# Further remarks on the taxonomy and relationships of the Linyphiidae, based on the epigynal duct conformations and other characters (Araneae)

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## Summary

The wide variety of epigynal duct conformations in the Linyphiidae have been studied, with particular reference to the double helical form and related forms. The duct conformations, coupled with other characters, indicate that the subfamily Erigoninae is closely related to the Mynogleninae, probably as a sister group, and that the Linyphiinae and the Lepthyphantinae/Micronetinae are probably most closely related to the Dubiaraneinae (new subfamily), being possibly directly derived from that subfamily. There are still a number of genera which do not at present fit easily into any of the six main subfamilies, and these remaining taxonomic problems are briefly discussed. The double helical duct conformations, coupled with certain other characters, indicate that the Linyphiinae probably share a common parentage with families of the Amaurobioidea/Dictynoidea; the closest relationship would appear to be with the cribellate families Titanoecidae and Dictynidae.

## Introduction

This paper is an extension of the work reported previously on the taxonomy of the Linyphiidae (Millidge, 1984a), based to a large extent on additional information on the internal epigynal characters of the family. The aim has been to clarify some aspects of linyphiid taxonomy, and to draw attention to the problems which are still unresolved.

## Methods and definitions

The methods are those previously employed (Millidge, 1984a); staining of the epigynum (e.g. with chlorazol black) is often essential to obtain a true picture of the epigynal structure, since some parts of the duct system may be so lightly sclerotised as to be virtually invisible without staining.

All figures of the epigyna are of the left-hand spermatheca as viewed from the dorsal side. The direction of rotation (clockwise or anticlockwise) of the sperm duct refers to the pathway of the duct, from this left-hand spermatheca, as it runs in the direction: spermatheca to genital opening (see Discussion). The direction of rotation of the duct of the right-hand spermatheca is the reverse of that of the left-hand spermatheca.

## Internal epigynal characters

### *Mynogleninae*

Several different conformations of the seminal duct are present in the Mynogleninae, a subfamily characterised by the presence of clypeal sulci in both sexes (Blest, 1979). In many species the duct pathway is in the form of a double helix located mesally to the spermatheca; there are three different versions of this. One form has the double helix inside a capsule (Fig. 1), another form has the helix free (Fig. 2), and a third has the duct running along the margins of a lightly sclerotised lamina, which is coiled into a helix (Fig. 3). The double helix has its longitudinal axis more or less parallel to the plane of the epigynum (cf. the Dubiaraneinae, below). The duct runs anteriorly, clockwise through one helix of the double helix, and at the distal end it reverses direction to run posteriorly through the second helix, still in a clockwise direction (see Discussion).

Another duct form, present in many mynoglenine species, is shown in Fig. 4; the duct runs from the spermatheca into a lightly sclerotised laminar structure, where it runs anteriorly up one side and posteriorly down the other, to the opening. This form is in effect an uncoiled version of the double helix shown in Fig. 3. Several species have the laminar structure bent over at the anterior end (Fig. 5); this bending may perhaps be an intermediate form between the helical lamina (Fig. 3) and the more or less straight lamina (Fig. 4).

There are a small number of species of the Mynogleninae which have neither the laminar nor the helical duct form. In these cases the duct forms a simple loop (Fig. 6), which probably is the result of simplification, with elimination of the lamina and shortening of the duct.

The spermathecae in the Mynogleninae are globular.

### *Dubiaraneinae, new subfamily*

The genera *Dubiaranea* Mello-Leitão and *Notiohyphantes* Millidge are now considered to constitute a new subfamily of the Linyphiidae. *Dubiaranea* contains a large number of species (Millidge, 1985, 1991) which have the seminal duct of the epigynum running along the margins of a lamina, as in the Mynogleninae; in the majority of the species, the lamina is coiled into a short, almost planar helix, the axis of which is more or less perpendicular to the plane of the epigynum (Figs. 7, 8); i.e. the axis is turned through 90° as compared with the helix of the Mynogleninae. The duct follows an almost flat double helical path; when observed from the dorsal side (as in Figs. 7, 8) the coiling from the spermatheca to the end of the lamina is anticlockwise, but reverses there to become clockwise as it runs back to the opening. There is at least one species in which the laminar structure is simple, bent over distally, but not coiled (Fig. 9); the lamina tends to be slightly folded along its longitudinal axis.

In the genus *Notiohyphantes*, which has very similar palps to those of *Dubiaranea*, the seminal duct is in the form of a long loop, and the external epigynal form also differs from those of *Dubiaranea*; the duct form bears some resemblance to those of the Lepthyphantinae.

The majority of the Dubiaraneinae have U-shaped spermathecae. In *Dubiaranea insulanus* Millidge (Fig. 9), one arm of the U is almost globular while the other is small and tube-like (hidden behind spermatheca in Fig. 9); this is similar to the spermathecal form of some members of the Linyphiinae.

### *Other haplotracheate genera with double helical seminal ducts*

*Labulla thoracica* (Wider) has the duct in the form of two long double helices (Fig. 10). The smaller helix is close to the spermatheca; the larger helix is mesal to the spermatheca, as in the Mynogleninae. The directions of rotation in the larger helix are the same as in the Mynogleninae, while those in the smaller helix are the reverse. The spermatheca is basically U-shaped, though slightly more complex.

The New Zealand genus *Diploplecta* (Millidge, 1988a) has more or less U-shaped spermathecae, and the duct runs through two encapsulated double helices.

The genera *Emenista* Simon and *Labullinyphia* Van Helsdingen, from south-east Asia (Van Helsdingen, 1985), appear to have the duct in the form of a double helix (Figs. 11, 12), set mesal to the spermatheca, but a shortage of specimens has prevented a detailed examination of these species. The spermathecae are globular with a tubular subsidiary chamber, as in some members of the Linyphiinae. The females do not have clypeal sulci, and no males are known.

A few of the haplotracheate genera of small spiders of erigonine appearance which are found in South America (Millidge, 1985, 1991) have the duct as an encapsulated double helix.

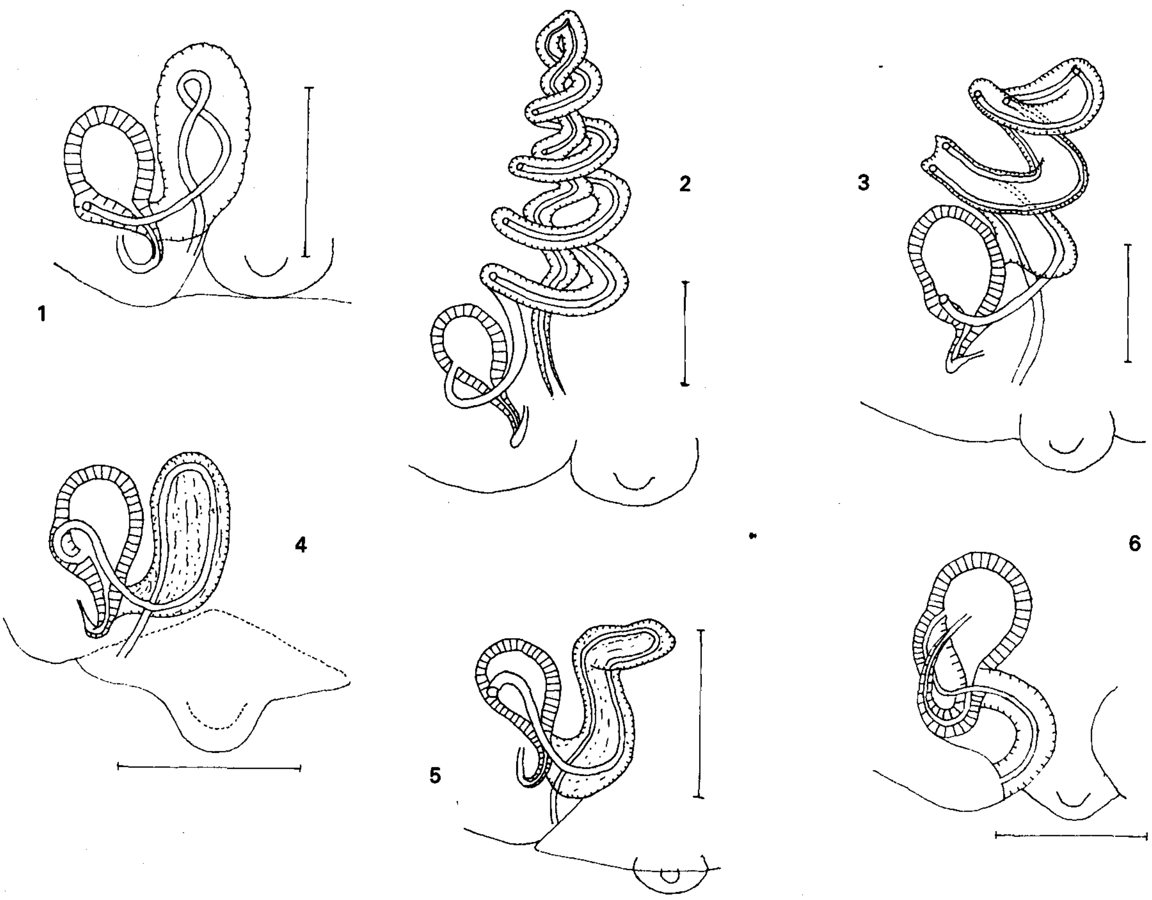
The Australian genus *Australolinyphia* Wunderlich has the duct in the form of a double helix (Fig. 13), but this is situated anterior to the spermatheca rather than mesal to it, and the directions of rotation in the helices are the reverse of those in the Mynogleninae. The genus *Novafrontina* Millidge, from Central America and northern South America, has the duct of basically the same form (Fig. 14) as in *Australolinyphia*. Both of these genera have globular spermathecae.

