The relatives of the Linyphiidae: phylogenetic problems at the family level (Araneae)

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Summary

The problems associated with the establishment of relationships at a family level are briefly discussed. It is concluded that only characters which are either plesiomorphic (or relatively so) for the family, or can with some confidence be related to the plesiomorphic character state, offer a reliable basis for a hypothesis of family relationship. A comparison of characters of the Linyphiidae with those of other families indicates that the closest relatives of the Linyphiidae are the Agelenidae (*s. lat.*), the Amphinectidae, and probably other sheet-web building families. There appear to be no valid characters which point to a close relationship between the Linyphiidae and any of the other families conventionally placed in Araneoidea auct.

Introduction

In the classification of spiders, the family Linyphiidae has commonly been placed in the superfamily Araneoidea, grouped with the families Araneidae, Metidae, Tetragnathidae, Symphytognathidae, Theridiidae, Nesticidae, Mimetidae and Archaeidae (Lehtinen, 1967). A few additional families have been added since Lehtinen's paper (e.g. Heimer & Nentwig, 1982). This grouping seems to have been accepted without question by the majority of arachnologists, though more recently it has been pointed out by Forster & Platnick (1984) that the evidence to support this superfamily as a monophyletic entity is of dubious validity. It is the purpose of this paper to draw attention to some character congruences which suggest that the closest relatives of the Linyphiidae are certain sheet-web builders, rather than orb-web builders, and that the Linyphiidae should be removed from the Araneoidea auct. Before presenting the data, however, it is necessary to examine the question of which characters can be accepted as valid for the determination of family relationships.

Selection of characters valid for supporting hypotheses of family relationships

In the early stages of the divergence of two (or more) evolutionary lines, the present-day members of which are regarded as families (or groups of families), the members of the two lines would presumably have shown character differences essentially no greater than those that exist today between species groups or closely related genera. Indeed, had a taxonomic intelligence existed at that time, the two branches would have been ranked no higher than genera within a single family, a family which has probably long since ceased to exist as a taxonomic entity. The characters shared by the two branches in the early stages of divergence would have

been derived from the characters of the parent species (i.e. would have been apomorphic with respect to the parent species), and would have been clearly discernible (to a taxonomist) at this early evolutionary stage. The early species in the branches would probably have been barely (if at all) diagnosable as members of the present-day families into which they evolved; in the course of time, however, the characters present in the two branches would have changed sufficiently to become recognisable as the primitive characters of the two family groups that we know today. In the very long period (probably well in excess of 100m. years) which has elapsed since the early stages of the branches, the two lines will have diverged more and more from one another, and it seems probable that many, or even most, of the original shared characters will have suffered a significant degree of change, to differing extents in the two branches; e.g. these characters will have become simplified, exaggerated, attenuated, drastically changed, or lost. Consequently many, or most, of the shared characters originally present may no longer be recognisable amongst the characters of the current members of the evolutionary lines (i.e. families) concerned. Clearly, therefore, it must be the characters which were present in the relatively early stages of the family line which are the most important for indicating relationships at a family level. Such primitive characters may include a genetic composition which manifests itself by a *tendency* to produce a certain character, but perhaps only in some members of the family. Characters shared in two (or more) present-day families cannot automatically be regarded as indicating relationships, since the primitive characters from which they were derived may have been so different from one another that they could not have ranked as shared characters in the early stages of the branches; congruence of such current characters would then be the result of convergence. This situation applies particularly to obviously simplified characters, which must be immediately suspect. For example, the character "simple serrate hairs" quoted (Lehtinen, 1967: 396) as characteristic of the Araneoidea, may have been derived by simplification of complex hair forms which were not identical in the early members of the families concerned. A similar argument applies to the character "scale-like ultrastructure of the skin", used as a synapomorphy for the Araneoidea (Lehtinen, 1975: 27). Likewise, the presence of a single trichobothrium on the metatarsi of present-day species in several families (Lehtinen, 1975) is no guarantee that the primitive members of the families had identical numbers of metatarsal trichobothria. The complete absence of a character in current groups is obviously more or less worthless for establishing relationship at a family level, since absence can have been derived from a wide selection of primitive characters! An example which illustrates that a comparison of current family characters can be invalid for establishing family relationships is given by Saaristo's work (1975) on the genitalia of *Rhabdoria* Hull (Linyphiidae) and *Araneus* Clerck (Araneidae): the somewhat similar genitalia in these two genera are not valid characters for showing a

relationship between the two families, since the genitalia of the *Lepthyphantes* Menge group, to which *Rhabdoria* belongs, are highly derived (Millidge, 1977, 1984) and bear little resemblance to the probably primitive genitalic forms in the Linyphiidae.

In the case of shared family characters which are rare, i.e. not widespread amongst families, it is probably more parsimonious, as a first hypothesis, to regard such characters as either plesiomorphic, or derived from the same plesiomorphic character, unless there is evidence to the contrary. An example of such a character could be the cheliceral peg teeth present in the Mimetidae, which link this family with others placed in the Palpimanoidea (Forster & Platnick, 1984).

The important point which emerges from this brief discussion is that the congruence of current characters in two (or more) families should not be used as a basis for a hypothesis of family relationship (e.g. in cladistic analysis) unless these characters can with some confidence be related to a congruence (or near congruence) of the corresponding primitive character in the families. In other words, family relationships should be based on the similarity of characters which are plesiomorphic, or relatively so, for the family; this requirement is not contrary to the Hennig principle, since such characters should of course be apomorphic with respect to the characters of the parent of the families concerned. The procedure suggested, making use of plesiomorphic characters, is in effect the reverse of outgroup comparison (Nelson & Platnick, 1981: 27).

Given the probably vast age of most spider families, and the probability that most or all of the very early species will have become extinct, it will not be surprising if some of the primitive characters to be looked for are recognisably present in only a small proportion of the current members of a family; at the same time it is possible that a small number of primitive characters may have survived in all current species of the family. In families which are comparatively young (if any exist), and in families which have relatively few species as a result of restricted diversification, the characters present today may be but little changed from the early characters of the family; but in large families, such as the Linyphiidae, Theridiidae, Araneidae and Salticidae, which have obviously undergone vigorous speciation and diversification, there is likely to have been a high degree of change in many of the early characters.

To sum up, shared present-day characters (i.e. apomorphic for the family) should be regarded as distinctly unreliable indicators of family relationships, unless there is good reason for considering these characters to be primitive (or relatively so) for the family, or unless the character can be related with some confidence to the primitive character state from which it was derived.

It seems probable that similar restrictions on character usage should also apply to the establishment of relationships between genera, many of which are probably fairly ancient groups.

Comparison of some characters of the Linyphiidae with those of other families

1. Chelicerae

The chelicerae of the Linyphiidae have a file ("stridulating file") on the lateral margin. This file is developed to a varying extent: in some species it is strong, in others it is weak, sometimes so weak as to be scarcely visible. The species with the weakest files are often those which belong to genera considered (e.g. on the basis of the genitalia) to be amongst the more primitive, e.g. *Haplinis* Simon (=*Mynoglenes*). The
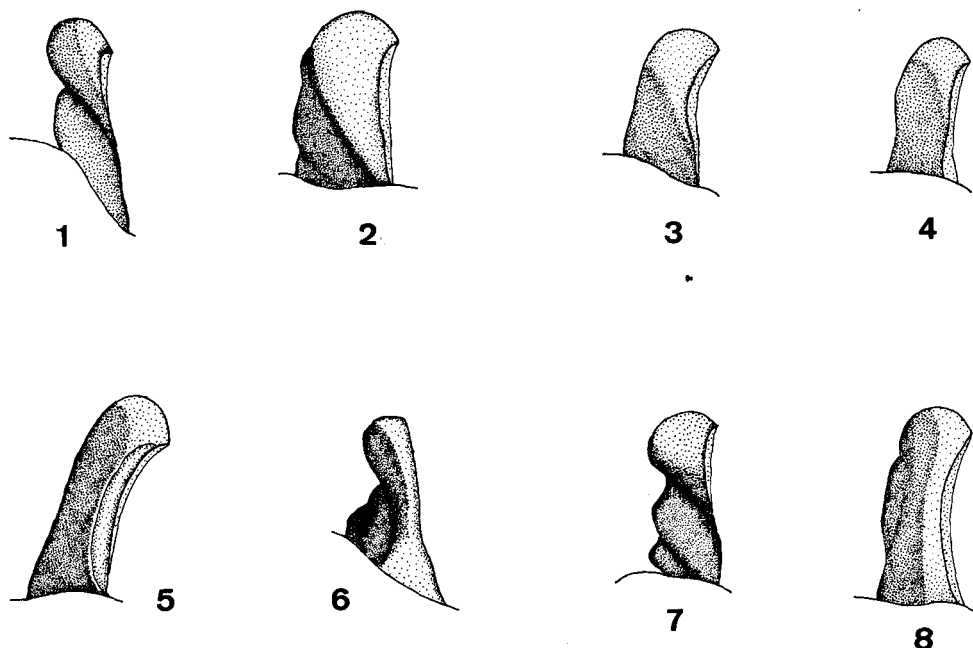
Figs. 1-8: Labia, lateral view, with maxillae removed and hairs omitted. **1** *Lepthyphantes nebulosus* (Sund.); **2** *Araneus diadematus* Cl.; **3** *Zygiella x-notata* (Cl.); **4** *Cryphoeca silvicola* (C. L. Koch); **5** *Tegenaria* sp.; **6** *Meta segmentata* (Cl.); **7** *Tetragnatha extensa* (L.); **8** *Mamoea rufa* (Berland).

character is present in all the linyphiid species, and is almost certainly primitive for the family. It is sometimes thought (e.g. Levi & Coddington, 1983: 152) that this cheliceral file is a character present only in the Linyphiidae. This is not so; Ero C. L. Koch (Mimetidae) has a strongly developed file, and weak files are discernible in some members of most entelegyne families, including the Araneidae and Theridiidae (cf. also Lehtinen, 1978: 259). The files in some members of the Agelenidae and Lycosidae are at least as strong as the weakest files present in the Linyphiidae.

