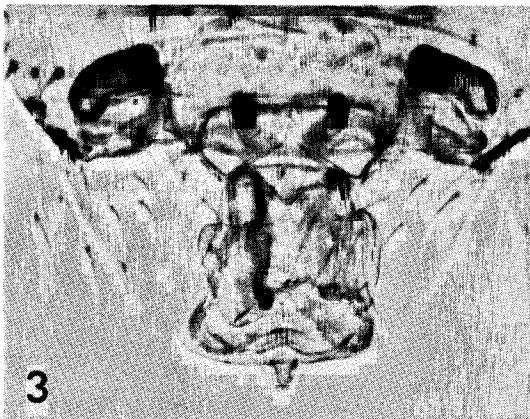
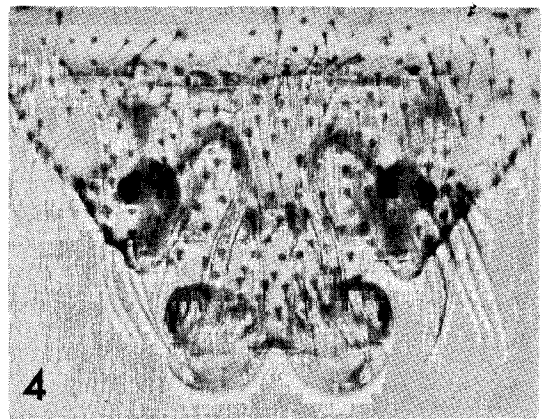
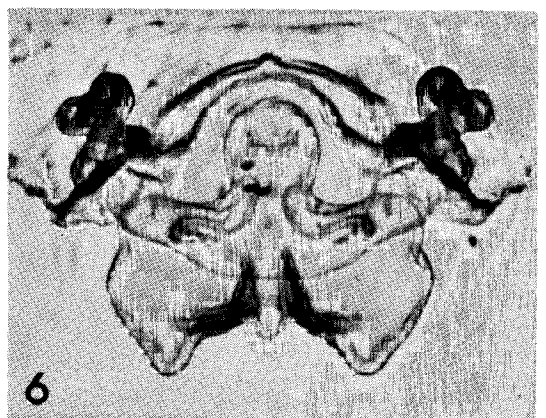
5 *L. flavipes*

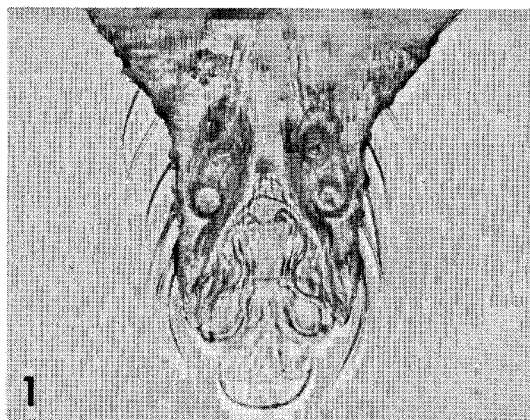
x 200



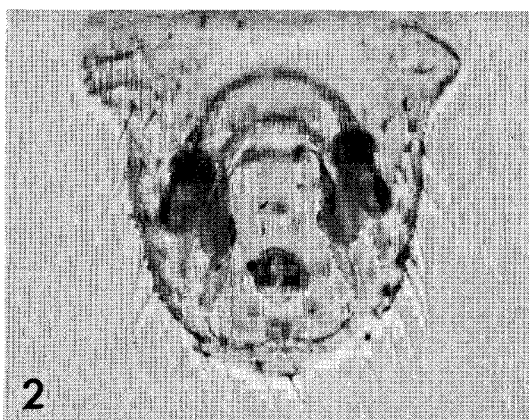
6 *L. mengei*

x 200

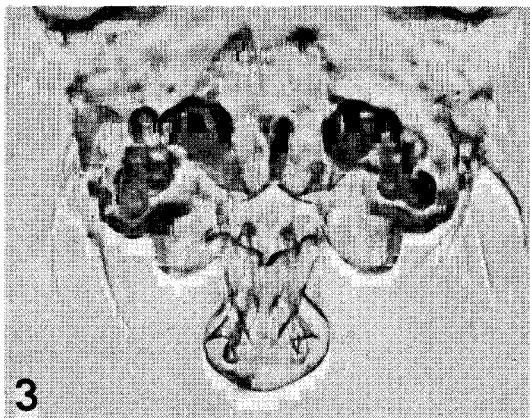
**1**
L. leprosus**x 90****2**
L. minutus**x 85****3**
L. alacris**x 120****4**
L. nebulosus**x 70****5**
L. whymeri**x 100****6**
L. obscurus**x 125**