### *Erigoninae*

Numerous members of the desmitracheate subfamily Erigoninae have a seminal duct conformation which is basically similar to the laminar form present in the Mynogleninae. The lamina is less planar than in the Mynogleninae, being somewhat curved or folded along the vertical axis, and is most often bent over to some extent distally. This form is present, for example, in some members of the following genera: *Walckenaeria* Bl. (Fig. 15), *Panamomops* Simon (Fig. 16), *Pelecopsis* Simon (Fig. 17), *Entelecara* Simon (Fig. 18), *Drepanotylus* Holm (Fig. 19), *Typhochrestus* Simon (Fig. 20).

In several erigonine species the lamina is coiled into a helix, to give the duct the form of a double helix, exactly as in the Mynogleninae: for example, *Walckenaeria obtusa* Bl. (Fig. 21 cf. Fig. 3), *Trematocephalus* Dahl (Fig. 22), *Nematogmus* Simon (Fig. 23). *Cineta* Simon (Fig. 24) has an encapsulated double helix. The directions of rotation in these helices are the same as in the Mynogleninae.

Many erigonines have lost the lamina, and have the duct in the form of a loop, which in its simplest form is basically similar to that present in a few mynoglenines; for example, *Walckenaeria atrotibialis* (O. P.-Cambr.)



Figs. 1–6: Epigyna, internal. **1** *Protoerigone otagoa* Blest; **2** *Mynoglenes mundenia* (Urquhart); **3** *Mynoglenes diloris* (Urquhart); **4** *Pseudafroneta pallida* Blest; **5** *Pseudafroneta incerta* (Bryant); **6** *Novafroneta vulgaris* Blest. Scale lines = 0.1 mm.

(Fig. 25), *Pelecopsis nemoralis* (Bl.) (Fig. 26), cf. *Novafroneta vulgaris* Blest (Fig. 6). The loop form is probably derived by loss of the lamina, which in some species (e.g. *Entelecara*, Fig. 18) appears to be weak.

The Erigoninae exhibit a considerable degree of diversification in the genitalia of the female, more so than in any other subfamily of the Linyphiidae. In many species the laminar or loop forms have acquired notable embellishments. For example: (i) the duct may form a double helix within the wall of the spermatheca before entering the lamina (Fig. 27), an arrangement rather similar to that in *Labulla* (Fig. 10); (ii) the duct may form a coil posterior to the spermatheca before it becomes a loop, as in some species of *Spirembolus* (Fig. 28); (iii) a short double helix may be displaced from the mesal to the ectal side of the spermatheca, as in *Lessertia* F. P. Smith (Fig. 29), and in a few species of *Spirembolus* (Millidge, 1980).

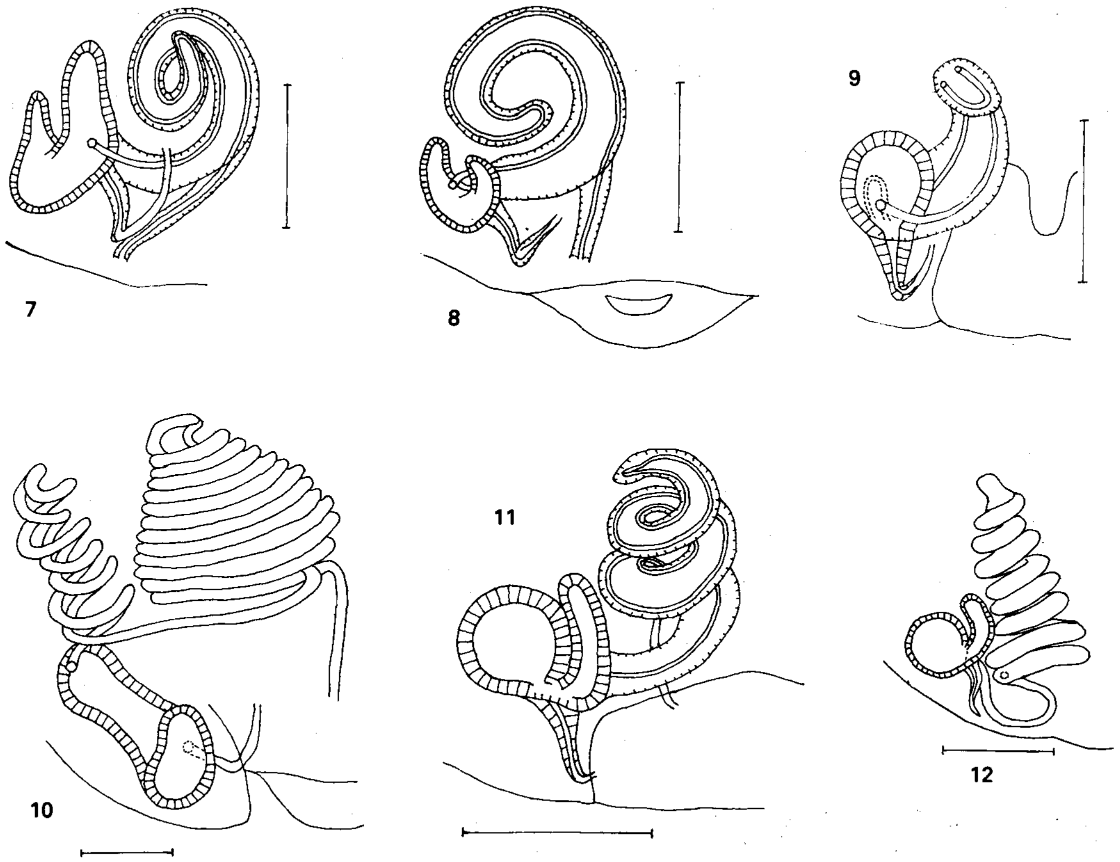
As mentioned above, there are several erigonines which have the double helical duct of the mynoglenine form; there are a few cases, however, in which the double helix is basically of the same form as in the Dubiaraneinae. *Gnathonarium* Karsch (Fig. 30), *Cnephalocotes* Simon (Fig. 31) and *Tmeticus* Menge (Fig. 32) are of this form; the directions of rotation in the double helix are the same as in *Dubiaranea*.