It is usually reported that the Linyphiidae do not have a basal cheliceral boss, such as that present in the Araneidae, the Agelenidae and many other families. Some of the probably more, primitive species of the Linyphiidae do, however, have a small basal boss (e.g. Microlinyphia impigra (O. P.-Cambr.), some Hormembolus Millidge species, some Laetesia Simon species), but only in the male sex. It is uncertain whether this boss, which is in the same position as in other families but differs somewhat in shape, is homologous with those of the other families.

A few species of a probably fairly primitive linyphiid genus, Dunedinia Millidge, from New Zealand, have the chelicerae of a form which is typical of the Dictynidae (Millidge, 1988); this cheliceral form is unusual, and points to the possibility that the Linyphiidae may lie in the same evolutionary branch as the Dictynidae.

2. Labium

It is usually stated, particularly in keys, that the Linyphiidae share, with the Araneidae, Metidae, Tetragnathidae and Nesticidae, the character of a rebordered labium, i.e. a labium with a thickened margin. The labium in the Linyphiidae is genuinely thickened on the anterior margin (Fig. 1), and this is also the case in many species of the Metidae and Tetragnathidae (Figs. 6, 7); in Zygiella F.O.P.-Cambr. (? Metidae) (Fig. 3), however, and in Nesticus Thorell (Nesticidae) the labium is not significantly different in shape (lateral view) from the labia of the Agelenidae (Figs. 4, 5). In the Araneidae the thickening is present (Fig. 2) but much reduced. The labium of the New Zealand species Mamoea rufa (Berland) (Amphinectidae, superfamily Amaurobioidea) is rebordered to a similar degree to that of Araneus (Araneidae) (Fig. 8, cf. Fig. 2), and in Zelotes apricorum (L. Koch) (Gnaphosidae) the labium is distinctly rebordered. It is the pale pigmentation of the rounded and polished anterior margin of the labium in the Araneidae and the Nesticidae which gives the impression of a significant degree of thickening. The tendency towards thickening of the labial margin which is exhibited both in the Amphinectidae and the Gnaphosidae indicates that the linyphiid form of labium is no more than a simple derivative form of the unthickened labium with the lightly pigmented anterior border; this latter form of labium is present not only in the Agelenidae, but also in many entelegyne families,

e.g. Clubionidae, Liocranidae, Salticidae, Thomisidae, Philodromidae, Gnaphosidae, Lycosidae, Pisauridae, Uloboridae, Mimetidae, Theridiidae, Zoridae, Sparassidae, Anyphaenidae and Pholcidae. Atypus Eichwald (Atypidae) has a distinctly rebordered labium, fused to the sternum, but without the pale pigmentation.

The character "rebordered labium" thus appears to be of little or no value in the assessment of family relationships.

3. Eye arrangement

In most linyphiids the eyes are subequal in size and arranged in two rows, with the laterals of both rows contiguous; in those erigonine males which have cephalic lobes of various forms, the arrangement of the eyes is obviously distorted. In the probably fairly primitive South American genus Hormembolus, however, the posterior median eyes are usually considerably enlarged, to give an arrangement (Fig. 9) which resembles that of Textrix Sundevall (Agelenidae) (Fig. 10), which itself approaches the arrangement in the Lycosidae.

4. Cephalic sulci

The species of the linyphiid subfamily Mynogleninae have two relatively deep sulci on the clypeus, more or less below the lateral eyes; internal glands open via pores in the floor of each sulcus (Blest & Taylor, 1977). The secretions from the glands do not appear to contain sexual pheromones, and it was suggested by Blest & Taylor that their role might be defensive. No other members of the Linyphiidae are known to have clypeal sulci of this form. The males of many species of the subfamily Erigoninae, however, have cephalic sulci which run posteriorly from the lateral eyes, and these sulci have a pit anteriorly, which leads into a deeply invaginated sac (Blest & Taylor, 1977); the secretion into the pit probably has a sexual function in these species (Blest & Taylor, 1977). It was suggested (Blest & Taylor, 1977; Blest, 1979) that the ocular sulci of the Mynogleninae and Erigoninae are homologous structures (though with different functions), and Blest (1979) proposed a hypothetical sequence for the evolution of the two forms.

Males of the theridiid genus Argyrodes Simon have a single clypeal sulcus into which internal glands discharge (Legendre & Lopez, 1974). It is uncertain whether this single sulcus should be considered to be homologous with the paired clypeal sulci of the Mynogleninae (Blest & Taylor, 1977).

In most erigonine species the sulci are absent in the female, but in the genus Erigone Audouin both sexes have two long sulci, which are situated on either side close to the margin of the carapace, and run posteriorly from a point between the chelicerae and the first pair of legs (Figs. 12, 13). These sulci are more strongly developed in the male, and in this sex they appear to have a pit anteriorly; the presence of coagulum in the pit in some cases indicates that a gland opens into the pit, but this has not been verified. A few pores in the

integument, outside the sulcus, are also present in some males (Fig. 46). *Prinerigone vagans* (Aud.) has sulci of the same form, but in this species they are very weak in the female. Some other erigonines have sulci of similar form though more weakly developed than in *Erigone,* e.g. *Erigonidium* F. P. Smith, *Gonatium* Menge, *Troxochrus scabriculus* (Westr.), *Hylyphantes nigritus* (Sim.). Some mynoglenines, particularly the larger species, have shallow, but distinct, pits near the carapace margin in the same position as the pits in *Erigone*; similar weak pits are visible in *Bolyphantes alticeps* (Sund.) and in species of *Meioneta* Hull. In *Eperigone* Crosby & Bishop the males of some species have a small shallow pit located well above the carapace margin (Fig. 14).

Thus the Linyphiidae have two different forms of cephalic sulci, namely those below or behind the eyes ("ocular sulci") and those near to the carapace margin ("marginal sulci").

During the course of the present work it has been found that females of *Textrix* (Agelenidae) have shallow cuticular depressions on the clypeus in approximately the same position (Fig. 10) as the ocular sulci of the Mynogleninae. Shallow depressions are also present below the lateral eyes of the females of *Cicurina cicur* (Fabr.) and *Agelena labyrinthica* (Clerck) (Figs. 11, 15); these depressions are similar in shape to the ocular sulci of the Mynogleninae, but are much more weakly developed. In the Mynogleninae the sulci tend to be weaker in the male than in the female, and this is also the case with these agelenids, to the extent that the sulci are scarcely visible in the

males. Even in the agelenid females, the sulci are very shallow; under the light microscope the floors of the depressions appear to be rugose or slightly punctate, but examination of those of *Textrix* by scanning electron microscopy failed to show the presence of any pores. Weakly developed sulci are also present below the lateral eyes in some members of the Lycosidae (e.g. *Pirata* Sund. (Fig. 16), *Hygrolycosa* Dahl (Fig. 17)), Pisauridae (*Pisaura* Sim.), Thomisidae (*Diaea* Thor.), Philodromidae (some species of *Tibellus* Sim., *Philodromus* Walck. and *Thanatus* C. L. Koch (Fig. 18)) and Gnaphosidae (e.g. *Haplodrassus signifer* (C. L. Koch), *Zelotes electus* (C. L. Koch)); there appear to be weak traces of sulci below the posterior lateral eyes in Zoridae (some species of *Zora* C. L. Koch) and in Liocranidae (some species of *Scotina* Menge and *Agroeca* Westr.). As in the Agelenidae, the sulci are usually visible only in the female; they are, however, extremely shallow, and can be somewhat difficult to see, but with the correct illumination the margins of the sulci are clear, and the floor is , differentiated from the surrounding integument. It seems doubtful that these poorly developed ocular sulci can have any function, although in one instance (*Cicurina*) a sulcus contained what might have been a trace of coagulum. It is proposed that these cuticular depressions, which occupy similar locations to those of the sulci of the Mynogleninae and Erigoninae, should be regarded as homologous with the linyphiid sulci, which represent extreme and specialised functional developments of the shallow sulci.
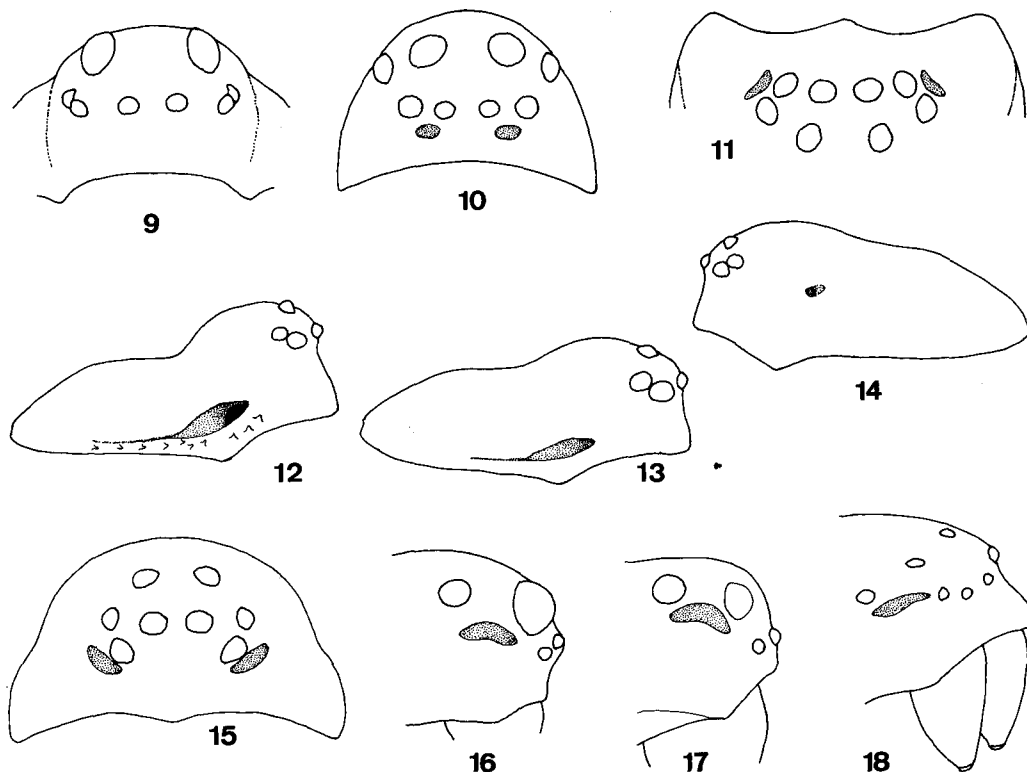
Figs. 9-18: Carapaces: cephalic depressions dotted. **9** *Hormembolus* sp., female, frontal; **10** *Textrix denticulata* (Olivier), female, frontal; **11** *Cicurina cicur* (Fabr.), female, above; **12** *Erigone atra* (Bl.), male, lateral; **13** *E. atra,* female, lateral; **14** *Eperigone fradeorum* (Berland), male, lateral; **15** *Agelena labyrinthica* (Cl.), female, frontal; **16** *Pirata latitans* (Bl.), female, lateral; **17** *Hygrolycosa rubrofasciata* (Ohlert), female, lateral; **18** *Thanatus formicinus* (Cl.), female, lateral.