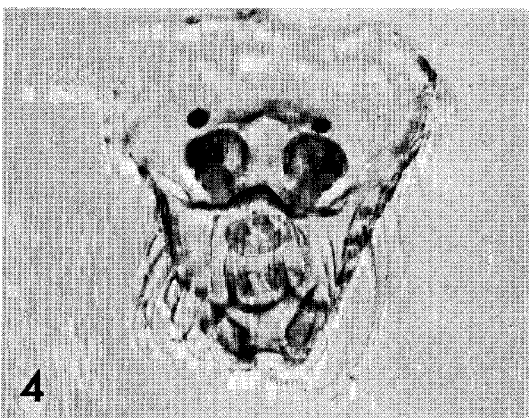
1
L. pinicola x 110



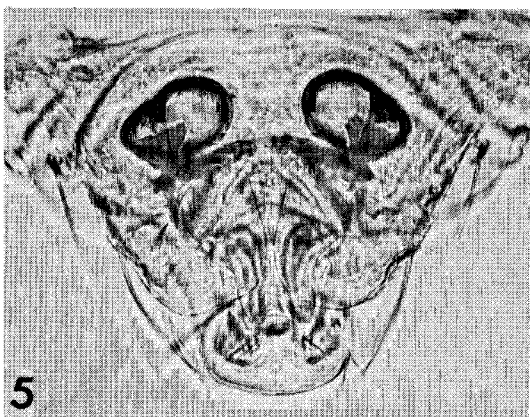
2
L. umbraticola x 150



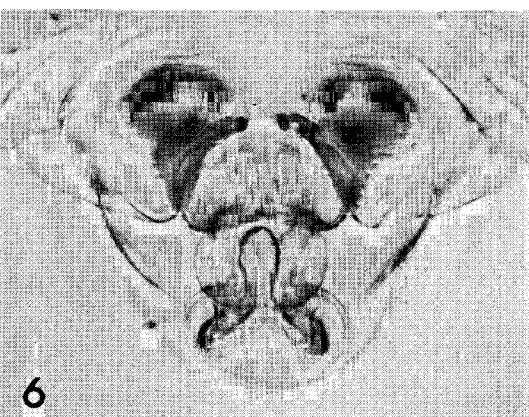
3
L. angulatus x 180



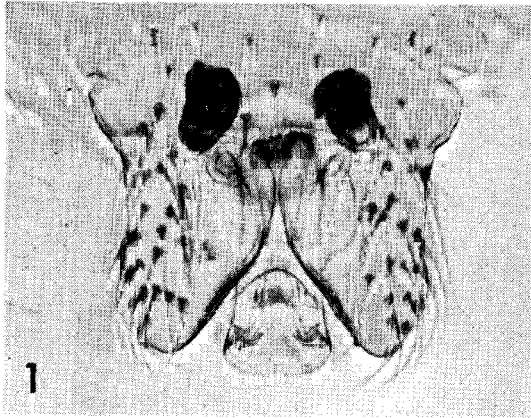
4
L. insignis (from below) x 110



5
L. ericaeus x 250

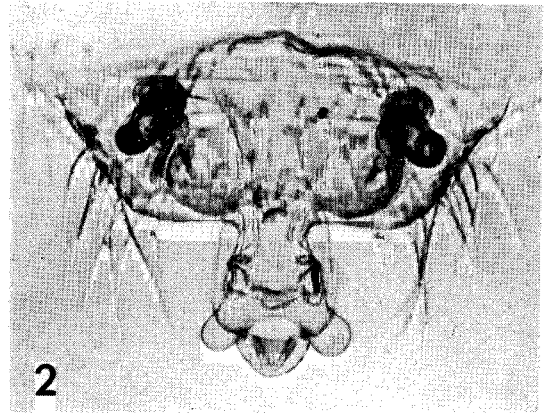


6
L. ericaeus (from below) x 250



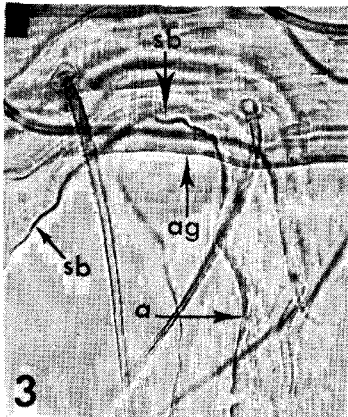
L. pallidus

x 140



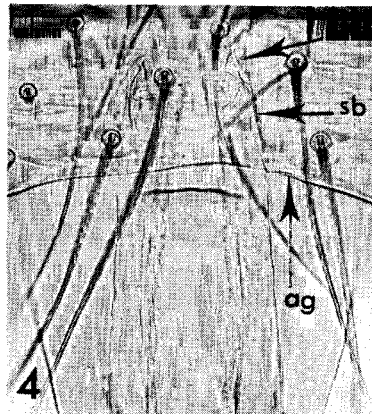
L. expunctus

x 180



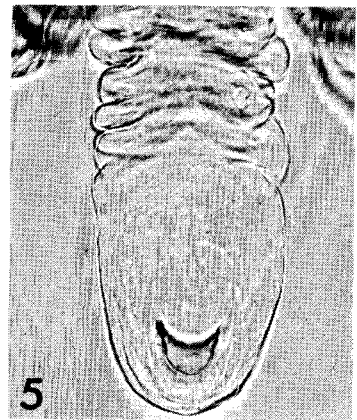
L. alacris, well developed scapoid base.

x 500



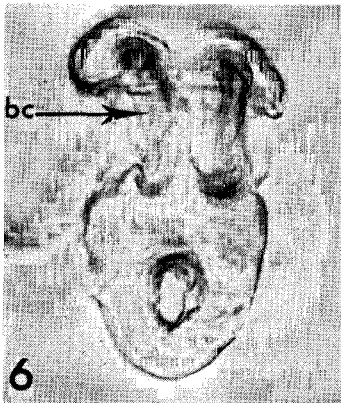
L. leprosus, weak scapoid base.

x 500



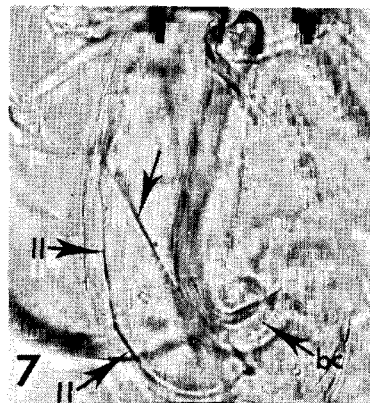
L. leprosus, stretcher.

x 435



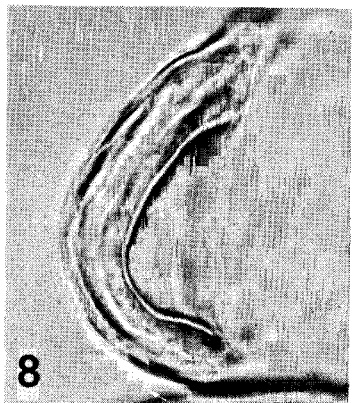
L. insignis, stretcher.

x 400



L. tenuis, lateral lobe.

x 700

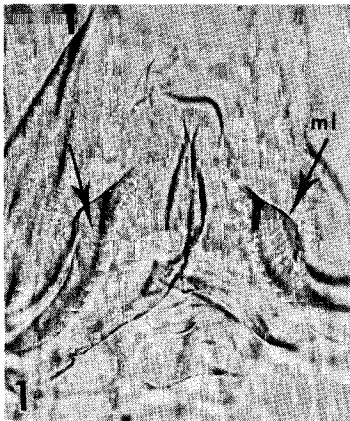


L. leprosus, lateral lobe.

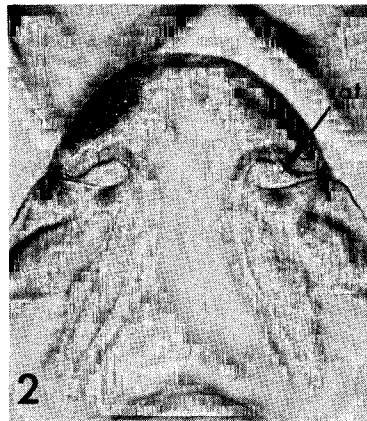
x 800

PLATE IV -

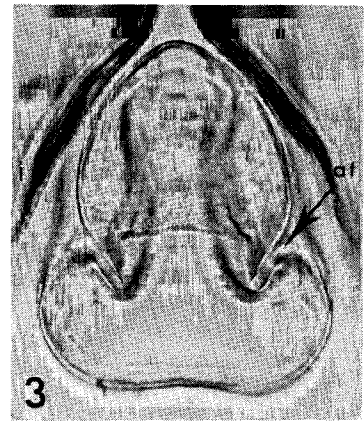
Vulvae: *Lepthyphantes* spp. high power photomicrographs of structural elements in the vulvae.