In the genus *Erigone* Audouin, which has the external epigynum in the form of a scape, the duct loop system has vanished, and the duct makes one turn around the base of the spermatheca before running posteriorly through the scape (Fig. 33); the single turn of the duct is anticlockwise. The close similarities of the palp, and of other characters, of *Erigone* with those of *Prinerigone* Millidge indicate that these two genera must be closely related; consequently it seems probable that the loss of the loop (which is present in a modified form in *Prinerigone* (Fig. 34), coupled with the coiling of the duct posterior to the spermatheca, is one duct route transformation which can take place readily in the Linyphiidae. A number of genera, e.g. *Eperigone* Crosby & Bishop and some South American genera (Millidge, 1991), have the same or a similar duct conformation to that of *Erigone*.

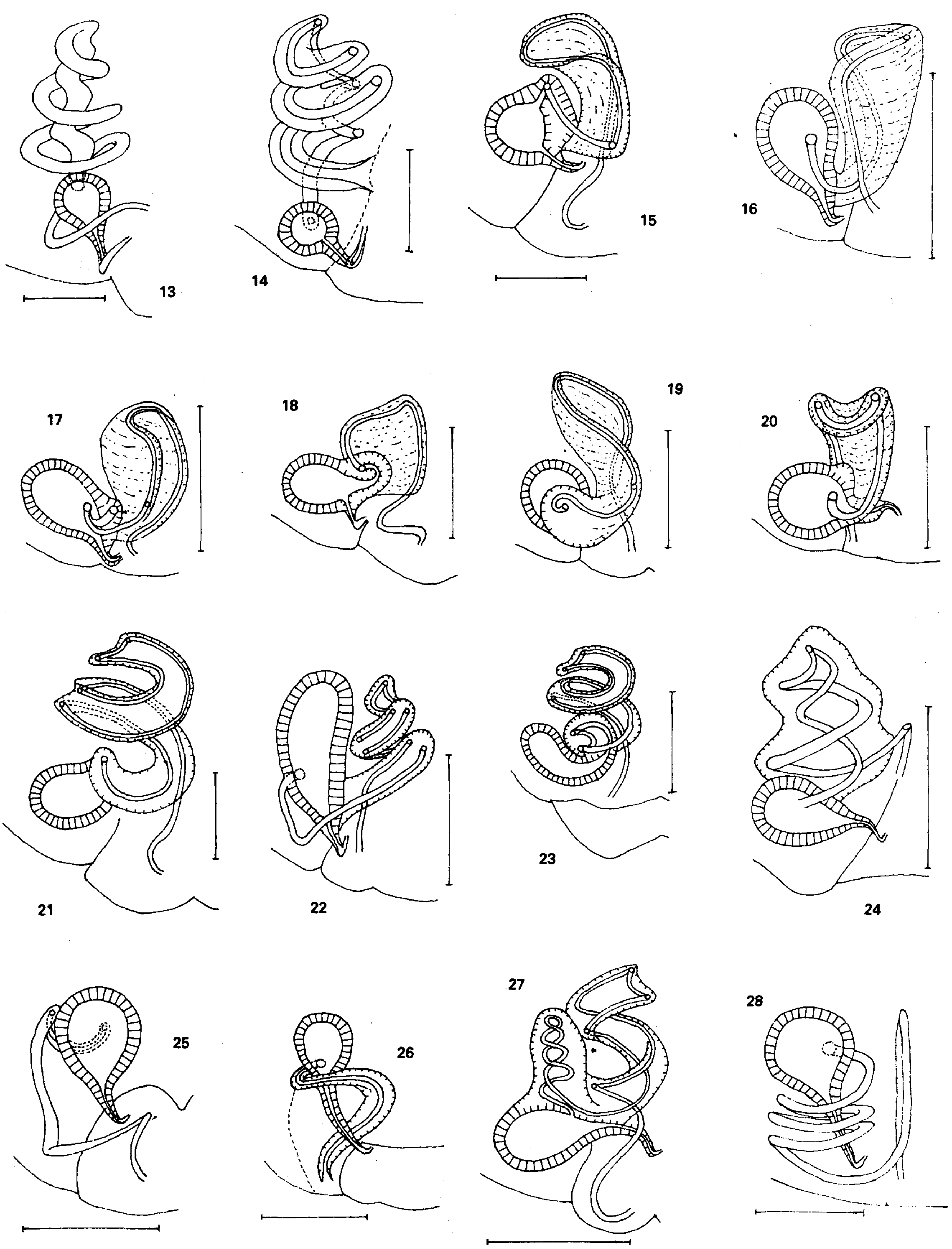
There are a number of erigonine genera with epigynal scapes in North America (Millidge, 1984b) and in South America (Millidge, 1985, 1991); some of these have the duct conformation very similar to those of *Erigone*, while others have a more complex conformation.

A similar duct form to that of *Erigone*, in which the duct makes a partial turn around the base of the spermatheca, is found in some other erigonine genera, for example *Erigonidium* F. P. Smith (Fig. 35), *Gongylidium* Menge (Fig. 36), *Pelecopsis mengei* Simon (Fig. 37), *Gongylidiellum vivum* (O. P.-Cambr.) (Fig. 38). This simplification of the duct conformation has probably taken place on a number of occasions during the evolution of the family.

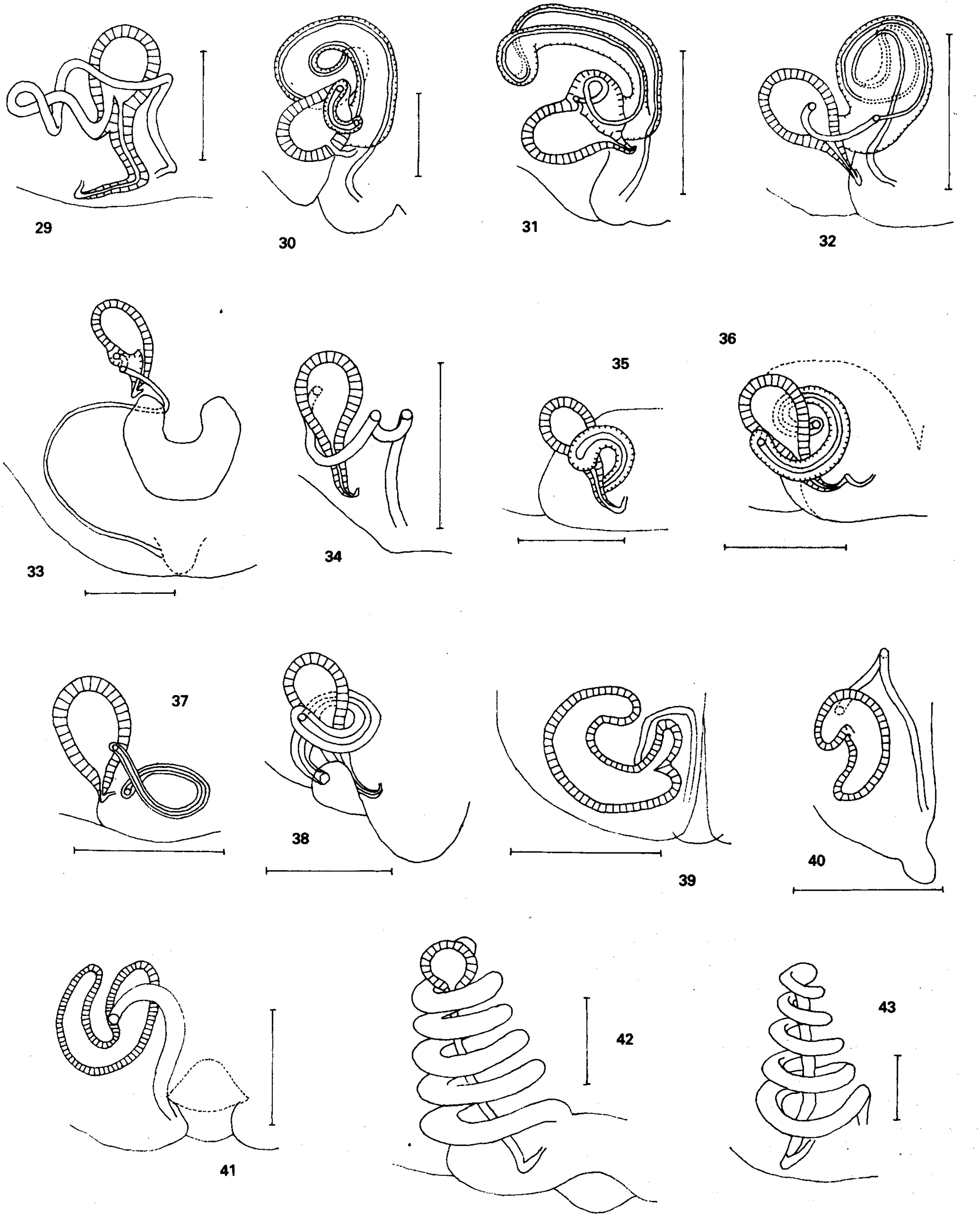
The majority of the erigonine genera have the spermathecae essentially globular in shape. There are several genera, however, in which the spermathecae are distinctly U-shaped; for example *Diplocephalus* Bertkau (Fig. 39), *Savignia* Bl. (Fig. 40), *Hypomma* Dahl (Fig. 41).