It has also been observed that weakly developed marginal sulci, situated in more or less the same position as those of the Linyphiidae, are present in members of many families, e.g. Lycosidae, Pisauridae, Gnaphosidae, Liocranidae, Philodromidae, Pholcidae, Theridiidae, Araneidae and Tetragnathidae. The sulci in these families are usually in the form of shallow pits, and tend to be stronger in the female than in the male.

5. Legs

A few linyphiid genera have a notch on the trochanters, particularly on legs III and IV; these taxa (e.g. *Haplinis, Stemonyphantes* Menge) are thought to be amongst the more primitive of the family. The notch is absent in the overwhelming majority of the linyphiid species, and is perhaps a primitive character of the family; or, more likely, the family lies in a branch of the Araneae in which the notching is present or potentially present. The notching is of little taxonomic value at the family level, however, since it is present in at least some members of a wide range of entelegyne families, e.g. Lycosidae, Pisauridae, Oxyopidae, Agelenidae, Clubionidae, Liocranidae, Philodromidae, Gnaphosidae, Zoridae, Anyphaenidae, Sparassidae, Mimetidae, Theridiidae, Nesticidae and Araneidae.

In the vast majority of the linyphiid species, the metatarsi I-III have a single trichobothrium. In a few of the probably more primitive species, however, the number of metatarsal trichobothria can be greater. *Allomengea scopigera* (Grube) has 5 on metatarsus I, and 2-3 on metatarsi II-IV; *Haplinis diloris* (Urquhart) female has 4-5 on metatarsus I, and 2-3 on metatarsi II-IV, while the male has 4 on each metatarsus; these multiple trichobothria are in a single row. It can be inferred that in the early members of the Linyphiidae the number of metatarsal trichobothria was much greater than one, and that the single trichobothrium now present in most species represents a reduction of the primitive character.

The single row of trichobothria on the metatarsi of the primitive linyphiids, and the double row on the tibiae of probably all linyphiids, are of increasing length towards the distal end (Figs. 19-21). This metatarsal pattern is regarded by Forster (1970: 12) as an ancestral character of the families which he and Lehtinen (1967) place in the superfamilies Dictynoidea and Amaurobioidea. No known linyphiid species has tarsal trichobothria, but these are also absent in some members of the Dictynoidea and Amaurobioidea.

6. Male palp

(a) *Cymbium.* Most of the probably primitive linyphiid genera (e.g. *Haplinis, Falklandoglenes* Usher, *Hormembolus*) have an elongated cymbium which is rather pointed anteriorly, and some of the species in these genera also have one or more stout spines distally on the mesal cymbial margin (e.g. Fig. 29). It may be inferred that a cymbium of this form is close to the primitive form of the family. A cymbium of similar shape is present in some species of a number of entelegyne families, e.g. Agelenidae, some families

currently placed in the Dictynoidea and Amaurobioidea (Forster, 1970; Forster & Wilton, 1973), Philodromidae, Gnaphosidae and Pisauridae, and also in some haplogyne families. In the Theridiidae and Araneidae the character appears to be only weakly developed. The mesal cymbial spines are present in some members of the Agelenidae (e.g. *Tegenaria* Latreille, *Orepukia* Forster & Wilton, *Neoramia* Forster & Wilton), of the Philodromidae (*Tibellus, Thanatus*), of the Gnaphosidae (some species of *Drassodes* Westr., *Haplodrassus* R. V. Chamberlin, *Gnaphosa* Latr. and *Micaria* Westr.) and of the Pisauridae. It is not known whether the mesal spines are primitive for these families, but their presence in only a few members of the families may indicate that this is the case.

In most (perhaps all) linyphiid genera the ectal margin of the cymbium is somewhat hollowed ("excavated"), particularly towards the posterior end; this character is present, though it is sometimes rather weak, in the probably more primitive genera of the family, and consequently it can probably be regarded as primitive or relatively so. In the genus *Sphecozone* O. P.-Cambr. (Linyphiidae), which lacks the linyphiid type of paracymbium, the basal end of the cymbium on the ectal side is extended along the anterior end of the tibia, and is very distinctly hollowed. This excavation on the ectal side of the linyphiid cymbium is very similar to that present in some members of the Agelenidae (*s. lat.*) (e.g. *Cicurina* Menge, *Coelotes* Bl., some species of *Tegenaria, Hahnia* C. L. Koch and *Antistea* Simon), the Thomisidae, the Philodromidae and the Salticidae. This cymbial character appears to be absent in the Araneidae and Theridiidae; in the Nesticidae (*Nesticus*) and Mimetidae the "paracymbium" is hollowed, but it seems doubtful that
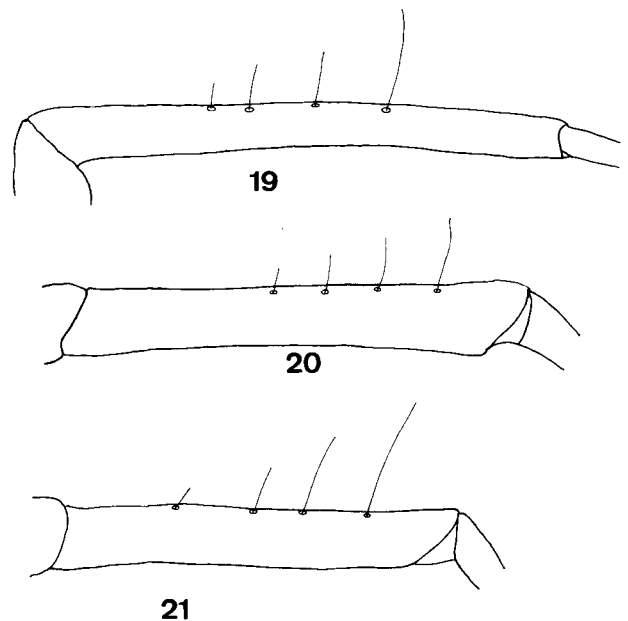
Figs. 19-21: Legs, with trichobothria. **19** *Haplinis diloris* (Urquhart), female, metatarsus I; **20** *H. diloris*, female, tibia I, posterior row of trichobothria; **21** *Grammonota* sp., male, tibia IV, posterior row of trichobothria.

this is homologous with the excavated cymbium of the Linyphiidae and other families mentioned above.

(b) *Paracymbium*. The paracymbium is defined by Foelix (1982: 181) as a basal appendage of the palpal tarsus. In practice, this term covers more than one form of appendage, and it is questionable whether the different forms can all be regarded as homologous.

In the Araneidae, the paracymbium is a basal knob-like projection from the ectal side of the cymbium, and is merely an extension or apophysis of the cymbium. This form can be described as an "integral" paracymbium. In the Theridiidae, the paracymbium (Heimer, 1982) is not a basal appendage, but a small projection, sometimes hook-shaped, usually arising from the antero-lateral margin of the cymbium; this paracymbium is also an integral paracymbium, though of a different form from that of the Araneidae.

The paracymbium of the Linyphiidae is usually described as a horseshoe-shaped sclerite which is hinged to the cymbium, but this is not strictly correct. The paracymbium is in fact a sclerite attached to the joint membrane which connects the tibia and the cymbium. Indeed, when the cymbium is detached from the palp, the paracymbium sometimes remains attached to the joint, rather than to the cymbium (Fig. 23). This form of paracymbium can be described as an "intersegmental" paracymbium, though from its position it might equally correctly be described as a "paratibia". In the probably primitive genus *Stemonyphantes* the paracymbium is attached both to

the joint membrane and to the cymbium, i.e. it is not a completely separate sclerite. Several taxa of the Linyphiidae have an integral paracymbium in addition to the intersegmental one: e.g. *Neomaso* Forster (Millidge, 1985), *Floronia* Simon, *Drapetisca* Menge.

In the Nephilinae, the paracymbium is intersegmental, as in the Linyphiidae, but in the few species that I have seen it is small and not horseshoe-shaped (Fig. 24).

In the Nesticidae, the form of the paracymbium is variable. In *Nesticus cellulanus* (Clerck) it is a large basal projection which is integral with the cymbium; in *Nesticella nepalensis* (Hubert) (if this is correctly placed in Nesticidae) it is in part attached to the cymbium, in part to the joint membrane.

In typical members of the Metidae, the paracymbium is a basal projection from the cymbium; there is no "hinge", and the paracymbium is integral. In the Tetragnathidae, the paracymbium is also an extension of the cymbium; the joint membrane from the tibia joins the cymbium at the base of this paracymbium, but the latter is not attached to the joint membrane, and the paracymbium must be regarded as integral. The metid and tetragnathid paracymbia are readily distinguishable from the araneid paracymbia, and, contrary to the statement of Coddington (1986: 337) they are also clearly different from those of the Linyphiidae.

