

The taxonomy of the Linyphiidae, based chiefly on the epigynal and tracheal characters (Araneae: Linyphiidae)

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Summary

The epigynal forms present in the Linyphiidae are described and analysed. The utility of the tracheal form and of the clypeal glands as taxonomic indicators is re-examined, and on the basis of these characters and the epigynal structures the known genera of the family are split into six groups, namely the *Stemonyphantes* group and the five subfamilies Mynogleninae, Linyphiinae, Drapetiscinae (new subfamily), Micronetinae and Erigoninae. There is evidence that the *Stemonyphantes* group is paraphyletic, but epigynal and other synapomorphies suggest that the subfamilies are monophyletic. It is argued that in the Linyphiidae the epigynal form may be more reliable than the palpal form as a taxonomic indicator, at least above the generic level, and that the classification proposed can be regarded as a useful working hypothesis which is capable of further development.

Haplinis Simon is established as a senior synonym of *Mynoglenes* Simon, and two new genera are erected: *Atopogyna* (type species *Erigone cornupalpis* O. P.-Cambr.) and *Palaeohyphantes* (type species *Mynoglenes simplicipalpis* Wund.). The female of *Palaeohyphantes simplicipalpis* is described. On the basis of the genitalia, most *Erigone* species appear not to be congeneric with the type species (*E. vagans* Audouin).

Introduction

There have been several publications which describe the epigynal structures of individual linyphiid genera or species (e.g. Blauvelt, 1936; Zorsch, 1937; Wiehle, 1956, 1960; van Helsdingen, 1965, 1969, 1970; Wanless, 1971, 1973; Saaristo, 1971, 1972, 1973a, b, 1974a, b; Lehtinen & Saaristo, 1972; Blest, 1979). No serious attempt has yet been made, however, to carry out comparative studies on the structures of the epigynes of the Linyphiidae as a whole. Such a study is reported in the present paper, and the epigynal characters are applied to the

development of taxonomic hypotheses.

Before these results are reported, however, it is essential to comment on two somatic characters in the Linyphiidae which are taxonomically relevant, namely, the form of the tracheae and the presence of clypeal pits and glands. These characters are therefore briefly discussed before the descriptions of the epigynal structures are given.

Methods

Representatives of as many genera as possible were examined during the course of this work. Fellow arachnologists have been extremely generous in providing specimens, but it has nevertheless proved impossible to obtain examples of all genera. Shortage of specimens has sometimes precluded the determination of the tracheal form, or a detailed study of the epigynal structure.

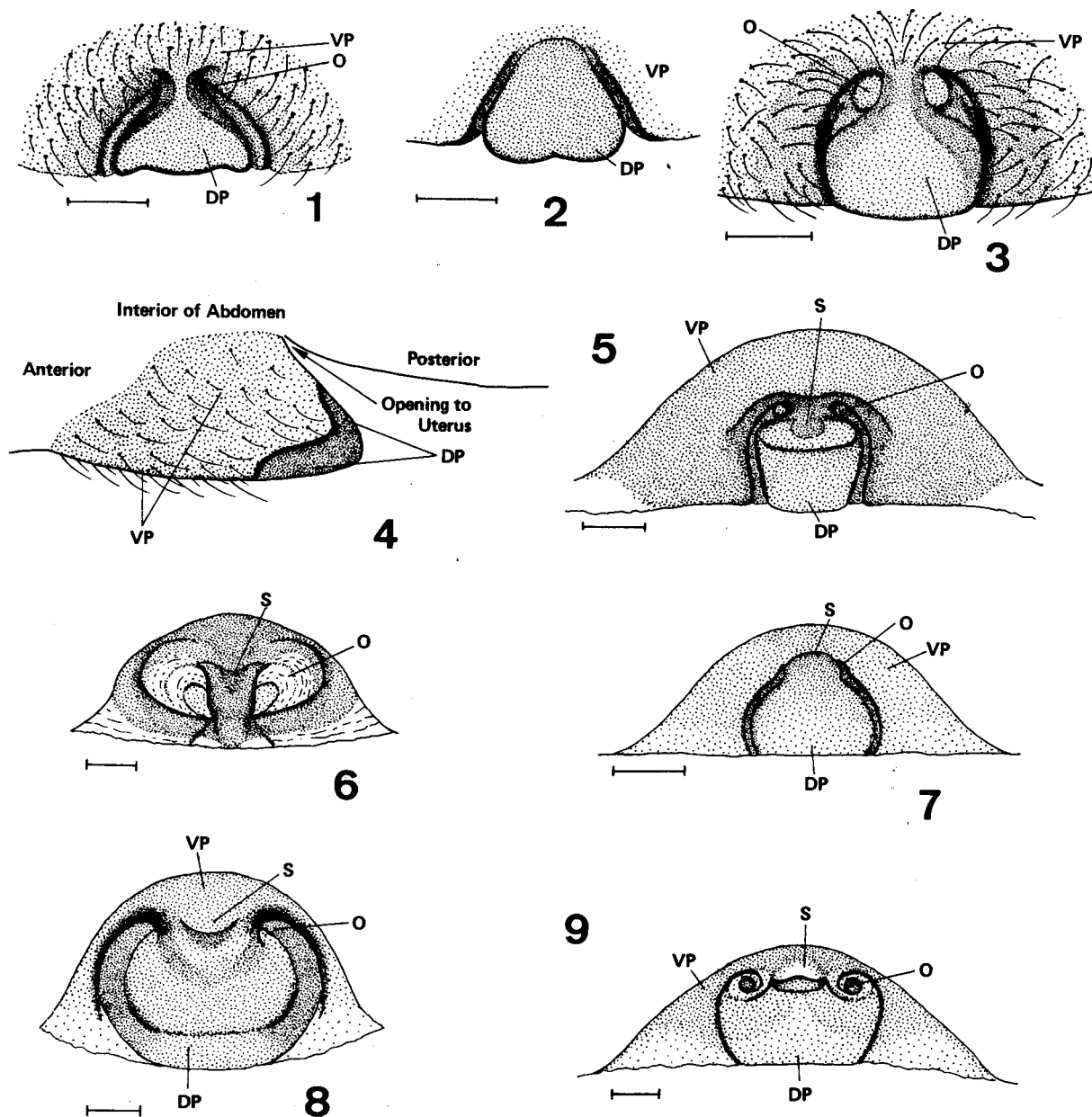
Epigynes: The excised epigynes have been examined by several procedures.

(i) The epigyne is immersed in clove oil or methyl salicylate and examined with a stereo-binocular microscope from a variety of angles by strong incident light against a white background. This is often the best method for establishing the locations of the internal ducts, etc. Where the epigyne is heavily pigmented, controlled bleaching in a weak sodium hypochlorite solution (c. 1% available chlorine), followed by washing, etc., before immersion in the clearing liquid, is beneficial.

(ii) In some instances it is advantageous to bleach the epigyne completely, or almost completely, in sodium hypochlorite, followed by examination under top light in water. The internal ducts often show up well by this procedure. Occasionally, after bleaching and washing, light staining, e.g. with chlorazol black, may be helpful.

(iii) Examination of the epigyne, immersed in a clearing liquid, by transmitted light with a monocular microscope may show additional details of the duct system, but because of refractive effects this procedure sometimes gives a confusing picture. In general, I regard it as a waste of time and material to make permanent slide mounts of epigynes, since it is essential to be able to examine them from all angles.

(iv) Examination of the dry epigyne by top light is probably the best method for observing the external shape of the epigyne, and for locating the



Figs. 1-9: Epigynes. 1 *Stemonyphantes lineatus* (Linn.), ventral, dry; 2 *S. lineatus*, dorsal, dry; 3 *Frontinella communis*, ventral, dry; 4 *S. lineatus*, lateral, semi-diagrammatic; 5 *Stemonyphantes abatensis*, caudal, dry; 6 *Estrandia nearctica*, caudal; 7 *Microlinyphia pusilla*, caudal; 8 *Frontinellina frutetorum*, ventral; 9 *Microlinyphia impigra*, caudal, dry. Scale lines 0.1 mm.

form and position of the genital openings. For this procedure, the epigyne should be as clean as possible, with foreign matter removed by short controlled washing in 10% potassium hydroxide or weak sodium hypochlorite solution (1% active chlorine), followed by water. The detached epigyne is taken through ethanol or isopropanol, transferred to a dry slide and allowed to dry for a few seconds under the binocular microscope. The dried epigyne tends to become electrically charged, and consequently liable to fly off and be lost, and should at this stage be attached temporarily to the slide by means of a tiny smear of viscous balsam mountant applied to the slide, close to the specimen, with the point of a fine needle. The epigyne can then be moved carefully on to the adhesive, and manipulated with a fine needle to expose the different surfaces for examination. The reflective and refractive effects present when the epigyne is examined in liquid are largely eliminated by examination of the dry epigyne; the image obtained is of the same kind as that obtained with the electron microscope, though of course with poorer definition and at reduced magnification. The epigyne can be recovered after examination, by covering it with a drop of xylene; after dispersal of the air bubbles present in the epigyne, it is transferred to alcohol. The drying for a limited period (up to several days) appears to cause no damage to the epigyne.

In order to obtain the most complete picture of the epigynal structure, more than one of these procedures must obviously be used.

Tracheae: Blest's procedure (1976) of boiling the spider in 10% sodium hydroxide gives satisfactory results, but in the present work the easiest method for revealing the tracheae was found to be treatment with cold dilute sodium hypochlorite solution (1% active chlorine), as follows. The limbs are removed from the spider, and a window is cut in the dorsal surface of the abdomen by means of a fine needle and forceps. The specimen is then rinsed in distilled water and transferred to the hypochlorite in a glass block at room temperature (15-20°C) for several hours, or overnight, until all the non-chitinous parts are dissolved. This treatment is gentle, and the undisturbed tracheae can be examined without removal of the specimen from the digestion liquid; the tracheae are readily visible when illuminated by strong oblique incident light against a dark

background. After the digestion, the specimen can if desired be washed in distilled water and then stained (Blest, 1976), but this was not found to be necessary in the present work. Spiders which have been stored in discoloured alcohol, particularly where this has been in contact with a rubber stopper, should be soaked in clean alcohol or isopropanol for 24 hours or longer, followed by water, to remove contamination as far as possible. With small spiders (up to 2 mm body length) cutting a window in the abdomen did not appear to be absolutely necessary.

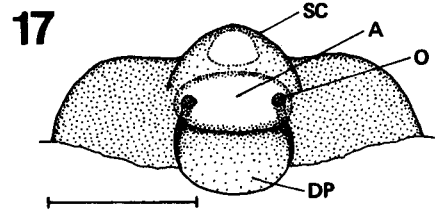
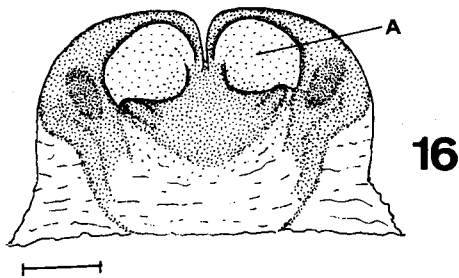
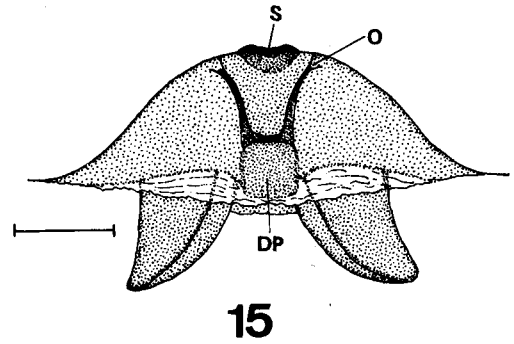
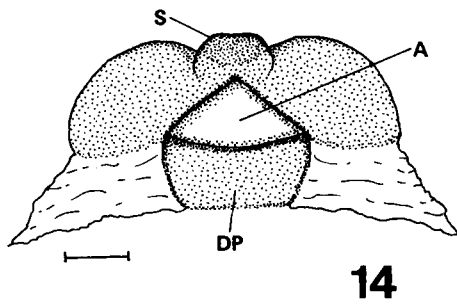
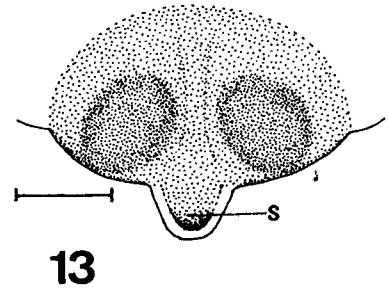
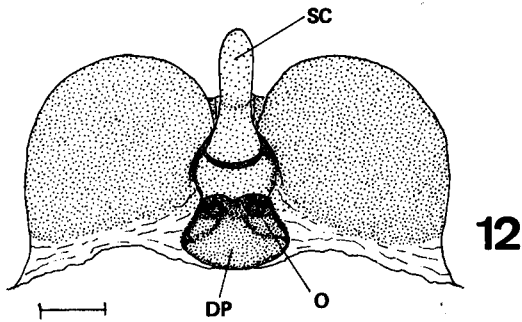
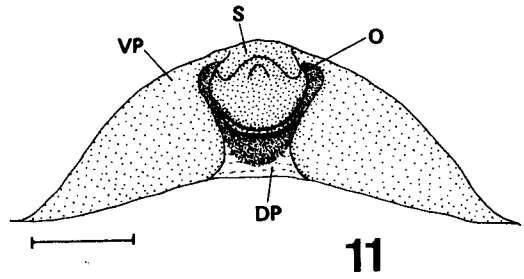
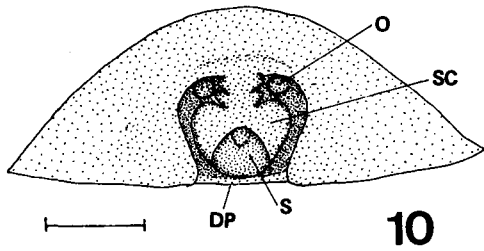
The digestion process destroys the spider, but the palps or epigyne can be removed before the treatment. In a few cases it was verified that a subadult specimen has the same tracheal structure as the adult, and it is probably safe to use a subadult for the tracheal determination, provided its identity is certain.

Blest (1976) noted that the median tracheal trunks in the erigonine species branch into bundles of either small tracheoles without taenidia, or of smaller tracheae with taenidia. The significance of these two forms is unclear; no attempt was made to distinguish between them during the course of the present work; future work may of course show that some additional information is produced by taking the two forms into account.

Tracheal structure

Several years ago it was suggested by Blest (1976) that the tracheal patterns within the Linyphiidae support the division of the family into two major groups, the subfamilies Linyphiinae and Erigoninae. In the former, the median pair of tracheae are short, slender, unbranched and confined to the abdomen (Fig. 130), while in the latter the median pair are thick trunks, which divide into numerous small branches which pass as two bundles through the pedicel into the prosoma (Fig. 131). All members of the family have the lateral tracheae simple and confined to the abdomen.

The genus *Allomengea* Strand, which was placed by Blest in the Linyphiinae, was anomalous in that the median tracheae were moderately branched, though confined to the abdomen. The genera *Aphileta* Hull, *Asthenargus* Simon, *Carorita* Duffey & Merrett, *Jacksonella* Millidge, *Lessertiella* Dumitrescu & Miller (= *Caviphantes* Oi), *Mioxena* Simon,



Figs. 10-17: Epigynes. 10 *Linyphantes tragicus* (Banks), ventral, dry; 11 *L. tragicus*, caudal, dry; 12 *Jalapyphantes cuernavaca* Gertsch & Davis, ventral; 13 *Smermisia tullgreni* Sim., ventral; 14 *Taranucnus setosus*, caudal; 15 *S. tullgreni*, caudal, dry; 16 *Taranucnus omithes*, caudal; 17 *Caviphantes saxetorum* (Hull), caudal, dry. Scale lines 0.1 mm.

Ostearius Hull and *Wiehlea* Braun, previously regarded as erigonine, were found to have tracheae of the "linyphiine" type, and were transferred by Blest to the Linyphiinae. The genera *Hilaira* Simon, *Donacochara* Simon, *Drepanotylus* Holm and *Leptorhoptum* Kulcz., previously regarded by some authors as "linyphiine", had tracheae of the "erigonine" form, and their position in the classification was considered to be problematical.

In the present paper, those taxa with simple unbranched median tracheae ("linyphiine" form of Blest) are referred to as "haplotracheate" (Greek *haplos* – simple, single), while those with median tracheal trunks which branch into two bundles of narrow tracheae ("erigonine" form of Blest) are referred to as "desmitracheate" (Greek *desme* – a bundle).

In two earlier papers (Millidge, 1977, 1980) I expressed some reservations on Blest's conclusions, on the grounds that the tracheal systems in other families appeared to be variable to a marked and indeed erratic degree. Reconsideration of the tracheal data, however, now suggests that Blest was almost certainly correct in stressing the taxonomic importance of the tracheal pattern, which in the Linyphiidae shows such a distinct dichotomy. At the same time it appears that some modification of Blest's conclusions is required, on the ground that it is highly probable that the haplotracheate form is the primitive form within the family. This view is supported by the facts that this simple tracheal form is the one present in what are probably the most primitive members of the Linyphiidae, namely the *Stemonyphantes* group and the Mynogleninae (see Discussion), and is also the form present in several other families, e.g. the Agelenidae (Petrunkevitch, 1942: 157), the Stiphidiidae and the Amphinectidae (Forster & Wilton, 1973). If the haplotracheate form is plesiomorphic for the family, then this character is not valid for inferring relationships within the family (Hennig, 1966), i.e., natural groups cannot be founded on symplesiomorphy. The Linyphiinae, as defined by Blest (1976) on the tracheal structure, cannot therefore be considered a monophyletic group. This was tacitly admitted later by Blest (1979) in a paper which shows (p. 172) the haplotracheate Linyphiinae as more closely related to the desmitracheate Erigoninae than to the haplotracheate Mynogleninae.

If the haplotracheate form is plesiomorphic, then the desmitracheate form must be apomorphic (derived), and this synapomorphy within the Erigoninae, as defined by Blest (1976), supports the hypothesis that the Erigoninae are a monophyletic group. This hypothesis is of course dependent on the assumption (based on the principle of Occam's Razor, or parsimony: Nelson & Platnick, 1981: 37) that within the Linyphiidae the desmitracheate system evolved only once from the primitive haplotracheate system.

Clypeal glands

The detailed study of the Mynogleninae carried out by Blest (1979) showed that all the members of this group were characterised by the presence in both sexes of a pair of clypeal pits, which contained numerous pores leading to internal secretory glands. These structures are absent from all those linyphiids (the *Stemonyphantes* group) which are probably the most primitive members of the family (see Discussion), and it seems probable that the clypeal pits are an apomorphic character which evolved in, and was confined to, a limited region of Gondwanaland. This synapomorphy within the Mynogleninae supports the hypothesis that the subfamily is monophyletic. There is no evidence, in either the New Zealand or the African linyphiid fauna, that any species lacking the clypeal pits is attributable to the Mynogleninae; therefore, the Mynogleninae appear to be strictly definable on the basis of the clypeal pits.