Figs. 7–12: Epigyna, internal. **7** *Dubiaranea aysenensis* (Tullgren); **8** *Dubiaranea caledonica* (Millidge); **9** *Dubiaranea insulanus* Millidge; **10** *Labulla thoracica* (Wider); **11** *Emenista bisinuosa* Simon; **12** *Labullinyphia tersa* (Simon). Scale lines = 0.1 mm.



Figs. 13–28: Epigyna, internal. **13** *Australolinyphia remota* Wunderlich; **14** *Novafrontina uncata* (F. O. P.-Cambr.); **15** *Walckenaeria acuminata* Bl.; **16** *Panamomops sulcifrons* (Wider); **17** *Pelecopsis radicicola* (L. Koch); **18** *Entelecara congenera* (O. P.-Cambr.); **19** *Drepanotylus uncatus* (O. P.-Cambr.); **20** *Typhochrestus digitatus* (O. P.-Cambr.); **21** *Walckenaeria obtusa* Bl.; **22** *Trematocephalus cristatus* (Wider); **23** *Nematogmus sanguinolentus* (Walck.); **24** *Cineta gradata* (Simon); **25** *Walckenaeria atrotibialis* (O. P.-Cambr.); **26** *Pelecopsis nemoralis* (Bl.); **27** *Walckenaeria spiralis* (Emerton); **28** *Spirembolus erratus* Millidge. Scale lines = 0.1 mm.



Figs. 29–43: Epigyna, internal. **29** *Lessertia dentichelis* (Simon); **30** *Gnathonarium dentatum* (Wider); **31** *Cnephalocotes obscurus* (Bl.); **32** *Tmeticus affinis* (Bl.); **33** *Erigone arctica* White; **34** *Prinerigone vagans* (Aud.); **35** *Erigonidium graminicola* (Simon); **36** *Gongylidium rufipes* (Sund.); **37** *Pelecopsis mengei* (Simon); **38** *Gongylidiellum vivum* (O. P.-Cambr.); **39** *Diplocephalus permixtus* (O. P.-Cambr.); **40** *Savignia frontata* Bl.; **41** *Hypomma cornutum* (Bl.); **42** *Microlinyphia pusilla* (Sund.); **43** *"Neriene" limbata* F. O. P.-Cambr. Scale lines = 0.1 mm.

### *Linyphiinae*

This haplotracheate subfamily was previously defined (Millidge, 1984a) by reference to the external epigynal form. It is now thought that this definition is too restrictive and should be broadened to comprise genera in which the seminal duct of the epigynum is coiled posterior to the spermatheca as in *Linyphia*; this will permit the inclusion in the subfamily of a number of genera/species which have the linyphiine type of palpal organ, but with an external epigynal form which does not meet the earlier definition. Examples of such taxa are *Microlinyphia* Gerhardt (Fig. 42), *Frontinellina* Van Helsdingen, *Cryptolinyphia* Millidge (1991), *Oilinyphia* Saito and several new genera from south-east Asia (Millidge & Russell-Smith, 1992). The species *"Linyphia" rita* Gertsch, *"L." catalina* Gertsch, *"Neriene" limbata* F. O. P.-Cambr. (Fig. 43) (all of which require one or more new genera) from Central and North America, which were previously excluded from the Linyphiinae, will now be included.

In some members of the Linyphiinae the seminal duct is a simple helix, with the direction of rotation anticlockwise. The fertilisation duct runs posteriorly from the spermatheca either more or less along the longitudinal axis of the helix (Fig. 42), or as a helix in parallel with the sperm duct (e.g. in *Linyphia*); the latter arrangement can be regarded as a more complex version of the former. As in *Erigone*, this duct structure could have been derived from a simple loop form; such a loop form is present in the *Kaestneria* group of genera which are included in the subfamily on the basis of their external epigynal structure (Millidge, 1984a).

Some of the genera in this subfamily have the spermathecae more or less globular, while in others (particularly the *Kaestneria* group and *Porrhomma* Simon, for example) the spermathecae are globular with a small, tubular subsidiary chamber. The latter form is similar to that in *Dubiaranea insulanus* (Fig. 9), and appears to be intermediate between the U-shaped and the globular spermathecae.

*Maro* O. P.-Cambr. can still be placed, provisionally, in the Linyphiinae, but *Wiehlea* Braun, *Labulla* and *Australolinyphia* must be excluded. *Stemonyphantes* Menge, which has the coiled duct conformation of the Linyphiinae, but encapsulated, is provisionally regarded as a separate development from the Linyphiinae.

### *Micronetinae and Lepthyphantinae*

It is proposed that the subfamily Micronetinae should be limited to the genera *Microneta* Menge, *Meioneta* Hull, *Agyneta* Hull, *Syedrula* Simon, *Tennesseellum* Petrunk. and probably *Theonina* Simon. These genera, apart from *Microneta* itself, differ from the other genera previously placed in the Micronetinae by the presence of a complex tracheal system (Millidge, 1986); they are grouped with *Microneta*, which is haplotracheate, because of the close similarity of the male palps and the epigyna. Most species in this subfamily have U-shaped spermathecae, but in *Microneta viaria* (Bl.) and a few *Meioneta* species they are globular with a tiny, tube-like subsidiary chamber. The seminal duct is in the form of a long loop.

The remaining members of the Micronetinae, as previously defined, now make up the haplotracheate subfamily Lepthyphantinae; most members of this subfamily have U-shaped spermathecae, and the seminal duct is a long loop as in the Micronetinae.

### *Miscellaneous genera*

Most of the genera previously placed in the *Stemonyphantes* group do not appear to fit readily into any of the major subfamilies described above, though it is possible that a few may in fact belong in the Mynogleninae or the Dubiaraneinae (see Discussion).

The genera previously placed (Millidge, 1984a) in the haplotracheate Drapetiscinae on the basis of the epigynal scape are now considered to be definitely heterogeneous, and it is no longer justifiable to group them in a single subfamily. They can be split into several groups, of uncertain relationship, as follows.

*Drapetisca* Menge and *Fageiella* Kratochvil have the spermathecae U-shaped, and the embolic division of the male palp has several sclerites as in the Lepthyphantinae. In *Arcuphantes* Chamberlin & Ivie and in *Doenitzius* Oi the scape tends to curl over at the extremity, perhaps moving towards the lepthyphantine form of scape, and the embolic division has several sclerites. It is possible that these four genera may represent side branches of the Lepthyphantinae.

*Neomaso* Forster, *Asthenargus* Simon, *Jacksonella* Millidge, *Aphileta* Hull and possibly *Saaristoa* Millidge have the epigynal scape and simple duct conformation very similar to those of *Erigone*, and the embolic division and suprategular apophysis of the male palp also bear some resemblance to those of *Erigone* (see Discussion).

*Allomengea* Strand and *Wubana* Chamberlin are fairly close in both epigynal and palpal forms (Van Helsdingen, 1974), and must be grouped together; they appear to be fairly primitive forms, but their relationships are unclear.

The genera *Helophora* Menge, *Sintula* Simon and *Typhlonyphia* Kratochvil are very different from one another, and their relationships are obscure. The South American genus *Laminacauda* Millidge has a distinct epigynal scape, and in some species at least has the seminal duct in the form of a short encapsulated double helix; its relationships are at present unknown.