Paracymbia, within the definition given by Foelix (1982), are to be found in families outside the
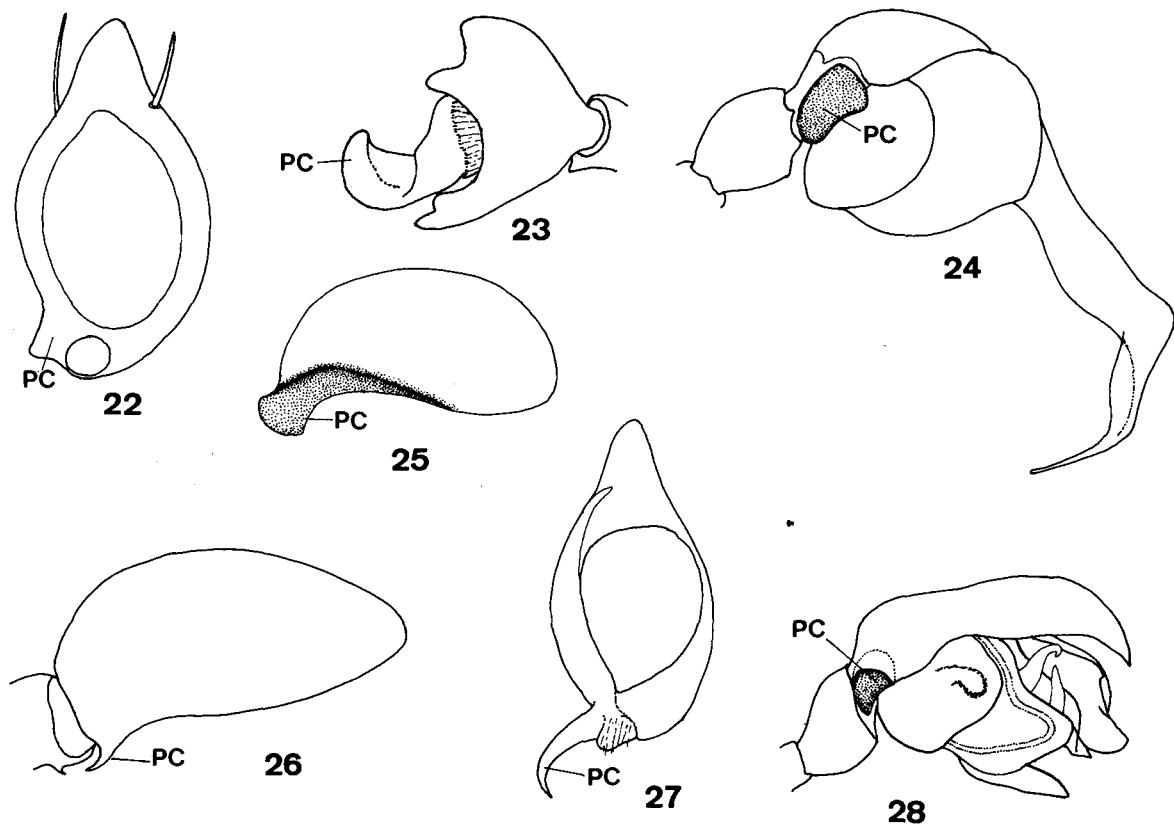
Figs. 22-28:   Male palps (right). **22** *Cicurina cicur*, cymbium, ventral; **23** *Eperigone agressa* Gertsch & Davis, palpal tibia with attached paracymbium, mesal; **24** *Nephila malabarensis* (Walck.), ectal; **25** *Xysticus bifasciatus* C. L. Koch, cymbium, ectal; **26** *Philodromus dispar* Walck., cymbium, ectal; **27** *Cheiracanthium virescens* (Sund.), cymbium, ventral; **28** S. American linyphiid species, undescribed. PC = paracymbium.

Araneoidea auct. In the Thomisidae and Philodromidae, the tutaculum, a basal projection from the cymbium (Figs. 25, 26), can justifiably be regarded as an integral paracymbium. *Cicurina* (Agelenidae) has a small integral paracymbium (Fig. 22), and basal cymbial projections are also present in some members of the Salticidae (e.g. *Marpissa* C. L. Koch). The extension on the posterior lateral margin of the cymbium of *Cheiracanthium* C. L. Koch (Clubionidae) must also presumably rank as a paracymbium (Fig. 27), and no doubt further examples of integral paracymbia can be found in other families.

Although the vast majority of the linyphiid species have an intersegmental paracymbium, there are quite a few in which this form of paracymbium is completely absent or greatly reduced in size. Members of the genus *Sphecozone,* which are in most respects typical linyphiids, have no trace of an intersegmental paracymbium, while certain other linyphiids from the Americas have the paracymbium greatly reduced (e.g. Fig. 28), and somewhat similar to that of *Nephila.*

The existence of the intermediate form of paracymbium, attached to both the joint membrane and the cymbium (in *Nesticella* and *Stemonyphantes*) may suggest that the intersegmental paracymbium was derived from some form of integral paracymbium. Since no member of the Araneidae appears to have developed the intermediate paracymbial form, however, it is a reasonable first hypothesis that the intersegmental paracymbium was not derived from the knob-like paracymbium of the Araneidae, but rather from some different form of integral paracymbium. It appears less likely (though it cannot be completely ruled out) that the polarity of the paracymbial change was in the reverse direction, i.e. that the integral paracymbia were derived from intersegmental paracymbia. The fact that some members of the Linyphiidae have a well developed integral paracymbium as well as the intersegmental one may be an indication that in the Linyphiidae the latter paracymbial type was not derived from the former. Nor, at this time, can it be totally excluded from consideration that the intersegmental paracymbium was formed by the transfer of a sclerite from the palpal tibia, rather than from the cymbium. Some palpal tibiae carry an apophysis attached via a region of reduced sclerotisation (e.g. in *Cambridgea* L. Koch (Linyphiidae), *Anyphaena* (Anyphaenidae), *Cyrba algerina* (Lucas) and *Gelotia syringopalpis* Wanless (Salticidae)), and there seems to be no logical reason why transfer of a sclerite to the joint membrane should be more probable from the cymbium than from the tibia. The origin of the intersegmental paracymbium must for the present, therefore, be accepted as unknown, and it is safer to regard this paracymbial form as neither identical with, nor derived from, the araneid paracymbial form.

(c) *Palpal bulb.* In the linyphiid bulb, only the basal haematodocha is functional, although in a few species there may be a trace of a second haematodocha between the subtegulum and the tegulum (Holm, 1984: fig. 17). The margin of the tegulum, on the mesal side adjacent to the cymbium, is relatively heavily sclerotised, usually thickened and forming a ridge with often some degree of overhang. The anterior end of this sclerotised region of the tegulum has developed into a projection, normally quite heavily sclerotised, the suprategulum, which often carries an apophysis of variable form, the suprategular apophysis. In a few, probably primitive, species, the suprategulum is absent or weakly developed. The tegulum may be heavily sclerotised in members of several entelegyne families, but the ridging on the mesal margin is absent in these families, with a few exceptions (see later).

The linyphiid embolus arises from the embolic division, which is a distinct sclerite connected to the tegulum by a lightly sclerotised neck, the stalk, through which passes the seminal duct. The embolic division may be quite simple or relatively complex. The stalk is possibly all that remains of the distal haematodocha. In most species, the stalk is narrow, and the embolic division can fairly readily be broken off from the tegulum; in a few species, however, and particularly in the primitive Mynogleninae, the junction between the embolic division and the tegulum is relatively broad (Fig. 29), and cannot accurately be described as a stalk. In what are probably the more primitive taxa of the family (e.g. Mynogleninae, *Stemonyphantes, Hormembolus*) the junction between the tegulum and the embolic division is located near to the posterior end of the organ, ventrally to the sclerotised margin of the tegulum, and this is probably the primitive position. In those members of the family which are probably more recent (e.g. most erigonines, *Lepthyphantes*), the junction has moved anteriorly, in some cases into the suprategulum. Hence it can be inferred that in the primitive linyphiid palp the junction was broad and near to the rear of the bulb. On this basis, it is probable that the palp of the African erigonine genus *Tybaertiella* Jocqué is a primitive form, not recent as proposed by Jocqué (1984).

From the stalk, the duct of the right hand palp, viewed ventrally, runs in a clockwise spiral through the tegulum, passing on the ectal side of the sclerotised margin of the tegulum, to the reservoir in the subtegulum; just within the subtegulum, before the duct ends in the fundus, the direction of rotation of the duct reverses (Fig. 30). This reversal of rotation, however, is present in members of many, if not all, entelegyne families, but is absent in the haplogynes.

The characters of the palpal bulb, viz. the sclerotised ridge of the mesal tegular margin, and the embolic division as a separate sclerite joined to the tegulum by a neck, appear to be characteristic of the Linyphiidae. There are, however, at least two families (Agelenidae, Amphinectidae) in the superfamily Amaurobioidea (Lehtinen, 1967: 308; Forster & Wilton, 1973: 15) which contain species with these two characters, and the palpal bulb in these taxa is basically similar in form to the linyphiid bulb. In these amaurobioid taxa, only the basal haematodocha is functional, as in the Linyphiidae, and expansion of this rotates the bulb in the same way as in the Linyphiidae; the rotation brings the embolus to the correct position on the ectal side of the palp, without the intervention of a paracym-

bium (cf. Heimer, 1982). In these taxa (e.g. *Cicurina* (Figs. 30, 32), *Cryphoeca* Thorell and *Textrix* (all in Agelenidae); *Mamoea* Forster & Wilton (Amphinectidae) (Fig. 31)) the embolus arises from a distinct embolic division which is attached to the tegulum, near to the posterior end of the bulb (as in primitive linyphiids) by a neck which is in part lightly sclerotised, in part more heavily sclerotised. The neck is somewhat broader in these genera than in *Haplinis* (Fig. 30 cf. Fig. 29), and is more strongly sclerotised on the posterior side. The conformation is nevertheless essentially the same as in the linyphiids, the differences being only that the loss of sclerotisation and the reduction in diameter of the neck have gone further in the Linyphiidae. The more heavily sclerotised regions of the embolic division in *Cicurina* (Fig. 30 "A") and *Mamoea* (Fig. 31 "A") are the equivalents of the lightly sclerotised "conductor" in *Haplinis* (Fig. 29 "C"). In the agelenids and *Mamoea* there is no suprategulum, which is also the case in a few probably primitive linyphiids. The combination of the sclerotised tegular ridge and the more or less distinct embolic sclerite has been found only in the Linyphiidae and the taxa just

mentioned, but the tegular ridge alone is strongly developed in the genus *Paravoca* Forster & Wilton (Amaurobiidae).

A study of the South American linyphiid fauna has disclosed the male of a species which is a typical linyphiid so far as the paracymbium, the labium and the cheliceral striae are concerned. The palpal bulb has the mesal margin of the tegulum sclerotised, and there is only a weak suprategulum; the embolic division is attached to the tegulum not by a narrow neck but by a broad, lightly sclerotised junction, and the duct follows a serpentine course within the embolic division (Figs. 33, 34) (Millidge, paper in preparation). The bulb is somewhat reminiscent of the Agelenidae, and were it not for the presence of the intersegmental paracymbium the species might well have been allocated to that family. This new species has presumably retained a palpal conformation which is fairly primitive for the Linyphiidae.