L. leprosus, median lobes. x 330



L. whymeri, atrium. x 300



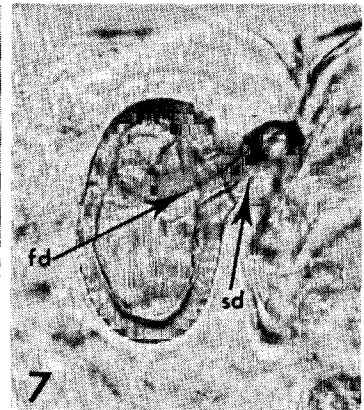
L. pallidus, atrium. x 410



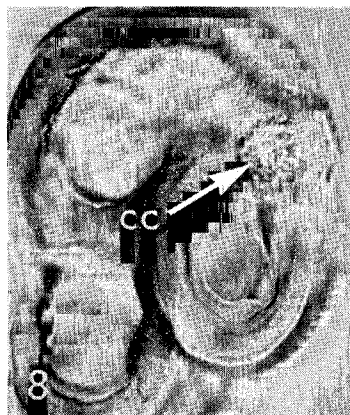
L. expunctus, bursa copulatrix of one side. x 600



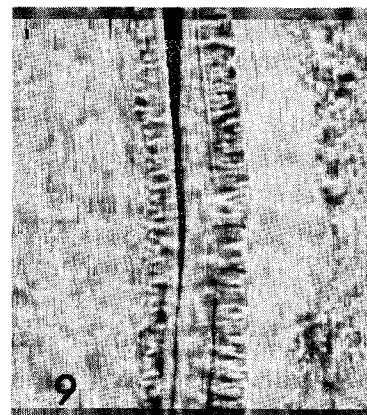
L. insignis, conical cells on primary lobe of spermatheca. x 1200



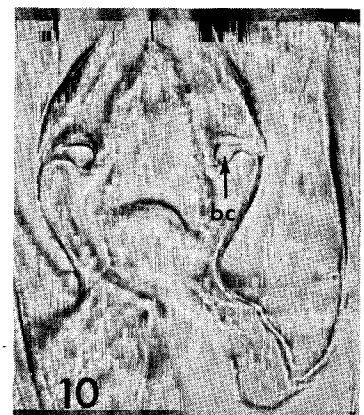
L. ericaeus, spermatheca. x 625



L. angulatus, distribution of conical cells. x 780

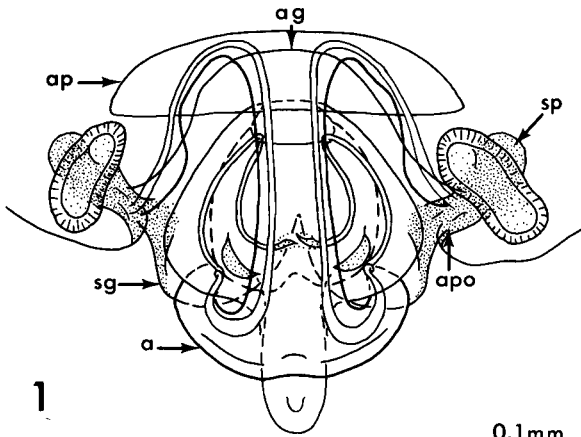


L. leprosus, sperm duct. x 1300

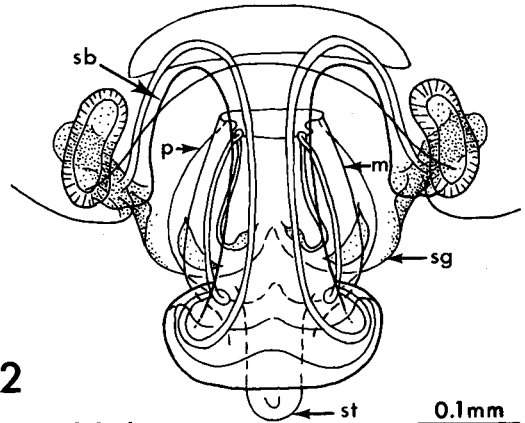


L. pinicola, posterior part of scape. x 700

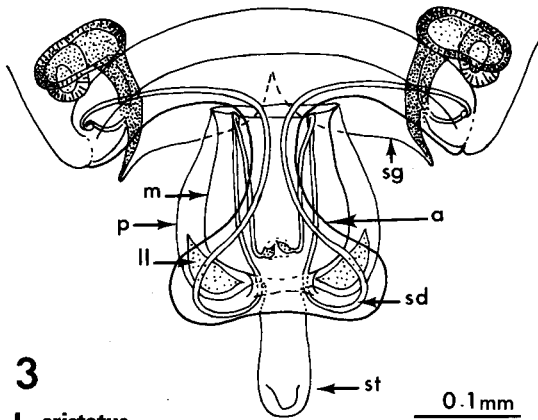
PLATE V — Vulvae: *Leptyphantus* spp. high power photomicrographs of structural elements in the vulvae.