## Discussion and conclusions

The work reported in this paper shows that many members of the haplotracheate subfamilies Mynogleninae and Dubiaraneinae have the seminal duct of the epigynum in the form of a double helix located on the mesal side of the spermatheca.

Two geometric forms are possible for a double helix. The first of these is characterised by a reversal in the direction of rotation as one helix joins the other; i.e. if the double helix is vertical, with the inlet and outlet both at the base, then the direction of rotation of the rising helix, *observed from above*, reverses at the top where it joins the descending helix. In the present paper, however, "direction of rotation" refers to the rotation of the duct on its passage in the direction spermatheca to opening; that is, upwards through the rising helix and downwards through the descending helix. Consequently the direction of rotation in the rising helix refers to the direction observed from *below* (which is the opposite of that observed from above), while the direction of rotation in the descending helix refers to that observed from *above*. Hence, in this first form of double helix the direction of rotation of the duct, running from inlet to outlet, is the same in both helices.

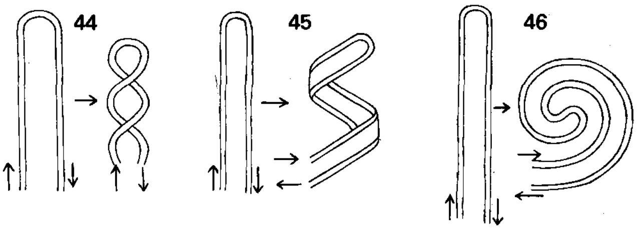
In the second form of double helix there is no reversal of direction of rotation, observed from above, as the rising helix starts to run downwards as the descending helix; as defined in this paper, however, the direction of rotation of the duct reverses as it moves from the rising helix to the descending helix. This second form suffers from the constraint that, in order that the two helices do not clash, one must be smaller in diameter than the other.

It is the first form of double helix which is present in the Linyphiidae, and in some other families discussed later. The second form is not present in any of the families examined.

Double helices of the first form can be derived, as a geometric entity, only from a loop, either by twisting the loop along its longitudinal axis to form a screw (Fig. 44), or by coiling the loop into a helix, as shown in either Fig. 45 or 46; the loop can be free, or the two arms can be joined by a lamina. The double helix shown in Fig. 44 corresponds with Fig. 2, while that in Fig. 45 corresponds with that in Fig. 3; the double helix in *Dubiaranea* corresponds with that in Fig. 46. In the Linyphiidae, it appears probable that the most primitive form of the double helix is the encapsulated form (e.g. Figs. 1, 24), which is retained in very few current linyphiids. This paired spermatheca + capsule form may possibly have been derived from a paired receptacula form present in haplogyne ancestors.

Although the actual shape of this double helix is different in the Mynogleninae and the Dubiaraneinae, the frequent presence of such an unusual character in both subfamilies suggests that these gondwanan, probably quite primitive, groups are descended from a fairly close common ancestor, which might be relatively close to the stem species of the family. The subfamilies are probably not sister groups, however, since there are a number of character differences:

(i) the Mynogleninae have well-defined clypeal sulci/glands (Blest & Taylor, 1977; Blest, 1979), which are absent in the Dubiaraneinae;



Figs. 44–46: Formation of double helical ducts — schematic. **44** By twisting loop along vertical axis; **45** By winding loop into helix, vertically; **46** By winding loop into helix horizontally.

(ii) the spermathecae in the Mynogleninae are more or less globular, whereas in the Dubiaraneinae they are U-shaped;

(iii) the posterior median eyes in the Dubiaraneinae are on black tubercles, which is not the case in the Mynogleninae;

(iv) the forms of the male palps are different: in the Mynogleninae the embolic division is small and simple in the vast majority of species, and the suprategular apophysis is a simple extension of the suprategulum. In the Dubiaraneinae the embolic division is larger and more complex in shape, and there is no true suprategular apophysis; instead there is a large sclerotised apophysis arising from the tegulum below the suprategulum (a "median apophysis" rather than a "suprategular apophysis"). This apophysis, absent in almost all other linyphiids, is probably a primitive character of the family.

Not all the mynoglenine species have the double helical duct; many have a simpler form in which the duct passes around the margins of a more or less flat lamina, and in a few species the lamina has gone and the duct forms a short, simple loop.

The Erigoninae resemble the Mynogleninae by the presence, among the species, of the double helical duct formed from a coiled lamina (Fig. 21 cf. Fig. 3), of the encapsulated double helical duct, and of the laminar and looped duct forms. Some members of the Erigoninae, however, have the double helical duct of the form present in the Dubiaraneinae. The Erigoninae are much less conservative than the Mynogleninae and the Dubiaraneinae in both the external epigynal forms and the duct conformations; in the Erigoninae, the latter exhibit wide variations and have acquired many embellishments not found in the Mynogleninae and Dubiaraneinae.

While most genera of the Erigoninae have more or less globular spermathecae, as in the Mynogleninae, there are several genera in which the spermathecae are U-shaped, as in the Dubiaraneinae; in at least one of these genera (*Hypomma*) the male has cephalic sulci. The U-shaped spermatheca, which appears to be almost universal in the Dubiaraneinae but is absent in a high proportion of other linyphiids, is thought to be the more primitive form; the globular form with the small tubular subsidiary chamber is thought to be an intermediate between the U-shaped and the globular.

It has been suggested (Blest & Pomeroy, 1978; Blest, 1979) that the Mynogleninae and the Erigoninae may be quite closely related, on the basis that (i) the mating behaviour of the Mynogleninae resembles that of the Erigoninae rather than that of the Linyphiinae (*s. lat.*), and (ii) that the post-ocular sulci present in many erigonine males probably represent a parallel development to the subocular (clypeal) sulci of the Mynogleninae. The latter hypothesis is strengthened by the recent discovery of clypeal sulci of the mynoglenine type in males of the genus *Blestia* (Millidge, 1993b), which in other respects appears to be a typical erigonine.

The work reported in this paper, coupled with Blest's work, shows that the Erigoninae possess characters which are present in the Mynogleninae (sub-ocular/post-ocular sulci, epigynal duct conformation, globular spermathecae, mating behaviour) together with characters present in the Dubiaraneinae (U-shaped spermathecae, epigynal duct conformation). This suggests that the three subfamilies have descended from a common parent, and that the Erigoninae might be a sister group of the Mynogleninae plus the Dubiaraneinae. The relationship of the Erigoninae with the Mynogleninae, however, appears to be much closer than with the Dubiaraneinae, and it seems more probable that the Mynogleninae and the Erigoninae have a close common parent (and are probably sister groups), and that this parent species and the Dubiaraneinae have themselves a close common parent, which was perhaps close to the stem species of the family. Between this stem species and the Mynogleninae, Erigoninae and Dubiaraneinae branches, however, there would probably have been a significant evolutionary period; this primeval stage in the family history has probably left few if any traces amongst the current fauna.

The Erigoninae have a complex tracheal system, extending into the prosoma, while the Mynogleninae and the Dubiaraneinae have a simple tracheal system restricted to the abdomen. If the Erigoninae and the Mynogleninae have a common parent, this parent must have had a respiratory system from which both the simple and the complex tracheal forms were derivable (see later).

The subfamily Linyphiinae has been redefined in this paper, to allow the inclusion of a number of species/genera previously excluded. The spermathecae in this subfamily are globular, or globular with a small tubular side chamber. In a number of the genera (*Linyphia* and allied genera) the seminal duct runs posteriorly from the spermatheca in an anticlockwise helix, which is quite distinct from the double helical system of the Mynogleninae and Dubiaraneinae. This single helical system is by no means unique to the Linyphiinae: as mentioned earlier, a similar (though clockwise) helix is present in some members of the erigonine genus *Spirembolus* (Millidge, 1980) and less clearly in *Scotinotylus* (Millidge, 1981).