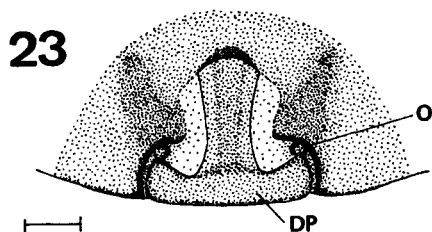
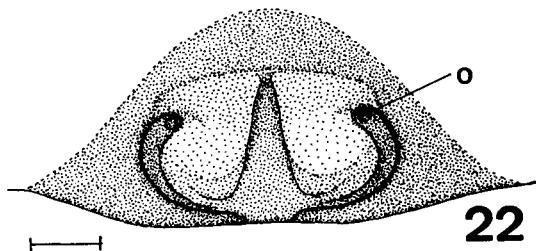
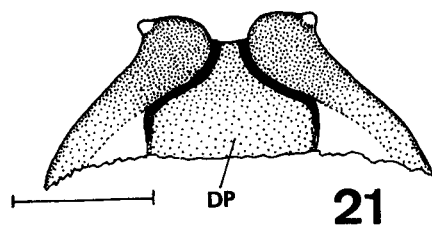
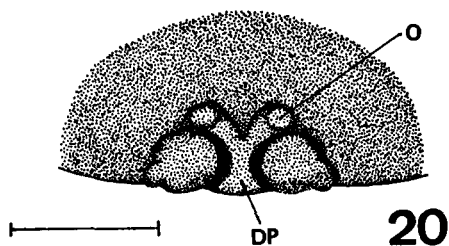
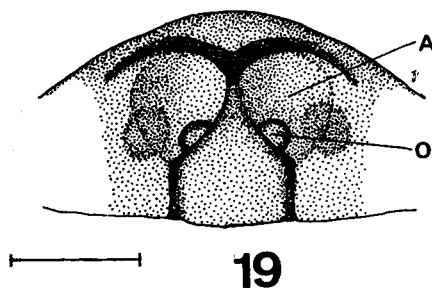
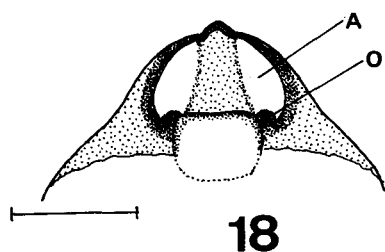
Epigynal structure

In its simplest form, the linyphiid epigyne comprises a cuticular envelope which holds the spermathecae and the associated duct system ("adnexae" of Roberts, 1983); the anterior end of the envelope is open to the interior of the abdomen. The envelope is made up of a ventral plate and a dorsal plate which are fused together at their margins (except anteriorly) (Fig. 4). The dorsal plate (DP in the figures) is small, occupying only part of the dorsal surface of the epigynal envelope (Figs. 2, 7), while the much larger ventral plate (VP) forms most or all of the ventral surface and part of the dorsal or caudal surface of the envelope (Figs. 2, 4, 7); the dorsal

plate may extend in some cases to the ventral surface of the epigyne (e.g. Figs. 1, 4), but always remains relatively small. The lateral junctions of the dorsal plate with the ventral plate are marked by two more or less longitudinal seams, composed of thickened cuticle. These thickened regions usually form part of the apodemal structures to which the spermathecae and ducts are attached internally; externally the seams (in this simple form of epigyne) are often in the form of shallow grooves which lead to or towards the genital openings (O) (e.g. Figs. 1, 9). The ventral plate has hairs on its ventral surface, but hairs are absent or very sparse on its dorsal surface; the dorsal

plate is hairless. This simple form of epigyne in most instances lies more or less flat on the ventral surface of the abdomen, but in some cases it may be erected to a varying degree (e.g. Fig. 4), and the epigynal surface described in this paper as "dorsal" may then lie more or less in the caudal position.

In many of the linyphiid taxa this simple epigynal form has undergone elaboration to give more complex derivative forms. The epigyne may be equipped with a small hollow or socket on the ventral surface, this "genital socket" (S) being actually or potentially functional for fixing the palpal position during copulation (e.g. *Lepthyphantes* Menge (van



Figs. 18-23: Epigynes. 18 *Eulaira schediana* Chamb. & Ivie, dorsal, dry; 19 *Ostearius melanopygius* (O. P.-Cambr.), caudal, dry; 20 *Palaeohyphantes simplicipalpis*, ventral; 21 *P. simplicipalpis*, dorsal, dry; 22 *Linyphia xylitla*, caudal; 23 *Linyphia rita*, ventral. Scale lines 0.1 mm.

Helsdingen, 1965); *Linyphia* Latr. (van Helsdingen, 1969, 1970); Mynogleninae (Blest & Pomeroy, 1978)). The ventral or dorsal plates may be extended posteriorly to produce a scape (SC), and there may be invagination of the epigynal integument to give an atrium (A). In these more complex epigynal forms, the dorsal plate is normally small and does not extend to the ventral surface of the epigyne.

An erected epigyne of the simple type, viewed from the side, might be regarded as a short scape (Fig. 4), but in this paper the term "scape" is reserved for certain specific modifications of the basic epigynal form. Several different forms of scape can be distinguished in the Linyphiidae. These are:

(i) Ventral scape (produced by posterior elongation of the ventral plate), which carries a genital socket on its ventral side, but does not carry the genital openings or ducts (e.g. Figs. 10, 44). This scape is usually short, and is present in some members of the *Stemonyphantes* group and in most members of the Mynogleninae.

(ii) Ventral scape, which carries the genital openings on its dorsal side, but has no genital socket. This form of scape, produced by elongation of the ventral plate, with the dorsal plate remaining small, can vary in length from short (e.g. Fig. 66) to quite long (e.g. Fig. 84); it is present in the Drapeticinae and in some members of the Erigoninae.

(iii) Ventral scape, which carries a socket on its ventral side and has the genital openings on its ventral or lateral sides. This form of scape, which is usually folded (e.g. Fig. 87), is present in the Micronetinae.

(iv) Dorsal scape (produced by posterior elongation of the dorsal plate), which carries a socket on its ventral side but no openings or ducts. This form of scape, which can be very short or quite long (e.g. Fig. 53), is present in the Linyphiinae. It is always associated with an atrium, and is referred to as the "parmula" by some authors (e.g. Comstock, 1940).

(v) Ventral scape, which carries neither genital openings nor socket. It may have a small hollow on its dorsal side, developed possibly to increase rigidity (a principle used in engineering design), but most probably of no functional use. This type of scape is referred to in this paper as a "pseudoscape" (e.g. Fig. 112: PS). Occasionally more than one pseudoscape is present on the ventral plate.

In the simplest external form of the epigyne, the

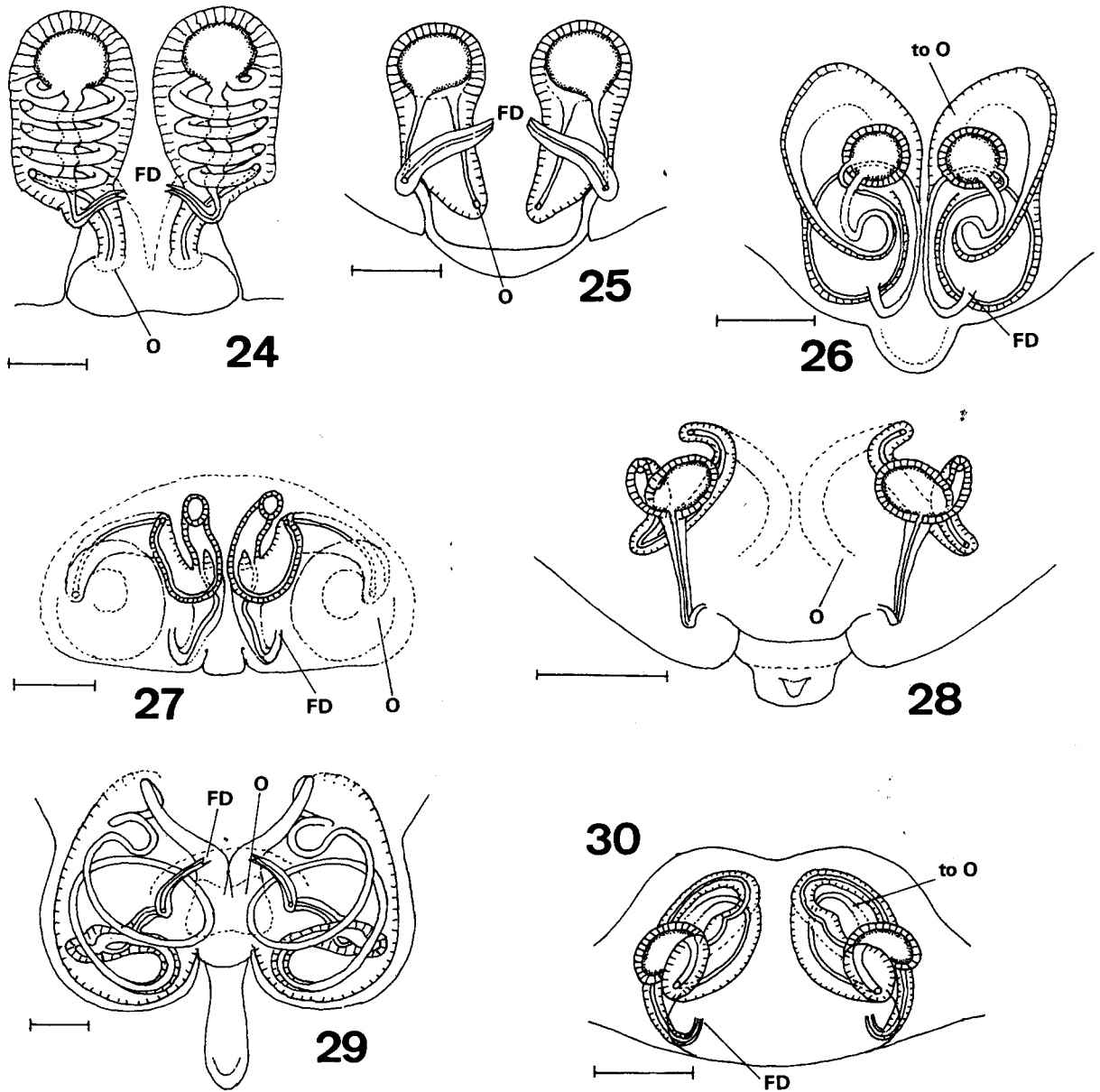
genital openings lie on the ventral surface, on or near the seams joining the ventral and dorsal plates (e.g. Fig. 1). In the more complex derivative forms of the epigyne, the openings are always associated with the ventral plate; they can lie on either the dorsal or ventral sides of a ventral scape, or can be located on the dorsal side of the ventral plate when this forms the ventral wall of an atrium.

Internally, sperm ducts lead from the genital openings to the spermathecae, and fertilisation ducts (FD) run from the spermathecae to open into the uterus on or near the margins of the dorsal plate. In some genera the fertilisation ducts run posteriorly from the spermathecae to the lateral margins of the dorsal plate, and then a short distance anteriorly to the openings, with the distal ends stout and normally clearly visible in the cleared epigynes; viewed from the dorsal side, they appear as in, e.g., Figs. 24, 48. In other genera the fertilisation ducts are shorter and slimmer, and run more or less laterally from the spermathecae to open between the spermathecae in the region of the dorsal plate; viewed from the dorsal side, this form appears somewhat sinuous, as in, e.g., Figs. 76, 115. Fertilisation ducts of this latter form are usually lightly sclerotised and difficult to see. The former type of duct, which is present in epigynes inferred to be primitive or relatively primitive, is considered to be the plesiomorphic form, while the latter type is regarded as an apomorphic form. In a few genera the fertilisation ducts run anteriorly, and open to the uterus anterior to the spermathecae (e.g. Figs. 75, 86); this is regarded as another apomorphic form.

In some linyphiid taxa (believed to be more primitive: see Discussion) there is obvious encapsulation of the sperm ducts, i.e. the duct is enclosed in part in a sclerotised capsule which also holds the spermatheca. The degree of encapsulation is variable: sometimes it is very clear (e.g. Figs. 24, 26), but in some cases, though present, it is less strongly developed. Probably encapsulation defined in this way is never completely absent, since the duct at its point of entry to the spermatheca is always within the spermathecal capsule.

Epigynal groups

In this paper the family Linyphiidae is subdivided into six sections, namely the subfamilies Mynoglen-



Figs. 24-30: Epigynes, internal. 24 *Stemonyphantes lineatus*, dorsal; 25 *S. abatensis*, dorsal; 26 *Smermisia tullgreni*, dorsal; 27 *Estrandia nearctica*, dorsal; 28 *Linyphantes tragicus*, dorsal; 29 *Jalapyphantes cuernavaca*, dorsal; 30 *Frontinella communis*, dorsal. Scale lines 0.1 mm.

inae Blest, 1979, Linyphiinae Simon, 1884, Drapetiscinae new subfamily, Micronetinae Hull, 1920 and Erigoninae Emerton, 1882, and the *Stemonyphantes* group. The Linyphiinae, the Drapetiscinae, the Micronetinae and the *Stemonyphantes* group are defined on the epigynal form, while the Erigoninae and the Mynogleninae are defined respectively on the tracheal structure and the clypeal glands (Blest, 1976, 1979). There is some evidence for considering the subfamilies to be monophyletic, but the *Stemonyphantes* group is almost certainly paraphyletic, and for this reason it is not designated as a subfamily (see Discussion).

The epigynal forms of these groups are now described. The *Stemonyphantes* group is dealt with first, as this comprises the genera which have epigynal forms considered to be the most primitive in the family (see Discussion).

Stemonyphantes group

The genera included in this group are: *Beauchenia* Usher, *Caviphantes* Oi (= *Lessertiella* Dumitrescu & Miller), *Estrandia* Blauvelt, *Eulaira* Chamberlin & Ivie, *Falklandoglenes* Usher, *Frontinella* F. O. P.-Cambridge, *Frontinellina* van Helsdingen, *Jalapyphantes* Gertsch & Davis, *Linyphantes* Chamberlin & Ivie, *Microlinyphia* Gerhardt, *Mioxena* Simon, *Ostearius* Hull, *Palaeohyphantes* new genus (see p. 264), *Selenyphantes* Gertsch & Davis (not examined), *Smermisia* Simon, *Stemonyphantes* Menge, *Tallusia* Lehtinen & Saaristo and *Taranucnus* Simon.

All the genera are haplotracheate, on the basis of determinations by Blest (1976), and by the author for *Estrandia nearctica* (Banks), *Eulaira dela* Chamberlin & Ivie, *Frontinella communis* (Hentz), *Frontinellina frutetorum* (C. L. Koch), *Linyphantes laguna* Chamberlin & Ivie and *Palaeohyphantes simplicialpis* (Wunderlich). Shortage of specimens prevented tracheal determinations for *Jalapyphantes* and *Smermisia*.

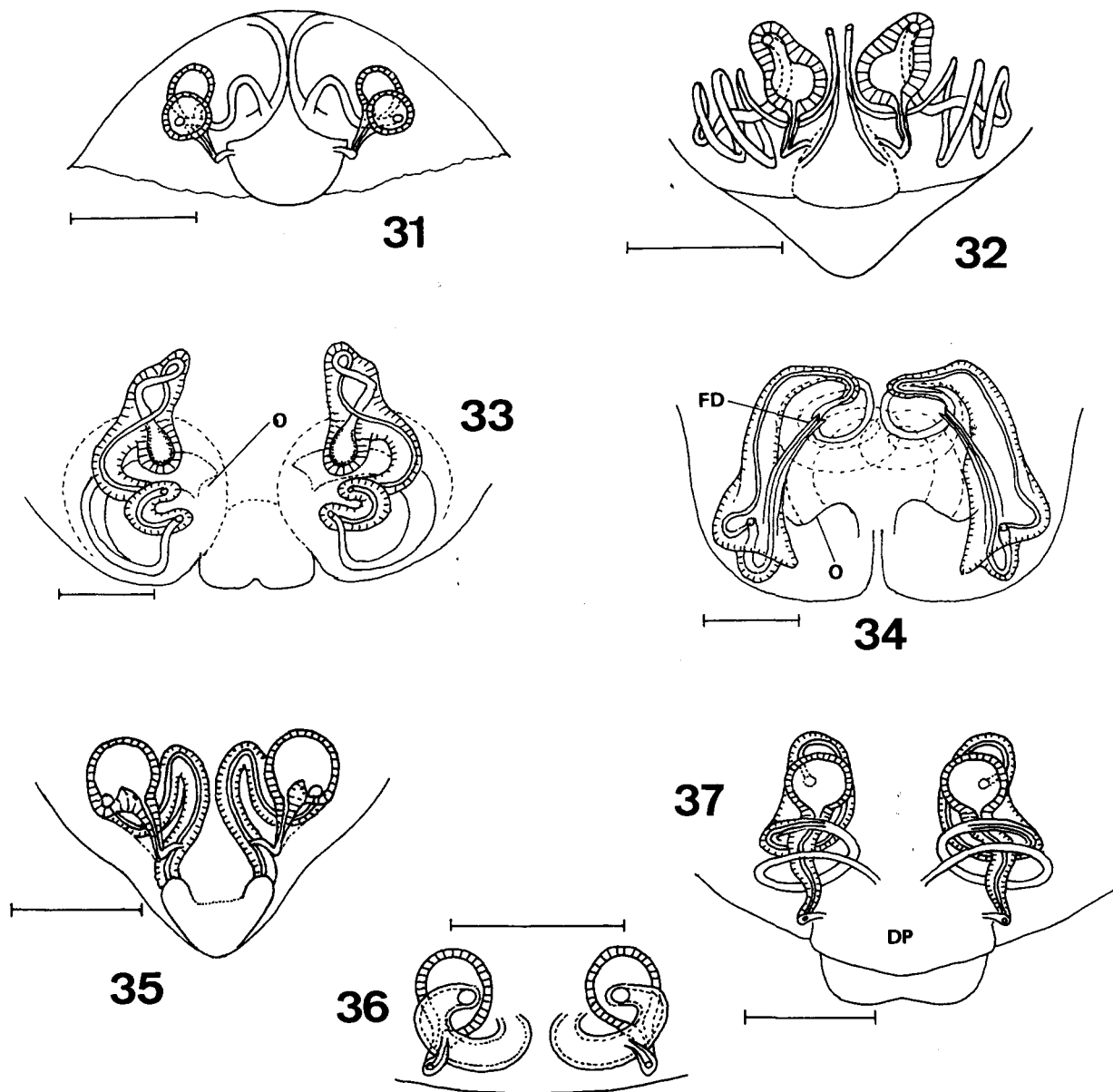
The characteristic feature of the epigynes of this group is that the genital openings are exposed on the ventral (or, occasionally, caudal) surface of the epigyne, typically at the anterior ends of two more or less longitudinal grooves (e.g. Figs. 1, 5, 10), which are the fused lateral margins of the ventral and dorsal plates. In a few members of the group the epigyne

lacks a genital socket (e.g. Fig. 1); many of the species, however, have a socket which usually lies at or near the anterior junction of the dorsal and ventral plates (e.g. Figs. 5, 9), with the dorsal surface of the socket forming part of the dorsal plate and the ventral surface forming part of the ventral plate. The socket shows varying degrees of development; in *Frontinellina* and *Stemonyphantes abatensis* Wund. it is no more than a shallow dimple (Figs. 5, 8), but in some other species it is well developed and located on a short scape (Figs. 10, 13).

In the genus *Linyphantes* the short scape/socket is attached to the ventral plate, and a shallow atrium has formed in the ventral plate; the genital openings are within the atrium but still exposed (Figs. 10, 11). In *Caviphantes* the ventral plate is extended into a short scape which has a rudimentary socket; this scape covers the dorsal plate, and between this plate and the scape there is a shallow atrium which holds the openings (Fig. 17). The epigyne of *Mioxena* is similar, but the scape lacks a socket. *Smermisia* is somewhat similar to *Caviphantes*, but the openings do not lie in an atrium (Fig. 15).

The size of the genital openings increases through *Stemonyphantes* (where they are small: Fig. 1) to *Frontinella* (where they are moderately large: Fig. 3) and *Estrandia* (where they are large: Fig. 6). *Taranucnus* is atypical, with the openings inside a deep atrium (Fig. 14). The female genitalia of *T. ornithes* (Barrows) (= *T. durdenae* Ivie) show little similarity to those of *T. setosus* (O. P.-Cambridge); there are two large openings (or atria), but no socket (Fig. 16), and the internal genitalia are different in form (Fig. 33 cf. Fig. 34). It seems unlikely that *ornithes* is congeneric with *setosus*.

The internal genitalia in this group are very heterogeneous: the spermathecae are not always well defined, there are widely varying duct configurations, and there is a variable degree of encapsulation. In *Stemonyphantes*, *Frontinella*, *Smermisia*, *Taranucnus*, *Jalapyphantes* and *Microlinyphia pusilla* practically the whole duct structure is enclosed within two capsules (Figs. 24, 30, 26, 33, 29); the capsule envelope is well sclerotised and clearly visible in most of these, but in *M. pusilla* the envelope is thin, lightly sclerotised and only faintly visible. In *Estrandia* (Fig. 27) and *Mioxena* (Fig. 37) there is partial encapsulation, while in *Linyphantes* (Fig. 28),



Figs. 31-37: Epigynes, internal. **31** *Ostearius melanopygius*, dorsal; **32** *Caviphantes saxetorum*, dorsal; **33** *Taranucus setosus*, ventral, FDs hidden; **34** *T. ornithes*, dorsal; **35** *Eulaira schediana*, dorsal; **36** *Palaeohyphantes simplicipalpis*, dorsal; **37** *Mioxena blanda* (Sim.), dorsal. Scale lines 0.1 mm.

