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Cladistics and the comparative morphology of linyphiid spiders and their relatives (Araneae, Araneoidea, Linyphiidae)

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This paper provides the first quantitative cladistic analysis of linyphiid morphology. Classical and novel homology hypotheses for a variety of character systems (male and female genitalia, somatic morphology, spinneret silk spigot morphology, etc.) are critically examined and studied within a phylogenetic context. Critical characters have been illustrated. A sample of linyphiid taxa (nine genera in four subfamilies), five species of *Pimoa* (Pimoidae), and two other araneoid families (Tetragnathidae and Araneidae, represented by *Tetragnatha* and *Zygiella*, respectively) were used to study the implications of the phylogeny of Pimoidae for the systematics of linyphiids. The phylogenetic relationships of these 16 exemplar taxa, as coded for the 47 characters studied, were analysed using numerical cladistic methods. In the preferred cladogram Pimoidae and Linyphiidae are sister groups, Stemonyphantinae are sister group to the remaining linyphiids, and Mynogleninae are sister group to the clade composed of Erigoninae plus Linyphiinae. These results agree with the relationships recently proposed by Wunderlich, except by finding erigonines as the sister group to linyphiines rather than to mynoglenines.

ADDITIONAL KEY WORDS:—Pimoidae–systematics–morphology–homology–phylogeny.

CONTENTS

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INTRODUCTION

The Linyphiidae is one of the most diverse spider families, containing more than 440 described genera and over 3600 species described up to 1987 (Platnick, 1989a). Linyphiids account for more than 10% of described spider diversity. Only the Salticidae, the jumping spiders, exceed linyphiids in diversity. For example, Roberts (1987) lists 618 spider species and 220 genera for the British fauna, of which 267 (43%) of them are linyphiid species, and 105 (48%) are linyphiid genera. While the European spider fauna is almost completely known (particularly the British and Middle and North European fauna), the picture changes quite dramatically in other parts of the world (Coddington & Levi, 1991). In a recent study of the poorly known South American linyphiid fauna (Millidge, 1991) 42 out of a total of 58 genera treated (72%) were new. In the same study 249 (93%) of the included species were new. In addition to their high taxonomic diversity, linyphiids are also numerically abundant, and are thus an important arthropod component of (at least) northern hemisphere temperate ecosystems. Bristowe (1941:503) estimated that more than half of the spider population of Britain belonged to the Linyphiidae.

Merrett (1963) has offered a detailed account of the taxonomic history of Linyphiidae, while Millidge (1980) has discussed more recent developments.

Although alpha-taxonomic papers on linyphiids are numerous, only a few workers have investigated the phylogenetic structure of the family and its placement within araneoid phylogeny. Wunderlich (1986; Fig. 32A) recently proposed a phylogenetic hypothesis for the linyphiid higher level phylogeny. Wunderlich (1986) suggested that pimoids (which he ranked as a linyphiid subfamily, Pimoinae) were the putative sister group of linyphiids (i.e. sister to the rest of linyphiids). More recently, Hormiga (1994) has found additional evidence in support of the sister group relationship of pimoids and linyphiids, and has delimited Linyphiidae to exclude the pimoines, which were ranked as a family (Hormiga, 1993). Wunderlich's (1986:106) cladogram for the subfamilies of Linyphiidae (Fig. 32A) can be summarized in parenthetical notation as follows: Stemonyphantinae (Linyphiinae (Mynogleninae, Erigoninae)). The subfamily Linyphiinae is composed by two tribes, the Micronetini and the Linyphiini. Wunderlich's cladogram provides diagnoses for the different linyphiid clades, but unfortunately his hypothesis is difficult to evaluate for several reasons. First, Wunderlich does not explicitly discriminate between diagnostic and synapomorphic characters in his clade diagnoses, and some of the character states used to define monophyletic groups are plesiomorphic (e.g. basal paracymbium). This distinction (character polarity) is a crucial one, because only synapomorphies should be used to delimit clades. Second, his hypothesis lacks clear and explicit character definitions, which in turn are needed to assess the different hypotheses of homology (and homoplasy) that have been suggested in the literature (e.g. are all linyphiid epigynal atria homologous?). Recent studies on higher classification of spiders (Goloboff, 1993; Griswold, 1993) suggest that, as Coddington & Levi (1991) have put it, the problem of phylogenetic inference largely resides in the allocation of homoplasy, rather than in finding characters. Third, character variation within the terminal taxa is not discussed, and a test of his hypothesis might be dependent on the taxa selected as exemplars for a particular clade. Fourth, some of the characters used in his study