7. Epigynum

The epigyna of the probably primitive linyphiid species have one constant character, namely the
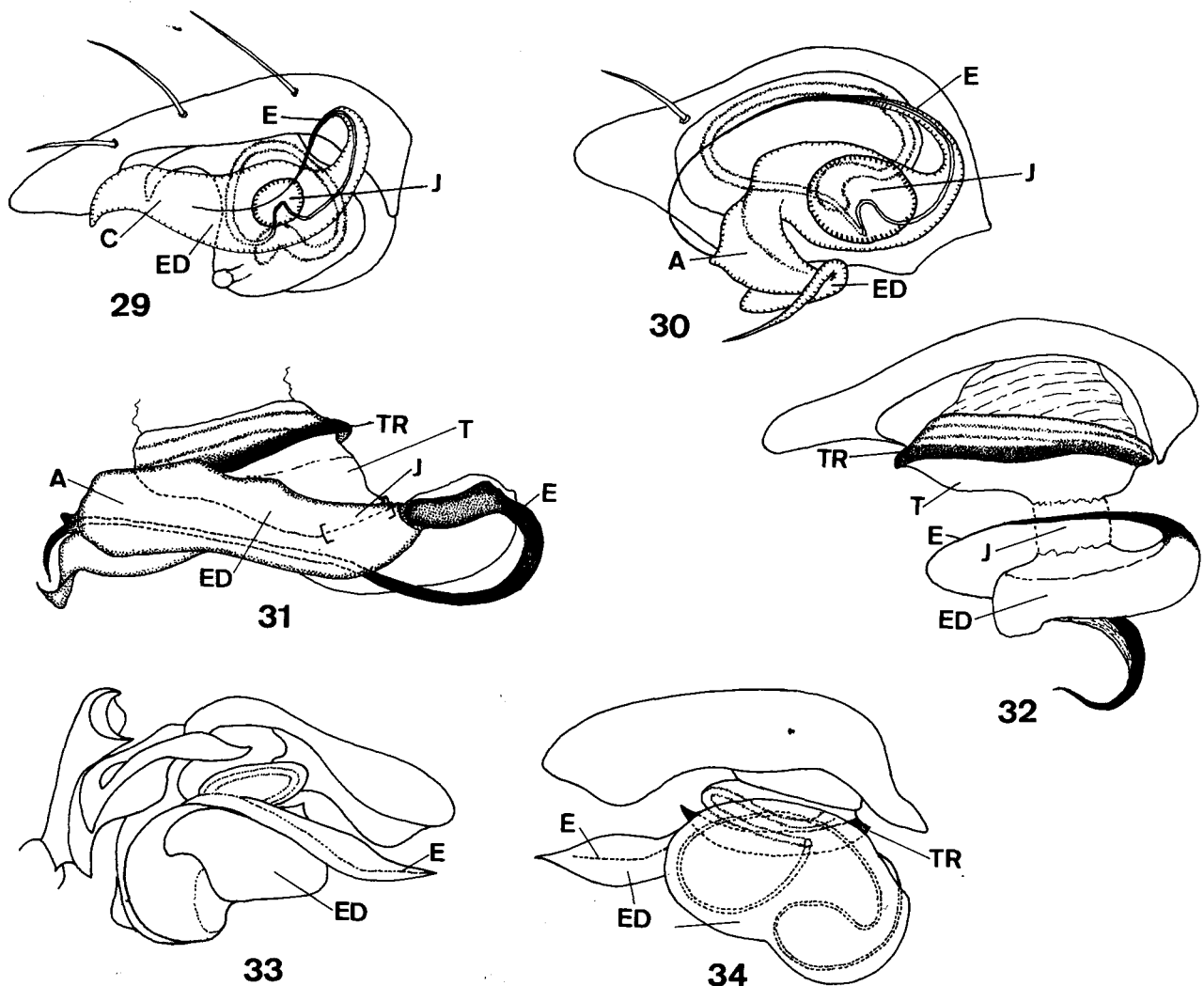
Figs. 29-34: Male palps (right). **29** *Haplinis titan* (Blest), mesoventral, cleared: ED margin and junction between ED and tegulum hatched; **30** *Cicurina cicur*, ventral, cleared: ED margin and junction between ED and tegulum hatched; **31** *Mamoea rufa*, detached bulb; **32** *C. cicur*, mesal, partly schematic to show junction; **33** S. American linyphiid species, ectal; **34** Ditto, mesal, cleared. A & C, see text; E = embolus; ED = embolic division; J = junction; T = tegulum; TR = tegular ridge.

position of the fertilisation ducts, which appear to be attached to, and open close to, the apodemes which form the margins of the dorsal plate at the posterior of the epigynum (Millidge, 1984); this character is present in most members of the family. The duct system in the epigyna of probably primitive linyphiids is often encapsulated. Some members of the Agelenidae, and of other families in the Amaurobioidea, have the fertilisation ducts in a similar position to those of the Linyphiidae, but in these taxa the dorsal plate, and the apodemal structures, are less clearly defined; hence there is not complete congruence of this epigynal character between the Linyphiidae and the members of these other families. In the Mimetidae (*Ero*) the fertilisation duct character is somewhat similar to that of the Linyphiidae, but in the Theridiidae, Araneidae, Metidae and Tetragnathidae the ducts are differently placed. The encapsulated duct character is present in some members of the Agelenidae and related families (Forster & Wilton, 1973), but not so far as I know in the Mimetidae, Theridiidae, Araneidae, Metidae or Tetragnathidae.

8. Tracheae

Several different tracheal systems are present in the Linyphiidae: in many taxa there are four slender, unbranched tubes limited to the abdomen, but in others the median tracheae are stouter, and split distally into a number of fine tracheoles which are either limited to the abdomen or extend into the prosoma (Millidge, 1986).

The Agelenidae are reported to have a simple tracheal system of four short, unbranched tubes limited to the abdomen (Forster & Wilton, 1973: 21), but the situation is in fact more complex (cf. Levi, 1967: 581). *Tegenaria* and *Textrix* do have simple tracheae of this form, but in *Cryphoeca* (Fig. 35) and *Tuberta* Simon the median tracheae are distally split into bunches of tracheoles which pass into the prosoma. This tracheal

form is very similar to that of the linyphiid genera *Meioneta* and *Agyneta* Hull, except that the tracheae open to the exterior via an atrium rather than via two spiracles. In *Cicurina* the median tracheae are also distally branched into tracheoles, but these are few in number and limited to the abdomen (Fig. 36); this is similar to the situation in the linyphiid genera *Allomengea* Strand and *Laminacauda* Millidge (some species). The genus *Argyroneta* Latr., which has usually been placed in the Agelenidae, and whatever the present view is certainly closely related to that family, has the tracheal spiracle well anterior to the spinnerets, and the tracheae are highly branched (Crome, 1952). This tracheal system, and particularly that of the juvenile (Crome, 1952: fig. 52), is very similar to that of the linyphiid species *Tennesseellum formicum* (Emerton) (Millidge, 1986: fig. 1), which also has the spiracle well anterior to the spinnerets. *Hahnia* and related genera, which like *Argyroneta* are closely related to the Agelenidae (and still placed in that family by some arachnologists), also have the tracheal spiracle well anterior to the spinnerets, and the tracheal system (Fig. 37) is practically identical with that of *Tennesseellum*.

It is possible that a few of the New Zealand genera/ species placed in the Amaurobioidea have highly branched tracheae which extend into the prosoma, but I have not been able to check this by examination of a wide enough range of taxa.

9. Web and spinnerets

Practically all members of the Linyphiidae spin a sheet web, and live on the underside, with no tubular retreat; the prey is bitten through the sheet, and then pulled through. The members of several families build sheet webs, e.g. the Agelenidae, other families of the superfamily Amaurobioidea, and some members of the Lycosidae. In most of these families, the spider lives and captures its prey on the upper side of the sheet, and
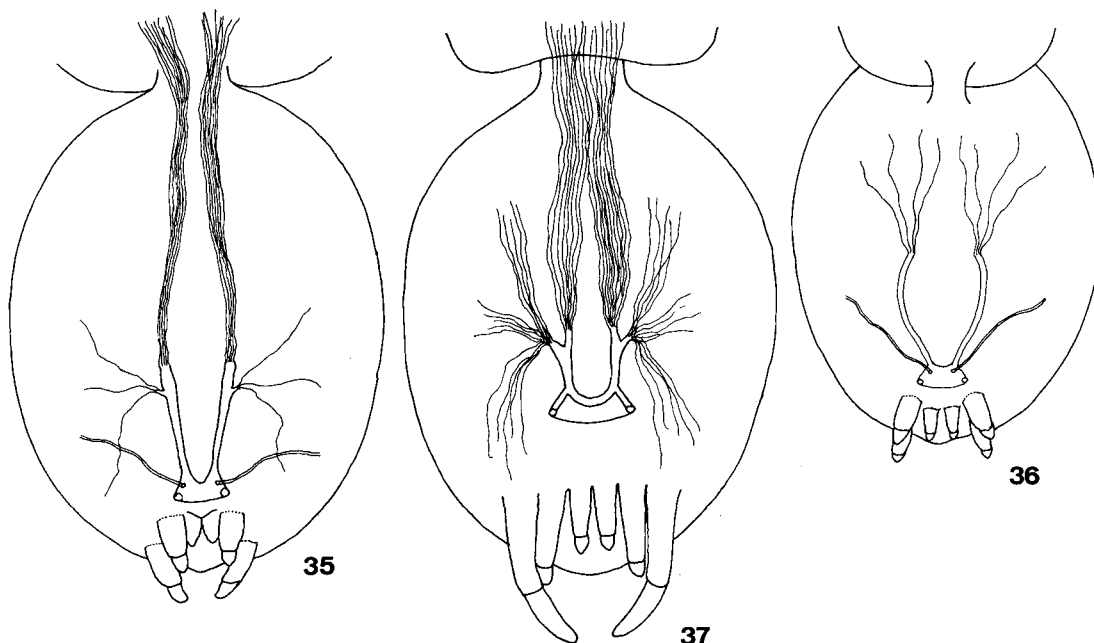
Figs. 35-37: Tracheae, ventral. **35** *Cryphoeca silvicola;* **36** *Cicurina cicur;* **37** *Hahnia helveola* Simon.

usually has a tubular retreat. In the New Zealand family Stiphidiidae (Amaurobioidea) however, the spider lives on the underside of the sheet (Forster & Wilton, 1973); the species *Cambridgea antipodiana* (White) spins a web which shows a clear similarity to the web of the linyphiid species *Frontinella pyramitela* (Walck.) (Forster & Wilton, 1973: fig. 396, cf. Kaston, 1981: fig. 2025). The legend to Forster & Wilton's figure reads: "The spider moves upside down beneath the sheet, biting through to insects knocked down onto the sheet. Occasionally it will move round on to the upper surface to capture prey". This legend is a more or less exact description of the behaviour of the linyphiid *Linyphia triangularis* (Clerck) (Bristowe, 1958: 261-263).