Caviphantes (Fig. 32), *Ostearius* and *Frontinellina* the encapsulation is weak or absent. The fertilisation ducts are fairly constant in form and position; in most instances they run posteriorly to the lateral margins of the dorsal plate, and then anteriorly to the openings, with the distal ends fairly stout (e.g. Figs. 24, 30). In *Caviphantes* and *Ostearius*, however, the fertilisation ducts are shorter and atypical (Figs. 31, 32).

The genus *Eulaira*, previously regarded as erigonine (Chamberlin & Ivie, 1945) is in fact haplotracheate, and fits into the *Stemonyphantes* group. The ventral plate is extended into a short scape, which carries a rudimentary socket; the openings lie in a shallow atrium situated between the dorsal plate and the scape (Fig. 18), and the internal duct system is relatively simple (Fig. 35). The epigyne of *Ostearius* is somewhat similar; the openings lie on the caudal side of a rudimentary scape, in two atria on either side of a median septum (Fig. 19).

Palaeohyphantes (new genus for *Mynoglenes simplicipalpis* Wund.) is included in the *Stemonyphantes* group on the basis of the epigyne (Figs. 20, 21), which is of the simplest form, without socket, scape or atrium; the duct system (Fig. 36) is simple, and different from that of the Mynogleninae. The genera *Beauchenia* and *Falklandoglenes* (Usher, 1983) do not fall in the Mynogleninae as defined either by Blest or in this paper, but form part of the *Stemonyphantes* group; the epigyne of *Falklandoglenes* appears to be basically of similar form to that of *Linyphantes* and certain as yet undescribed genera from South America.

Several species allocated in the literature to the genus *Linyphia* are almost certainly not correctly placed in that genus, and should be transferred to the *Stemonyphantes* group; for example, *L. xylylla* Gertsch & Davis (Fig. 22), *L. catalina* Gertsch (Fig. 47), *L. chiapas* Gertsch & Davis (1946) and *L. rita* Gertsch (Figs. 23, 46). *L. mimonti* Simon (female) is perhaps assignable to *Stemonyphantes* or some related genus (van Helsdingen, 1969: fig. 73, cf. Fig. 25 of this paper).

Selenyphantes seems to fall in the *Stemonyphantes* group, on the basis of the figure of the epigyne given by Gertsch & Davis (1946). The epigynes figured for *Bathyphantes spedani* Locket and *B. dubius* Locket (Locket, 1968) indicate that these species may also

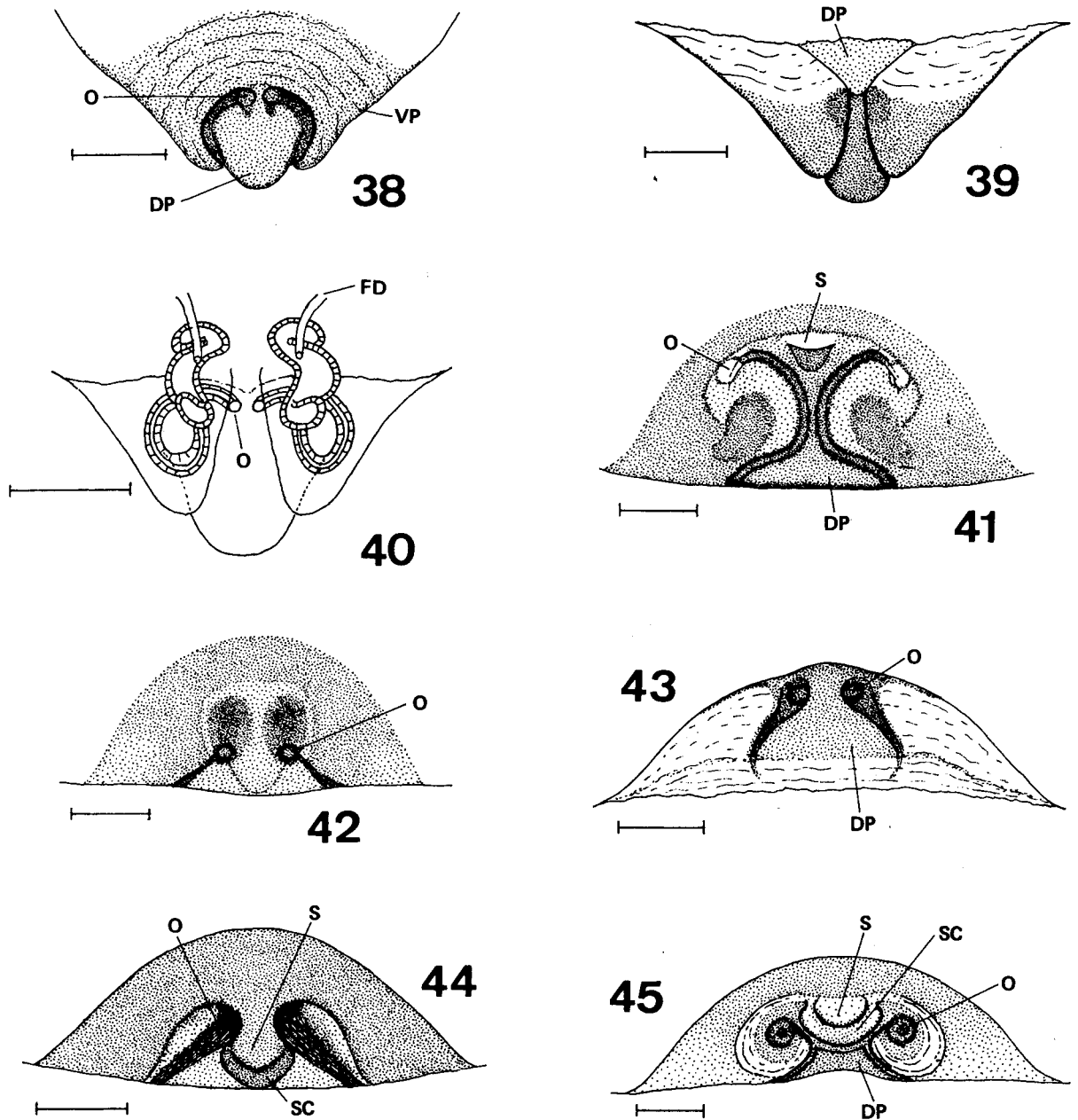
be assignable to this group.

Tallusia is included provisionally in the *Stemonyphantes* group. Externally the epigyne is of the correct form, with two pronounced grooves leading to the exposed genital openings on the ventral surface (Figs. 38, 39), but internally the fertilisation ducts are atypical (Fig. 40). The epigynal form has some features in common with that of the Drapetiscinae, and possibly *Tallusia* should be regarded as a sister group of that subfamily (see later).

The genus *Microlinyphia* must be regarded as to some extent intermediate between the *Stemonyphantes* group and the Linyphiinae. *M. pusilla* and *M. impigra* (O. P.-Cambr.) appear to be closely related, having similar palpal organs (Merrett, 1963; van Helsdingen, 1970) and similar internal genitalia in the females (Wiehle, 1956; van Helsdingen, 1970). In *M. impigra* the external epigyne, which has a socket at the junction of the ventral and dorsal plates (Fig. 9), is quite typical of the *Stemonyphantes* group, and not at all like the epigynes of the Linyphiinae (q.v.). The external epigyne of *M. pusilla* (Fig. 7) is also not untypical of the *Stemonyphantes* group, but in this species a small cavity has opened between the short scape/socket and the ventral plate, leaving the scape/socket attached to the dorsal plate as in the Linyphiinae. The internal genitalia of *Microlinyphia* have a coiled duct configuration similar to that present in some members of the Linyphiinae (e.g. *Bathyphantes approximatus* (O. P.-Cambr.), *Lessertinella*: Fig. 62). In *M. pusilla* the coiled duct is inside a thin capsule, which appears to be absent in *M. impigra* and in the North American species of *Microlinyphia*.

Frontinellina has the duct system similar to that of *Microlinyphia*, but the external epigyne (Fig. 8) is quite typical of the *Stemonyphantes* group. *Mioxena* also has a coiled duct configuration (Fig. 37) rather similar to that of *Microlinyphia*; as in that genus, the posterior coils are lightly sclerotised and difficult to see.

The inclusion of *Microlinyphia* and *Frontinellina* in the *Stemonyphantes* group rather than in the Linyphiinae will be regarded as questionable by many arachnologists. It must be remembered, however, that the *Stemonyphantes* group is not a subfamily, but an interim repository for genera which have an inferred primitive type of epigyne. These two genera could be transferred to the Linyphiinae if the definition (in



Figs. 38-45: Epigynes. **38** *Tallusia experta* (O. P.-Cambr.), ventral, dry; **39** *T. experta*, dorsal, dry; **40** *T. experta*, internal, dorsal; **41** *Metafroneta sinuosa* Blest, ventral; **42** *Novafroneta vulgaris* Blest, ventral; **43** *Afroneta bidentata* Holm, caudal; **44** *Parafroneta confusa* Blest, ventral; **45** *Haplinis mundenia* (Urquhart), caudal. Scale lines 0.1 mm.

this paper) of this subfamily were somewhat widened (see Discussion, p. 261); if this were done, the epigynes of these two genera should be regarded as probably primitive forms of the linyphiine epigynal form.

Subfamily Mynogleninae

Although the generic name *Mynoglenes* is now a junior synonym of *Haplinis* (see p. 264), the subfamily name Mynogleninae (Blest, 1979) is still valid (Art. 40, ICZN Rules).

The genera included in this subfamily are: *Afroneta* Holm, *Cassafroneta* Blest, *Haplinis* Simon, *Hyperafroneta* Blest, *Megafroneta* Blest, *Metafroneta* Blest, *Metamynoglenes* Blest, *Novafoneta* Blest, *Parafroneta* Blest, *Poecilafoneta* Blest, *Promynoglenes* Blest, *Protoerigone* Blest, *Pseudafoneta* Blest and *Trachyneta* Holm.

A detailed account of this subfamily, which is sharply characterised by the presence of clypeal pits and clypeal glands, has been given by Blest (1979). All the genera are haplotracheate; this has been confirmed by the author in the case of *Afroneta bidentata* Holm.

The external epigynes are basically similar to those of the *Stemonyphantes* group, and the presence of the clypeal pits is the only reliable character for distinguishing the Mynogleninae from members of the *Stemonyphantes* group. In a few genera (*Hyperafroneta*; *Metafroneta*: Fig. 41; *Novafoneta*: Fig. 42; *Afroneta*: Fig. 43) the epigynes are of the simplest form, with the genital openings small, at the anterior ends of two curved grooves, and with either no genital socket or a rudimentary one. In other genera there is a broad socket on a short scape which is attached to either the ventral or the dorsal plate (Figs. 44, 45), and an atrium which holds the genital openings. The atrium is much less developed than in the Linyphiinae (q.v.), and consists of little more than a shallow hollow in the ventral plate. When the scape is on the ventral plate, it occupies most of the atrium; when the scape is on the dorsal plate, there is a longitudinal ridge running across the atrium to the dorsal plate and scape, and the scape can be regarded, in some degree, as shared between the dorsal and ventral plates.

In *Megafroneta* (Blest, 1979: fig. 529) the scape

is longer than normal, and there are two short lateral projections from the ventral plate.

The basic arrangement of the internal genitalia appears to be constant throughout the subfamily. The spermathecae are simple in form, without the accessory chamber sometimes present in the Linyphiinae; the fertilisation ducts are of similar form to those of the *Stemonyphantes* group. The sperm duct lies mesal to the spermathecae for most of its length, and joins the spermatheca near its base at a side entry (Fig. 48). In those members of the subfamily which are regarded by Blest (1979) as "typical" the sperm duct follows a double spiral pathway of one form or another (Figs. 48, 49); in many of the species, however, the ducts do not have an obviously spiral form (Fig. 50). In most genera there is some encapsulation of the ducts.

The form of the epigyne in the Mynogleninae seems to have remained remarkably constant, being very similar in *Parafroneta* (New Zealand) and *Afroneta* (central Africa) despite a probable separation of these populations for some 70-80 million years.

Subfamily Linyphiinae

The genera included in this subfamily are: *Australolinyphia* Wunderlich, *Bathypantes* Menge, *Cresmatoneta* Simon, *Diplostyla* Emerton, *Kaestneria* Wiehle, *Labulla* Simon, *Laetesia* Simon, *Laperousea* Dalmas, *Lessertinella* Denis, *Linyphia* Latreille, *Maro* O. P.-Cambridge, *Neriene* Blackwall, *Pityohyphantes* Simon, *Porrhomma* Simon, *Sisicus* Bishop & Crosby and *Wiehlea* Braun.

All the genera are haplotracheate, on the basis of determinations by Blest (1976), and by the author for *Australolinyphia remota* Wund., *Cresmatoneta mutinensis* (Canest.), *Laetesia* sp. (New Zealand), *Laperousea cupidinea* Simon, *Lessertinella kulczynskii* (L essert), *Pityohyphantes phrygiamus* (C. L. K.) and *Sisicus apertus* (Holm).

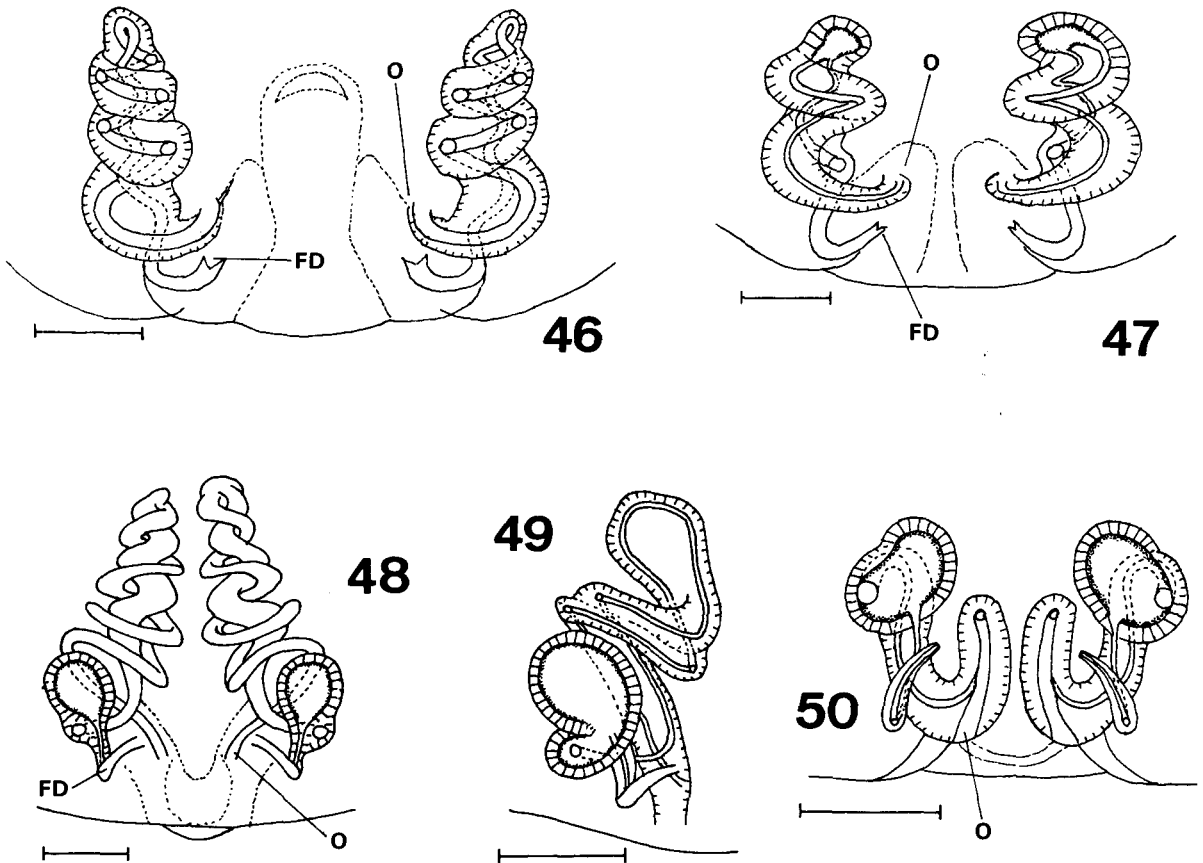
The epigynes of this subfamily are characterised by the presence of a scape/socket on the dorsal plate, and by the location of the genital openings inside a well-defined atrium between the ventral and dorsal plates. The atrium may be a single chamber (as in e.g. *Neriene clathrata* Sund.) or divided into two chambers by a median septum (as in *Pityohyphantes*, *Kaestneria dorsalis* (Wid.) and *Linyphia hortensis*

Sund.). Inside the main atrium of *Linyphia* and *Neriere* there are two wide conical or dome-shaped sub-atria, which are tailored to fit the terminal apophysis of the male palp (van Helsdingen, 1969). The scape is frequently very short.

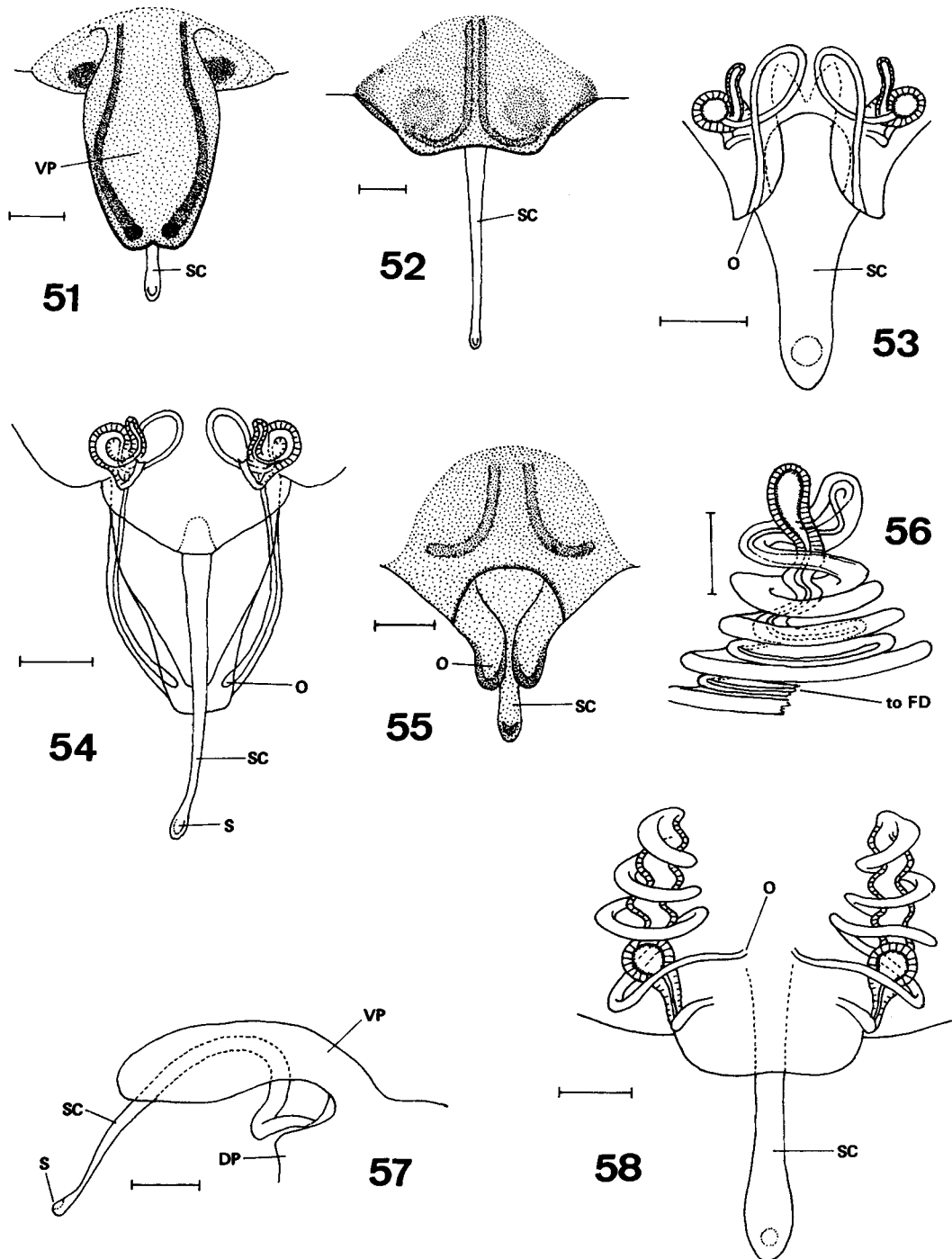
In many of the *Bathyphantes* species the ventral plate is extended posteriorly to give a pseudoscape which does not carry a ventral socket; this pseudoscape is often longer than the true (dorsal) scape. The apparent presence of a socket near the tip of this pseudoscape, as shown for example in the figures given by Ivie (1969) in his paper on the numerous North American *Bathyphantes* species, is an illusion, produced by a dorsal hollow near the posterior end. A similar pseudoscape is present in *Diplostyla*, but here the true scape is miniscule. In the Australasian genus *Laperousea*, the ventral plate of the epigyne is

extended posteriorly to form a broad shield, which still functions as the ventral wall of the atrium, and carries the genital openings on its dorsal side (Figs. 51, 54, 57); the true scape, carrying a minute socket, originates from the dorsal plate, and is long, thin and flexible. The European genus *Cresmatoneta* has the external epigyne somewhat similar to that of *Laperousea*, but the extension of the ventral plate is short (Fig. 52). In *Kaestneria* (Fig. 53) and *Laetesia* (Fig. 55) the ventral plate is extended in two arms which cover the atrium and carry the openings; these arms have twisted so that the openings are on the mesal, or even the ventral, surface.