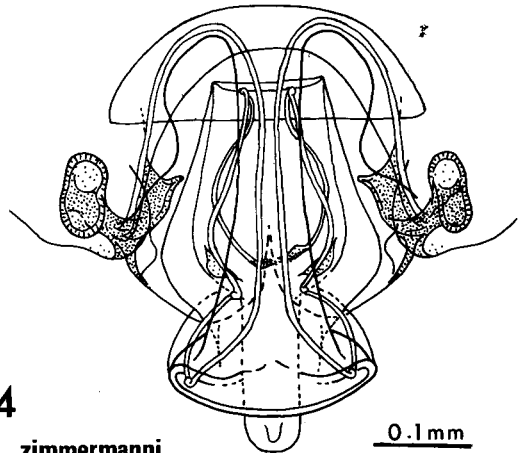
1
L. tenuis



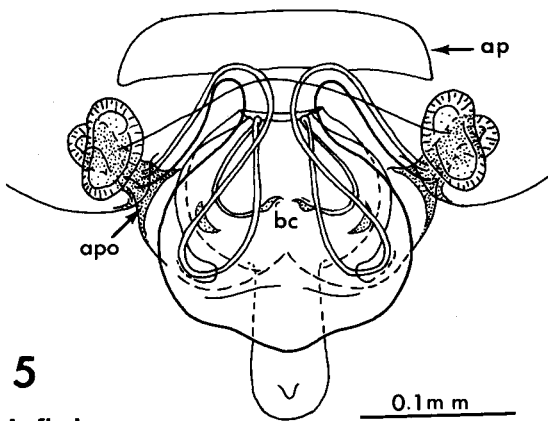
2
L. tenebricola



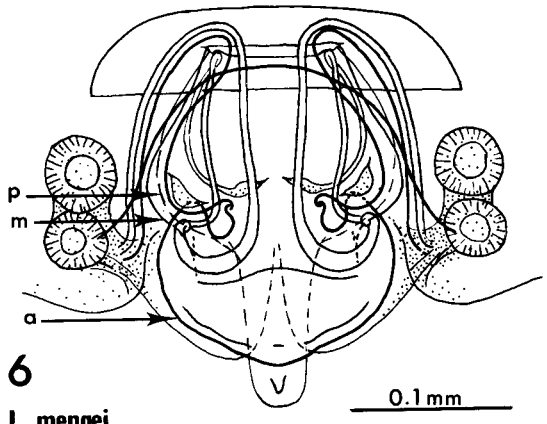
3
L. cristatus



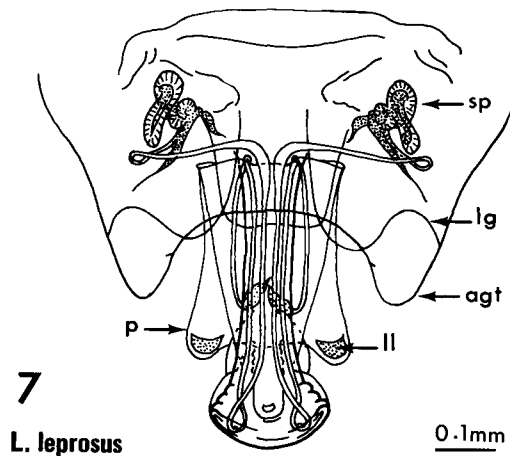
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L. zimmermanni



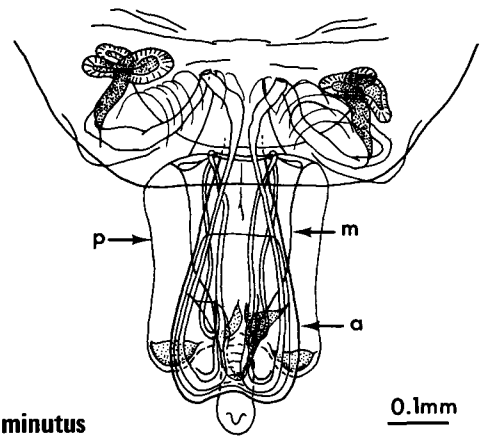
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L. flavipes



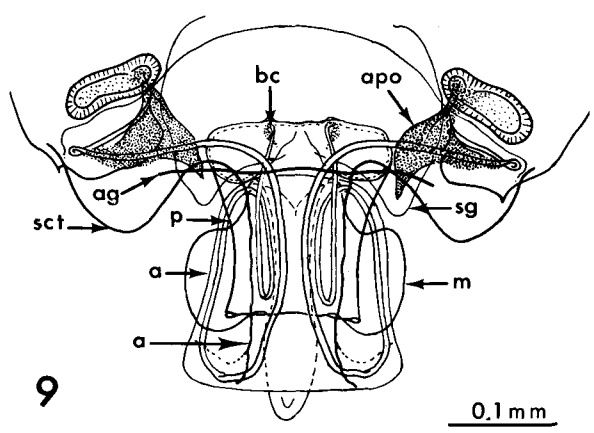
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L. mengei



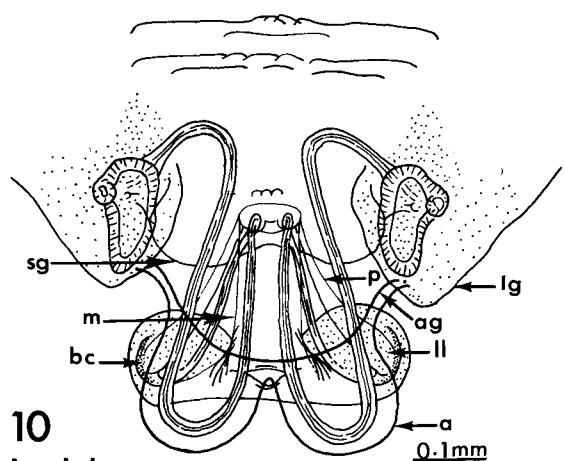
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L. leprosus



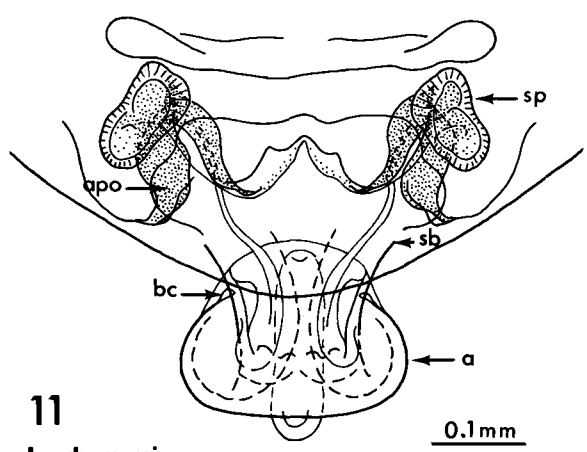
8
L. minutus



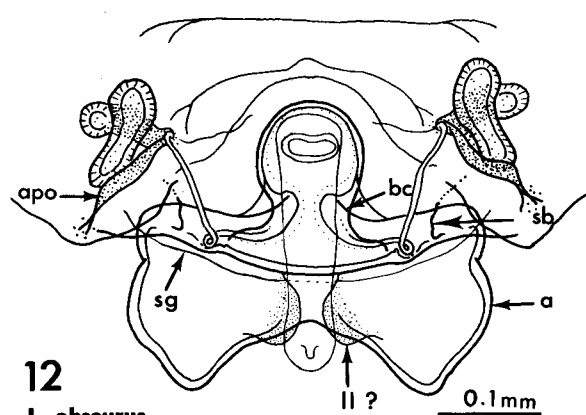
9
L. alacris



10
L. nebulosus



11
L. whymperi



12
L. obscurus

PLATE VII - Figs. 7-12, Vulvae: *Leptyphantus* spp., camera lucida drawings.