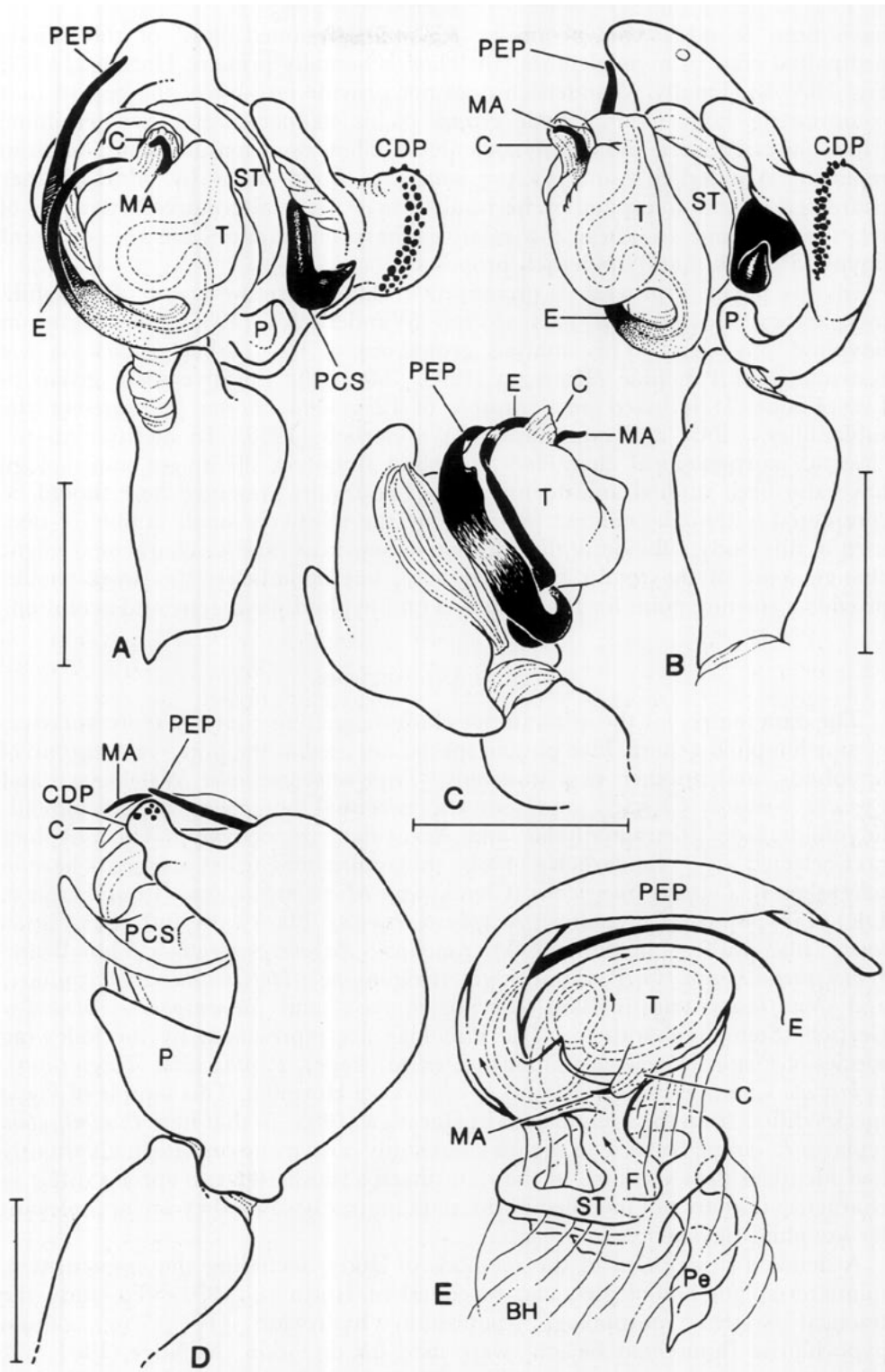


Figure 1. Male palp morphology of *Pimoa*. A, *P. crispa*, ventral. B, Ditto, ectal. C, *P. rupicola*, mesal. D, *P. hespera*, dorsal. E, *P. altioculata* (schematic, scale bars = 0.5 mm).

have been found to be erroneous, e.g. the presumed 'loss' of the female pedipalpal claw of mynoglenines (the claw is actually present; Hormiga, 1993; Fig. 19A, B). Finally, Wunderlich does not provide any list of the genera that comprise the large monophyletic groups of his cladogram (i.e. the linyphiine tribes, the erigonines, and the mynoglenines). These omissions make it difficult to replicate Wunderlich's analysis (or worse, to build on it by adding either characters or taxa to expand on his results), to evaluate alternative hypotheses of relationship, and to assess the relative character support for the different linyphiid clades that Wunderlich proposes.

In this paper I provide a quantitative cladistic reassessment of linyphiid morphology, designed in part to test Wunderlich's (1986) hypothesis on linyphiid phylogeny. This analysis grows out of two earlier studies on the systematics of Pimoidae (Hormiga, 1993, 1994), the putative sister group to Linyphiidae. It is based on a sample of 12 genera chosen to represent the subfamilies, tribes, and outgroups of Wunderlich (1986). In addition to the classical morphological characters, linyphiid spinneret silk spigot morphology have also been studied and documented. The results presented here should be considered within the context provided by the relatively small sample of taxa used in this study. Obviously the addition of new taxa (and/or characters) might change some of the results presented here, but nonetheless this work should provide a starting point for future studies on linyphiid phylogeny and evolution.

MATERIAL AND METHODS

The data matrix for the quantitative cladistic analysis contains representatives of nine linyphiid genera. Five pimoid species are used as the putative outgroup of linyphiids, and another two araneoids (*Tetragnatha versicolor* Walckenaer and *Zygiella x-notata* (Clerck)) represent the potential outgroups to the pimoid-linyphiid clade (Tetragnathidae and Araneidae, respectively). The linyphiid taxa selected are (Wunderlich's (1986) subfamilies and tribes are given here in parentheses): *Linyphia triangularis* (Clerck) and *Microlinyphia dana* (Chamberlin & Ivie) (Linyphiinae, Linyphiini); *Bolyphantes luteolus* (Blackwall) and *Lepthyphantes tenuis* (Blackwall) (Linyphiinae, Micronetini); *Erigone psychrophila* Thorell and *Walckenaeria directa* (O. P.-Cambridge) (Erigoninae); *Haplinis diloris* (Urquhart) and *Novafroneta vulgaris* Blest (Mynogleninae); and *Stemonyphantes blauveltae* Gertsch (Stemonyphantinae). The Pimoidae are represented by the following species of *Pimoa*: *P. rupicola* (Simon), *P. crispa* (Fage), *P. altioculata* (Keyserling), *P. breviata* Chamberlin & Ivie, and *P. edenticulata* Hormiga. This sample of *Pimoa* species differs from the sample used in Hormiga (1993) in that here *P. edenticulata* replaces *P. curvata* because in the previous study *curvata* and *breviata* inadvertently had identical data columns in the data matrix (the latter two species differ in characters that are not included in this data matrix because they are not relevant for linyphiid phylogeny).

A detailed description of the methods of study, including the assessment of spinneret spigot homologies, can be found in Hormiga (1994). To study the tracheal system morphology, potassium hydroxide (10%) or sodium hypochlorite (household bleach) were used for digestion (Millidge, 1984; 5% solution at room temperature). The digested specimen was then washed in distilled water, stained with an aqueous solution of chlorazol black, and