The distal ends of the fertilisation ducts are of similar form to those of the *Stemonyphantes* group and the Mynogleninae, but tend to be less stout (e.g. Figs. 53, 54). The spermathecae are often equipped



Figs. 46-50: Epigynes, internal. 46 *Linyphia* *rita*, dorsal; 47 *Linyphia* *catalina*, dorsal; 48 *Haplisis mundenia*, dorsal; 49 *H. titan* (Blest), left side, dorsal; 50 *Afroneta bidentata*, dorsal. Scale lines 0.1 mm.



Figs. 51-58: Epigynes. **51** *Laperousea* sp. (New Zealand), ventral; **52** *Cresmatoneta mutinensis* (Canestr.), ventral; **53** *Kaestneria pullata* (O. P.-Cambr.), internal, ventral; **54** *Laperousea* sp., internal, dorsal; **55** *Laetestia aucklandensis* (Forst.), ventral; **56** *Linyphia triangularis* (Clk.), internal, dorsal, left spermatheca with initial coils of ducts; **57** *Laperousea* sp., lateral; **58** *Australolinyphia remota* Wund., internal, dorsal. Scale lines 0.1 mm.

with an accessory chamber (Fig. 53).

The configuration of the ducts is variable in this subfamily. In *Linyphia* and *Neriere* both the fertilisation duct and the sperm duct are incorporated as coiled tubes in the walls of the sub-atria (Fig. 56); the fertilisation duct terminates as usual near the lateral margins of the dorsal plate, and the sperm duct appears to open at the base of the sub-atrium, and not near its apex as stated by Wiehle (1967: 188). Despite the differing mechanics of the copulatory process in *Linyphia* and *Neriere* (van Helsdingen, 1969), there appears to be no essential difference in the structure of the epigynes in these two genera, and this must call into question whether the separation of *Neriere* from *Linyphia* is justified. In *Bathyphantes approximatus* and *Lessertinella* (Fig. 62) the spermathecae are set well forward, and the sperm duct forms a broad coil which opens into the atrium, while the fertilisation duct runs along the axis of this coil as a narrow corkscrew to the dorsal plate. The other *Bathyphantes* species have a similar fertilisation duct, but the sperm duct is much shorter, and the coiling, though present, is much less obvious; the *Porrhomma* species have similar epigynes to these *Bathyphantes* species. In *Kaestneria* (Fig. 53) the sperm duct does not have a coiled configuration and the spermathecae are set more posteriorly, with the fertilisation ducts consequently shorter. *Laetesia*, *Laperousea* (Fig. 54), *Cresmatoneta*, *Diplostyla* and *Pityohyphantes* have the duct system essentially similar to that of *Kaestneria*.

The genus *Lessertinella*, though previously regarded by most authors as erigonine (Thaler, 1972; Weiss, 1979), has the epigyne (Fig. 62) (and the male palp) typical of those of the Linyphiinae (as pointed out by Thaler, 1972: 44); the genital socket/scape is weak, rather as in some *Porrhomma* species. *Lessertinella* is haplotracheate, and despite its "erigonine" chaetotaxy there can be no doubt that it should be included in the Linyphiinae.

The epigynes of the *Maro* species have a short scape/socket arising from the dorsal plate (Fig. 59), and the genital openings are located inside a small atrium (Figs. 60, 61); owing to the pale colour and small size the full detail of the fertilisation ducts could not be seen. This genus has usually been considered to be close to *Centromerus* or to *Meioneta* (Locket & Millidge, 1953; Saaristo, 1971). The

presence of the scape/socket on the dorsal plate, and the location of the openings within an atrium, however, show that *Maro* cannot be placed in the subfamily Micronetinae (q.v.); it seems most probable that this genus is composed of dwarf, and perhaps somewhat degenerate, members of the Linyphiinae.

Wiehlea is placed provisionally in the Linyphiinae: the genital openings lie inside a shallow atrium (Fig. 63), there is a small rudimentary socket attached to the dorsal plate, and the sperm duct follows a spiral pathway. *Sisicus* is also included provisionally in this subfamily. The openings (in *S. penifusciferus* Bishop & Crosby) appear to lie inside a fairly deep atrium, and there is a rudimentary socket attached to the dorsal plate; the pale colour and minute size make it difficult to be certain of the duct arrangement. With these tiny species it is not easy to determine with any certainty whether their correct position is in the Linyphiinae or in the *Stemonyphantes* group.

In *Australolinyphia* the external epigyne is completely typical of the Linyphiinae, but the internal duct system appears at first sight to be very similar to that of many *Haplinis* species. Blest (1979) suggested that *Australolinyphia*, which also has an odd palpal structure in the male, should be placed in a separate group in close conjunction to the Mynogleninae. The similarity of the duct system in these two genera is, however, superficial. In *Haplinis* (Fig. 48) there are well-defined spermathecae, with the inner coil of the duct joining the posterior end of the spermatheca at a side entry. In *Australolinyphia* (Fig. 58) the spermatheca is little more than a continuation of the wide inner coil of the duct system; indeed the genitalia are not dissimilar to those of "*Linyphia*" *rita* (Fig. 46). The aberrant palpal structure of *Australolinyphia* may be of no significance, since *Diplostyla*, which has the female genitalia, both externally and internally, completely typical of the Linyphiinae, also has an aberrant palpal structure. In *Labulla* the internal duct structure (Wiehle, 1956: fig. 483) is more complex than usual for the Linyphiinae, and the male palpal structure is also aberrant. *Australolinyphia*, *Diplostyla* and *Labulla* are regarded as probably primitive branches of the subfamily, but it is possible that they should rank as sister groups of the Linyphiinae as here defined (see Discussion).

The genera *Microlinyphia* and *Frontinellina*,

usually placed with *Linyphia* and *Neriene*, have been allocated to the *Stemonyphantes* group: see pp. 239, 261.

Subfamily Drapetiscinae – new subfamily

The genera included in this subfamily are: *Allomengea* Strand, *Aphileta* Hull, *Arcuphantes* Chamberlin & Ivie, *Asthenargus* Simon & Fage, *Carorita* Duffey & Merrett, *Doenitzius* Oi, *Drapetisca* Menge, *Fageiella* Kratochvil, *Helophora* Menge, *Saaristoa* Millidge, *Simplicistilus* Locket, *Sintula* Simon, *Tibioplus* Chamberlin & Ivie, *Typhlonyphia* Kratochvil and *Wubana* Chamberlin.

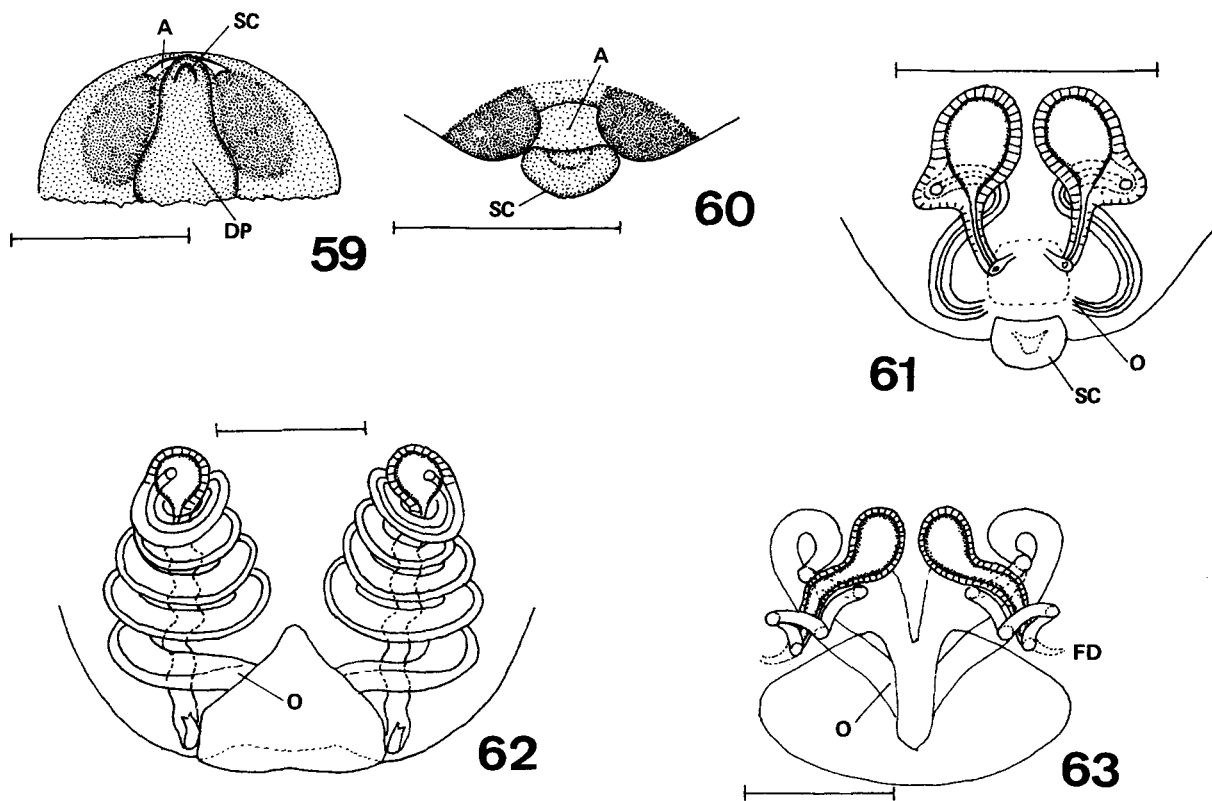
The members of this subfamily are haplotracheate, on the basis of determinations by Blest (1976), and by the author for *Arcuphantes fragilis* Chamb. & Ivie, *Fageiella patellata* (Kulcz.), *Tibioplus diversus* (L. Koch), *Typhlonyphia reimoseri* Kratochvil and *Wubana drassoides* Chamberlin. Shortage of material

precluded determinations for *Doenitzius* and *Simplicistilus*. In *Allomengea*, the median tracheae have some short branches, which do not however extend into the prosoma (Blest, 1976).

In this subfamily the epigynes are characterised by the prolongation of the ventral plate into a scape which carries the genital openings and ducts, but lacks a socket (e.g. Figs. 72, 73, 76). The genital openings are located on the dorsal side of the scape, towards or at the distal end.

Internally, the duct configuration can be relatively complex (Figs. 80, 83) or quite simple (e.g. Figs. 76, 81, 85). The fertilisation ducts are of two forms, either moderately stout, usually opening to the uterus anterior to the spermathecae (e.g. Figs. 82, 84, 85), or rather thin and sinuous, opening to the uterus in the area between the spermathecae (Fig. 81).

The scape can be more or less straight (Fig. 72), bent (Fig. 64) or rolled into a curve or coil (Figs. 69,



Figs. 59-63: Epigynes. **59** *Maro minutus* O. P.-Cambr., dorsal; **60** *M. minutus*, caudal, dry; **61** *M. minutus*, internal, dorsal; **62** *Lessertinella carpatica* Weiss, internal, dorsal; **63** *Wiehlea calcarifera* (Sim.), internal, dorsal. Scale lines 0.1 mm.

71); it can be long (Fig. 84) to short (Fig. 66). In a few genera (e.g. *Sintula*, Fig. 86) the scape is bifid distally. On the dorsal side the scape usually has two longitudinal depressions or grooves (Figs. 65, 67, 68); the openings lie more or less at the distal ends of these channels, which possibly act as guides for the palpal organ. Occasionally the scape is somewhat hollowed dorsally.

In the genus *Doenitzius* (Fig. 71) and in some species of *Arcuphantes* (Figs. 69, 70) (Oi, 1960) the scape is less simple, though still showing the same basic characters, namely with the openings on the dorsal side and with no genital socket.

Saaristoa (Figs. 72, 73, 76) falls in the Drapetiscinae, and is regarded as quite distinct from *Oreonetides* (which lies in the Micronetinae), despite the contrary opinions of recent authors (Thaler, 1981; van Helsdingen, 1981). The epigynal structure of *S. abnormis* (Bl.) is quite different from that of the type species of *Oreonetides* (i.e. *vaginatus* Thor.), as is the palpal structure (Saaristo, 1972; Millidge, 1977).

Simplicistilus (Locket, 1968; Locket & Russell-Smith, 1980) is small and almost colourless, and the detail of the epigyne is difficult to see; there seems to be no socket, and the openings appear to be on the dorsal side of the scape (Fig. 79). The inclusion of this genus in the Drapetiscinae must be regarded as provisional.

In the cave genus *Typhlonyphia* the genital openings lie on the mesal sides of two short side branches of the ventral plate (Figs. 74, 75), rather as in *Sintula*, and two grooves run from the dorsal plate to the openings. The scape is distinctly hollowed out dorsally, and within this hollow there is a small pit. The fertilisation ducts are similar in form to those of some members of the Drapetiscinae. The epigynal form is not completely typical of this group, but does not fit into any of the other subfamilies proposed.

The Drapetiscinae could be split into two groups on the basis of the form of the fertilisation duct. Such a division would place the genera *Arcuphantes*, (?) *Doenitzius*, *Drapetisca*, *Fageiella*, *Helophora*, *Sintula* and *Typhlonyphia* in one group, and *Allomengea*, *Aphileta*, *Asthenargus*, *Carorita*, *Saaristoa*, (?) *Simplicistilus*, *Tibioplus* and *Wubana* in another. In the latter group the fertilisation ducts are of similar form to those of the Erigoninae.

Subfamily Micronetinae

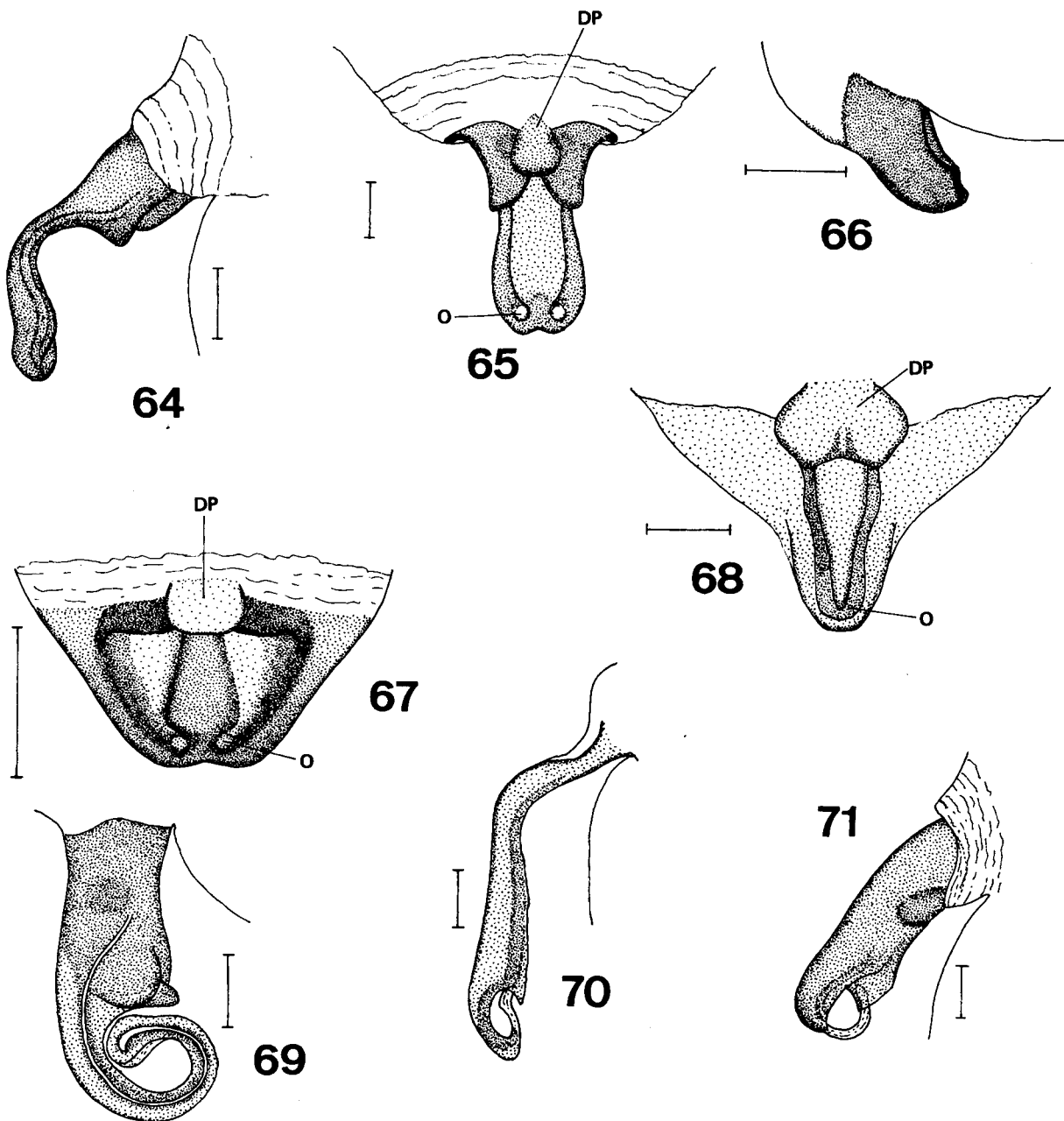
The name Micronetinae was used by Hull (1920) for a suprageneric group which comprised *Microneta*, *Agyneta*, *Meioneta* and other genera. This name must therefore have priority over the name *Lepthyphantinae* used by Saaristo (e.g. 1973a). The female genitalia of members of this subfamily have been extensively studied by Saaristo, and the genera included in the subfamily in the present paper are for the most part those given by Saaristo (1973a, b, 1974a, b), with a few additions. A detailed investigation of the epigynal forms of some *Lepthyphantes* species was published by Wanless (1971, 1973), following some earlier work by van Helsdingen (1965) and Zorsch (1937).

This subfamily comprises the following genera: *Agyneta* Hull, *Bolyphantes* C. L. Koch,[‡] *Centromerita* Dahl, *Centromerus* Dahl, *Centrophantes* Miller & Polenec (not examined), *Floronia* Simon, *Gnathantes* Chamberlin & Ivie (not examined), *Labullula* Strand, *Lepthyphantes* Menge, *Locketidium* Jocqué, *Macrargus* Dahl, *Meioneta* Hull, *Metaleptyphantes* Locket, *Microneta* Menge, *Oreonetides* Strand, *Poecilonea* Kulczynski, *Syedra* Simon, *Syedra* Simon, *Tapinopa* Westring, *Tennesseeillum* Petrunkevitch, *Theonina* Simon and *Troglohyphantes* Joseph.