One feature of web building which is said to be peculiar to members of the superfamily Araneoidea is the inclusion of sticky threads, believed to be associated with the presence of aggregate glands, which open through special spigots on the posterior spinnerets (literature summarised by Kovoor, 1977; Coddington, 1986: 331). The Linyphiidae are reported to have aggregate glands, though only one or two *Linyphia* species appear to have been examined. The presence of sticky threads in the linyphiid web has been denied by Bristowe (1958: 261), but I have been able to confirm the observation of Wiehle (1956: 9) that there are very small droplets on some of the threads of a *Linyphia* sheet; the sticky threads lie erratically over the upper surface of the sheet, and their number is variable from web to web. The microdroplets are clearly visible with oblique illumination against a black background; their spacing on the threads ranges from almost contiguous to well separated. The droplets are sticky,

as can be demonstrated by touching them with a dry fine needle, but the stickiness is weak. The sticky threads are usually very slender, with a diameter (in the webs of *L. triangularis* and *L. montana* (Clerck)) of 0.001 mm or less, with the droplets around 0.0025 mm diam.; the droplets may be larger, however, in webs taken after rainfall or wet mist. The sheet webs of *Erigone, Monocephalus* F. P. Smith, *Ostearius* Hull, *Lepthyphantes* and *Microneta* Menge have also been found to contain similar threads coated with microdroplets, and it is probable that these microdroplets are present in most or all linyphiid sheets.

The sheet webs of some agelenid spiders are slightly adhesive (as most housewives know), and examination of the webs of *Tegenaria* and *Coelotes* species showed that slender threads coated with microdroplets, similar to those of the linyphiids, were present. In some *Tegenaria* webs these sticky threads were plentiful, in others they were sparse; this may possibly relate to the age of the web, since it has been noted (G. H. Locket, pers. comm.) that the sticky droplets on linyphiid webs can decline or vanish, presumably as the result of evaporation, when the web is kept in a fairly dry atmosphere. *Coelotes* webs contain areas of fairly close network composed of very fine threads carrying numerous microdroplets. A *Pardosa* sp. (immature) in captivity produced stout drag lines, but also spun small areas of finer silk which contained some threads coated with microdroplets.

Examination of webs spun by *Pholcus phalangioides* (Fuess.) showed that sticky threads of more than one kind were present, and some of these threads were very fine, coated with microdroplets similar to those present in the linyphiid and agelenid webs. The microdroplets
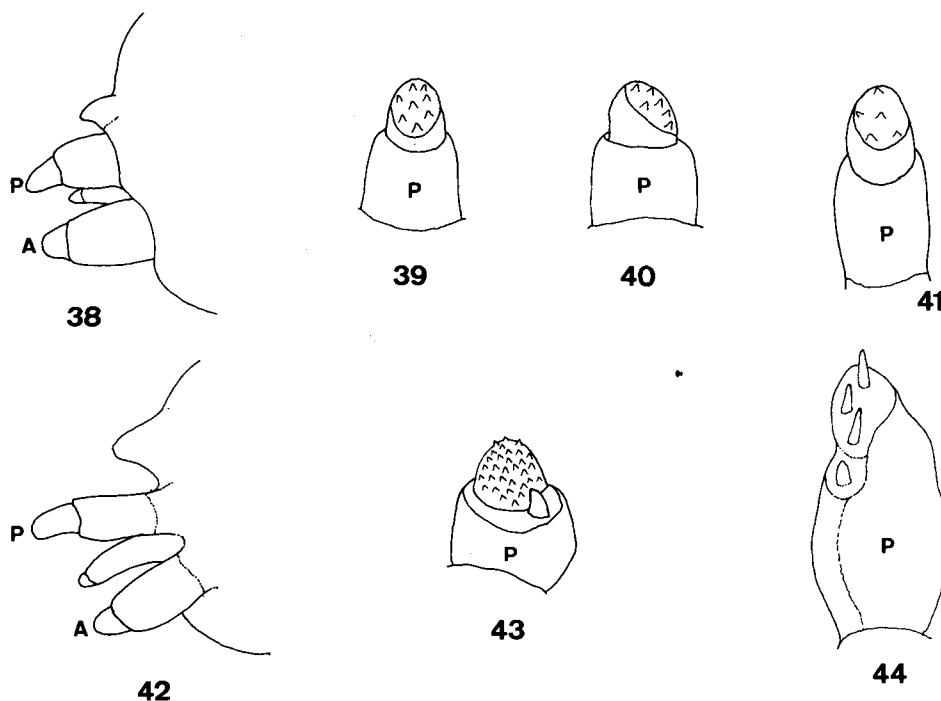
Figs. 38-44: Spinnerets, hairs omitted. **38** *Hormembolus* sp., lateral; **39** *Hormembolus* sp., mesal; **40** *Hormembolus* sp., meso-dorsal; **41** *Cicurina cicur,* mesal; **42** *C. cicur,* lateral; **43** *Linyphia triangularis* (Cl.), mesal; **44** *Cambridgea antipodiana* (White), mesal. A = anterior spinneret; P = posterior spinneret.

in all the webs mentioned above are a good deal smaller than the droplets on the sticky spiral of an araneid web, but it was found that the araneid web also contains some slender threads coated with microdroplets, particularly in the hub. As with the *Linyphia* web, the microdroplets increase in size after wet weather, and this is also true of the large droplets of the capturing spiral. The sparse scaffolding web of *Robertus lividus* (Bl.) (Theridiidae) also contains a few threads coated with microdroplets.

The posterior spinnerets of the Linyphiidae are often relatively long, with two clear segments (e.g. Fig. 38), and the spinning field of the distal segment is equipped with a number of simple spigots (Figs. 39, 40) (observations with light microscope). In both respects these spinnerets are similar in form (though smaller in size) to those of the Agelenidae (Figs. 41, 42). In most "linyphiine" genera (i.e. those which have the simple tracheal form) there is an additional, fairly large, spigot, situated at the base of the distal segment, on the joint between the two segments of the posterior spinnerets (Fig. 43); this additional spigot is carried by the female, but is absent in the adult male (juveniles not examined). Though present in most linyphiine genera, including the probably primitive genera *Haplinis* and *Stemonyphantes*, there are some exceptions; it appears to be absent, for example, in *Taranucnus* Simon, *Asthenargus* Simon & Fage, *Mioxena* Simon, *Hormembolus* and *Florinda* O. P.-Cambr. The absence seems not to be associated with small size, since the spigot is present in *Sintula cornigera* (Bl.) (length 1.7 mm). The additional spigot is well developed in *Drapetisca*, which spins no web, and in *Tapinopa* Westr., which spins a small sheet of shiny silk (Bristowe, 1958: 264). It is interesting that the extra spigot is present in the linyphiine genus *Donacochara* Simon, but absent in the very similar erigonine genus *Tmeticus* Menge; the extra spigot in fact appears to be absent in all the erigonine species. It seems unlikely that this spigot is associated with the presence and operation of aggregate glands.

The New Zealand species *Cambridgea antipodiana*, which as mentioned above spins a web similar to those of some of the larger linyphiid species, has 3-4 long spigots on the distal segment of the posterior spinnerets, and there is an additional spigot on the joint between the distal and basal segments (Fig. 44); as in the linyphiines, this spigot is absent in the adult male. It is not known whether *Cambridgea* has aggregate glands, nor whether the sheet webs of this or other stiphidiid species contain sticky threads. The British species of the Agelenidae do not have the additional spigot.

Discussion

In the current classification schemes for the Araneae (summarised by Bonnet, 1959: 5017; Lehtinen, 1967) the Linyphiidae are placed in the superfamily Araneoidea, which comprises the Araneidae, Tetragnathidae, Metidae, Theridiidae, Nesticidae, Theridiosomatidae, Symphytognathidae, Mimetidae,

Archaeidae and possibly others (Lehtinen, 1975; Heimer & Nentwig, 1982). The evidence to support this grouping as a monophyletic entity is hardly convincing, as pointed out recently by Forster & Platnick (1984). The characters given by Lehtinen (1967, 1975) for defining the group are more or less valueless (Coddington, 1986: 329, 331), and assertions (e.g. Lehtinen, 1967, 1975; Heimer & Nentwig, 1982) that the Araneoidea are a clearly defined group are patently false. Despite the lack of any firm evidence, the inclusion of the Linyphiidae in the Araneoidea seems to have been accepted without demur by practically all arachnologists. A critical appraisal of the taxonomic schemes proposed by various authors for the Araneae makes it fairly clear, however, that the principal reason for grouping together most of the families currently included in the Araneoidea was a negative one, viz. not that they *shared* characters which linked them together, but that they *lacked* (or appeared to lack) characters which would fit them into any of the other groupings (or superfamilies) then proposed.

Most of the previous work dealing with the relationships of families has been based on the subjective evaluation of the relative importance of many characters; e.g. Bristowe (1938: 287 — "cumulative assessment of all differences and resemblances") or Lehtinen (1967: 279). Such personal assessments by expert arachnologists are no doubt valuable, but because they are subjective they are not susceptible to scientific analysis. Furthermore, this method of assessment does not seriously relate to the evolutionary changes which must have taken place over the very long period of development of the families. In order to make the assessment of family relationships less subjective, and hopefully to bring it more into the realms of science, it is necessary to be able to identify those characters present in current families which can be considered to be valid for indicating relationships between such ancient groups as families or groups of families. This question was discussed earlier in this paper, and it was concluded that hypotheses of relationship at a family level should be based only on characters which are themselves relatively plesiomorphic for the family, or which can with some confidence be related to the character form which was plesiomorphic for the family.