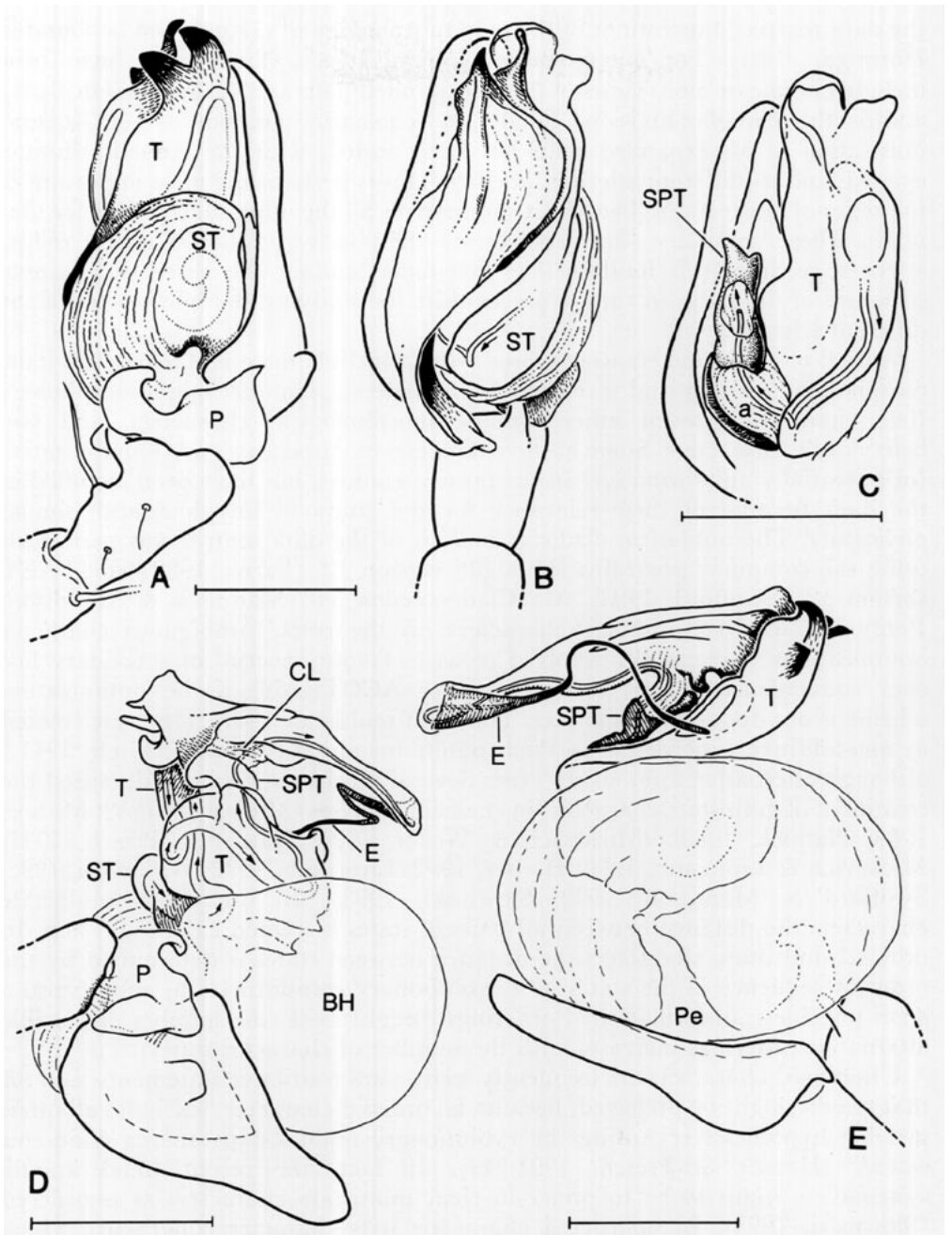


Figure 2. *Stemonyphantes blauveltae*, male palp morphology. A, Ectal. B, Ventral. C, Ventral, embolic division removed ('a' is the membranous hinge of the suprategulum). D, Expanded, dorsoectal. E, Ditto, mesal (scale bars = 0.5 mm).

mounted on a slide with a drop of an 85% aqueous solution of lactic acid. Overall, the method followed has been modified from Ray Forster (personal communication).

Palp morphology has been illustrated for every linyphiid species included in

the data matrix (illustrations of the palp morphology in pimoids can be found in Hormiga, 1994). For every species camera lucida illustrations have been included of one or more views of the unexpanded palp and of the expanded palp and/or the embolic division. Finally, a schematic (i.e. not camera lucida) illustration of an expanded palp has been added, with the embolic division excised, and its different sclerites labelled. This is perhaps the most important of the series of illustrations, because it summarizes all the other illustrations for that taxon. These 'summary' illustrations show the relative position of all the palpal sclerites because it is fundamental for understanding the three dimensional structure of the palp, in turn a prerequisite for studying the homologies of the different sclerites.

A total of 47 characters were scored, which include male and female genitalic morphology (30 male and three female characters), spinneret spigot morphology (five characters), seven other somatic morphological characters, and two behavioural characters. Some of the characters in Appendix 2 are uninformative (or potentially uninformative) in the present context, but have been included in the data because of their relevance for the study of linyphiid and pimoid phylogeny. The numerical cladistic analysis of the data matrix was performed using the computer programs Hennig86 version 1.5 (Farris, 1988) and PAUP version 3.1 (Swofford, 1993). MacClade version 3.0 (Maddison & Maddison, 1992) was used to optimize characters on the trees. Ambiguous character optimizations were usually resolved so as to favour reversal or secondary loss over convergence (Farris optimization or ACCTRAN) if the optimization scheme is not discussed in the text. The eight multistate characters were treated as non-additive (unordered or Fitch minimum mutation model; Fitch, 1971), although alternative approaches exist. Several recent papers have discussed the treatment of multistate characters in cladistic analyses (Mickevich, 1982; Mabee, 1989; Platnick, 1989b; Mickevich & Weller, 1990; Hauser & Presch, 1991; Mickevich & Lipscomb, 1990; Hauser, 1992; Lipscomb, 1992; Wilkinson, 1992; Swofford & Maddison, 1992; Slowinski, 1993). In unordered multistate characters the distance between all pairs of states is treated as a single step. In ordered multistate characters the distance between states is determined by the order or sequence of the states in a evolutionary transformation, and several *a priori* possible transformations ('orderings') might exist (the number of possible alternative orderings increases with the number of character states).

Unordered characters are frequently seen as less restrictive statements, and for that reason might be preferred, because an ordered character "excludes all other possible hypotheses regarding the evolutionary relationships among character states" (Hauser & Presch, 1991:244). In fact, the recent trend among systematists seems to be to prefer to treat multistate characters as unordered (Slowinski, 1993). In unordered characters it is character congruence which determines the state order and no non-falsifiable hypotheses are constructed (Hauser & Presch, 1991; Hauser, 1992). Hauser & Presch (1991) have argued that if character congruence is used as a falsifying criterion to assess character evolution, it is inappropriate to order multistate characters, because ordered characters cannot be falsified by character congruence except in an *a posteriori* fashion that is independent of the tree building algorithm. Swofford & Maddison (1992:216) have also suggested the use of unordered character states (and equal costs for all transformations) "as a suitable starting point, loosely analogous