All the genera are haplotracheate, on the basis of determinations by Blest (1976), and by the author for *Tennesseeillum minutum* Petrunkevitch and *Theonina cornix* (Simon). Shortage (or absence) of material precluded determinations for *Centrophantes*, *Gnathantes*, *Labullula*, *Locketidium* and *Metaleptyphantes*.

In this subfamily the epigynes are characterised by the prolongation of the ventral plate into a scape, which has a genital socket distally on the ventral side, and which carries the genital openings on the ventral surface (or occasionally on the lateral sides). There is a well-defined cavity between the ventral and dorsal plates, into which the scape is recessed. The "lateral plates" of some authors (van Helsdingen, 1965; Wanless, 1973) are the barely differentiated lateral areas of the ventral plate; the "scapoid base" (Wanless, 1973) is a thickened part of the ventral plate at the base of the scape.

Internally, the sperm ducts follow a simple course from the spermathecae along the length of the scape to the openings. The fertilisation ducts, which are usually lightly sclerotised and difficult to see, are



Figs. 64-71: Epigynes. **64** *Drapetisca socialis* (Sund.), lateral; **65** *D. socialis*, dorsal; **66** *Asthenargus paganus* (Sim.), lateral; **67** *A. paganus*, dorsal; **68** *Allomengea scopigera* (Grube), dorsal; **69** *Arcuphantes osugiensis* (Oi), lateral; **70** *A. longiscapus* (Oi), lateral; **71** *Doenitzius peniculus* Oi, lateral. Scale lines 0.1 mm.

either narrow and sinuous (Fig. 95) or somewhat stouter and slightly funnel-shaped distally (Fig. 100; also Dumitrescu & Georgescu, 1980: figs. 9, 15, 19), in both cases opening into the uterus in the area between the spermathecae.

With the exception of certain species currently placed in *Lepthyphantes* (see later), all members of the Micronetinae have a basic epigynal form which is covered by the above definition. There is, however, much variation in the detail, particularly in the form of the scape. In many species, the posterior part of the scape is recessed into the cavity in a double fold roughly in the form of an S (e.g. Figs. 87, 88; Saaristo, 1973b: fig. 68), with the posterior part almost completely hidden behind the anterior part, when viewed from the ventral side. In a few species (e.g. *Lepthyphantes alacris* (Bl.) and *Macrargus rufus* (Wid.): Fig. 89) the scape is slightly coiled near its distal end, but still retains the basic S-shape. It is well known that the long scape with this sigmoid form can be partially expanded (unfolded) and its detail made more visible by soaking the epigyne in 10% alkali hydroxide solution, or by treatment with hot lactic acid, followed by transfer to water or aqueous alcohol. This form of scape may also be unfolded to some extent by the male during copulation (van Helsdingen, 1965).

In many species of this subfamily, however, the scape is much shorter, and the sigmoid shape, though still present, is less developed; for example, in *L. pallidus* (O. P.-Cambr.) (Fig. 90), *L. expunctus* (O. P.-Cambr.) (Fig. 91), the *Bolyphantes* species and many *Centromerus* species (Fig. 92) (the shape of the scape in *L. pallidus* and *L. expunctus* appears to be shown incorrectly by Wanless (1973: fig. 24 H, I)). When it is short, the scape appears to be more or less rigid, and little if any expansion is produced by treatment with alkali or lactic acid; this lack of flexibility presumably precludes any appreciable unfolding during copulation. Another relatively rigid type of scape, capable of only limited expansion, is found in other species, e.g. *L. nebulosus* (Sund.) (Fig. 93), *Centromerus pabulator* (O. P.-Cambr.) (Fig. 96); in these species the ventral plate is prolonged posteriorly, representing in effect the anterior part of the scape, and the overall S-shape is well developed.

The epigyne, particularly in those species which

have a short scape, is sometimes located at the tip of a finger projecting from the epigastric area, e.g. *L. angulifer* Simon, *Oreonetides vaginatus* and *Metaleptyphantes* species.

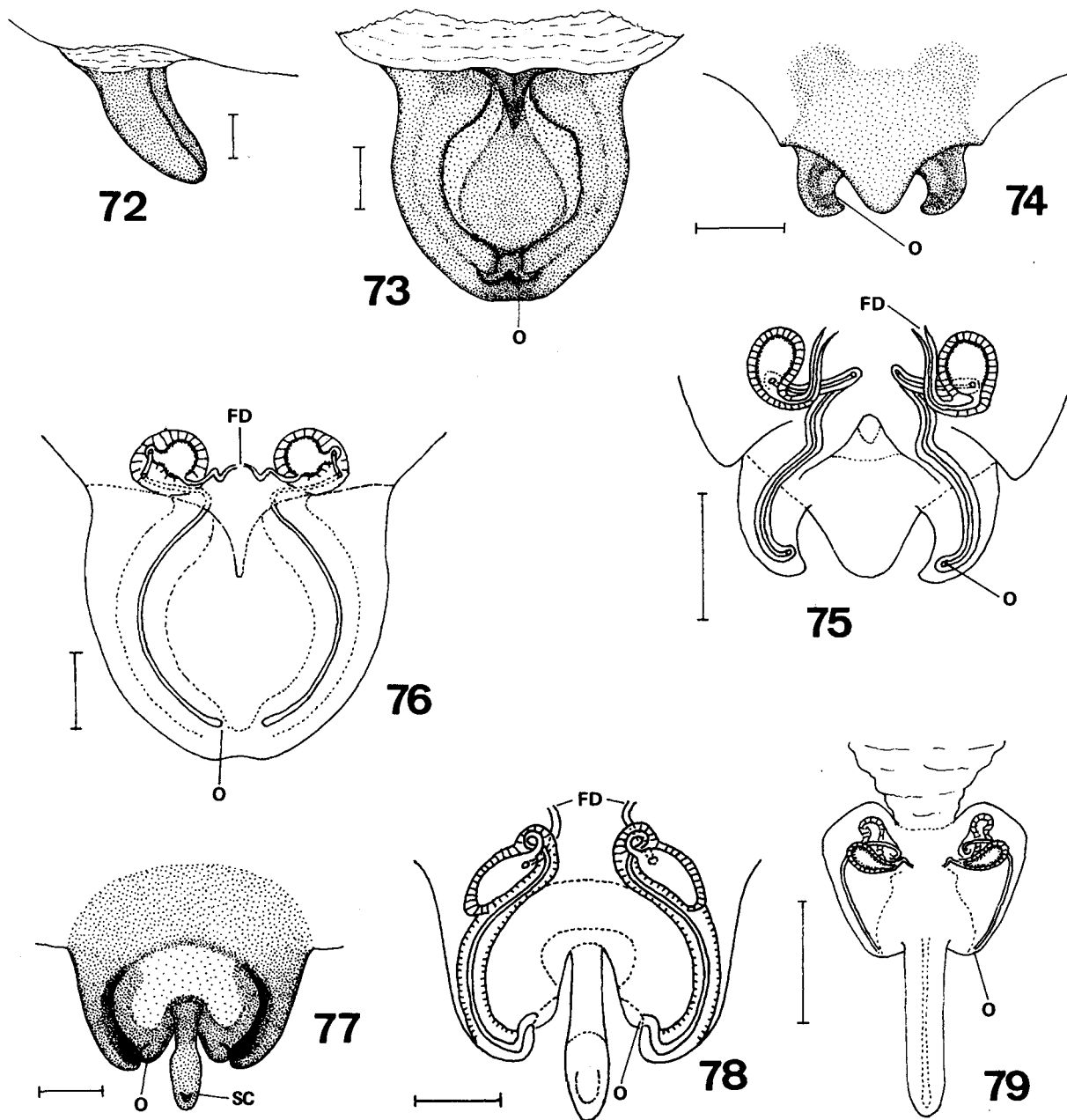
In some *Centromerus* species the scape does not have the sigmoid form, but is more or less finger-like; the genital socket is still located on the distal end of the scape in these species, but the openings lie on the ventrolateral sides of the scape, fairly near to the base (e.g. *Centromerus arcanus* (O. P.-Cambr.): Figs. 97, 98).

The scape is frequently furnished with lateral lobes, which may lie on the anterior part adjacent to the first fold, or near the distal end, or both. If distal lobes are present, these may carry the genital openings in shallow depressions (Wanless, 1973); when distal lobes are absent, the openings may lie further from the distal end of the scape (e.g. *Oreonetides glacialis* (L. Koch): Figs. 94, 95).

The variety of epigynal forms present in the genera *Lepthyphantes* and *Centromerus* (as currently delimited) may suggest that these large genera could with advantage be subdivided; *Oreonetides* (excluding *Saaristoa*) also has a somewhat wide spread of epigynal forms (van Helsdingen, 1981; Thaler, 1981).

The genus *Metaleptyphantes* is placed provisionally in the Micronetinae. The epigyne appears to be of the correct form, but the species are small and weakly pigmented, and the details of the epigyne are difficult to see. A shortage of specimens prevented a more detailed study of this genus.

Some African species currently placed in *Lepthyphantes*, e.g. *L. biseriatus* Simon & Fage, *L. obtusicornis* Bosmans (Bosmans, 1978), have epigynes which are not fully in accord with the definition given for the Micronetinae. The scape is recessed into a cavity between the ventral and dorsal plates, but is short and not significantly sigmoid, and a genital socket appears to be absent; the openings are on the sides of the scape, and the internal duct system is very simple (Fig. 99), though of the same general form as in the Micronetinae. In some members of this subfamily (e.g. *L. pallidus*) the socket is only weakly developed, and it is possible that loss of the socket has proceeded even further in these African species. At the present time it seems best to retain these species provisionally in *Lepthyphantes*, and hence in the Micronetinae; certainly they will not fit readily



Figs. 72-79: Epigynes. 72 *Saaristoa abnormis* (Bl.), lateral; 73 *S. abnormis*, dorsal, dry; 74 *Typhlonypbia reimoseri* Kratoch., ventral; 75 *T. reimoseri*, internal, dorsal; 76 *S. abnormis*, internal, dorsal; 77 *Atopogyna cornupalpis* (O. P.-Cambr.), ventral; 78 *A. cornupalpis*, internal, dorsal; 79 *Simplicistilus venustus* (Lockett), internal, dorsal. Scale lines 0.1 mm.

into any of the other subfamilies proposed in this paper.

The species *Erigone cornupalpis* O. P.-Cambr., transferred in recent years to *Centromerus* (van Helsing, 1973) on the basis of its palpal configuration, has an epigynal form which appears to preclude its inclusion in that genus. The ventral plate extends posteriorly as a broad scape (Fig. 77), which carries the genital openings and the ducts. The scape is divided posteriorly into two short arms, and a narrow subsidiary scape, carrying a socket, arises from the median notch. The openings are on the mesal sides of the two posterior arms of the scape, and there are grooves running from the small dorsal plate to the openings (Fig. 77). The sperm duct system is simple (Fig. 78); the fertilisation ducts are relatively stout, similar to those in some members of the Drapetiscinae (e.g. Fig. 85), and open to the uterus anterior to the spermathecae. Because of its epigynal form, this species is assigned to a new genus, *Atopogyna* (see p. 264). In some respects the epigynal form is similar to that of the Drapetiscinae, and particularly to that of *Typhlonypbia* (Figs. 74, 75), but an important difference lies in the presence of the subsidiary scape. Although the palpal organs of *Atopogyna* show similarities to those of the Micronetinae (genus *Centromerus*), the epigyne is not of the form characteristic of this subfamily: i.e. there is no hollow (atrium) between the dorsal and ventral plates, and the genital openings are not located on the scape which carries the socket. Thus the epigynal form of *Atopogyna* is inconsistent with its inclusion in either the Drapetiscinae or the Micronetinae, as defined. It cannot perhaps be ruled out at this stage that the epigynal form is a primitive form of the micronetinine epigyne, but there is no firm evidence to support this possibility. Alternatively, if this possibility is rejected, it may eventually prove necessary to allocate *Atopogyna* to a new subfamily. It will be interesting to see whether any other genera with a similar epigynal form are discovered in the New World.

Subfamily Erigoninae

This subfamily is defined as comprising all the desmitracheate species of the Linyphiidae (see p. 233). In addition to the genera/species listed by Blest (1976), the following have been determined as

desmitracheate during the present work:—

Abacoproeces saltuum (L. Koch), *Alioranus pauper* (Sim.), *Caracladus aviculus* (L. Koch), *Ceraticelus fissiceps* (O. P.-Cambr.), *Elgonella nemoralis* Holm, *Emenista bisinuosa* Sim., *Eperigone tridentata* (Emert.), *Eridantes erigonoides* (Emert.), *Erigonophus jarmilae* (Miller), *Exechophysis bucephalus* (O. P.-Cambr.), *Gnathonargus unicornis* (Banks), *Grammonota inornata* Emert., *Hylyphantes nigrinus* (Sim.), *Islandiana alata* (Emert.), *Microcyba tridentata* Holm, *Minicia marginella* (Wid.), *Origanates rostratus* (Emert.), *Phanetta subterranea* (Emert.), *Sciastes truncatus* (Emert.), *Scotinotyclus antennatus* (O. P.-Cambr.), *Scylaceus pallidus* (Emert.), *Scytiella mirifica* Georgescu, *Sisicottus montanus* (Emert.), *Souessoula parva* (Banks), *Spirembolus maderus* Chamberlin, *Stajus truncatifrons* (O. P.-Cambr.), *Strongyliceptus allaundi* (Fage & Sim.), *Tachygyna pallida* Chamb. & Ivie, *Trichoncoides piscator* (Sim.), *Tunagyna debilis* (Banks) and *Zornella cultrigera* (L. Koch).

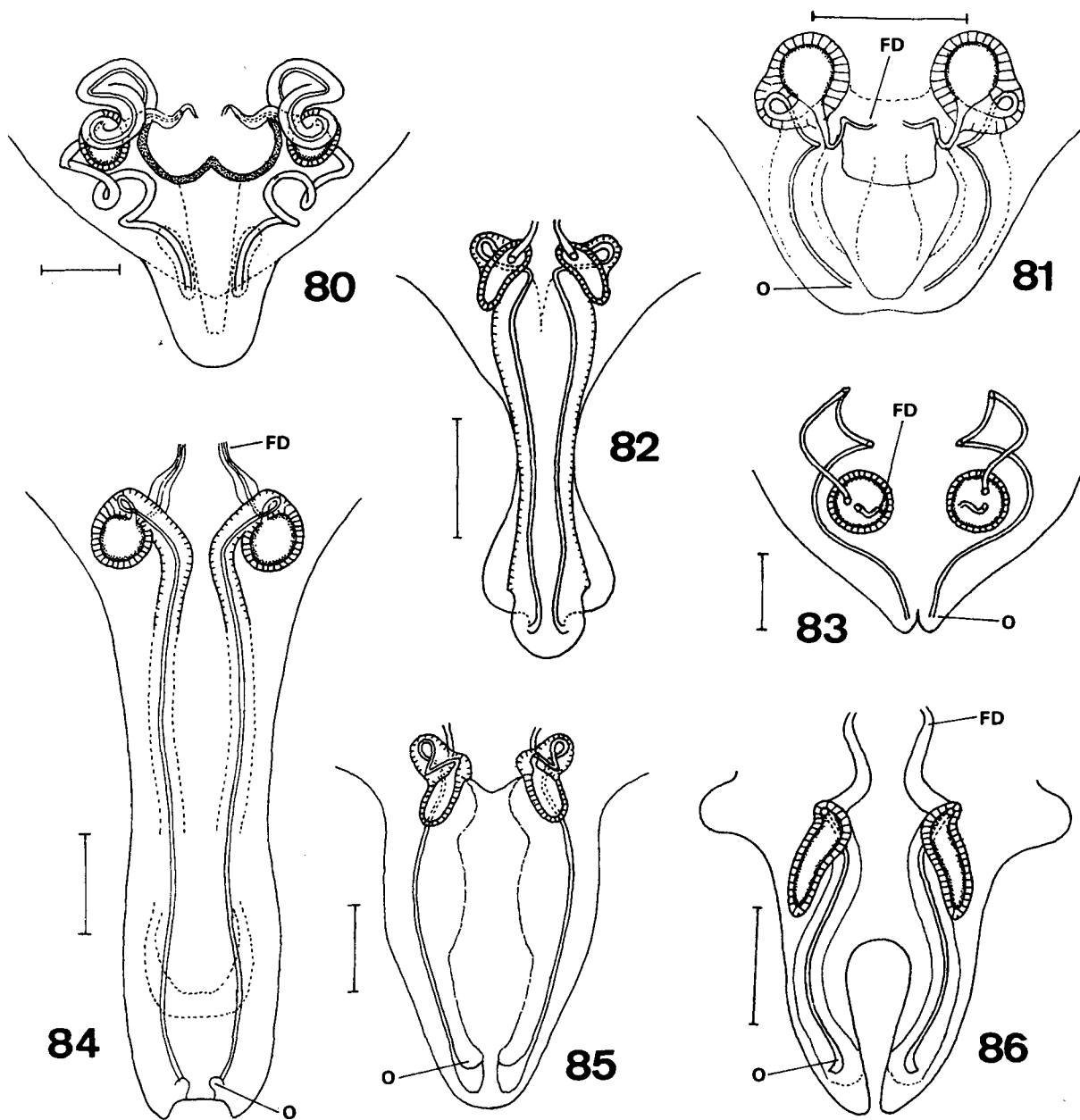
The majority of the genera of the Erigoninae have the external epigyne of the same basic form as that of the *Stemonyphantes* group; that is, the genital openings lie on the ventral (or occasionally the caudal) surface of the epigyne, close to the anterior ends of the two more or less longitudinal grooves which mark the lateral junctions of the ventral and dorsal plates. In common with the *Stemonyphantes* group, the openings can vary in size from small (e.g. Figs. 101, 102) to large (e.g. *Gonatium rubellum* (Bl.): Millidge, 1981a: fig. 25); or the openings can lie within an atrium. The atrium may be single or divided by a median septum; it may be reasonably deep, as in e.g. *Micrargus* (Millidge, 1975: fig. 1) and *Satilatlas* (Millidge, 1981b: fig. 245), or it may be no more than a shallow depression in the ventral plate, as in e.g. *Scotinotyclus* and *Thyreosthenius* (Fig. 104). In a few genera (e.g. *Micrargus*, *Scotinotyclus*, *Thyreosthenius*: Fig. 104) the epigyne carries a genital socket; this is always on the ventral plate.

Within the Erigoninae the epigynes exhibit many variants and elaborations of the basic external form. For example, in the *Savignya/Diplocephalus* group of species the ventral plate is bisected longitudinally into two wing-like branches (Fig. 103) which cover the dorsal plate; the genital openings are located on the dorsal surface of the wings (Fig. 106), which are

presumably lifted by the male during mating. In this form of epigyne, the openings lie in effect inside an atrium enclosed by the ventral and dorsal plates.

In some erigonine genera the epigyne is in the

form of a scape, which carries the genital openings on the dorsal side near the posterior end (e.g. most *Erigone* species (see p. 265): Fig. 119; *Tachygyna*: Fig. 107); the scape can be long (Fig. 110) to short



Figs. 80-86: Epigynes, internal. **80** *Allomengea scopigera*, dorsal; **81** *Asthenargus paganus*, dorsal; **82** *Arcuphantes fragilis* Chamb. & Ivie, dorsal; **83** *Wubana drassoides* (Emert.), dorsal; **84** *Helophora insignis* (Bl.), dorsal; **85** *Fageitella patellata* (Kulcz.), dorsal; **86** *Sintula cornigera* (Bl.), dorsal. Scale lines 0.1 mm.

(Fig. 105). This epigynal form is similar to that present in the Drapetiscinae. The European species "*Troxochrus*" *nasutus* Schenkel (which is desmitracheate) has an epigyne of this form (Figs. 109, 111), and cannot therefore be a member of the genus *Troxochrus*, which has an epigyne quite different in form, both externally and internally.