In the early stages of the separation of two lines which ultimately led to current families, the characters present in the two branches will presumably have been quite similar to one another: there will have been only small differences in both the genitalic and somatic characters, and if the branches comprised web spinners the web forms will also have been very similar. Which of these early shared characters are likely to be still recognisable after so long a period of time? Many of the original shared genitalic characters, in both sexes, must have developed in differing directions, so that by today they have become unrecognisable (at least at first sight) as related forms. Nevertheless it is not altogether unlikely that elements of a few of the early genitalic characters will have been retained in at least the more primitive members of the current families: the problem

lies in the recognition of these elements. In most species of the Araneomorphae, the structures of the genitalia, more than any other character, are significant for inferring relationships at a specific or generic level, and meaningful congruences of the genitalic characters at a family level should at least be looked for when considering possible family relationships. In theory, it should be possible to deduce the elements of the parent genitalic form from which the two (or more) family groups under consideration were derived. This ideal may not be achievable on present knowledge, but it is only by attempting to find such correlations between two or more families that our knowledge of the evolutionary pathways of the sex organs can be advanced.

So far as non-genitalic characters are concerned, it seems probable that the web forms of the groups under consideration should still share some of the early characters of the web; indeed, the basic web form, once established as a successful means of prey capture, may have altered but little. Some unusual or specialised somatic characters may also still be recognisable in the lines concerned, but more simple or generalised somatic characters, such as those based on the nature, number and position of hairs, spines or trichobothria, are likely to have undergone change to varying degrees, so that the primitive form of the character is no longer perceivable with any certainty.

Bearing in mind what has been argued above, a number of characters of the Linyphiidae have been studied and compared with the corresponding characters in other families.

The presence of a paracymbium on the male palp has been put forward as a character which defines the Araneoidea (e.g. Shear, quoted by Coddington, 1986: 333). The term "paracymbium" has, however, been used rather loosely in the arachnological literature, and in fact covers various different forms of cymbial appendage. The linyphiid paracymbium is intersegmental, and is readily distinguishable from the integral paracymbia carried by most members of the Araneoidea auct. The origin of the linyphiid paracymbial form is obscure (it could have been transferred to the joint membrane from either the cymbium or the tibia), and there is no evidence that it is homologous with the knob-like paracymbia of the Araneidae. Integral paracymbia appear to be fairly widely but erratically distributed throughout the entelegyne families, and are not limited to members of the Araneoidea auct. Thus not only is the paracymbium (s. lat.) eliminated as a synapomorphy for the Araneoidea, but also it does not apparently indicate any close relationship between the Linyphiidae and the Araneidae, Metidae, Tetragnathidae or Theridiidae. It must be concluded that at the present time this character is of little if any value for the establishment of family relationships.

The palpal bulb of the Linyphiidae exhibits at least two characters which appear to differentiate it from the bulb of almost all other families. These are, firstly, the sclerotised and thickened, often projecting, tegular margin on the mesal side, and, secondly, the presence of an "embolic division", a distinct sclerite linked to the

tegulum by a narrow or relatively narrow neck. These two palpal characters seem to be absent in the Araneidae, Metidae, Tetragnathidae, Theridiidae, Nesticidae and Mimetidae, and so far as is known are shared only with some members of the Agelenidae and the Amphinectidae. The first character is present also in a New Zealand genus of the family Amaurobiidae, and it is not impossible that both characters may be present in some species of other genera allocated to New Zealand families of the Amaurobioidea and Dictynoidea (Forster, 1970). These two bulbal characters appear to be primitive for the Linyphiidae, but whether they are primitive for the Agelenidae and Amphinectidae is not known. The development of both of these unusual characters in each of the family lines can nevertheless be taken as a good indication of a common ancestry. This relationship between the Linyphiidae and the Agelenidae is also supported by the sharing of two characters of the palpal cymbium, viz. the presence of mesal spines and the excavated ectal margin. These characters are also shared with some species of other amaurobioid families, and with members of the Philodromidae and the Gnaphosidae (see later).

The Linyphiidae have a number of different tracheal forms, and it is of interest that the Agelenidae (s. lat.) exhibit a very similar range of forms. Both families have some genera in which the median tracheae are stout and divided anteriorly into numerous fine tracheoles which may or may not extend into the prosoma, and both families have taxa in which the tracheal spiracle is well anterior to the spinnerets. The close congruence of the tracheal forms in the two families is in agreement with the hypothesis that these families share a common ancestry. It is not known whether other amaurobioid families have multiple tracheal forms.

The web of practically all members of the Linyphiidae is a simple sheet, with the spider living on the underside; in some of the larger species the sheet is embellished with a superstructure of knockdown threads. It must be very probable that the primitive web form of the family was a sheet. As pointed out earlier, species of the genus *Cambridgea* (Stiphidiidae: Amaurobioidea) build a web very similar to that of some linyphiids, and live on the underside, rather than on the upper side which is the usual position for members of this superfamily. The procedure of prey capture of *Cambridgea* is also very similar to that of *Linyphia*. The change from living on the upper surface of the web to living beneath the web is not a great one; when the early sheet and tube builders began to move out from a protected environment, e.g. in crevices, under rocks, etc., to more exposed positions amongst vegetation, then movement to below the sheet would have given increased protection from predators, while at the same time eliminating the need for a tubular retreat. An upside-down life would present no problem for a spider, since this is its inevitable position when moving along a thread. The method of prey capture of linyphiids and stiphidiids, viz. biting through the sheet, is also used by *Atypus,* but this is presumably a case of

convergence.

The posture of *Cambridgea* on its web disposes of the suggestion (Heimer, 1982: 285) that living on the underside of the web is a defining character for the Araneoidea.

It is usually stated (e.g. Coddington, 1986) that the linyphiid web contains sticky threads, and the present work has confirmed Wiehle's observation (1956) that the sheet web of *Linyphia* has some threads which carry minute droplets; these microdroplets were also found to be present in the webs of other linyphiid species. Aggregate glands, which open via special spigots on the posterior spinnerets, and which are reported to be the source of the sticky droplets on the trapping spiral of orb-web builders (Kovoor, 1977), have been demonstrated in only one or two species of the Linyphiidae. It appears unlikely that aggregate glands (if they are indeed present in most linyphiids) are responsible for the production of the microdroplets of the linyphiid web, since similar threads coated with microdroplets are present in the sheet webs of agelenids which are reported not to have aggregate glands.

It is not known whether sticky microdroplets are present in the sheet webs spun by families other than the Agelenidae, although fragments of web spun by a captive juvenile *Pardosa* sp. (Lycosidae) also contained threads with the microdroplets. The web of *Pholcus* (Pholcidae) was found to have an assortment of sticky threads, some of which are very slender and coated with microdroplets as in the Linyphiidae. Similar microdroplets are also present on some threads of the araneid orb web, particularly on the hub; these are quite distinct from those on the sticky spiral. The tiny web of *Robertus* O. P.-Cambr. (Theridiidae) also contains threads with microdroplets. The microdroplets in the linyphiid and agelenid webs are only weakly adhesive, and it seems unlikely that they can make much contribution to prey immobilisation; the slight adhesion to the prey, however, may be advantageous by serving to amplify the vibrations produced by prey movement.

Since the microdroplets are present in the webs of several families which do not spin orb webs, the presence of such sticky threads in the linyphiid web cannot be used as a character to indicate a close relationship between the Linyphiidae and the Araneidae and other orb-web spinning families. The general similarity of the sheet webs of the Linyphiidae, the Agelenidae, the Stiphidiidae and other amaurobioid families, the posture of *Cambridgea* on its web, the presence of similar microdroplets on the threads of the linyphiid and agelenid webs, and the absence on these webs of the large, araneid-type sticky droplets, together support the hypothesis of a close relationship between the sheet webs spun by the linyphiids and the various sheet webs spun by the agelenids and related families; that is, they indicate that these families have a common parentage.

Protagonists of the superfamily Araneoidea, however, maintain that the linyphiid web is a derived (reduced) form of the orb web (e.g. Coddington, 1986:

324), which presumably was itself evolved from some earlier, less organised, web form. The hypothesis that the linyphiid sheet was evolved by the stages of elaboration of some earlier web form to an orb, followed by reduction to a sheet, is obviously less parsimonious than the hypothesis that the linyphiid web is simply a sheet, like other sheet webs. The data reported here support the more parsimonious hypothesis, and there appears to be no evidence to support the less parsimonious; consequently there is no longer any need to pretend that the linyphiid web is anything but what it appears to be, namely a sheet web of the same general form as other sheet webs, and probably sharing the same parentage.

The wide distribution of the microdroplet character makes it probable that the production of threads coated with sticky droplets, of one form or another, may be a relatively plesiomorphic character for the Araneae, and that the threads with microdroplets represent a more primitive stage of development of the sticky droplet character than the trapping spiral of the orb web. If aggregate glands are truly the source of the large sticky droplets of the araneid web, and if aggregate glands are derived from aciniform glands (Coddington, 1986: 340), then it may be that the microdroplets are the product of the aciniform glands, and that the higher demand for sticky material during the course of development of the orb web led to the conversion of some aciniform glands into aggregate glands, which were capable of a higher productivity of the sticky liquid.

The results presented in this paper highlight the problems involved in identifying characters which can be accepted as reliable indicators of family relationships, at least so far as the larger and more developed families are concerned. A few characters of the palpal bulb, and the web form, appear to be satisfactory characters to support the hypothesis that the Linyphiidae are most closely related to the sheet web building families, particularly to the Agelenidae and Amphinectidae, and perhaps also to some related families currently placed in the superfamily Amaurobioidea, e.g. the Stiphidiidae and the Amaurobiidae. The similarities of the multiple tracheal forms of the Linyphiidae and Agelenidae, of the cymbial characters, of the trichobothrial pattern of the metatarsi and tibiae, and some features of the epigynal form, are in accord with the hypothesis (i.e. do not falsify it), though taken individually these characters would probably not be sufficient to justify the hypothesis. The absence of the rebordered labium in the Agelenidae also does not falsify the hypothesis, since the rebordered labium seems to be a normal development of the labial form present in many entelegyne families, and at least one genus of the Amphinectidae has a rebordered labium. The hypothesis is not necessarily falsified by the presence of the intersegmental paracymbium in the Linyphiidae, and its absence in the Agelenidae, since the origin of this form of paracymbium is not definitely known. Some members of the Agelenidae, like some members of the Linyphiidae, have an integral paracymbium.