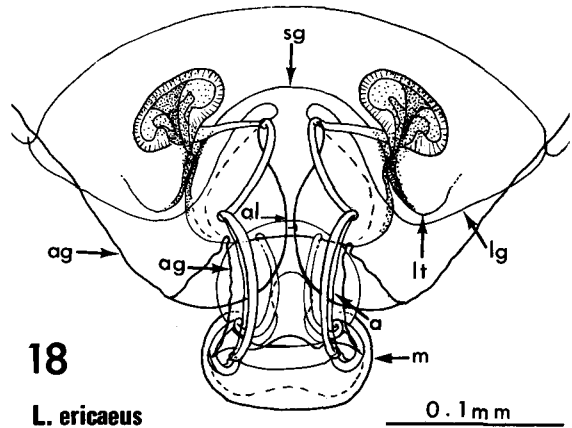
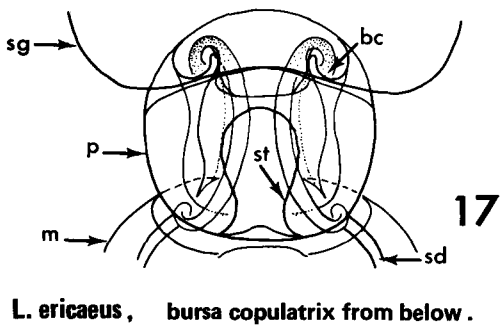
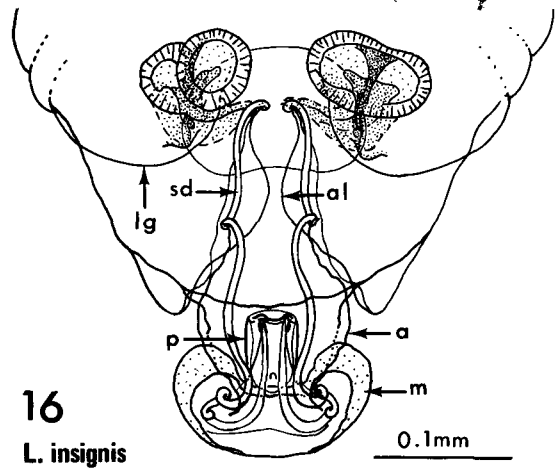
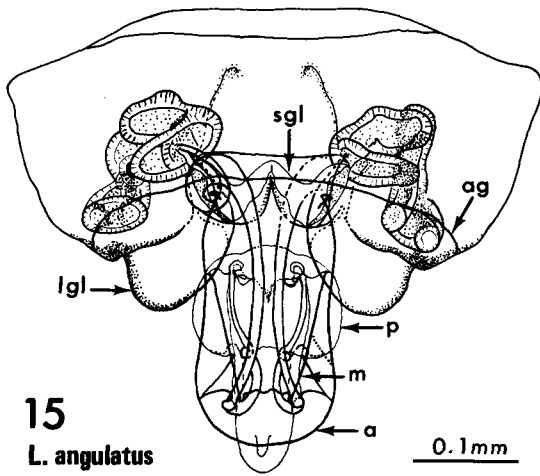
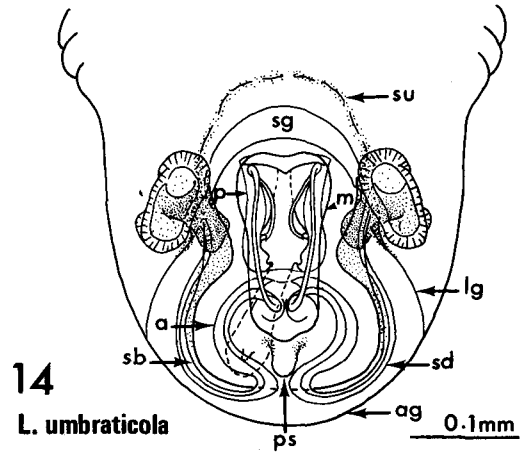
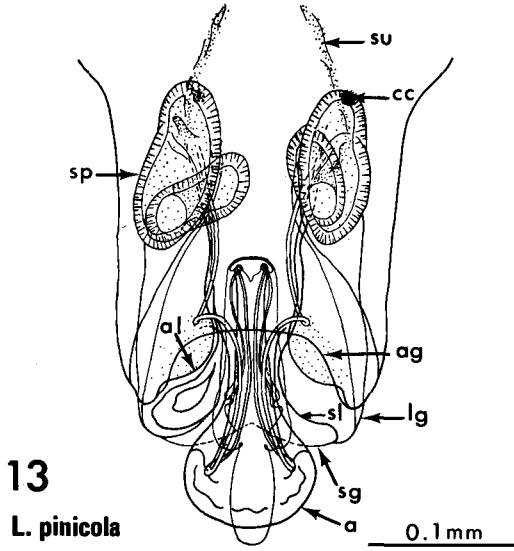
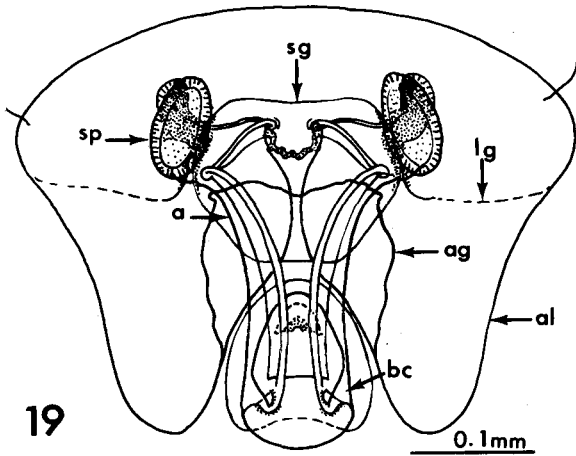
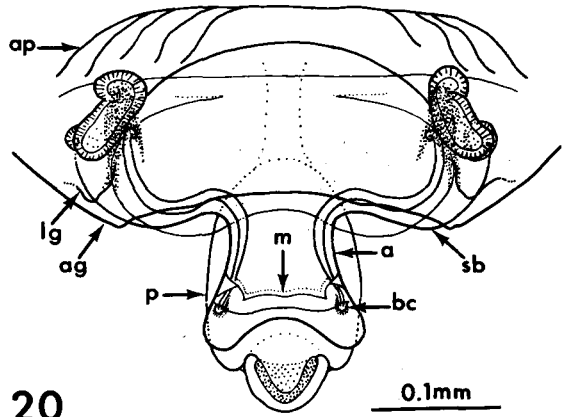


PLATE III - Figs. 13-18, Vulvae: *Lepthyphantes* spp., camera lucida drawings.