Occasionally the ventral plate of the epigyne carries one or two finger-like extensions, e.g. *Maso gallica* Sim. (Fig. 112) and "*Trichopterna*" *rufithorax* Sim. (Fig. 113); these pseudoscapae carry neither sockets nor ducts, though there may be a dimple on the dorsal side.

The spermathecae in most instances lie adjacent to the dorsal plate; in a few species, however, they are set more anteriorly (e.g. *Dicymbium*: Fig. 114; *Lessertia*: Fig. 117). The sperm duct system exhibits widely varying degrees of complexity. In many species there is at least partial encapsulation with the spermathecae, e.g. *Trematocephalus* (Fig. 116), *Hypselistes* (Fig. 115); in *Walckenaeria spiralis* (Emert.) the duct is partially encapsulated in the form of a double helix (Millidge, 1983: fig. 23). There are many other configurations of the sperm duct, some simple, some complex.

The fertilisation ducts are normally short and slender, of sinuous appearance, lying more or less between the spermathecae (e.g. Fig. 115), with the openings within the area of the dorsal plate. In a few species where the spermathecae are set more anteriorly, a probably more primitive configuration of the fertilisation duct has been retained, with a longer duct running posteriorly to the region of the dorsal plate (e.g. Figs. 114, 117).

A complete investigation of the epigynal variations in the Erigoninae has yet to be carried out.

Discussion

It was proposed by Blest (1976) that the Linyphiidae should be split into two subfamilies, the Linyphiinae and the Erigoninae, on the basis of the tracheal structure. In the present paper it is concluded (p. 233) that the haplotracheate tracheal character ("linyphiine" form of Blest) is plesiomorphic for the family, and cannot be used to support the existence of the subfamily Linyphiinae as defined by Blest. The desmitracheate form of the

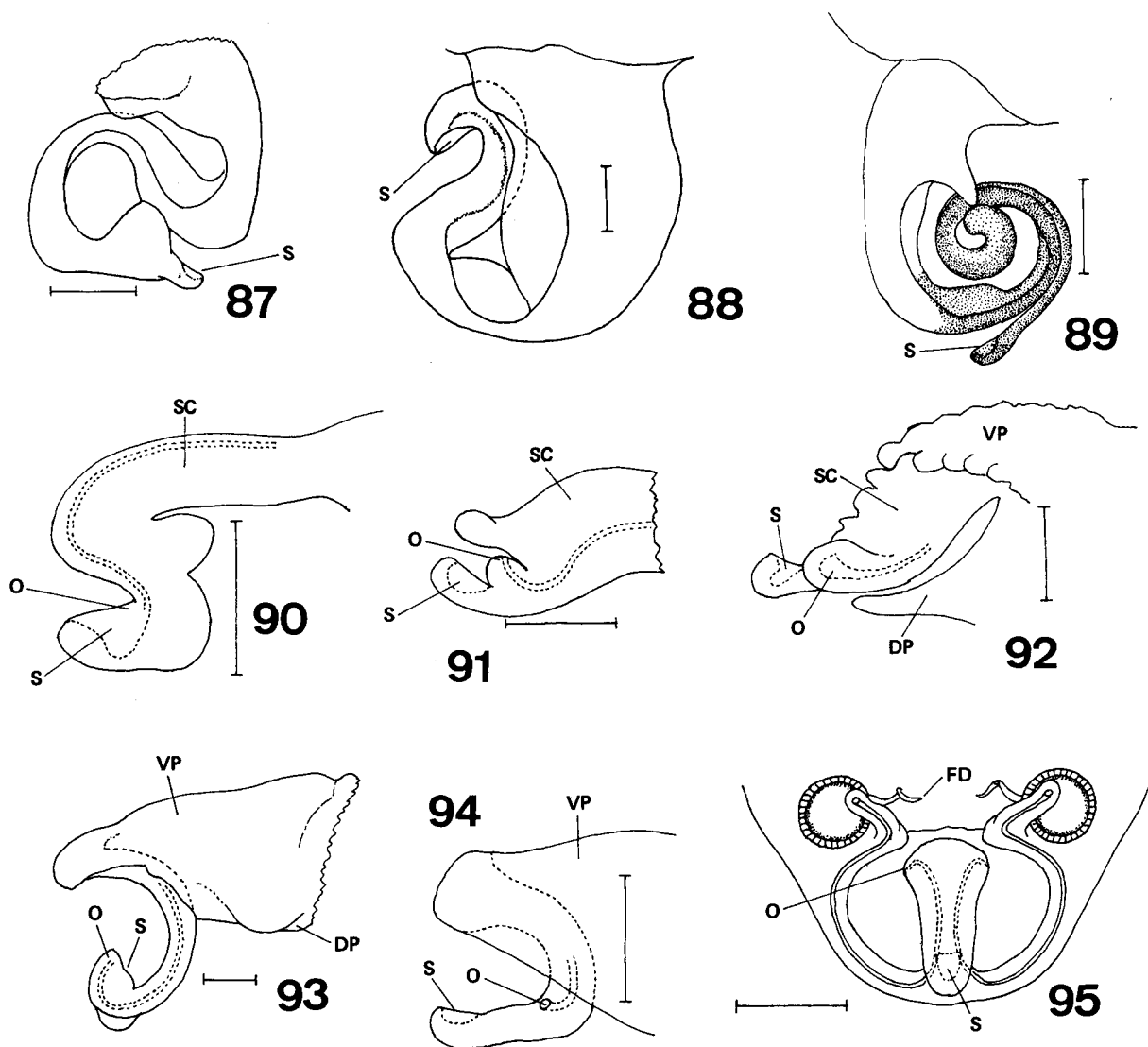
tracheal character is inferred to be apomorphic, and is thus a valid character to support the hypothesis that the Erigoninae form a monophyletic group.

After the erection of the haplotracheate subfamily Mynogleninae, the subfamily Linyphiinae (*sensu* Blest, 1979: 172) appears to be definable only as the residue of the Linyphiidae remaining after removal of the Mynogleninae, the Erigoninae and the genus *Australolinyphia*, which is really no definition at all. This important part of the Linyphiidae appears not to be definable on the basis of any known character, e.g. the tracheal form, the male or female genitalia, or the chaetotaxy. The subfamily Linyphiinae (*sensu* Usher, 1983: 558) suffers from the same lack of positive definition. Before the existence of the subfamily Mynogleninae was recognised, it was suggested by several authors, either overtly or by inference (e.g. Wiehle, 1956; Merrett, 1963; Lehtinen & Saaristo, 1970; Saaristo 1973a) that the division of the Linyphiidae into the two traditional subfamilies, the Linyphiinae and the Erigoninae, was altogether too simple a concept, and that additional subfamilies would be required. In the present paper, the Linyphiinae (*s. lat.*) are split into four parts, namely the subfamilies Linyphiinae (redefined), Micronetinae and Drapetiscinae, and the *Stemonyphantes* group. The two former subfamilies are not new, but in past publications they were somewhat amorphous groups which lacked adequate definition; in the present paper, they are defined, in common with the Drapetiscinae and the *Stemonyphantes* group, on their epigynal structures. In addition, the family contains the two subfamilies Erigoninae and Mynogleninae, defined respectively (following Blest, 1976, 1979) on the tracheal structure and the clypeal glands. Practically all the established genera of the Linyphiidae can be fitted into one or other of these groups, though the position of a small number of genera must be regarded as provisional.

The *Stemonyphantes* group is defined on the basis of the external epigynal structure. In some members of this group the epigyne shows marked similarities to the epigynes in other families (e.g. some families of the Amaurobioidea: Forster & Wilton, 1973) in respect of (i) the external form: genital openings on the ventral surface at the anterior ends of grooves which mark the lateral junctions of the dorsal and ventral plates; and (ii) the form and position of the

fertilisation ducts (Fig. 24, cf. Fig. 127). The distinct encapsulation of the ducts present in some members of the *Stemonyphantes* group is also sometimes present in other families (Fig. 25, cf. Fig. 125; Figs. 126, 127). It seems probable that these epigynal features are plesiomorphic for the Linyphiidae; if so,

the *Stemonyphantes* group must almost certainly be paraphyletic (Hennig, 1966). As noted under the discussion of tracheal structure (p. 233), a subfamily should not be founded on symplesiomorphy, and consequently this group has not been designated as a subfamily. The group is a convenient interim repos-



Figs. 87-95: Epigynes. **87** *Microneta viaria* (Bl.), partly expanded, lateral; **88** *Tapinopa longidens* (Wid.), lateral; **89** *Macrargus rufus* (Wid.), partly expanded, lateral; **90** *Lepthyphantes pallidus* (O. P.-Cambr.), scape, lateral; **91** *L. expunctus* (O. P.-Cambr.), scape, lateral; **92** *Centromerus sylvaticus* (Bl.), lateral, with part of VP removed to show scape; **93** *Lepthyphantes nebulosus* (Sund.), lateral; **94** *Oreonetides glacialis* (L. K.), lateral; **95** *O. glacialis*, internal, dorsal. Scale lines 0.1 mm.

itory for some miscellaneous genera which, because of their epigynal form, do not at once fit into any of the subfamilies defined. The erection of this group is a recognition of the practical situation facing the taxonomist, i.e. that it is impossible at the present time to fit all the linyphiid genera into *properly defined* subfamilies. The *Stemonyphantes* group, though not a natural grouping, does have the justification that it is based on a defined character; it is designed to sort out those genera with epigynal characters inferred to be primitive.

The presence of the primitive epigynal characters probably indicates that the members of this group were derived from early branches of the primitive family stock; the group presumably represents the products of several diverse but on the whole unsuccessful evolutionary experiments (unsuccessful on the basis of the relatively few species surviving today), initiated during the early history of the Linyphiidae. The diverse male palpal structures in this group, which in most instances are different from those present in the haplotracheate subfamilies, also support this hypothesis. Eventually, as further information becomes available, it will be necessary to move the genera from this group into the present subfamilies or into new subfamilies; this procedure is illustrated with the genera *Microlinyphia* and *Frontinellina*, which can be transferred to the Linyphiinae if the definition of this subfamily is somewhat relaxed (see p. 261).

The external epigyne in some members of the *Stemonyphantes* group is very simple, with no genital socket, no scape and no atrium. The absence of these characters is considered to be the plesiomorphic state in the Linyphiidae, while the presence (widespread within the family) of any of these characters is considered to be apomorphic. The socket/scape in the *Stemonyphantes* group is sometimes located on the ventral plate of the epigyne, but in a few cases it is on the dorsal plate; often, however, it is situated at the anterior junction of the ventral and dorsal plates (on the ventral surface), and this may have been the most primitive position. The initial stage in the formation of an atrium could then have been the production of a transverse sulcus by invagination of the integument on either the dorsal or the ventral side of this primitive socket. Such a sulcus could join the two genital openings, and subsequent enlargement

and deepening of the sulcus would lead to the formation of an atrium.

The internal genitalia of the *Stemonyphantes* group show a wide degree of variation, but include the most complex formations within the family. The simplification of the internal genitalia (e.g. reduction of encapsulation, change to less complex and more straightforward duct pathways) is considered to be apomorphic. Thus the evolution of the linyphiid epigyne is thought to have been towards more complex external structures, but less complex internal structures.

The males of many (but not all) of the *Stemonyphantes* group have a long, somewhat coiled embolus, and this is also present in many members of the Mynogleninae. The hypothesis is therefore proposed that this form of embolus is plesiomorphic, or at least relatively plesiomorphic, for the family.

The subfamily Mynogleninae (Blest, 1979) is regarded as monophyletic on the basis of the clypeal pits/glands, a well-developed character which is almost certainly apomorphic. There is no evidence amongst the New Zealand or central African populations of the Mynogleninae of loss of the clypeal glands, and hence their presence is regarded as a decisive character for the definition of the subfamily. Externally the epigynes are of essentially similar form to those of the *Stemonyphantes* group, and were it not for the clypeal glands it would be difficult or impossible to differentiate the Mynogleninae from the *Stemonyphantes* group. Although a few genera in this subfamily have the simplest form of external epigyne, with no socket, scape or atrium, or only rudimentary ones, there is a progressive transformation to epigynes which have a shallow atrium, inside which lie the genital openings. In most genera the epigyne carries a socket on a short scape, which is located on either the ventral or the dorsal plate (see p. 241). The fertilisation ducts are always of the primitive form present in the *Stemonyphantes* group; the sperm duct is usually encapsulated, and its basic arrangement is remarkably constant.

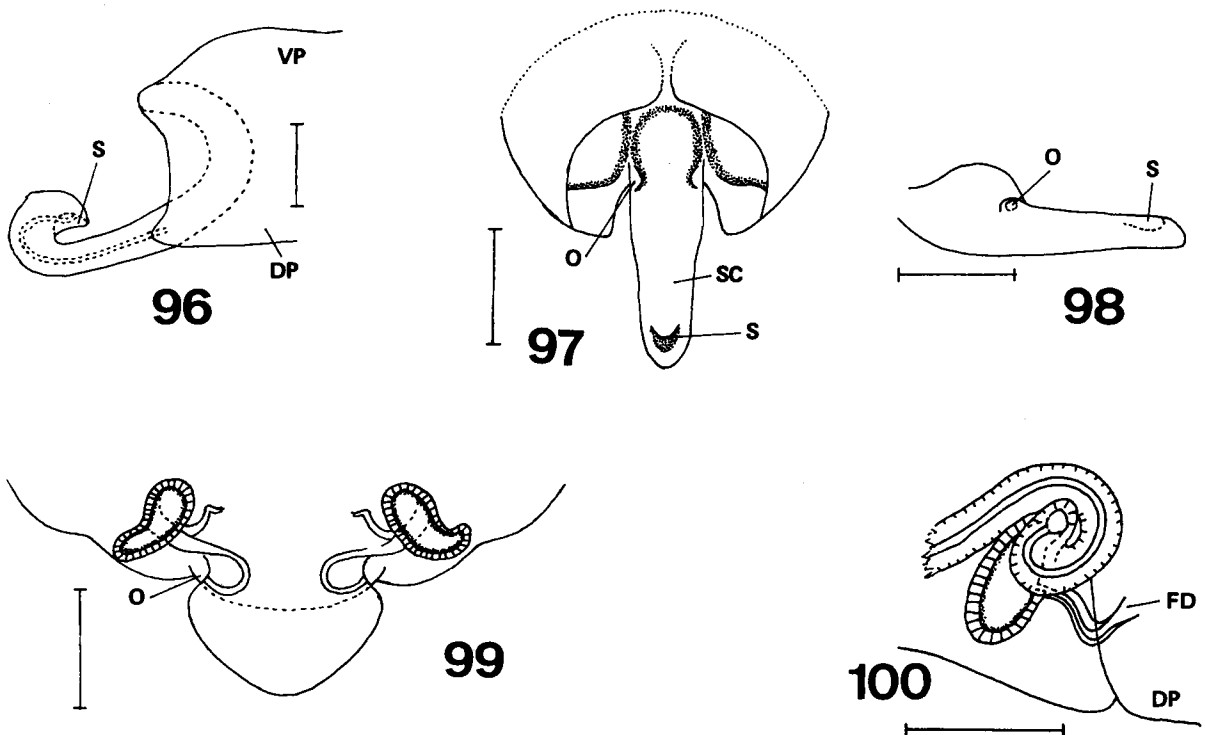
The external epigynal structure of the scape-bearing Mynogleninae is very similar to that in the genus *Linyphantes* (*Stemonyphantes* group) from western North America; the epigynes of this genus have a shallow atrium which holds the genital openings, and a short ventral scape/socket which

occupies most of the atrium. Members of the *Stemonyphantes* group with epigynes of a similar basic form are also present in southern South America (paper in preparation); the sperm ducts in some of these species appear to have a similar configuration to that in the Mynogleninae. The genus *Falklandoglenes* has the external epigynal structure of the *Linyphantes* form, and is considered to be part of the *Stemonyphantes* group; it is probably related to the undescribed South American species. Although the palpal structures of these South American species show similarities to those of the genus *Microlinyphia*, the epigynal structure (which is of a form present only in the Mynogleninae and in this group of species) would indicate that this group and the Mynogleninae are related, perhaps as sister groups (see later).

The epigynes of the Linyphiidae also have an atrium which holds the genital openings; in this subfamily, however, the atrium is more highly developed

than in the Mynogleninae, forming a distinct chamber enclosed between the ventral and dorsal plates, with the dorsal plate constituting the floor of the atrium. There is a scape/socket attached to the dorsal plate, i.e. the atrium has opened on the ventral side of the socket. In contrast to the Mynogleninae, there are in the Linyphiidae no species in which the scape/socket is on the ventral plate, although in a few species the ventral plate is joined to the dorsal plate and scape by a longitudinal septum. In this subfamily, the configuration of the duct system is variable, but sometimes in the form of a long helix; the fertilisation duct always has the primitive form present in the *Stemonyphantes* group and in the Mynogleninae.

Within the Linyphiidae, extension of the ventral plate to give a scape of one form or another has taken place in every one of the groups described in this paper, and it must be concluded that this extension has been a relatively facile evolutionary event. Extension of the dorsal plate to give a scape/socket,



Figs. 96-100: Epigynes. **96** *Centromerus pabulator* (O. P.-Cambr.), expanded, lateral; **97** *C. arcanus*, ventral; **98** *C. arcanus*, scape, lateral; **99** *Lepthyphantes biseriatus*, internal, ventral; **100** *Floronia bucculenta* (Clk.), internal, spermatheca, FD and part of sperm duct. Scale lines 0.1 mm.

a character which is almost certainly apomorphic, is present however only in the Linyphiinae and in some members of the Mynogleninae. The synapomorphy within the Linyphiinae of the dorsal scape, coupled with the particular form of the atrium, support the hypothesis that the Linyphiinae are a monophyletic group. The South American species mentioned above have palpal organs somewhat similar to those of the genus *Microlinyphia*, while their epigynes are similar to those of the Mynogleninae. If *Microlinyphia* can be regarded as a primitive member of the Linyphiinae (see later, p. 261), then this presence of both mynoglenine and linyphiine characters in one genus may suggest that the Mynogleninae and the Linyphiinae have arisen from a common parent.

The presence within the Linyphiinae of several different internal epigynal arrangements, and of several different palpal configurations, suggests that this subfamily is composed of several branches; for example, *Linyphia/Neriene*, *Bathyphantes/Porhomma/Lessertinella* and *Kaestneria/Cresmatoneta/Laetesia*(?) *Laperousea*, and probably others to hold the remaining genera, the positions of which are not immediately clear.

A spiral duct configuration of somewhat similar form to that in some members of the Linyphiinae is present in the genera *Microlinyphia*, *Frontinellina* and *Mioxena*, and in the New World species "*Linyphia*" *catalina* and "*L.*" *rita*, all of which are placed in the *Stemonyphantes* group because of the external form of the epigynes. On the basis of the internal duct configuration, these taxa are probably related to the Linyphiinae (see later).

The members of the Drapetiscinae have the epigyne in the form of a scape, which lacks a socket. The genital openings lie on the dorsal side of the scape, at the posterior ends of grooves which extend from the margins of the small dorsal plate. The sperm ducts follow a fairly simple pathway in most instances, and the fertilisation ducts are not of the primitive form present in the *Stemonyphantes* group. This form of scape could have arisen by extension of the ventral plate of the simplest epigynal form (i.e. lacking both socket and atrium) present in the family.