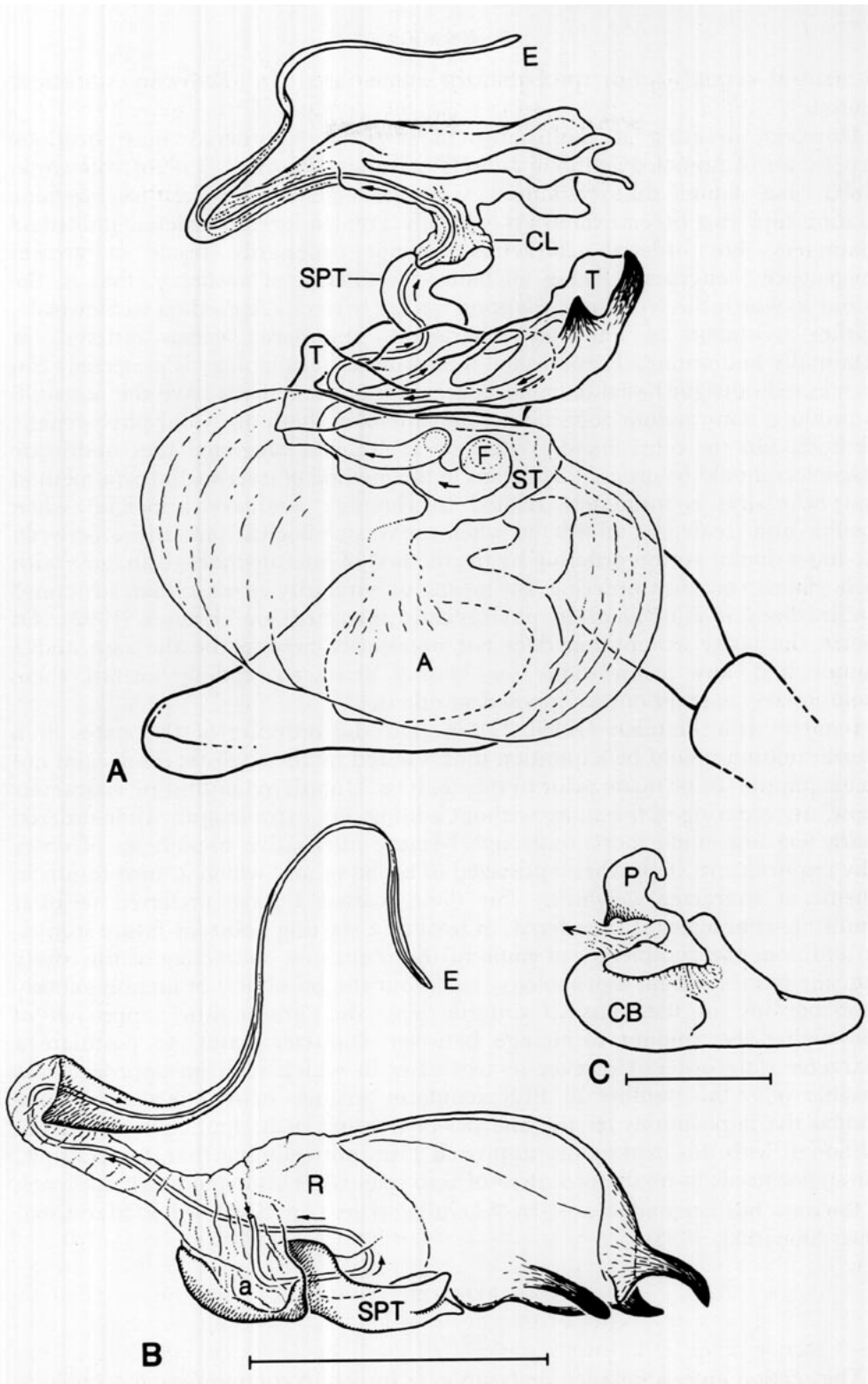


Figure 3. *Stemonyphantes blauweltae*, male palp morphology. A, Expanded (schematic). B, Embolic division ('a' is the membranous hinge of the suprategulum). C, Paracymbium, ectoventral (scale bars = 0.5 mm).

to neutral (equal) prior probabilities often used in Bayesian statistical analysis".

However, treating a multistate character as unordered may overlook hypotheses of homology among subsets of states (Platnick, 1989b). Slowinski (1993) has found that resolution (i.e. the extent to which phylogenetic relationships can be recovered) is typically greater for the ordered multistate characters, but ordered characters do not necessarily result in greater congruence (congruence being an indirect estimator of accuracy, that is, the extent to which the recovered relationships are correct). According to Slowinski, neither treatment of multistate characters (unordered versus ordered, or maximally and minimally connected if Slowinski's terminology is preferred) can be rejected outright based on congruence, and both methods have the potential to produce non-random congruence, and therefore both are valid phylogenetic methods. On the other hand, Wilkinson (1992) has suggested that multistate characters should be ordered by means of the method of intermediates (a method that he claims is intimately related to Hennig's auxiliary principle) when possible and treated as unordered when the morphological similarities between the states do not permit ordering by the method of intermediates. I disagree with such claims, because ordering by means of similarity *assumes* that structural intermediacy is equivalent to phylogenetic intermediacy (Hauser, 1992). Of course the latter assumption does not necessarily need to be the case and I cannot find any justifications for biasing character coding toward these evolutionary assumptions as opposed to others.

I agree with Platnick (1989b:23) in that the ordering of the states in a transformation should be a question that is tested by the cladistic results and not an assumption to be made prior to the analysis. Unordered multistate characters allow any ordering of the states without adding any extra length, while ordered characters are much more restrictive because alternative hypotheses of order may require extra steps when optimized in a cladogram, which in turn results in scheme of character weighting. For these reasons I have preferred to treat multistate characters as unordered, at least as a starting point for future studies. In addition, the complexity of some of the multistate characters of this study (e.g. the paracymbium morphology) ruled out the possibility of unambiguously applying any of the classical criteria (e.g. the 'gradualistic' approach of minimizing the amount of change between character states) to postulate a character state order. However in two cases in which such an approach was possible (e.g. the number of PLS aciniform spigots: many-one-zero) I have studied the implications for the analysis of treating such characters as ordered (although with this exploratory approach I am not claiming that, for example, one spigot needs to be the precursor of zero spigots). This exploratory approach to the data has been advocated by several workers (e.g. Swofford & Maddison, 1992; Slowinski, 1993).

RESULTS

Characters

This section gives a detailed description of linyphiid comparative morphology and its coding into the characters and character states used in the phylogeny reconstruction. Some of the characters are applicable only to the pimoids, and