Several south-east Asian genera (Millidge & Russell-Smith, 1992) have the linyphiine single helical duct conformation, but have male palps very similar to those of the Dubiaraneinae, both as regards the form and position of the tegular apophysis and the form of the embolic division, though the latter has a small additional sclerite which is absent in the Dubiaraneinae. The close resemblance of the palpal form in these Asian genera to those of *Dubiaranea* suggests that the Linyphiinae and the Dubiaraneinae are quite closely related; it suggests, indeed, that the Linyphiinae may have been directly derived from the Dubiaraneinae. This suggestion of a close relationship is supported by the location (in some linyphiine genera) of the posterior median eyes on shallow black tubercles, and by the frequent presence in the Linyphiinae of the probably intermediate spermathecal form (globular, with tubular side chamber), which is present in at least one species of *Dubiaranea* but apparently absent in the Mynogleninae.

As mentioned earlier, the species of the Dubiaraneinae have a large tegular apophysis, which is almost certainly a primitive character. It appears possible that, in the course of the evolution of some branches related to, or derived from, the Dubiaraneinae, this tegular apophysis may have migrated towards the anterior end of the suprategulum, and there amalgamated with an extension of the suprategulum to give a suprategular apophysis with a posterioventral extension of the kind present in the Linyphiinae (e.g. Fig. 47). The presence of this modification of the suprategular apophysis may in fact be another pointer to a closer relationship of the Linyphiinae with the Dubiaraneinae than with the Mynogleninae.

The development of an additional sclerite on the embolic division of the Asian genera mentioned above can be taken as a probable indication that the multiplication of sclerites on the embolic division in many linyphiids is a character derived from the Dubiaraneinae branch of the family, since the Mynogleninae and the Erigoninae do not appear to have developed additional sclerites to any noticeable degree.

The restriction of the subfamily Micronetinae, because of the complex tracheal form of the genera *Meioneta*, etc., was dealt with earlier. As in the case of the Mynogleninae/Erigoninae, the parent species of the Micronetinae, as now defined, must have had a respiratory system from which both the simple and the complex tracheal systems were derivable (see later). Most of the species of the Micronetinae and the Lepthyphantinae (which comprises most of the genera previously placed in Micronetinae) have the spermathecae U- or V-shaped, and the duct forms a long loop.

The embolic division of the male palp in the Lepthyphantinae/Micronetinae has several sclerites, and the suprategular apophysis (e.g. Fig. 48) often has a posterioventral extension as in the Linyphiinae. Both of these characters, together with the U-shaped spermathecae, can be taken as pointers to a closer relationship of these two subfamilies to the Dubiaraneinae than to the Mynogleninae.

The haplotracheate genera previously grouped together in the Drapetiscinae appear to be too heterogeneous to justify their retention in a single subfamily, and in most cases their relationships are still unclear; some may eventually be found to fall into the Lepthyphantinae.

There are a number of haplotracheate genera of small spiders of erigonine appearance which cannot at present be fitted easily by character congruences into any of the major subfamilies dealt with above; a few of these genera are found in the northern hemisphere, but a greater number are present in South America. Some of these taxa have U-shaped spermathecae, some have globular; some have the seminal duct as an encapsulated double helix, some have the duct as a simple loop. The palps vary widely in form. These genera certainly appear to be closer to the Mynogleninae/Erigoninae than to the Dubiaraneinae, and can be regarded, provisionally, as an offshoot from the Mynogleninae/Erigoninae branch, though of uncertain relationship.

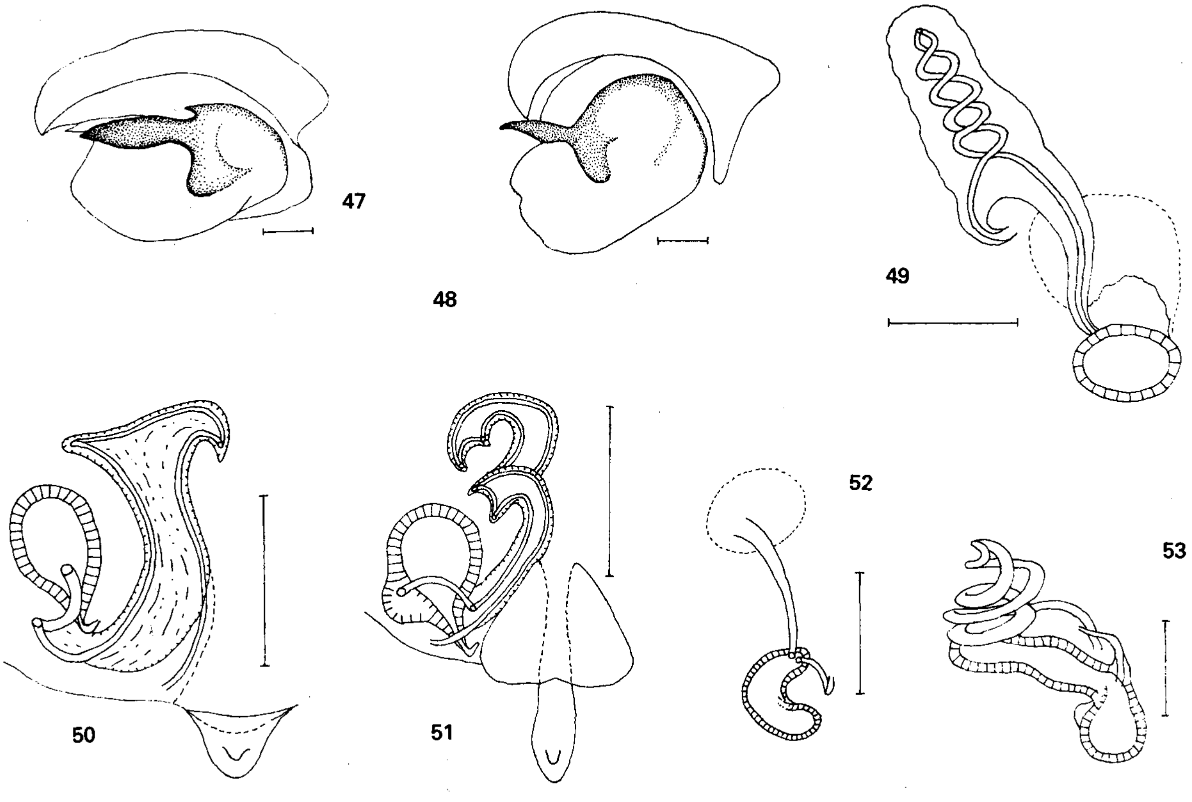
The Erigoninae comprise species with and without cephalic sulci (in the male), and this suggests the possibility that the Mynogleninae may also be found to contain a few species which lack the clypeal sulci. A *possible* candidate for inclusion in the Mynogleninae would be the North American genus *Linyphantes* Chamberlin; this genus is haplotracheate, and the seminal duct of the female is laminar or in the form of a short double helix (Figs 50, 51). Among the haplotracheate subfamilies, these duct characters are found only in the Mynogleninae. The palpal structure of *Linyphantes* is more complex than in most mynoglenines, but might not rule out its inclusion in the Mynogleninae. A few other genera in the *Stemonyphantes* and *Drapetisca* groups may eventually be found to fit into the Mynogleninae or the Dubiaraneinae branches of the family.

To sum up so far, the data currently available indicate that the family comprises six main branches (Mynogleninae, Dubiaraneinae, Linyphiinae, Micronetinae, Lepthyphantinae and Erigoninae), plus a number of genera which are at present unassignable. Of the main branches, the Erigoninae appear to be closely related to the Mynogleninae, probably as a sister group. The Linyphiinae, the Lepthyphantinae and Micronetinae seem to be more closely related to the Dubiaraneinae than to the Mynogleninae; the Linyphiinae have quite probably arisen as a direct branch from the Dubiaraneinae, and this may also prove to be the case with the Lepthyphantinae and the Micronetinae.

The Mynogleninae have retained the following characters thought to be relatively primitive, though not necessarily plesiomorphic for the family: the double helical duct systems (including the encapsulated form, considered to be the most primitive) in the female; the attachment of the embolic division to the tegulum by a broad junction rather than a narrow neck in the male; the clypeal sulci in both sexes. The Dubiaraneinae have retained the following probably primitive characters: the double helical duct system and the U-shaped spermatheca in the female; the distinctive tegular apophysis in the male. The Linyphiinae, Lepthyphantinae and Micronetinae have retained only the U-shaped spermatheca in the female, and perhaps the remnants of the migrated tegular apophysis in the male.