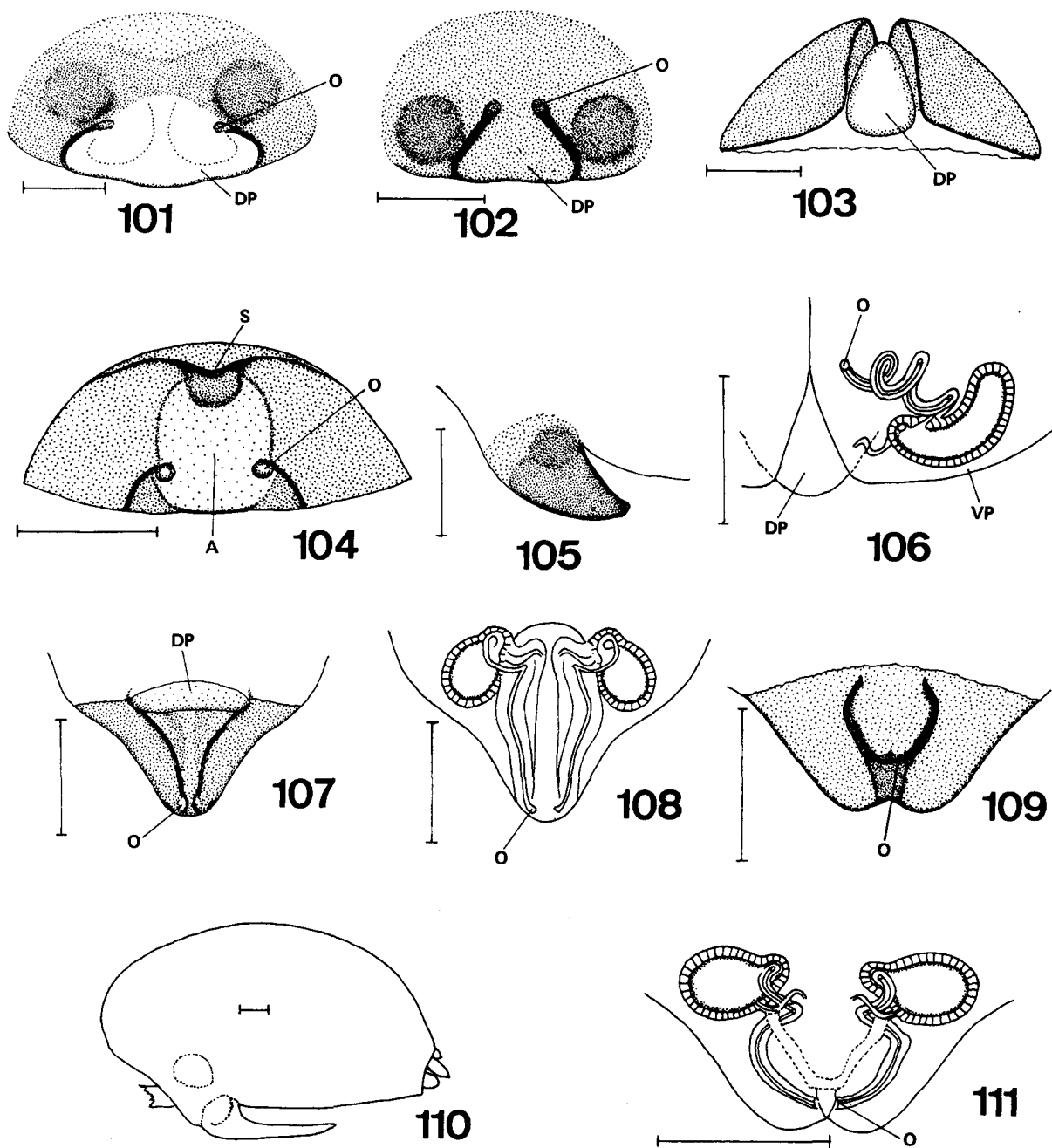
As mentioned above, the posterior lengthening of the ventral epigynal plate to give a scape of one form

or another is general throughout the Linyphiidae. Although the specific form of the scape characteristic of the Drapetiscinae is also present in some members of the desmitracheate Erigoninae, it may be permissible to cite this almost certainly apomorphic character to support the hypothesis that the Drapetiscinae form a monophyletic group within the haplotracheate members of the Linyphiidae. When this form of scape is long, it represents a distinctive and easily recognisable character; but when it is short, there is only a small difference between this epigynal form and that in some members of the *Stemonyphantes* group. For example, the epigynes of *Aphileta* and *Asthenargus* (Figs. 67, 81) differ from those of *Caviphantes* (Figs. 17, 32), *Mioxena* (Fig. 37), *Ostearius* (Figs. 19, 31) and *Eulaira* (Figs. 18, 35) only to the extent that in the former genera the ducts run along the scape to the openings, while in the latter the openings lie in an atrium between the dorsal plate and the scape, with the scape itself devoid of ducts and openings. Although in addition the form of the fertilisation duct will distinguish members of the Drapetiscinae from most members of the *Stemonyphantes* group, this distinction is less clear in the small species of the genera *Caviphantes*, *Ostearius* and *Eulaira*, where the fertilisation ducts are barely different from those of some members of the Drapetiscinae.

The Drapetiscinae can be regarded provisionally as a monophyletic group, but it cannot be ruled out that the simple extension of the ventral plate to give this form of scape may represent a minor and relatively facile modification of the primitive epigynal form, a modification which has taken place more than once.

The members of the Drapetiscinae exhibit a wide variety of palpal forms, which presumably indicates that the subfamily has a number of branches.

The members of the Micronetinae also have the epigyne in the form of a scape derived from the ventral plate, but in this subfamily the scape, which has a socket distally on the ventral surface, lies partly recessed within a well-defined hollow enclosed by the ventral and dorsal plates; the genital openings are situated on the ventral (or occasionally lateral) surface of the scape. The sigmoid form of the scape (see p. 248), equipped with lateral lobes, is the most complex and probably the most apomorphic form; the asigmoid form, as in *Centromerus arcanus*, is



Figs. 101-111: Epigynes. **101** *Spirombolus vallicolens* Chamb., ventral, dry; **102** *Pelecopsis elongata* (Wid.), ventral, dry; **103** *Diplocephalus cristatus* (Bl.), caudal, with "wings" slightly lifted; **104** *Thyreosthenius parasiticus* (Westr.), ventral, dry; **105** *Tachygyna pallida* Chamb. & Ivie, lateral; **106** *Diplocephalus cristatus*, internal, ventral, right side; **107** *Tachygyna pallida*, dorsal, dry; **108** *T. pallida*, internal, dorsal; **109** "*Troxochrus*" *nasutus* Schenkel, dorsal, dry; **110** *Tunagyna debilis* (Banks), abdomen and epigynal scape, lateral; **111** "*Troxochrus*" *nasutus*, internal, dorsal. Scale lines 0.1 mm.

considered to be probably the most primitive form in the subfamily. The sperm ducts follow a consistently straightforward pathway from the openings along the scape to the spermathecae, and the fertilisation ducts are not of the primitive type.

The ventral scape in the Micronetinae could have arisen from a primitive epigynal form which carried a socket on the ventral plate. The epigyne of the *Centromerus arcanus* type could represent an early form of the micronetinine epigyne; subsequent elaboration, coupled with some extension of the ducts and movement of the genital openings, would give the more advanced forms of the epigyne.

The epigynal form which is characteristic of the Micronetinae is quite specific, and is present in no other group in the family; on this basis, the Micronetinae are considered to be a monophyletic group. The most advanced epigynal forms of the Micronetinae are, externally, the most complex in the whole of the Linyphiidae, and are considered to be probably the most apomorphic. On the basis of the genitalia, both female and male, the Micronetinae appear to represent the most highly developed branch of the Linyphiidae.

The Drapetiscinae and the Micronetinae both have ventral scapes, but the epigynal forms show a number of significant differences. At the present time there appears to be no positive evidence which either supports or excludes a close relationship between these two subfamilies.

The Erigoninae are defined in this paper by the desmitracheate form of the tracheae, as proposed by Blest (1976). The subfamily is regarded as monophyletic, the essential supports for this hypothesis being that the desmitracheate character is apomorphic, and that (based on parsimony) this character was evolved only once within the family. The character most frequently used in the literature to diagnose the erigonines, namely the chaetotaxy (e.g. Locket & Millidge, 1953; Wiehle, 1960) was never completely satisfactory, and is certainly no longer valid if the tracheal definition is accepted. At the present time the only acceptably rigid definition of the Erigoninae is that based on the tracheal form.

In the majority of the genera of the Erigoninae the external epigyne has essentially the same form as that present in the *Stemonyphantes* group, and in some members of the Mynogleninae; that is, with the

genital openings located on the ventral surface at or near the anterior ends of the lateral seams joining the ventral and dorsal plates. As in the *Stemonyphantes* group, a few erigonine genera have the genital openings within an atrium. In some species there is a genital socket (which may be rudimentary), and this is always on the ventral plate. Some erigonine genera have the epigyne in the form of a scape, which is very similar to the scapes of some members of the Drapetiscinae. The primitive epigynal form present in many erigonine genera has undergone some elaboration in other genera, but the basic epigynal pattern is usually discernible.

The internal genitalia of the Erigoninae are frequently less complex than in the *Stemonyphantes* group, but there are many examples where more primitive characters (e.g. duct encapsulation, complex duct pathways) have persisted. In those erigonines where the epigyne is a scape, the internal genitalia are virtually identical with those of some members of the Drapetiscinae. The fertilisation ducts in the Erigoninae differ from those of the *Stemonyphantes* group, being of the probably more apomorphic form which is present in many members of the Drapetiscinae and the Micronetinae.

Some males of the Erigoninae have subocular pits which house the openings to internal glands, somewhat like the clypeal pits/glands of the Mynogleninae (Blest & Pomeroy, 1978). These organs, though fulfilling different functions in the two subfamilies, appear to be anatomically similar, and may indicate some relationship between the two subfamilies.

Several epigynal forms and many palpal forms are present in the Erigoninae, and undoubtedly it will be necessary eventually to split this subfamily into several branches.

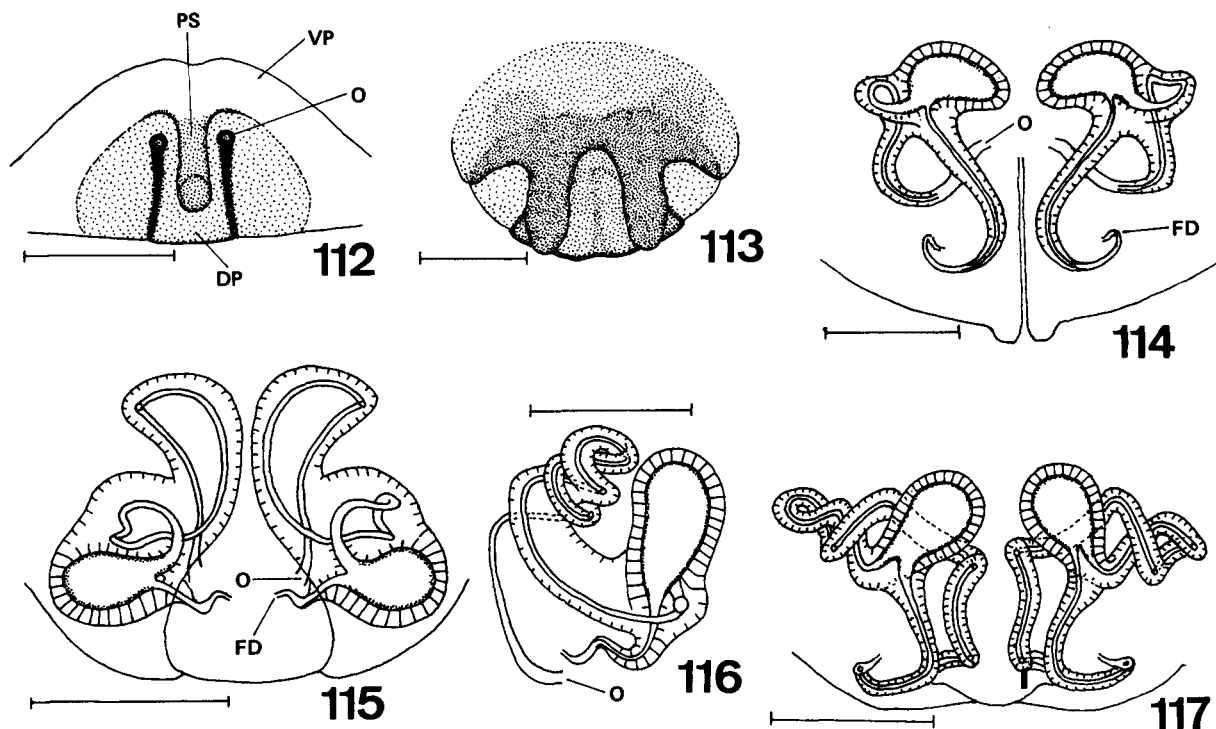
Many erigonine species have a slender coiled embolus in the male palp, and this probably represents an inheritance from primitive ancestors; such whip-like or coiled emboli are not infrequent in the more primitive members of the family, viz. the *Stemonyphantes* group and the Mynogleninae. Some erigonines have retained other probably primitive features in the palpal conformation, e.g. the embolic division of *Tunagyna* (Fig. 128) shows distinct similarities to that of some *Haplinis* species, having a broad stalk leading to the embolic division at the

posterior end of the organ, and a long slender embolus the distal end of which rests on a membranous conductor arising from the stalk/tegulum. The apophyses present on the palpal segments in many male erigonines are also probably a retained primitive character, which has undergone development and diversification in this subfamily. Such apophyses are present in some members of the *Stemonyphantes* group, appear to be absent in the Mynogleninae, are found very sparsely in the Linyphiinae and the Drapetiscinae, and more frequently in the Micronetinae.

The retention in the Erigoninae of several primitive, or relatively primitive, genital characters, both male and female, suggests that this subfamily diverged from the primitive stock fairly early in the history of the family. Perhaps as a result of their decrease in size, and changes in habitat, however, the members of this subfamily have lost most of the probably primitive somatic characters, e.g. multiple tibial and metatarsal spines, multiple metatarsal trichobothria, tarsal

claw on female palp.

Among the large number of erigonine species known, none possesses the characteristic epigynal features of the Linyphiinae or the Micronetinae. There are epigynal congruences between some members of the Erigoninae and some members of the Drapetiscinae, and between the Erigoninae and the *Stemonyphantes* group, but in the latter case the congruence is based on plesiomorphy. The epigynal congruences between the Erigoninae and the Drapetiscinae, and the presence of the subocular pits/glands in both the Erigoninae and the Mynogleninae, may indicate that the Erigoninae are more closely related to the Drapetiscinae and the Mynogleninae than to the Linyphiinae or the Micronetinae. The presence in one genus (*Allomengea*) of the Drapetiscinae of a tracheal system to some extent intermediate between the haplotracheate and desmitracheate forms (with the median tracheae branched, but not passing into the prosoma: Blest, 1976) also suggests the possibility that the Erigoninae and



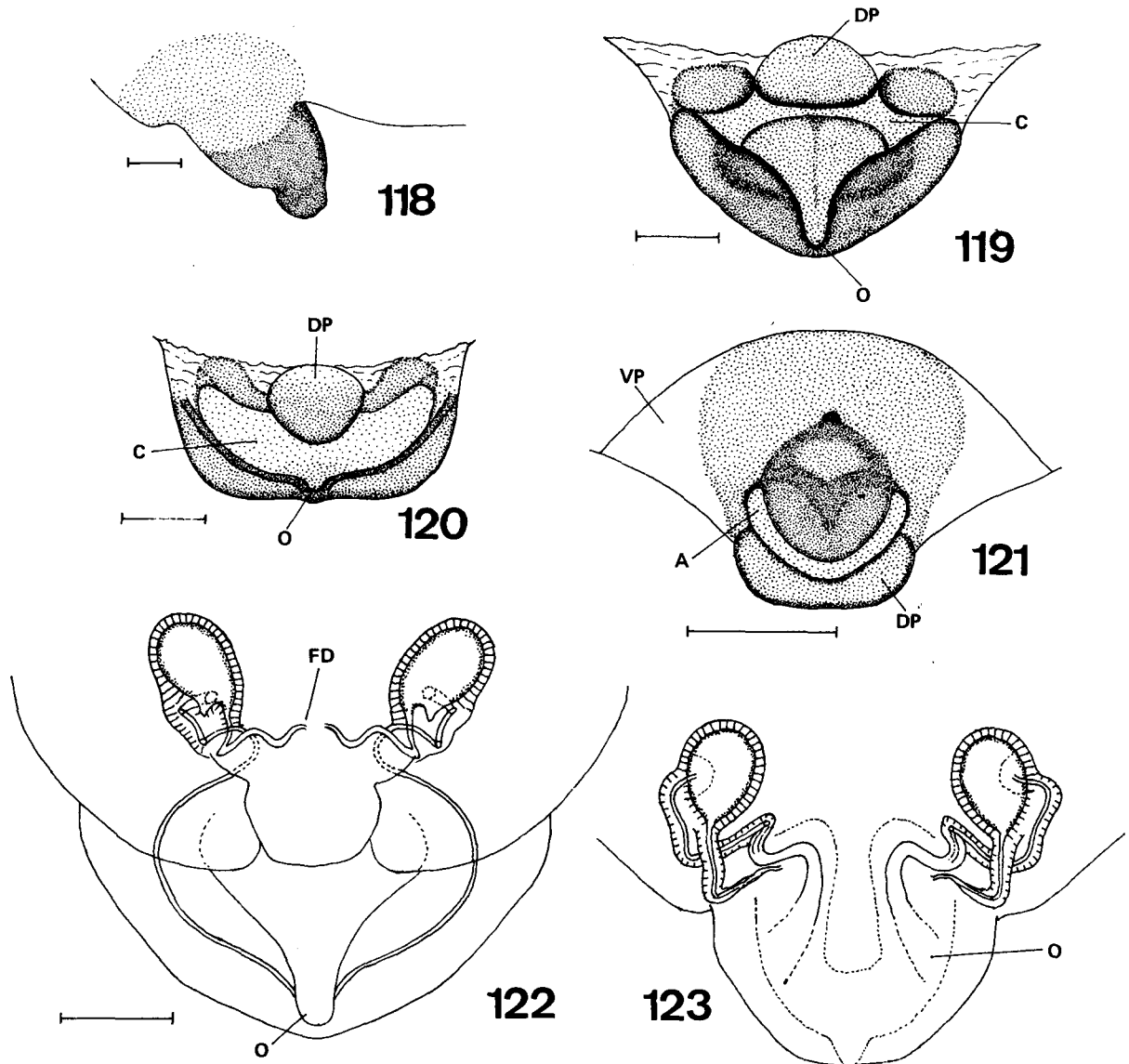
Figs. 112-117: Epigynes. 112 *Maso gallica* Sim., ventral, dry; 113 "*Trichopterna*" *rufithorax* Sim., ventral; 114 *Dicymbium nigrum* (Bl.), internal, dorsal; 115 *Hypselistes jacksoni* (O. P.-Cambr.), internal, dorsal; 116 *Trematocephalus cristatus* (Wid.), internal, dorsal, right side; 117 *Lessertia denticelis* (Sim.), internal, ventral. Scale lines 0.1 mm.

Drapetiscinae are near relatives. The relationships suggested are shown in the diagram (Fig. 129), but it must be emphasised that these are very tentative.

Although it is impossible at this stage to draw any firm conclusions, the present investigation does not support the splitting off of the Erigoninae as a separate family, since the possible relationships mentioned indicate that the Linyphiidae minus the Erigoninae

would not constitute a monophyletic group.

The taxonomic system proposed in this paper enables the linyphiid genera to be assigned fairly easily either to one of the current subfamilies or, if the epigyne appears to be of a primitive form, to the *Stemonyphantes* group. If a new genus is discovered which apparently fits into none of the groups described, it could well become necessary to assign



Figs. 118-123: Epigynes. **118** *Erigone longipalpis* (Sund.), lateral; **119** *E. longipalpis*, dorsal, dry; **120** *Erigone atra* (Bl.), dorsal, dry; **121** *Erigone vagans* Aud., caudal, dry; **122** *Erigone longipalpis*, internal, dorsal; **123** *Erigone vagans*, internal, dorsal. Scale lines 0.1 mm.

it to a new subfamily.

The next step in the development of the proposed taxonomic system would be the transfer, on the basis of the epigynal structures, or other relevant characters, of some genera/species from the *Stemonyphantes* group to the defined subfamilies, to give enlarged subfamilies. These new subfamilies would, for priority reasons, retain the same names, but it might be necessary for the present groups, as defined on pp. 241-246, to be relegated to the status of tribes. For example:

(i) On the basis of the external epigynal form, and possibly also on the internal duct configuration, the genera *Linyphantes*, *Falklandoglenes*, possibly *Caviphantes*, and possibly some as yet undescribed genera from South America, would be transferred to an enlarged Mynogleninae, as one or more sister groups of the group defined on p. 241.