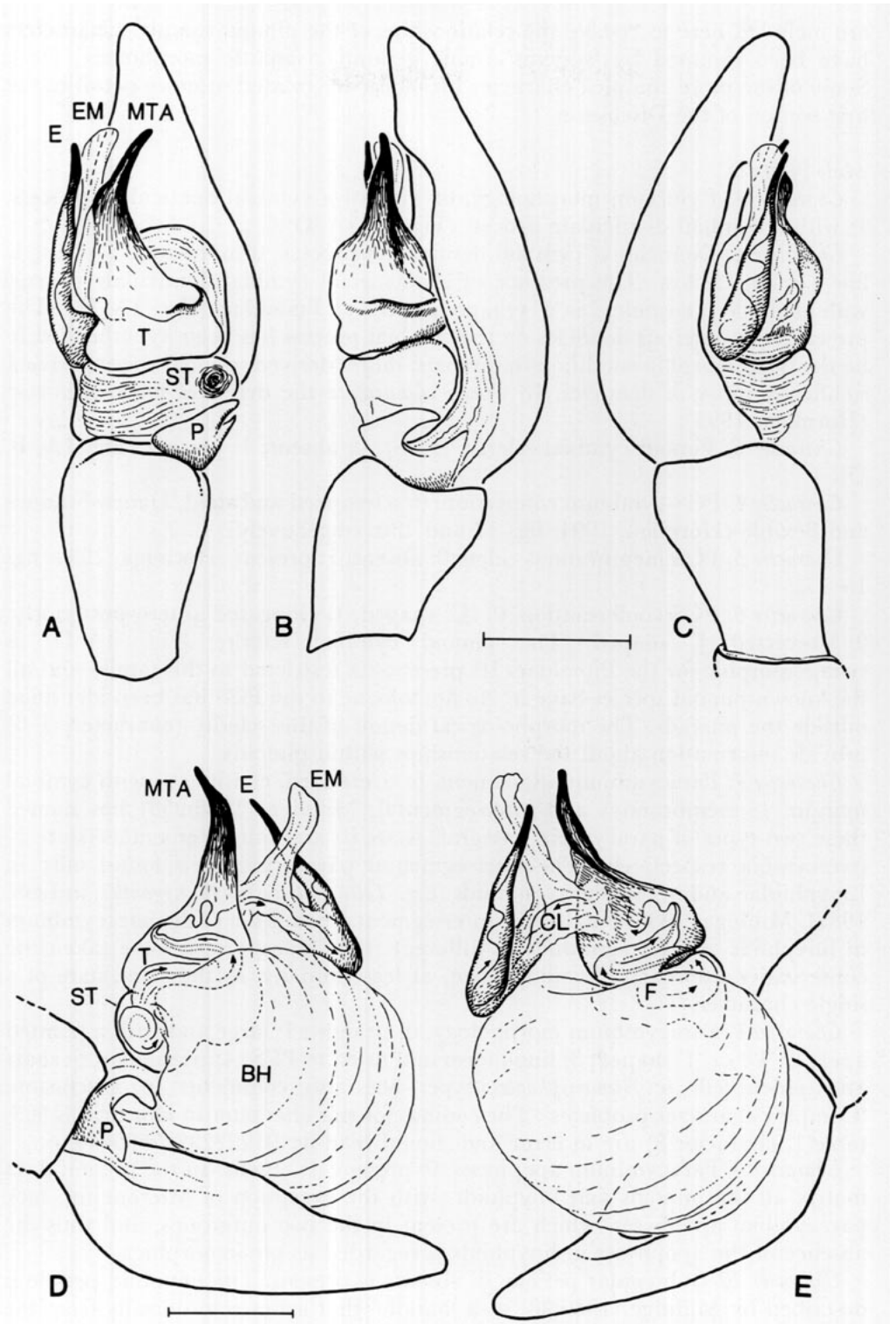


Figure 4. *Novafroneta vulgaris*, male palp morphology. A, Ventral. B, Ectal. C, Mesal. D, Expanded, ectal. E, Expanded, mesal. (scale bars: A–c = 0.2 mm; D & E = 0.1 *mm*)

are included here to resolve the relationships of the pimoid sample. Characters have been grouped by 'systems' (male genitalia, somatic morphology, etc.). Some of the more complex character problems are treated in more detail in the first section of the Discussion.

Male genitalia

Character 1. Cymbium morphology. 0: without a cymbial denticulate process; 1: with a cymbial denticulate process (Figures 1A–D).

Character 2. Denticles of cymbial denticulate process. 0: numerous (> 20); 1: few (< 20); 2: lost. The presence of a dorsoectal cymbial denticulate process with denticles (cuspules) is a synapomorphy of Pimoidae (Fig. 1A–D). The presence of numerous denticles on the cymbial process has been hypothesized to be the plesiomorphic condition in pimoids; more 'derived' pimoid species have a smaller number of denticles. In *Pimoa edenticulata* the denticles have been lost (Hormiga, 1994).

Character 3. Pimoid cymbial sclerite (PCS). 0: absent; 1: present (Fig. 1A, B, D).

Character 4. PCS-cymbium connection. 0: sclerotized and rigid; 1: membranous and flexible (Hormiga, 1994: figs 17 and 130, respectively).

Character 5. PCS membranous ridge. 0: absent; 1: present (Hormiga, 1994: figs 15–17).

Character 6. PCS conformation. 0: 'U' shaped; 1: elongated antero-posteriorly; 2: 'reversed J' shaped. The pimoid cymbial sclerite (Fig. 1A–D) is synapomorphic for the Pimoidae. Its presence is restricted to this family and all the known pimoid species have it. No homologue to the PCS has been identified outside the pimoids. The morphological details of this sclerite (characters 4–6) provide information about the relationships within pimoids.

Character 7. Paracymbium attachment. 0: sclerotized, continuous with cymbial margin; 1: membranous and intersegmental. Millidge (1988:258) has named these two types of paracymbia 'integral' (state 0) and 'intersegmental' (state 1) paracymbia respectively. The intersegmental paracymbium is found only in Linyphiidae and in some tetragnathids (e.g. *Tetragnatha* and *Pachygnatha,* in Levi, 1981). Millidge (1988) regards the intersegmental condition of the paracymbium in linyphiids and tetragnathids as different (see Discussion). I have taken the conservative approach of coding them, at least initially, as the same state of a single character.

Character 8. Paracymbium morphology. 0: straight; 1: large and with a pointed apex; 2: 'U' or 'J' shaped; 3: linguiform and fused to PCS; 4: triangular; 5: short and procurved; 6: *Stemonyphantes* type. See also comments in Discussion: 'Complex character problems'. The codings for this character in Hormiga (1993, table 1, character 8) are in error and should read as: 0122222222635444.

Character 9. Paracymbium apophyses. 0: present; 1: absent. In the present data matrix all the pimoids and linyphiids, with the exception of Micronetini, lack paracymbial apophyses, which are present in the two outgroups, and thus the absence of the apophyses in linyphiids is regarded as plesiomorphic.

Character 10. Subtegular petiole. 0: absent; 1: present. The linyphiid petiole is described by Millidge (1980:98) as a 'handle' that arises ecto-dorsally from the subtegulum. The presence of a subtegular petiole seems to be restricted to araneids and linyphiids (Coddington, 1990a).