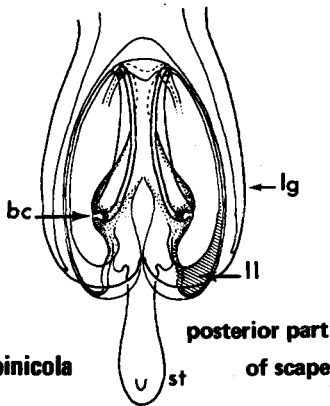
19

L. pallidus



20

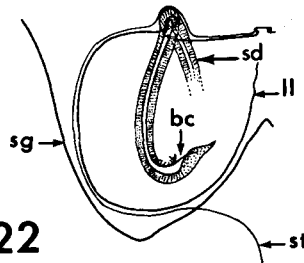
L. expunctus



21

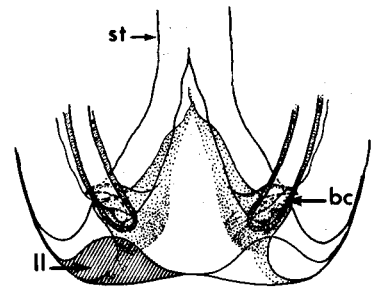
L. pinicola

posterior part
of scape



22

L. alacris, bursa copulatrix



23

L. angulatus, bursa copulatrix

Abbreviations used in the figures

a anterior part of scape
at atrium type of bursa copulatrix
ag anterior genital sclerite
agt anterior genital tooth
al anterior genital lobe
ap arched plate
apo apodeme
bc bursa copulatrix
cc conical cells

cp cuticular process
fd fertilization duct
lg lateral genital sclerite
ll lateral lobe
lt lateral genital tooth
m median part of scape
ml median lobes
p posterior part of scape

ps pseudostretcher
sb scapoid base
sct scapoid tooth
sd sperm duct
sg subgenital sclerite
sp spermatheca
st stretcher
su suture

The scape (Pl. VI) shows considerable variation in its development. The majority of vulvae have a flexible sigmoid scape, the anterior (*a*), median (*m*) and posterior (*p*) parts being well developed and showing independent structural modifications that characterise the species. In other species, a more compact and less flexible scape results from the apparent fusion between the parts. The cuticle in those parts of the scape lying within the epigynal cavity has a membranous appearance while the exposed regions are usually more robust and better sclerotized. The scapoid base (*sb*) has not previously been named in the literature, although Wiehle has included it in a number of his illustrations. Van Helsdingen divided the scape into two regions which he called the straight and arched parts, the former corresponding with the anterior part described here, while the latter includes both the median and posterior parts.

The stretcher (*st*), the function of which was first described by van Helsdingen, is used by the male to extend the scape during copulation and is found in all British *Lepthyphantes*. It consists of a base that gives rise to a trunk (Pl. IV; 5), the distal portion of which is spoon-shaped with a central sclerotized depression. In some species the trunk is reduced (Pl. IV; 6), the distal part originating directly from its base.

The *lateral lobes* (*ll*) have been shown by van Helsdingen to be typically pocket-like structures (Pl. IV; 8), which retain the pointed end of the embolus during copulation. When the membranes of the lateral lobes are homogenous (Pl. IV; 7), they are difficult to locate and as such may pass unrecognised in those species where one expects to find them. In some species they are absent, while in others there are homogenous structures (Figs. 21, 23) that resemble the lateral lobes but may not necessarily be homologous with them.

The term *bursa copulatrix* (*bc*) is used in its most general sense to include the range of structures which house the copulatory pore. Basically two structural types can be distinguished. In the first, the bursa copulatrix consists of two lobes (Pl. V; 1), which are the modified distal parts of each sperm duct. These median lobes (Pl. V; 1: *ml*) which were described by van Helsdingen, are found in many species but unfortunately their precise nature and the location of

the copulatory pore cannot be ascertained with certainty, for their internal position and sclerotization combine to give a poor optical image. Similarly the second type of bursa copulatrix is difficult to distinguish (Pl. V; 2, 3), for it has the form of a chamber or atrium (*at*) that appears to be formed from the folded parts of the scape (Pl. V; 2); often the point at which the sperm duct joins the atrium is not clear and the relation between the two is uncertain. In some species the bursa copulatrix appears to be of an intermediate form (Pl. V; 4).

The *sperm ducts* (*sd*) have a typically striated appearance (Pl. V; 9). In the more flexible type of scape the ducts are long and run a more or less parallel course throughout the length of the organ, at the base of which they turn sideways to join the spermatheca (*sp*). Shorter ducts, not extending the full length of the scape, are usually found in the less flexible type of organ. At either side of each duct is a fine membrane which, in some species, appears to form a wide outer sheath.

The *spermatheca* (*sp*) is a pouch lined with cuticle in which spermatozoa are stored. In this genus each epigyne has two spermathecae which are usually oval (Pl. V; 7) or kidney shaped and may be folded to form one or more lobes. Their outer surface is heavily sclerotized and covered with cuticular pores which suggests the presence of glands opening into the lumen. At the apex of each spermatheca is a circular patch of conical shaped cells (Pl. V; 5, 6), and arising from each cell is a fine cuticular process which is just resolvable with the light microscope. These cells together with their processes are often difficult to find, their presence being indicated by a brighter circular patch on the surface of the spermatheca (Pl. V; 8).

The *fertilization duct* (*fd*) is an indefinite structure that is closely associated with the apodeme (Pl. V; 7). In contrast to the sperm ducts it is very short, has no striations and appears to open directly into the epigynal cavity.

The *apodemes* support the spermathecae and provide a site for the attachment of muscles. They are heavily sclerotized, amorphous structures that appear to be invaginations of the lateral and subgenital sclerites. Further support for muscles is given by sutures that are seen in the walls of the sclerites.

Affinities suggested by the structure of the vulvae

The structure of the vulvae suggests relationships that may be relevant to the phylogeny of the genus. The groups suggested here are based entirely on the morphology of the vulvae, other characters not having been taken into account. Moreover, in some cases these groups are based on an incomplete understanding of the vulvae, and should not be considered as an attempt to reclassify the genus.