(ii) On the basis of the internal genitalia, viz. the particular coiled duct configuration, the genera *Microlinyphia*, *Frontinellina*, possibly *Mioxena* and *Stemonyphantes*, the species "*Linyphia*" *rita* and "*L.*" *catalina* and probably other New World species, would be transferred to an enlarged Linyphiinae, as two or more sister groups of that group of genera which comprise the Linyphiinae as described on pp. 241-244. In the cases of *Microlinyphia* and *Frontinellina*, such a move would also be supported by the palpal structure (Merrett, 1963; van Helsdingen, 1969, 1970). As mentioned earlier, *Australolinyphia*, *Diplostyla* and *Labulla* might also be considered to be sister groups of the group defined on pp. 241-244.

(iii) On the basis of the external epigynal form, *Eulaira* and *Ostearius* might be considered for transfer to an enlarged Drapetiscinae, as sister groups to the subfamily as defined on pp. 245-246.

Such moves would leave a group of genera of currently uncertain relationships, viz. *Beauchenia*, *Estrandia*, *Frontinella*, *Jalapyphantes*, *Palaeohyphantes*, *Selenyphantes*, *Smermisia* and *Taranucnus*, some at least of which would probably need to be accommodated in new subfamilies.

These suggestions are put forward as an indication of the possibilities inherent in the proposed taxonomic scheme, but it would be wise to delay positive proposals of this nature until additional information has accumulated on the haplotracheate genera, particularly those of the New World, Africa,

eastern Asia and Australasia. It is clear that the definition of such enlarged subfamilies would present some problems.

With the exception of the Mynogleninae and the Erigoninae, the taxonomic groupings proposed in this paper are based on the epigynal structures. It is legitimate to question whether the genitalic structure of the female should be preferred over that of the male as a character to support hypotheses of relationship within the Linyphiidae. The palpal organs of all members of this family have the same basic structure, but the embolic divisions and the supra-tegular apophyses have undergone considerable diversification in form. It is the structure of the embolic division that has been most frequently employed as a taxonomic indicator. Within each major line of development, as represented by the subfamilies proposed in this paper, it may be reasonable to infer that the component parts of the embolic division should be more or less homologous. Since each subfamily will have undergone independent evolutionary change, however, it cannot be taken for granted that such homology will extend from one line to another, and neither can it be ruled out that apparent similarities in the palpal structures may be attributable in some instances to convergence. Such possibilities could account for some of the difficulties encountered in past attempts to homologise the complex palpal structures, and to achieve an unambiguous classification of the Linyphiidae on the basis of the palpal structure (e.g. Wiehle, 1960; Merrett, 1963). The same criticism is equally applicable to the author's earlier attempt (Millidge, 1977) to develop a linyphiid classification on the basis of the palpal structures; this attempt was in addition based on the probably erroneous premise that the embolic division of the primitive linyphiid palp was simple in form, whereas it now appears probable (from our knowledge of the Mynogleninae (Blest, 1979) and of the *Stemonyphantes* group) that the primitive palp was relatively complex.

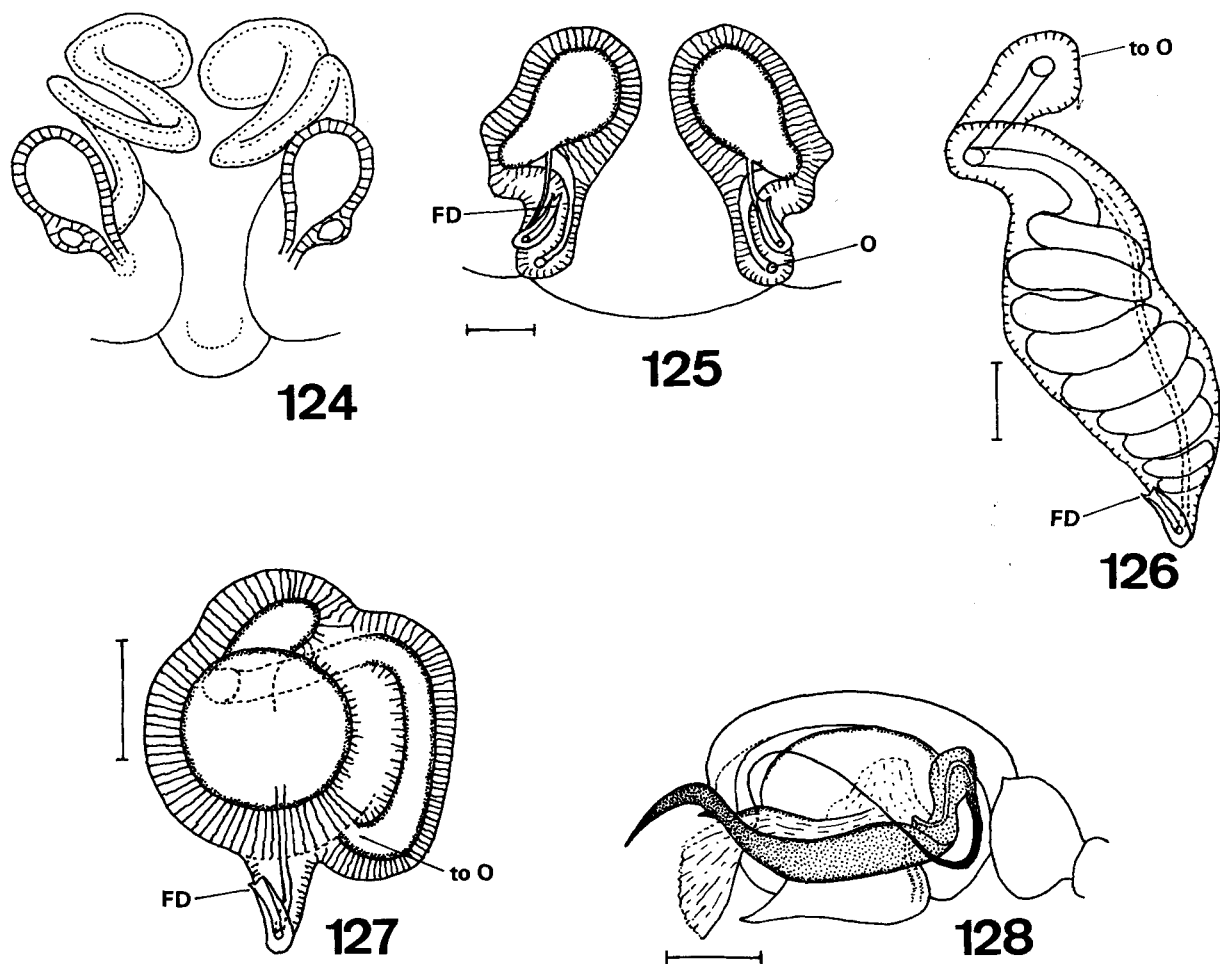
The component parts of the male palp exhibit a very wide variety of forms, some quite exotic, whereas the epigynes are, at least externally, much more conservative in their range of forms. As a consequence of this epigynal stability, the genera of the Linyphiidae can be allocated with comparative ease into the *Stemonyphantes* group, the Linyphiinae,

the Drapetiscinae and the Micronetinae. The palpal structures, on the contrary, cannot be used to give unambiguous diagnoses of any of these groups, and this is also true in the cases of the Mynogleninae and the Erigoninae which are defined on non-epigynal characters. The palpal structure exhibits significantly greater plasticity than the epigynal structure, the basic forms of which are remarkably constant.

As mentioned in the discussion above, the epigynal forms of all the subfamilies appear to be derivable from the primitive epigynal form by relatively simple (though hypothetical) geometric changes. Possible

derivations of the multitudinous palpal forms of the Linyphiidae from some presumed primitive palpal form would clearly be much more difficult, and would undoubtedly be complicated by convergences.

It is of course undesirable to base taxonomic groupings such as subfamilies on one character alone; it would be very convenient if other, non-genitalic, characters were available for taxonomic use. Unfortunately no such characters are known in the Linyphiidae, and consequently if the epigynal and palpal characters point in different taxonomic directions then priority must be given to one or the other. The



Figs. 124-128: **124** *Haplisis subclathrata*, epigyne, internal (by clearing whole spider); **125** *Orepukia nota* Forster & Wilton (Agelenidae), epigyne, internal, dorsal; **126** *Tegenaria saeva* Bl. (Agelenidae), epigyne, internal, dorsal, right side; **127** *Orepukia popplewelli* Forster & Wilton, epigyne, internal, dorsal, left side; **128** *Tunagyna debilis*, male palp, mesal. Scale lines 0.1 mm.

suggestion made in this paper is that, where this circumstance arises, the more conservative epigynal structure is likely to be a more reliable taxonomic character than the more volatile palpal structure. In many instances a consideration of the palpal form will lead to essentially the same taxonomic conclusions as consideration of the epigynal form; for example, as noted by Merrett (1963: 451) almost all the members of Wiehle's Lephyphantaeae, Centromereae and Microneteae (Wiehle, 1956), which correspond by and large with the Micronetinae as defined in the present paper, have similar palpal structures. The very different epigynal structures in *Drapetisca* and *Maro*, however, show that the inclusion of these genera in the same group is almost certainly erroneous.

The taxonomic systems so far proposed for the Linyphiidae (Wiehle, 1956; Merrett, 1963, who also summarised earlier proposals; Blest, 1979; Usher, 1983) do not cope satisfactorily even with the known linyphiid genera, and additional problems arise with new material now coming forward in increasing quantities from areas such as Australasia, Africa, South America and eastern Asia. The subdivision of the family into the groups proposed in this paper

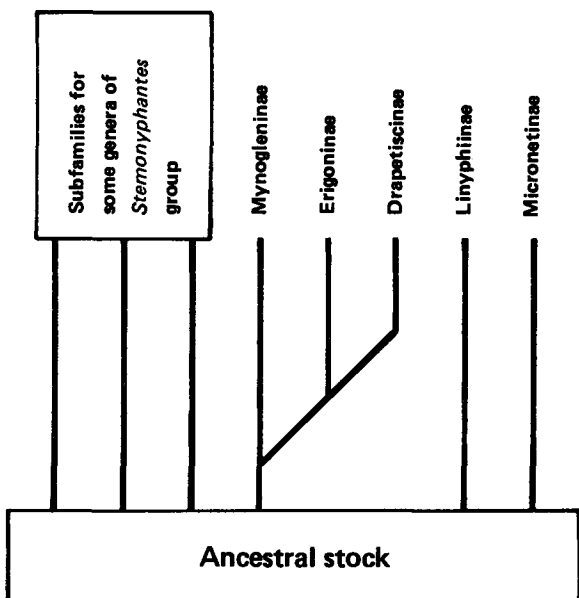
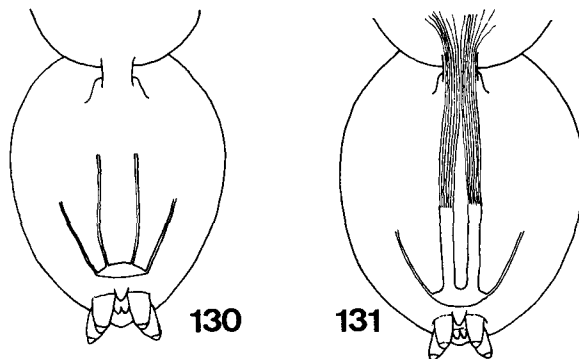


Fig. 129: Diagram showing tentative relationships of subfamilies proposed.

offers an alternative taxonomic hypothesis which is reasonably logical and straightforward; the subfamilies used are for the most part not new, but most are more clearly defined than hitherto on the basis of certain selected synapomorphies. Because of the scope for further development of the hypothesis, the potential for dealing with new genera is improved. The scheme proposed, like all such schemes, is of course open to criticisms, but it is nevertheless suggested that it may be acceptable for the time being as a working hypothesis.

Acceptance of the hypothesis would require that the adjective "linyphiine" be restricted to those genera/species which are assignable to the Linyphiinae as defined in this paper; and where this subfamily name is used, e.g. in faunal lists, it would be likewise restricted. The adjective "erigonine" would be applied only to the desmitracheate Erigoninae, i.e. the haplotracheate species previously regarded as erigonine would be excluded. It is desirable that future descriptions of new species/genera of the Linyphiidae should record the tracheal form.

As a final comment, it is important to bear in mind that the hypotheses proposed are, like other scientific hypotheses, potentially falsifiable, for example by the discovery of character congruences which point more strongly in a different direction, or of evidence that the desmitracheate character was evolved more than once in the family. It would be a useful discipline for students of linyphiid taxonomy to examine whether the taxa on which they are working will, or will not, fit these (or other)



Figs. 130-131: Tracheal systems, dorsal view. **130** Haplotracheate; **131** Desmitracheate.

hypotheses; and if not, what modifications to the hypotheses are required or what alternative hypothesis will better fit the data. It is only by erecting taxonomic hypotheses of this kind, and later modifying or discarding them *on the basis of the data available*, that the order which undoubtedly exists in this (and other) families can eventually be uncovered.

Descriptions of new genera, etc.

Genus *Palaeohyphantes* new genus

Type species: Mynoglenes simplicipalpis Wunderlich, 1976.

Derivation of name: From the Greek *palaios*, ancient; *hyphantes*, a weaver. The gender is masculine.

This genus is erected for the Australian species *Mynoglenes simplicipalpis*, which is not a *Mynoglenes* (Blest, 1979).

The genus is defined by the form of the genitalia of the type species. The epigyne is of a simple form, with the genital openings lying on the ventral surface (Fig. 20), at the anterior ends of the lateral junctions of the dorsal and ventral plates. There is no scape, socket or atrium. Posteriorly the ventral plate has a rounded swelling on either side of the dorsal plate, and each of these swellings has a small nipple-like elevation (Fig. 21). The internal duct system is very simple (Fig. 36). The male palp (Wunderlich, 1976; Blest, 1979) is of very simple form, and appears to lack a suprategulum.

The genus is haplotracheate.

Palaeohyphantes simplicipalpis (Wunderlich) (Figs. 20, 21, 36)

Mynoglenes simplicipalpis Wunderlich, 1976: 136; Brignoli, 1983: 318.

The male of this species was described by Wunderlich (1976). Both sexes were later taken together by Blest (1979), and a description of the female is given here.

Total length: 2.1-2.3 mm. *Carapace:* Length 0.95-1.0 mm. Yellow-brown to brown, with dusky fovea and markings. *Eyes:* Moderately large, with posteriors all less than one diam. apart. *Chelicerae:* Orange-brown, suffused anteriorly with some black; four teeth in anterior row. *Abdomen:* Rather variable in colour. Grey to blackish dorsally, with 2-3 irregular

broad white or pale yellow bars; sides grey to black with white blotches; ventrally grey to black with irregular lighter markings. *Sternum:* Brown to almost black. *Legs:* Yellow-brown, with tibiae and metatarsi weakly annulated with black or brown. All femora with one dorsal spine, femur I with one or two pro-lateral spines. All tibiae with two dorsal spines and a crown of 3-4 short spines distally; tibiae I and II with one prolateral and one retrolateral spine. All metatarsi with one dorsal spine. Except for the distal tibial spines, the spines are long. Metatarsi I-III with a trichobothrium dorsally; TmI c. 0.15. *Female palp:* Without a tarsal claw. *Epigyne:* Figs. 20, 21, 36; description given under Genus above.

Genus *Haplinis* Simon, 1894

Haplinis Simon, 1894: 701; Roewer, 1942: 536; Bonnet, 1957: 2086. Type species *H. subclathrata* Simon, 1894 by original designation.

Mynoglenes Simon, 1905: 418; Roewer, 1954: 95; Bonnet, 1957: 2996; Blest, 1979: 101. Type species *Linyphia rufocephalia* Urquhart, 1888 (= *Mynoglenes insolens* Simon, 1905), by original designation.

The female holotype of *Haplinis subclathrata* (MNHN, Paris), from New Zealand, is a typical member of the Mynogleninae, with well-defined clypeal pits. The unique specimen has lost all the leg spines, but the size (carapace length 1.6 mm, abdomen length 2.15 mm), the trichobothria (TmI 0.70), and the epigyne, both externally and internally (Fig. 124) are very similar to those of *Mynoglenes similis* (Blest, 1979: 118). Although it was not possible to carry out a thorough comparison of the internal genitalia of *H. subclathrata* with those of *M. similis*, it is very probable that *M. similis* is a junior synonym of *H. subclathrata*; since there is no male of *H. subclathrata*, however, this can never be established with complete certainty. There can be no doubt, however, that *Mynoglenes* is a junior synonym of *Haplinis*.

Genus *Atopogyna* new genus

Type species: Erigone cornupalpis O. P.-Cambridge.

Derivation of name: From the Greek *atopos*, strange; *gyna*, female. The gender is feminine.

The genus is characterised by the form of the epigyne. The ventral plate is drawn out posteriorly into a broad scape (Fig. 77), which holds the genital

openings and the ducts. The scape is split posteriorly into two short arms, and arising from the median notch there is a narrow subsidiary scape which carries a well-defined socket. The ducts run near the lateral margins of the scape, and the openings are on the mesal sides of the posterior arms of the scape; grooves run along the dorsal side of the scape from the small dorsal plate to the openings (Fig. 77). The internal duct system is simple (Fig. 78), with the fertilisation ducts relatively stout, opening into the uterus anterior to the spermathecae.

The male palp has been well described and illustrated by van Helsdingen (1973); the cymbium is drawn out posteriorly into a long horn, and the palpal organs are fairly similar to those of *Centromerus*.

The type species is haplotracheate.

The genus at present comprises only *A. cornupalpis*; *Microneta tennapax* Barrows (van Helsdingen, 1973) may also belong in *Atopogyna*, but it has not been possible so far to examine this species.

The species *Centromerus persolutus* (O. P.-Camb.), *C. latidens* (Emerton) and *C. longibulbus* (Emerton), described with *cornupalpis* by van Helsdingen (1973), appear to be true *Centromerus* species.

Note on the genus *Erigone* Audouin

The genus *Erigone*, as currently defined, is a large one, with species distributed throughout the world. The type species of the genus is *Erigone vagans* Audouin. Examination of the epigynal form of *E. vagans* and other *Erigone* species, however, offers strong evidence that the large majority of the species currently assigned to *Erigone* are not congeneric with the type species.

In the majority of the "*Erigone*" species the epigyne is in the form of a scape, which carries the ducts leading to the genital openings, located on the dorsal side near the distal end (Figs. 118-120). The scape is hollowed out on the dorsal side, to give a distinct cavity between the ventral and dorsal plates (Figs. 119, 120).

The epigyne of *E. vagans* is quite different. The detail of the epigyne is concealed behind a translucent gummy mass which is trapped in the long hairs on the ventral surface; this deposit can be removed with a fine needle and forceps after soaking the specimen for a few minutes in cold 10% caustic soda or potash, and the epigynal form is then

disclosed. The genital openings are on the ventral plate inside an atrium which lies behind a short, broad extension of the ventral plate (Fig. 121). This epigyne, both in its form and in the deposit which conceals the atrium, shows some resemblance, externally, to those of the genus *Satilatlas* (Millidge, 1981b). Internally the duct arrangement is relatively simple (Fig. 123).

This incongruence of the majority of the "*Erigone*" species with *E. vagans* is confirmed by the structure of the palpal organs. The embolic division of *E. vagans* is distinctly different from those of the majority of the "*Erigone*" species (Wiehle, 1960; Merrett, 1963: figs. 58, 59). The suprategular apophysis of *E. vagans* is also somewhat different from those of most "*Erigone*" species.

The males of all the species currently placed in *Erigone* do share a few characters, in particular the presence on the palps of a ventral spur on the patella and of pointed tubercles or teeth ventrally on the femur, and the presence on the anterior face of the chelicerae of rows of pointed tubercles. The significance of these shared characters is diminished, however, by the fact that they are also present in the genus *Eperigone*, in which the epigynal form and the embolic division of the male palp are quite distinct from those of *Erigone*.

It is unfortunate that the type species of *Erigone* now appears not to be congeneric with the vast majority of the species currently assigned to the genus. Many of these species are common, and appear frequently in faunal lists, etc. In order to preserve the maximum nomenclatural stability, therefore, an application is to be made to the International Commission on Zoological Nomenclature to suppress *E. vagans* as the type of *Erigone*, and to designate instead the species *Linyphia longipalpis* Sundevall. If the proposal is agreed by the Commission, a new genus will be created for *E. vagans* and the few related species.

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