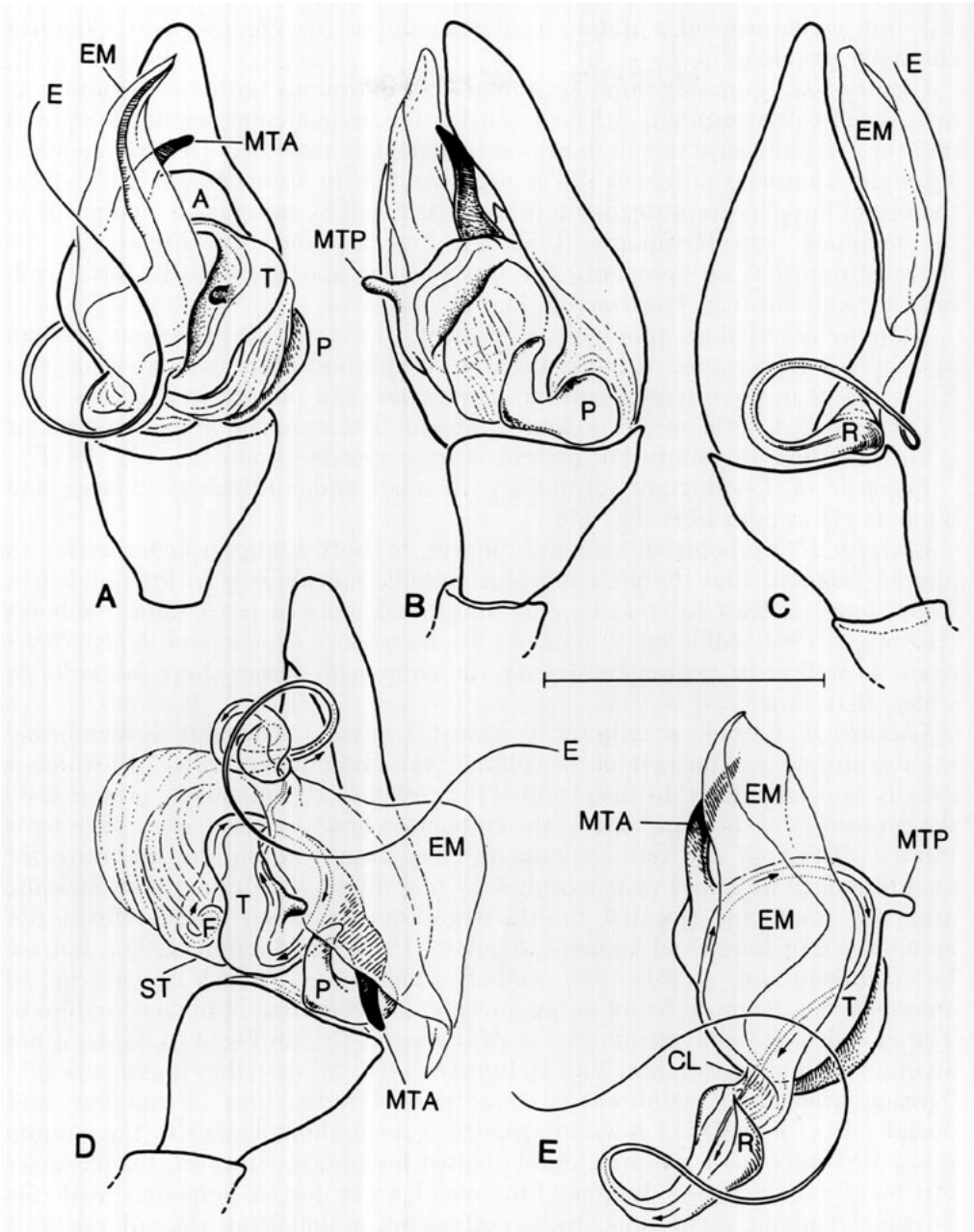


Figure 5. *Haplinis diloris*, male palp morphology. A, Ventral. B, Ectal. C, Dorsomesal. D, Expanded, ectal. E, Embolic division and tegulum (schematic, scale bar = 0.5 mm).

Character 11: Tegular suture. 0: conspicuous; 1: subtle or absent. This character is restricted to the pimoids, which have the tegulum divided into a distal and basal region by means of a suture that runs from the anteroectal towards the posteromesal margin of the tegulum (Hormiga, 1994: fig. 16).

Character 12: Mynoglenine tegular apophysis. 0: absent; 1: present. I have coded mynoglenines as lacking the typical linyphiid suprategulum (see character

13), but having instead a unique tegular apophysis (see comments in 'Complex character problems').

Character 13: Suprategulum. 0: absent; 1: continuous with the tegulum; 2: articulated to the tegulum. I have regarded the mynoglenine tegular apophysis and the linyphiid suprategulum as non-homologous structures (see comments in 'Complex character problems'). The suprategulum in *Stemonyphantes* differs from the rest of linyphiid suprategula in being articulated by means of a membrane to the tegulum (van Helsdingen 1968:124; Figs 2C and 3B). Frequently the suprategulum has an apophysis, the suprategular apophysis, on its distal end, near the column (e.g. *Walckenaeria*, Fig. 6C, SA).

Character 14. Median apophysis. 0: present; 1: absent. The araneoid median apophysis, which is present but reduced in size in most of the pimoids (Fig. 1A–E), is absent in the linyphiids and in *Tetragnatha*, and present in *Zygiella*.

Character 15. Conductor. 0: present; 1: absent. The araneoid tegular conductor is absent in the linyphiids, but present in most species of pimoids (Fig. 1A–E).

Character 16. Conductor morphology. 0: small and undivided; 1: large and bilobate (Hormiga, 1994: fig. 368).

Character 17. Embolus. 0: long and filiform; 1: short. Outgroup comparison to pimoids suggests that the plesiomorphic embolic morphology in linyphiids is a rather long (at least twice as long as wide), and more or less filiform, embolus (Hormiga, 1994; Millidge, 1984:254). In *Bolyphantes luteolus* and *Lepthyphantes tenuis*, as well as in *Erigone psychrophila*, the embolus is rather short (as wide, or wider, than long).

Character 18. Embolic membrane. 0: absent; 1: present. The embolic membrane is a membranous outgrowth of the column (van Helsdingen, 1986:123), which is usually associated with the distal end of the embolus. Its function is, presumably, the protection of the distal end of the embolus, where the ejaculatory opening is located. Although the term 'conductor' has been used in the literature for descriptions of linyphiid palp morphology (e.g. Blest, 1979), linyphiids lack the araneoid conductor (located on the tegulum, and such usage reflects not homology, but functional analogy (Saaristo, 1971; Coddington, 1990a, but see his comment on p. 16). The embolic membrane, which is absent in *Stemonyphantes*, seems to be an autapomorphic development of higher linyphiids. The so called 'embolic membrane' in *Microlinyphia* ('m' in Fig. 11B, C, E) is not an outgrowth of the column. Van Helsdingen (1970:6) describes it as a structure "arising from (the) membranous connection of radix, base of embolus, and dorsal side of lamella". I have interpreted it as nonhomologous to the column positioned embolic membranes found in other linyphiids. However, the nature of this membrane remains dubious. One could argue for its homology with the linyphiid embolic membrane, by hypothesizing a shift from the column to a radical position. This latter hypothesis produces no change in the cladogram topology. Another alternative hypothesis is to consider the membrane in *Microlinyphia* as homologous to that associated with the terminal apophysis of some 'derived' linyphiids (see character 25). See also comments in 'Complex character problems'.

Character 19. Pimoid embolic process (PEP). 0: absent; 1: present. This structure is an autapomorphic development of the embolus in pimoids (Fig. 1A–E).

Character 20. PEP conformation. 0: undivided; 1: divided.