The presence of stout median tracheal trunks seems to be a characteristic of most members of Forster's entelegyne superfamily Dictynoidea (Forster, 1970), in which he includes the genera *Argyroneta* and *Hahnia* which are close to the Agelenidae and often included in that family. The presence of such trunks in members of the Linyphiidae and the Agelenidae may be indicative of a fairly close link between these two families and the families of the Dictynoidea. In this connection, it may be of relevance that the males of a few linyphiid species from New Zealand have (? retained) the dictynid form of chelicerae. It is not known whether the New Zealand amaurobioid families contain, like the Agelenidae, some species with the median tracheal trunks.

The clypeal sulci of the Mynogleninae and the post-ocular sulci of the males of some erigonine species were regarded by Blest (1979) as homologous structures, but of uncertain provenance. The presence of the character in the Mynogleninae might indicate that it is primitive for the family, but perhaps more likely that the Linyphiidae lie in a branch of the Araneomorphae where this character ("ocular" sulci) is present or potentially present. The current work has shown that shallow ocular sulci are present in some members of the families Agelenidae, Lycosidae, Pisauridae, Thomisidae, Philodromidae, Gnaphosidae and Liocranidae. These sulci are located in essentially the same positions as the ocular sulci in the Linyphiidae, and this suggests that the sulci in these families should be considered to be structurally homologous with those of the Linyphiidae. The poorly developed sulci present in these families correspond with stage (ii) of Blest's hypothetical evolutionary sequence which led to the more highly developed linyphiid sulci (Blest, 1979: 169). Although the ocular sulci are present in members of the few families given above, the character does not appear to be widespread in the Araneae; thus there is no evidence at present that the character is plesiomorphic for the Araneae as a whole. As a first (most parsimonious) hypothesis it must be assumed that the ocular sulci have evolved only the once, and consequently that all the families which carry the character lie in the same evolutionary branch, i.e. form part of the same monophyletic group. This is not in disagreement with the hypothesis of a close relationship between the Linyphiidae and the Agelenidae. A relationship between the Linyphiidae, Agelenidae (and

some other families of the Amaurobioidea), Philo-dromidae and Gnaphosidae is also supported by the cymbial characters.

The presence of "marginal" cephalic sulci in some members of the Linyphiidae is probably of no value for establishing family relationships. This character seems to be present in a wide range of families, and consequently it appears likely to be a relatively plesiomorphic character of the Araneae. In most families the character is represented only by weak depressions, but in the Malkaridae (Moran, 1986; Platnick & Forster, 1987) and the Micropholcommatidae (Platnick & Forster, 1986) the sulci are more strongly developed, and like the ocular sulci of the Mynogleninae and the Erigoninae, and the marginal sulci of *Erigone*, they have acquired pores which open to secretory glands. Although described here as "marginal" sulci, these cuticular depressions appear in fact to be associated with the junction of "head" and "thorax", and in some instances they are not adjacent to the carapace margin, e.g. in *Atypus* and *Eperigone*.

Several of the characters examined (cheliceral file, labial form, trochanteral notch and reversed palpal duct rotation) are present in some members of a wide range of entelegyne families, and this suggests that many (if not all) of the entelegyne families share a common ancestry. None of the characters examined, however, gives any credence to the existence of a close relationship between the Linyphiidae and the orb-web spinning families, the Theridiidae, the Nesticidae or the Mimetidae.

Although the data available point to the families of sheet web builders as the closest relatives of the Linyphiidae, it would be unsafe to designate any one of these families as the sister group of the Linyphiidae. It is probably prudent to assume that Nature, like Truth, is "rarely pure and never simple" (Wilde, 1895), and it seems unlikely that evolution has been considerate enough to produce family branches in neat pairs. A more credible situation would probably be as shown schematically in Fig. 45, where the sister group of Family A would be the complex of families B-H, and the only families to have a single family as a sister group would be G and H; the situation that the sister group of one family is another family is likely to be the exception rather than the rule. Of course, some families in a sister group complex will be closer in characters to the family concerned than others, e.g. in Fig. 45 it is likely that B will be closer in characters to A than will H, and on the basis of its characters B might well be considered (erroneously) to be the sister group of A. It seems probable, on the basis of available data, that the sister group of the Linyphiidae will be made up of a group of families which include the Agelenidae (*s. lat.*) and the Amphinectidae, and probably some other families currently placed in the Amaurobioidea and Dictynoidea. On the basis of the cephalic sulci character (and possibly the cymbial characters) this group of families would itself form part (not necessarily a branch) of a larger group comprising at least the Lycosidae (some of which build sheet webs similar to those of the Agelenidae), Pisauridae, Thomisidae,
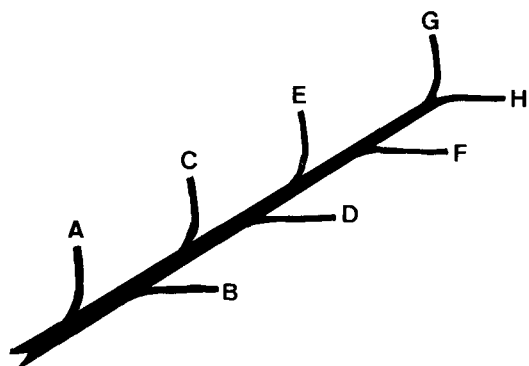

Fig. 45: Diagrammatic scheme of evolution of families A-H: see text.

Fig. 46: *Erigone jugorum* Simon, male. Left marginal sulcus, anterior end, showing plugged pit and 3 pores exterior to sulcus, × 1100.

Philodromidae, Gnaphosidae, Zoridae and Liocranidae.

The superfamily Araneoidea auct. has already been depleted by the removal from it of the Archaeidae and Mimetidae (Forster & Platnick, 1984), and on the basis of the present work it must be further depleted by the removal of the Linyphiidae. I would personally regard it as virtually certain that a critical reappraisal of the characters of the Theridiidae and Nesticidae will necessitate the removal of these families also.

The superfamily Araneoidea appears to have been erected on somewhat weak foundations, and this is probably true of most of the named superfamilies so far proposed. These large groups often appear to owe more to subjective assessments and speculation than to scientific method, and all should be regarded with a healthy scepticism by the scientific taxonomist. One example is the Amaurobioidea (Lehtinen, 1967; Forster & Wilton, 1973), into which the Linyphiidae, on the evidence presented in this paper, might appear to fall; despite Lehtinen's statement that the limitation of this superfamily is not difficult, the definition in fact given is so general that it is really no definition at all. It may be true that this, and other superfamilies, bring together certain families which appear to be generally similar in *current* characters, but it would be unwise to take such superfamilies very seriously unless they are based on at least one *eligible* shared character.

The designation of named superfamilies (presumed to be monophyletic) for the Araneomorphae is effectively an assumption that the phylogenetic tree of this arm of the Araneae has a number of substantial side branches. At the present time, when our knowledge of family relationships in the Araneae is, from the scientific viewpoint, distinctly nebulous, it is not desirable that the phylogeny of the group should be pre-empted in this way; there must be other possibilities which should not be excluded from consideration. For example, if the evolution of the Araneomorphae has been essentially serial (of the form shown schematically in Fig. 45), there will have been few, if any, large side branches which could count as monophyletic superfamilies. Alternatively, it is

tempting to speculate that the most important characters for defining the phylogenetic groups in the Araneomorphae are the form of the web, and the technique of prey capture, both of which may well represent ancient and enduring habits which are resistant to change or loss. Three such phylogenetic lines would comprise (i) those families which spin sheet webs or modified sheets, (ii) those which spin orb webs or webs which are clearly modified orb webs (i.e. a more realistically defined Araneoidea), and (iii) those which have the distinctive theridiid prey capture technique of combing silk over the prey with the tarsi of the fourth legs (Theridiidae, Nesticidae, ? Pholcidae, ? Hadrotarsidae). Each of these three groups would have originated, in separate evolutionary lines, from ancestors which lived in tubular retreats equipped with a few threads (radii) around the entrance. Some, or even many, of the current taxa which do not build snares, but hunt in one way or another, may have been derived from web-building ancestors; for example, many of the three-clawed taxa placed by Forster in the Dictynoidea (Forster, 1970) are hunters, some being quite like thomisids in appearance, and some members of the Lycosidae (also three-clawed) still build agelenid-like sheet webs (Brady, 1962). It would seem more probable that such hunters evolved from tube or sheet web builders, the prey capture technique of which was the simple one of rushing out and seizing their victim, rather than from the orb-web builders or those of the theridiid group, both of which had developed (or were developing) more sophisticated techniques of prey capture. Other hunters, with more specialised techniques of prey capture, e.g. Mimetidae, Archaeidae, might however have descended from members of the theridiid group or the orb-web builders.

A phylogenetic scenario of this kind, in which each of the three separate lines of web builders (and their derivative hunting forms) had followed serial evolutionary sequences of the type shown in Fig. 45, could be responsible for the difficulties which are encountered in trying to identify characters (other than web form) which will define most of the superfamilies so far proposed, since with such a scenario these superfamilies would be no more than convenient fictions, and the search for synapomorphies to substantiate them as monophyletic groups would be a search for the non-existent.

These speculative thoughts are put forward less as definite hypotheses than as matters which require discussion. It is to be hoped that more taxonomists will be encouraged to cast a critical and questioning eye on the classical hypotheses of spider phylogeny, most of which were erected to a large extent on the basis of the work and ideas of nineteenth century arachnologists.

characters mentioned under "paracymbium" in this paper, and for the production of scanning electron micrographs; and to Mr G. H. Locket for the loan of specimens, for allowing me to examine the webs spun by several spiders in captivity, and for helpful comments on an earlier draft of this paper.

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