The Erigoninae have retained, distributed amongst its numerous species, more relatively primitive characters than any other subfamily, namely: the double helical duct forms and the laminar duct form present in the Mynogleninae; the double helical duct form present in the Dubiaraneinae; the U-shaped spermatheca; the cephalic sulci in the male, including clypeal sulci in one instance; and possibly (see later) the absence of a paracymbium on the male palp. It is also possible that the complex tracheal form present in the Erigoninae (and in *Meioneta* and related genera) is more primitive than the simple form present in many linyphiids. The possibility that the two tracheal forms are interconvertible (at least in the Linyphiidae) receives some support from the presence of a few species with intermediate tracheal forms (*Allomengea* and some *Laminacauda* species). The erigonine tracheal form appears to be itself intermediate between the even more complex form present in *Tennesseellum* (Micronetinae) (Millidge, 1986) and the simple form.

If the reduction of the complex tracheal form to the simple form were regarded as feasible, it would be easier to rationalise the close similarities of some desmitracheate erigonine taxa to some haplotracheate taxa; for example, *Erigone* to *Asthenargus*/*Neomaso*, *Tmeticus* to *Donacochara* Simon and of *Meioneta*/*Agyneta* to *Microneta*, which differ from one another mainly in the tracheal form. Similarly, many of the small haplotracheate species of erigonine appearance differ from members of the Erigoninae principally in



Figs. 47–53: **47, 48**: Right palps, mesal, embolic divisions removed. **49–53**: Epigyna, internal. **47** *Microlinyphia impigra* (O. P.-Cambr.); **48** *Centromerus sylvaticus* (Bl.); **49** *Dictyna arundinacea* (Linn.); **50** *Linyphantes* sp.; **51** *Linyphantes orcinus* (Emerton); **52** *Argenna subnigra* (O. P.-Cambr.); **53** *Arangina pluva* Forster. Scale lines = 0.1 mm.

the tracheal form. The polarity of the tracheal transformation (simple to complex, or vice versa), if it occurs, is not in fact known; irrespective of the polarity, however, these taxonomic problems in the Linyphiidae would be simplified if the two tracheal forms could be accepted as interchangeable.

The Linyphiinae appear to be quite closely related to the Dubiaraneinae, and indeed the evidence suggests that the Linyphiinae may be no more than a side branch of the Dubiaraneinae. Similarly it appears possible that the Lepthyphantinae may be an offshoot from the Dubiaraneinae; the Micronetinae may be in a similar position, but this case is complicated by the tracheal question. Thus it might, in the future, be necessary to combine the Dubiaraneinae, the Linyphiinae, the Lepthyphantinae and (?) the Micronetinae into a single subfamily. The Erigoninae appear to be quite closely related to the Mynogleninae, and in this case too it might be found that these two subfamilies form a single branch of the family; again, however, the question of the tracheal interconversion needs to be resolved. Although it is more convenient, for the present, to retain the subfamilies described in this paper, taxonomists should bear in mind the possibility that the Linyphiidae may in fact comprise only two main groups (subfamilies), namely the Dubiaraneinae/Linyphiinae/Lepthyphantinae/?Micronetinae (for which priority would demand the name Linyphiinae), and the Mynogleninae/Erigoninae (for which priority would demand the name Erigoninae); thus the hypotheses on linyphiid taxonomy would have come full circle!

The geographical distribution of the various parts of the Linyphiidae merits some consideration. As mentioned earlier, there are clear indications that the Mynogleninae, Dubiaraneinae and Erigoninae arose from a fairly close common parent, probably during the early stages of the evolution of the family; the Linyphiinae, Lepthyphantinae and Micronetinae are probably somewhat less ancient groups, which appear to be probably closely related to the Dubiaraneinae. It is somewhat curious, therefore, that the Mynogleninae and the Dubiaraneinae appear to be restricted to separate remnants of Gondwana, with no overlap whatsoever (so far as known at present), while the Erigoninae, Lepthyphantinae, Micronetinae and Linyphiinae are very numerous in genera and species in the northern hemisphere (Laurasia) but sparse or completely absent in the southern hemisphere (Gondwana) (except where there has been invasion from elsewhere, e.g. probably Africa). Judging from their wide range of habitats, and the high degree of speciation, the Erigoninae and Lepthyphantinae, at least, are very adaptable, and there is no obvious reason why these subfamilies could not have thrived equally well in many of the gondwanan remnants, given the opportunity. Possible hypotheses to explain this distribution would be, either that these subfamilies originated in Laurasia after the separation from Gondwana, or that it was only in a separated Laurasia that the ancestors of these subfamilies acquired, by mutations, their marked ability to diversify and adapt to a wide range of habitats. Possibly the acquisition of an ability to aeronaut at that stage could have played some part in the process. The Mynogleninae certainly, and the Dubiaraneinae possibly, show less adaptability, and any members of these two subfamilies resident in Laurasia after the break-up may have been eliminated later by competition from their more aggressive cousins. It cannot be ruled out, however, that a few of the species of unknown provenance present in the northern hemisphere today (e.g. some of those consigned to the *Stemonyphantes* or *Drapetisca* groups of genera) may be descendants of early members of the Mynogleninae or Dubiaraneinae which have so changed in characters as to be unrecognisable (for the time being) as such.

The U-shaped spermatheca, the laminar form of the seminal duct, and especially the double helical form of the seminal duct (encapsulated or free), are characters which are widespread within the Linyphiidae. In the Araneae as a whole, however, these characters appear to be somewhat rare, and consequently they may be useful pointers to family relationships. Based on current knowledge, these characters seem to be found only in the Linyphiidae and in several cribellate families which have been variously placed in the Amaurobioidea (Lehtinen, 1967) or in the Dictynoidea and Amaurobioidea (Forster, 1970). The Linyphiidae include taxa which have slender and unbranched tracheae (which Forster (1970) regards as characteristic of the Amaurobioidea) and taxa which have the median tracheae strongly branched (which Forster takes as characteristic of the Dictynoidea).

Apart from the Linyphiidae, all three of these epigynal characters appear to be present only in the Dictynidae. For example, *Argenna subnigra* (O. P.-Cambr.) has the spermatheca U-shaped (Fig. 52); *Dictyna arundinacea* (Linn.) has an encapsulated double helix (Fig. 49), but on the lateral rather than the mesal side of the spermatheca, as the free double helix is in several erigonines; *Arangina pluva* Forster has the duct as a small free double helix (Fig. 53); *Dictyna uncinata* Thorell has a somewhat similar double helix but encapsulated (Fig. 54); *Nigma puella* (Simon) has the duct passing around the margins of a somewhat folded lamina (Fig. 55).

The double helical duct is present in other families of the Dictynoidea (according to Forster); for example, *Notiomachia hirsuta* (Marples) (Desidae) has the duct as a free double helix (Fig. 56), and *Panoa* Forster (Desidae) is very similar. A number of other species with probably double helical ducts are to be found figured in Forster (1970).

Double helical duct systems of the linyphiid type are even more clearly developed in the Titanoecidae, which were excluded, probably incorrectly, from the Amaurobioidea by Lehtinen (1967). Most species of the genus *Titanoeca* Thorell have the seminal duct as an encapsulated double helix, located more or less on the mesal side of the spermatheca (Figs. 57, 58) (Hubert, 1966); this is true of the North American as well as the European species. In most of the *Titanoeca* species the directions of rotation of the helices are the same as in the Linyphiidae, and these encapsulated forms are, apart from the number of turns in the helix, very similar to those of *Protoerigone* Blest (Mynogleninae) (Fig. 58, cf. Fig. 1). *T. sequeirai* Simon has lost the encapsulation, and has a clear, free double helix (Fig. 59); the duct leaves the spermatheca in an anticlockwise curve (viewed posteriorly), rather than clockwise as in the Linyphiidae and in most other *Titanoeca* species, and the directions of rotation in the double helix are the reverse of those in the other *Titanoeca* species and in the majority of linyphiids. Since *T. sequeirai* appears, on the basis of somatic and palpal characters, to be a normal member of the genus, it would seem that both the loss of encapsulation and the reversal of the direction of rotation are relatively facile transformations. As mentioned earlier, there are isolated examples of the reversal of direction of rotation within the Linyphiidae (*Australolinyphia, Novafrontina*). Apart from the directions of rotation, the internal epigynal form of *T. sequeirai* is remarkably similar to that of many species of the Mynogleninae (Fig. 59, cf. Fig. 2).