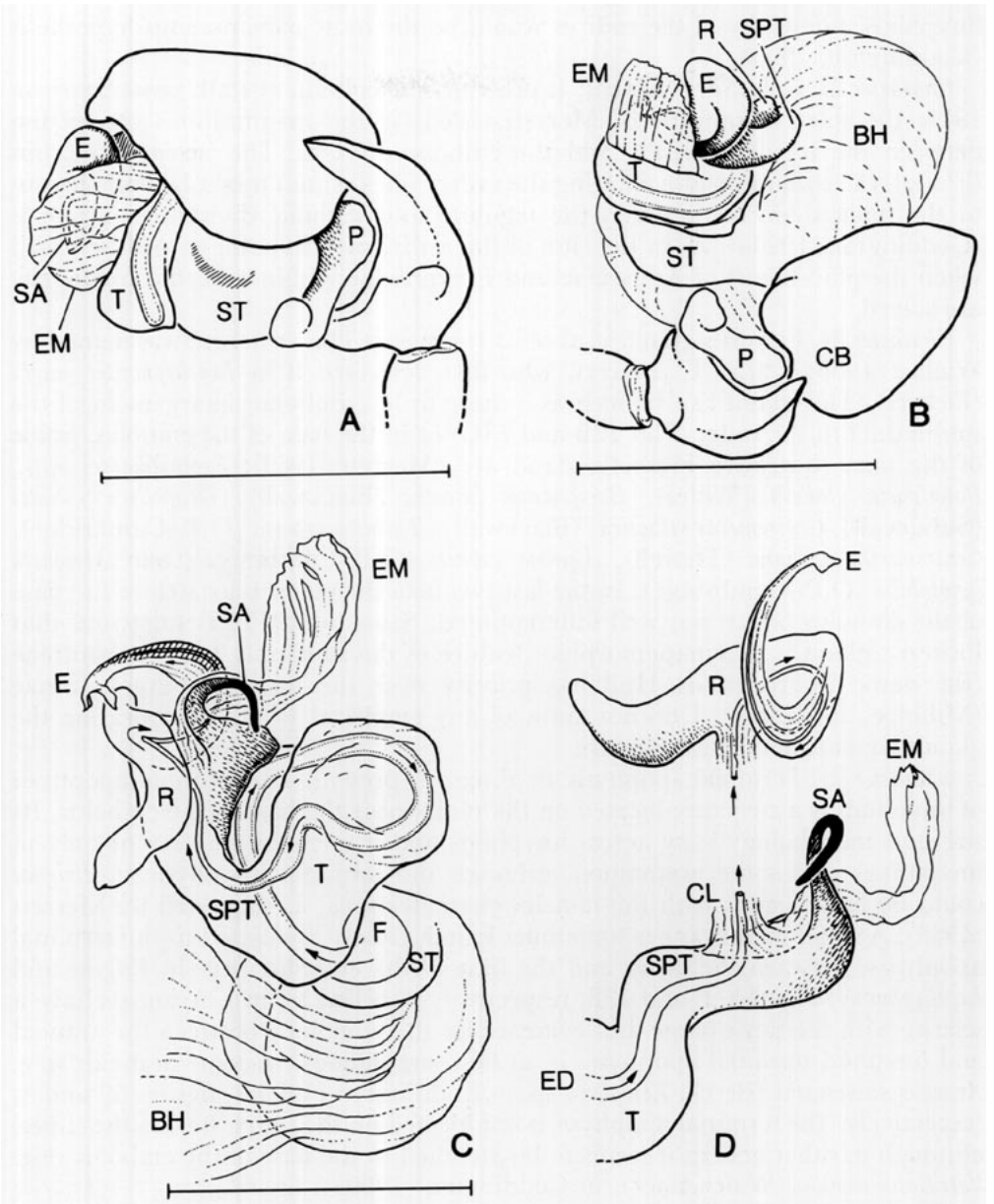


Figure 6. *Walckenaeria directa,* male palp morphology. A, Ectal. B, Expanded, ectal. C, Embolic division, tegulum, and subtegulum. D, Embolic division (schematic, scale bar = 0.5 mm).

Character 21. PEP base. 0: narrow; 1: wide and lamelliform.

Character 22. Radix. 0: absent; 1: present. The radix is a palpal sclerite, of varying size and morphology, on which the embolus and any of the rest of the components of the embolic division are located. The sperm duct enters into the radix, from the column, before entering the embolus. A sclerite of the same name can be found in *Zygiella* and in many other araneids, but the homology between these two sclerites is quite dubious. If araneids are sister to pimoids plus

linyphiids, homology of the radices would be the most parsimonious hypothesis (Coddington, 1990a).

Character 23. Column. 0: absent; 1: present. The column or stalk (*sensu* Saaristo, 1971; the duct membrane of Merrett, 1963) is the membranous connection between the tegular division and the embolic division. The sperm duct runs through the column before entering the radix. The column might be homologous to the haematodocha between the tegulum and embolic division in araneids (Coddington, 1990a). As in the case of the radix, such hypotheses will be tested when the placements of Araneidae and Linyphiidae within araneoid phylogeny are solved.

Character 24. Fickert's gland. 0: absent; 1: present. This structure was named by Wiehle (1956:6) after C. Fickert, who first described it in *Lepthyphantes mughi* (Fickert). This gland can be seen as a more or less globular enlargement of the sperm duct in the radix (Figs 12B and 13C) or in the base of the embolus. Some of the taxa that have Fickert's gland are (Merrett, 1963): *Lepthyphantes* spp., *Poeciloneta globosa* (Wider), *Bolyphantes luteolus* (Blackwall), *Drapetisca socialis* (Sundevall), *Centromerus sylvaticus* (Blackwall), *Tallusia experta* (O.P.-Cambridge), *Centromerita concinna* (Thorell), *Agyneta subtilis* (O.P.-Cambridge), and *Meioneta innotabilis* (O.P.-Cambridge). In the last two taxa the gland is located in the base of the embolus and is not well differentiated. Saaristo (1975:23) suggested that Fickert's gland is a (synapomorphic) feature of the subfamily Lepthyphantinae (the name Micronetinae Hull has priority over the name Lepthyphantinae (Millidge, 1984:246)). I do not know of any empirical work corroborating the glandular nature of this structure.

Character 25. Terminal apophysis. 0: absent; 1: present. The terminal apophysis of linyphiids is a structure located on the radix, near the base of the embolus. Its size and morphology vary across linyphiids and it seems to be present only in linyphiines and some erigonines, although the terminal apophysis in *Erigone* could be homologous with the lamella characteristica, as suggested by Merrett (1963). A small membrane is sometimes found, closely associated to the terminal apophysis, between the latter and the base of the embolus (e.g. in *Erigone* and *Lepthyphantes,* Figs 7A–F and 13B, respectively, labelled as 'm'). Araneids have a sclerite with the same name, but evidence for the homology between the araneid and linyphiid terminal apophyses is, at best, ambiguous. In some araneids (e.g. *Araneus diadematus* Clerck, *Eriophora* sp. in Coddington (1990a), figures 59 and 8, respectively) the terminal apophysis is not located on the radix, but on the stipes, although in other genera it seems to be attached to the base of the embolus (e.g. *Verrucosa arenata* (Walckenaer), in Coddington (1990a): fig. 64).

Character 26. Lamella characteristica. 0: absent; 1: present. The lamella characteristica is a sclerite of the linyphiid embolic division, located in the basal part of the radix, adjacent and posterior to the terminal apophysis. This sclerite is particularly large and conspicuous in some genera (e.g. *Lepthyphantes, Helophora, Microlinyphia,* etc.). While the lamella is absent in the erigonine sample of this study (but see character 25 for an alternative hypothesis), many erigonine genera have a radical sclerite that Merrett (1963) homologized with the lamella characteristica (e.g. *Hilaira frigida* (Thorell), *Tapinocyboides pygmaeus* (Menge), and *Milleriana inerrans* (O.P.-Cambridge), depicted in Merrett's figures 48, 53 and 54, respectively).