In this study the vulvae are divided into seven groups, some of which are split into sections:

- Group 1** (a) *L. tenuis* (Blackwall); *L. tenebricola* (Wider);
L. cristatus (Menge); *L. zimmermanni* Bertkau;
L. flavipes (Blackwall); *L. mengei* Kulczynski.
 (b) *L. alacris* (Blackwall).
 (c) *L. leprosus* (Ohlert); *L. minutus* (Blackwall).
Group 2 *L. nebulosus* (Sundevall).
Group 3 (a) *L. whymperi* F.O.P.—Cambridge.
 (b) *L. obscurus* (Blackwall).
Group 4 *L. ericaeus* (Blackwall); *L. insignis*
 O.P.—Cambridge.
Group 5 *L. pallidus* (O.P.—Cambridge).
Group 6 (a) *L. pinicola* Simon
 (b) *L. umbraticola* (Keyserling).
 (c) *L. angulatus* (O.P.—Cambridge).
Group 7 *L. expunctus* (O.P.—Cambridge).

Locket & Millidge (1953) arranged the British species in five groups on the basis of the position of the trichobothria, the spinal armature of the legs and the dorsal pattern of the abdomen (Table 1). Wiehle (1956) arrived at the same groupings after a study of the genitalia and spinal armature of the legs and it is interesting to compare these groups with those given above.

Group 1 (a), *L. tenuis*, *L. tenebricola*, *L. cristatus*, *L. zimmermanni*, *L. flavipes* and *L. mengei* have a flexible sigmoid scape that arises from a well developed scapoid base. The genital atrium is limited by an arched plate and forms a distinct well, even in

those species where it is covered by the scape. The lateral lobes are membranous pocket-like structures which lie either side of the bursa copulatrix (which is made up of two median lobes). The spermathecae are simple, each with one lobe.

Group 1 (b), *L. alacris* differs from group 1 (a), in that the median part of the scape is invaginated, resulting in an extra fold that locates the bursa copulatrix in an anterior position. This may account for the difficulty in identifying the lateral lobes which are indicated in Fig. 22 as a thin chitinous plate, devoid of pigmentation and lacking any pocket-like features. The arched plate is absent. The well developed scapoid base suggests that *L. alacris* is more closely related to group 1 (a) than it is to group 1 (c). Locket and Millidge include this in their group 1, and the absence of the arched plate supports this view. On balance, *L. alacris* shows affinities to both groups and is therefore placed in an intermediate section.

Group 1 (c), *L. leprosus* and *L. minutus* are alike in vulva structure. They differ from the other sections to which they are closely related in possessing a weakly developed scapoid base. Other differences may in part be accounted for by the increased size of the vulva; the median lobes and lateral lobes are prominent structures; the spermathecae are more complex; sutures are distinct but the arched plate is absent.

Group 2, *L. nebulosus* shows affinities with group 1 because of the general similarity in the form of the vulva. As in group 1, the scape has a sigmoid shape but the parts differ in their development. The anterior part of the scape is well developed and completely covers the epigynal cavity. The median and posterior parts are weakly developed. The lateral lobes are large pigmented structures that occupy much of the space in the posterior part of the scape,

Group 1	Group 2	Group 3	Group 4	Group 5
<i>L. nebulosus</i>	<i>L. obscurus</i>	<i>L. tenuis</i>	<i>L. ericaeus</i>	<i>L. expunctus</i>
<i>L. leprosus</i>		<i>L. zimmermanni</i>	<i>L. pallidus</i>	
<i>L. minutus</i>		<i>L. cristatus</i>	<i>L. pinicola</i>	
<i>L. alacris</i>		<i>L. tenebricola</i>	<i>L. insignis</i>	
<i>L. whymperi</i>		<i>L. mengei</i>	<i>L. angulatus</i>	
		<i>L. flavipes</i>	<i>L. umbraticola</i>	
			<i>L. carri</i>	

Table 1: Distribution of species within the groups of Locket and Millidge (1953).

giving the impression that it is well developed. In contrast to group 1, the lateral lobes are located on the outer surface of the posterior part of the scape. The stretcher is aberrant, being no more than a pocket-like fold: the sperm ducts are wider and the median lobes more diffuse. These differences in detail are thought to justify the inclusion of this vulva in a separate group, although this is not in agreement with either Locket & Millidge or Wiehle, who included it in their group 1.

Group 3 (a), *L. whymperi*, (b) *L. obscurus*, both these vulvae are clearly distinct from groups 1 and 2, but their affinity to each other is uncertain. They are alike in that the distal parts of the short sperm ducts open into an atrium that is similar in both vulvae. While the form of the scape would appear to limit the flexibility of both organs, the relationship between these species is in doubt because the parts of the scape cannot be clearly distinguished. In fact, the terms anterior, median and posterior cannot be strictly applied to either vulva, for exactly which membranes represent the median and posterior parts is uncertain. The development of an atrium has possibly led to a degree of fusion between the parts; its shape and the absence of lateral lobes in *L. whymperi* suggests that it may combine the functions of the lateral lobes and copulatory pore into one structure. In *L. obscurus* there are no lateral lobes, there are, however, dark lobe-like structures on the underside of the anterior part of the scape, their sclerotization indicating that they may function as lateral lobes. Other differences are found in the shape of the spermatheca, the development of the apodeme and the form of the subgenital sclerite. Locket and Millidge include *L. whymperi* in group 1 and *L. obscurus* in group 3. Placing these vulvae into one group is therefore not in agreement with other taxonomic characters.

Group 4 (a), *L. ericaeus*, (b), *L. insignis* are alike in vulva structure and show affinities to group 1 in the development of the flexible sigmoid scape. They are placed in a separate group on account of the complex nature of the epigynal cavity. In both vulvae the well of the epigynal cavity is reduced by prominent anterior genital lobes, part of which lies under the scape and is associated with the sperm ducts. The anterior genital sclerite extends to cover the weakly

developed anterior part of the scape and is responsible for the membranous appearance of the epigynes. Detail within the scape cannot be clearly distinguished, there are no structures that resemble the lateral lobes and the form of the bursa copulatrix is obscure. In *L. insignis* the sperm ducts simply fade out in the base of the stretcher (Pl. IV; 6), while in *L. ericaeus* they terminate in a system of folds that have the appearance of an atrium (Fig. 17). However, these folds must be interpreted with great care as the definition in this region is extremely poor. The most interesting difference between these two vulvae is a wedge-shaped gutter which is derived from the folded edges of the median part of the scape of *L. insignis*.

Group 5, *L. pallidus* has prominent anterior genital lobes and simple spermatheca indicating an affinity to group 4. It is placed in a separate group on account of its general form (Fig. 24-1), size and the structural differences in the parts of the scape. The most important feature to note is that the sperm ducts do not extend the full length of the scape as in group 4, but terminate in an atrium that resembles those of group 3.