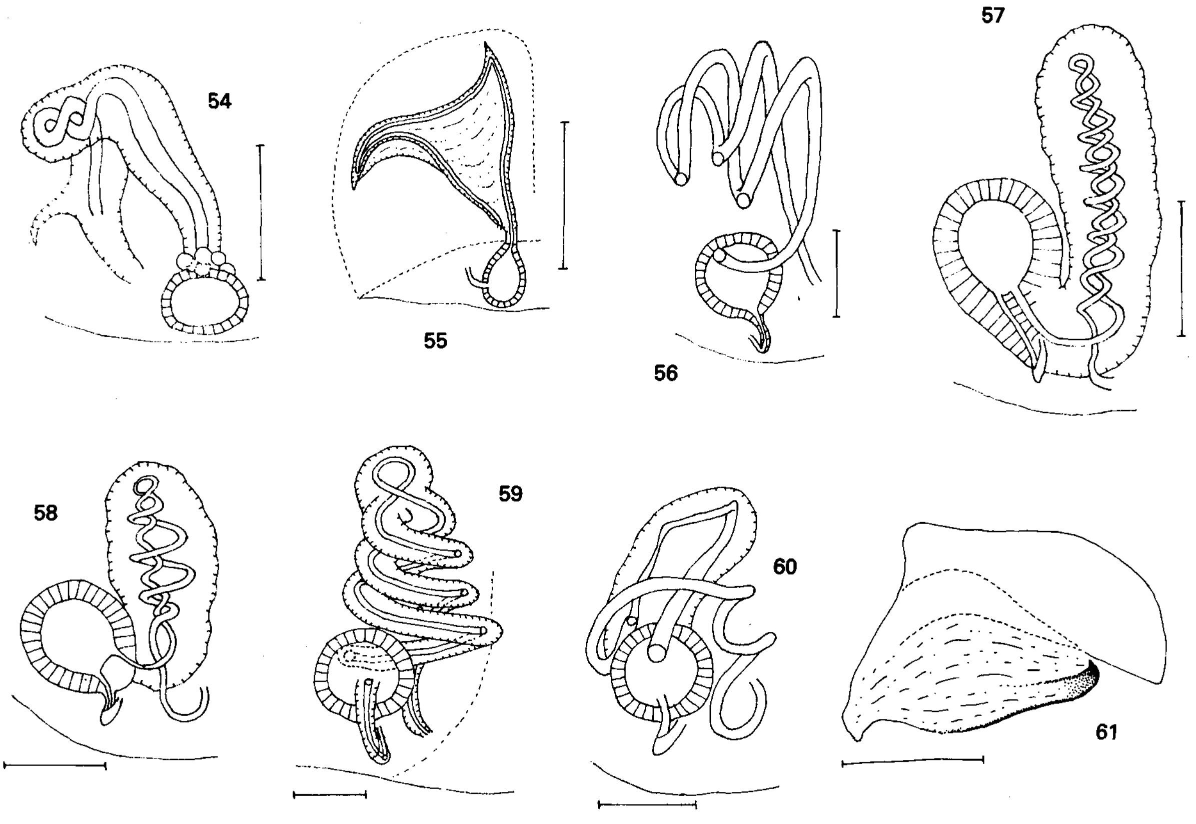
In *T. albomaculata* (Lucas) the double helical duct has been reduced to an encapsulated loop (Fig. 60); it is possible that an encapsulated loop of this type may be an intermediate, in some cases, in the conversion to the laminar form, which could result from subsequent flattening of the capsule.

The form and position of the tegular apophysis in the Dubiaraneinae is judged to be primitive. A similar form of apophysis is present in e.g. *Amaurobius* C. L. Koch, but absent in some members of the Amaurobioidea/Dictynoidea, e.g. in Dictynidae, as it is in most members of the Linyphiidae. Another character present in some members of the Dictynidae and Linyphiidae, and perhaps in no other family, is the distinctive bowed form of the chelicerae of the male; this occurs in the linyphiid genus *Dunedinia* Millidge (New Zealand and Australia) and in a new genus from Western Australia (Millidge, 1993a).

Since the days of Simon there has been a strong bias amongst taxonomists towards the hypothesis that the Linyphiidae are closely related to the Araneidae and the Theridiidae. The congruence of the somewhat unusual characters, mentioned in this paper, in members of the Linyphiidae and of the Amaurobioidea/Dictynoidea suggests, however, the probability of a close relationship between the Linyphiidae and some of the cribellate families of the Amaurobioidea/Dictynoidea; and that the Linyphiidae, Dictynidae and Titanoecidae may be particularly close within this group of families. The fact that the Linyphiidae are ecribellate is no bar to such a relationship. It is perhaps worth noting that the family Agelenidae, previously suggested (Millidge, 1988b) as a possible close relative of the Linyphiidae, is also regarded as an ecribellate member of the Amaurobioidea by some taxonomists (e.g. Lehtenen, 1967).

Two recent publications (Platnick & Forster, 1989: figs. 38, 39; Forster, Platnick & Coddington, 1990: figs. 202, 203), which were not seen until after this paper was written, show that the encapsulated double helix is probably present in a few members of the Synotaxidae (some of the members of which have been confused with linyphiids) and of the Anapidae. The presence of this epigynal character may indicate that these two families are, basically, quite closely related to the Linyphiidae and Amaurobioidea/Dictynoidea; that is, they may form a group, all the members of which have evolved from a single, probably haplogyne, ancestor.

If this hypothesis that the Linyphiidae should probably be included in the Amaurobioidea/Dictynoidea is to be taken seriously, it must be pursued a little further, and some



Figs. 54–61: **54–60**: Epigyna, internal. **61**: Right palpal cymbium, ectal. **54** *Dictyna uncinata* Thorell; **55** *Nigma puella* (Simon); **56** *Notiomachia hirsuta* (Marples); **57** *Titanoeca obscura* (Walck.); **58** *Titanoeca monticola* (Simon); **59** *Titanoeca sequeirai* Simon; **60** *Titanoeca albomaculata* (Lucas); **61** *Ceraticelus fissiceps* (O. P.-Cambr.). Scale lines = 0.1 mm.

explanation given for the presence of the paracymbium in the Linyphiidae but not in those superfamilies. The obvious, and by no means illogical, reason for this could be that the earliest members of the Linyphiidae did not in fact have the paracymbium, which is a more recent development. As pointed out earlier in this paper, the Erigoninae have retained, among the species, a number of probably relatively primitive characters. Thus the *absence* of a paracymbium in the South American erigonine genera *Sphecozone* O. P.-Cambr., *Brattia* Simon, *Gymnocymbium* Millidge, *Gonatoraphis* Millidge and *Dolabritor* Millidge (Millidge, 1991) may be simply another retained primitive character, rather than the result of reduction and loss of the paracymbium. The cymbium of *Sphecozone* is very similar to those of the *Amaurobius* species, as well as to those of the agelenid genera mentioned previously (Millidge, 1988b). The paracymbium is also absent in some linyphiine genera from south-east Asia (Millidge & Russell-Smith, 1992). The paracymbium in the Linyphiidae may have been evolved more than once, and possibly by more than one route. For example, *Dolabritor ascifer* Millidge has a tiny hook on the posterior end of the cymbium, which might represent the beginning of a paracymbium; and the peculiar paracymbium which lies along the ectal margin of the cymbium in sôme species of *Ceraticelus* Simon (Fig. 61) appears to have been produced by sclerotisation of a laminar margin of the cybium, with only a minimal degree of fission from the cymbium. Several linyphiine genera, from South America (*Eurycolon* Millidge) and south-east Asia (Millidge & Russell-Smith, 1992) have only a rudimentary paracymbium, a tiny sclerite attached to the membrane which connects the tibia with the cymbium, and this too may represent one early stage in the evolution of a paracymbium.

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