Group 6 (a), *L. pinicola*, (b) *L. umbraticola*, (c) *L. angulatus* have vulvae of varied form. The configuration of the scape shows an affinity to groups 1, 4 and 5. *L. pinicola* and *L. angulatus* have a flexible sigmoid scape that ends in a typical stretcher, the scape of *L. umbraticola* differs in form but is flexible and also terminates in a typical stretcher. In all three vulvae the epigynal cavity is well developed, possessing anterior and lateral genital lobes in *L. pinicola*, lateral lobes in *L. angulatus* and extending in *L. umbraticola* to form a cover that almost encloses the scape. Apart from these general considerations, the only feature common to all three vulvae is the suture that lies in the subgenital sclerite. *L. pinicola* and *L. umbraticola* differ from *L. angulatus* in possessing a unique posterior scape (Fig. 21), while that of *L. angulatus* is more typical of group 1, having a superficial resemblance to that of *L. alacris*. The presence of lateral lobes cannot be established with certainty in any of these vulvae; the structures indicated in Fig. 21 and 23 may prove to be folds that play no part in holding the embolus. The bursa copulatrix of *L. angulatus* has a distinct form (Fig. 23), and while those of *L. umbraticola* and *L.*

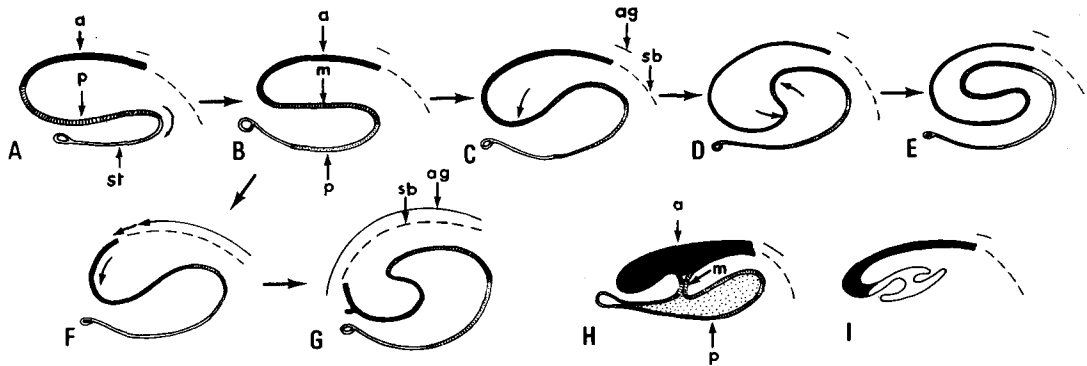


Fig. 24. Diagram showing how the scape of *L. alacris* and *L. umbraticola* may have evolved.

A Primitive hypothetical scape. B Scape of *L. flavipes* type, showing flattened form. C Scape of *L. tenebricola* type, with swelling of the knob-shaped turning point. D Hypothetical scape, showing early stage of invagination. E Scape of *L. alacris*, showing complete invagination. F Hypothetical scape showing early stage of inversion. G Scape of *L. umbraticola*. H Scape of *L. expunctus*. I Scape of *L. pallidus*.

pinicola are very similar to each other, their precise form is uncertain, the ducts appearing to fuse over an aperture. Structures peculiar to *L. angulatus* are found in the complex spermatheca and the accessory lip of the subgenital sclerite. In *L. pinicola* this sclerite has fused with the lateral sclerite, while in *L. umbraticola* it remains simple, having the form of a crescent-shaped plate.

It is interesting to note that the spiders of groups 4, 5 and 6 above, which all have lateral lobes, composed the group 4 of Locket & Millidge.

Group 7, *L. expunctus*, the form of the epigynal cavity, the arched plate and well developed scapoid base suggests an affinity to group 1. This vulva is placed in a separate group because the configuration of the scape (Fig. 24-H) differs from that of any other group in having the form of a horizontal letter H. Further differences include the nature of the stretcher, the absence of lateral lobes and the poorly defined bursa copulatrix (Pl. V; 4) which is not lobe-like as in group 1, and appears too small to form a typical atrium. This vulvae cannot be placed with confidence near any other group. As Locket and Millidge place *L. expunctus* alone in their group 5, the above observations would appear to be in agreement.

Possible evolutionary stages in the development of the scape

The vulvae of group 1 show a remarkable similarity in structure and can be arranged in a morphological series, Figs. 24 A-E show the possible evolutionary relationships of the types of scape found in members of this group from a hypothetical "primitive" condition through intermediate stages represented by certain contemporary species to that found in *L. alacris*.

It is suggested that the scape of *L. alacris* may have evolved by a process of invagination.

The theoretical "primitive" scape (Fig. 24-A) has a flattened form with a U-shaped invagination separating the anterior and posterior parts. Such an organ could show functional similarities to *L. alacris* if the stretcher was long and the bursa copulatrix located in an anterior position. The development of the posterior part along the line of the stretcher could give rise to the compressed sigmoid scape of the type found in *L. flavipes* and *L. mengei* (Fig. 24-B). The gradual enlargement of the knob-shaped turning point that may have preceded invagination can be seen in a number of contemporary species, various stages being represented by *L. tenuis*, *L. tenebricola*, *L. cristatus*, and *L. zimmermanni*. Unfortunately the critical stage

of early invagination, (Fig. 24-D) is not represented by a contemporary British species, although it is conceivable that such a scape may be found among foreign *Lepthyphantes*.

It has been shown above that there is an affinity between group 1 and *L. umbraticola*. The scape of this species is inverted, the median part lying above the anterior part. In addition, the anterior genital sclerite is extended posteriorly so as almost to completely cover the scape. The ancestral vulva may have passed through the stage shown in Fig. 24-F, where small arrows show the direction in which the inversion may have occurred.

Conclusions

The practice of clearing epigynes as a means of investigating their structure has its limitations because the appearance and spatial relationships between the parts are difficult to interpret. These problems can only be solved by using histological techniques involving serial sectioning of the epigynes. A better understanding of the structure of the genitalia and the affinities between them would result from a study of foreign *Lepthyphantes* and other related genera. A knowledge of the functional relationship between the genitalia is vital if the structural elements are to be understood. Van Helsdingen's work on *L. leprosus* was important to this study, for without it some of the structural features in the vulva would not have been recognised.

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Summary

The vulvae of 19 British species of the spider genus *Lepthyphantes* are described in detail and grouped according to affinities indicated by the structural evidence. Possible stages in the evolution of the scape are also briefly discussed.

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