Character 27. Male pedipalpal retrolateral tibial apophysis. 0: absent; 1: present

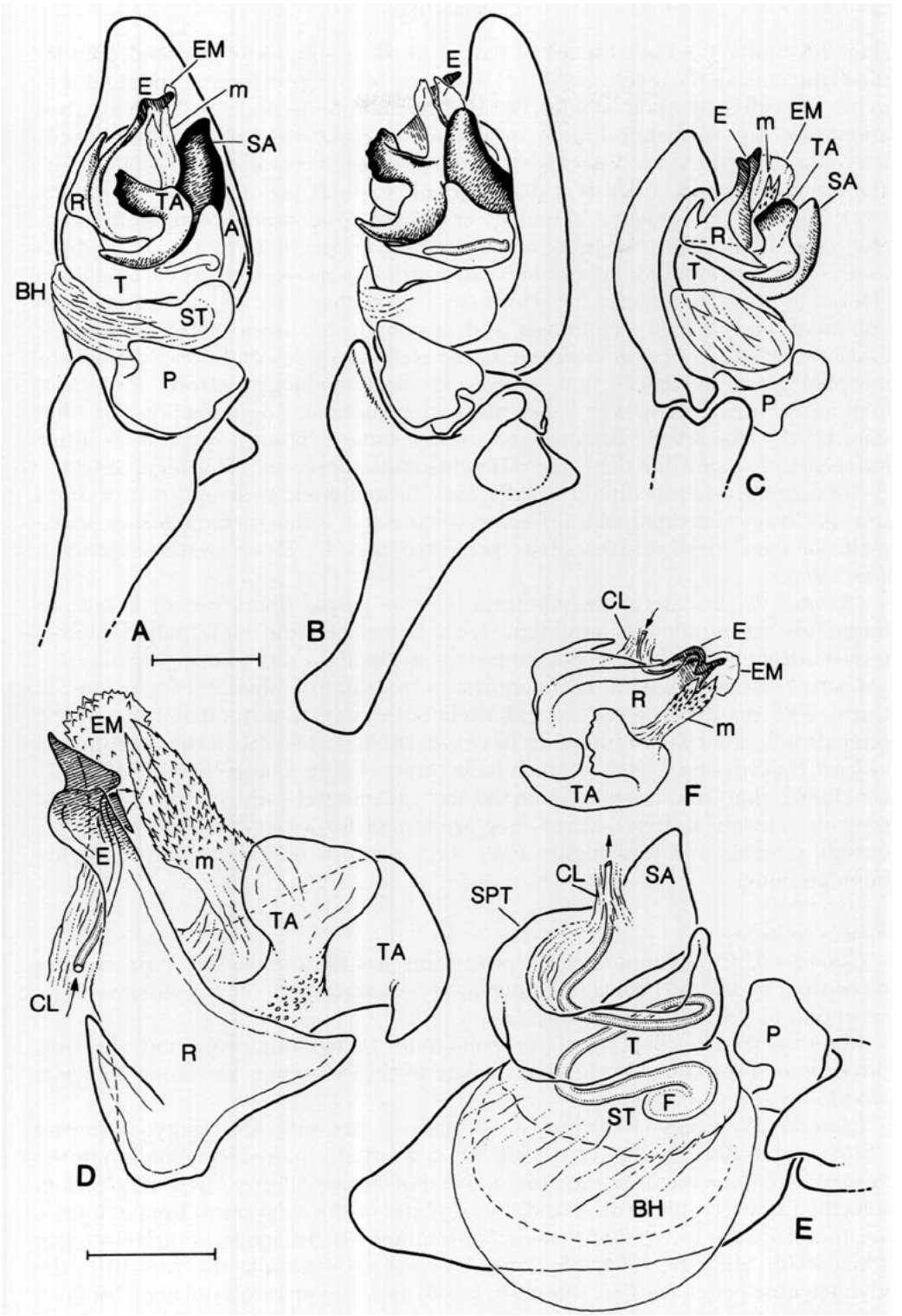


Figure 7. *Erigone psychrophila*, male palp morphology. A, Ventral. B, Ectal. C, Partially expanded, mesoventral (schematic). D, Embolic division. E, F, Schematic, embolic division excised (scale bars = 0.2 mm, except D, 0.1 mm).

(Figs 6A and 7A). The absence of palpal tibial apophyses is plesiomorphic for the Orbiculariae (Griswold, 1990:14) and therefore its presence in linyphiids has to be regarded as apomorphic. Within the linyphiids male pedipalpal tibial apophyses are restricted to the erigonines (retrolateral and usually heavily sclerotized, Figs 6A and 7A) and to *Stemonyphantes* (ventral and hook-like, Fig. 7B). In the pimoids there is a dorsal rounded tibial protuberance (Hormiga, 1994; Fig. 1B). The classical homology criteria of position and detailed similarity (Remane, 1956) do not suggest homology of the erigonine retrolateral apophysis to the tibial apophyses of pimoids and *Stemonyphantes*. In previous analyses (Hormiga, 1993, character 27; Hormiga, 1994, character 33) the male tibial apophysis morphology in pimoids and linyphiids has been coded in a single multistate character (with 'absence' as the plesiomorphic condition), despite the morphological evidence that suggested non-homology across the three mentioned taxa. However, the most parsimonious optimization of that unordered character, despite its conservative coding, suggested three independent origins for the three different tibial apophyses (Hormiga, 1993).

Character 28. Male pedipalp tibial spines. 0: scattered; 1: arranged in a distal row. A cluster of pedipalpal tibial spines arranged in a row is characteristic of the males of some 'derived' pimoids (represented here by *Pimoa edenticulata* and *P. altioculata*).

Character 29. Prolateral trichobothria in male palpal tibia. 0: two; 1: one. In linyphiids the number of prolateral trichobothria on the male palpal tibia is reduced from two (pimoids and outgroups in the data set) to one.

Character 30. Retrolateral trichobothria in male palpal tibia. 0: two; 1: four; 2: three. The presence of retrolateral trichobothria in male palpal tibia of the pimoids is apomorphic. Linyphiids have two trichobothria (with the exception of at least *Haplinis* and *Linyphia*, which have three). Using a larger sample of taxa I concluded that characters 29 and 30 are meaningful only in the context of pimoids (Hormiga, 1994); when they are scored for a larger suite of taxa (i.e. outside pimoids and at a higher level) they seem to be uninformative (highly homoplasious).

Female genitalia

Character 31. Epigynum form. 0: protruding less than its width; 1: protruding more than its width. Protruding epigyna are characteristic of pimoids, with the exception of the basal *Pimoa rupicola*.

Character 32. Dorsal plate of the epigynum. 0: without projections; 1: with projections. Projections of the dorsal plate of the epigynum are found in *Pimoa edenticulata* and in *P. breviata*.

Character 33. Epigynal atrium. 0: absent; 1: present. The epigynal atrium ('bursa copulatrix' in Blauvelt, 1936:90) is a usually paired epigynal chamber formed by enlargements of the proximal end of the copulatory ducts. The atrium is located between the ventral and dorsal plates of the epigynum. Epigynal atria are found in the Linyphiini genera *Linyphia* and *Microlinyphia* (van Helsdingen 1969, 1970; Millidge, 1984:235, 255). An epigynal atrium is also present in the mynoglenine genus *Haplinis* (Blest 1979:100) but absent in *Novafroneta* (Millidge 1984:241). Similar epigynal atria are also present in other linyphiids not included here that are not closely related to the Linyphiini (Millidge, 1984; van Helsdingen, *in litt.*).

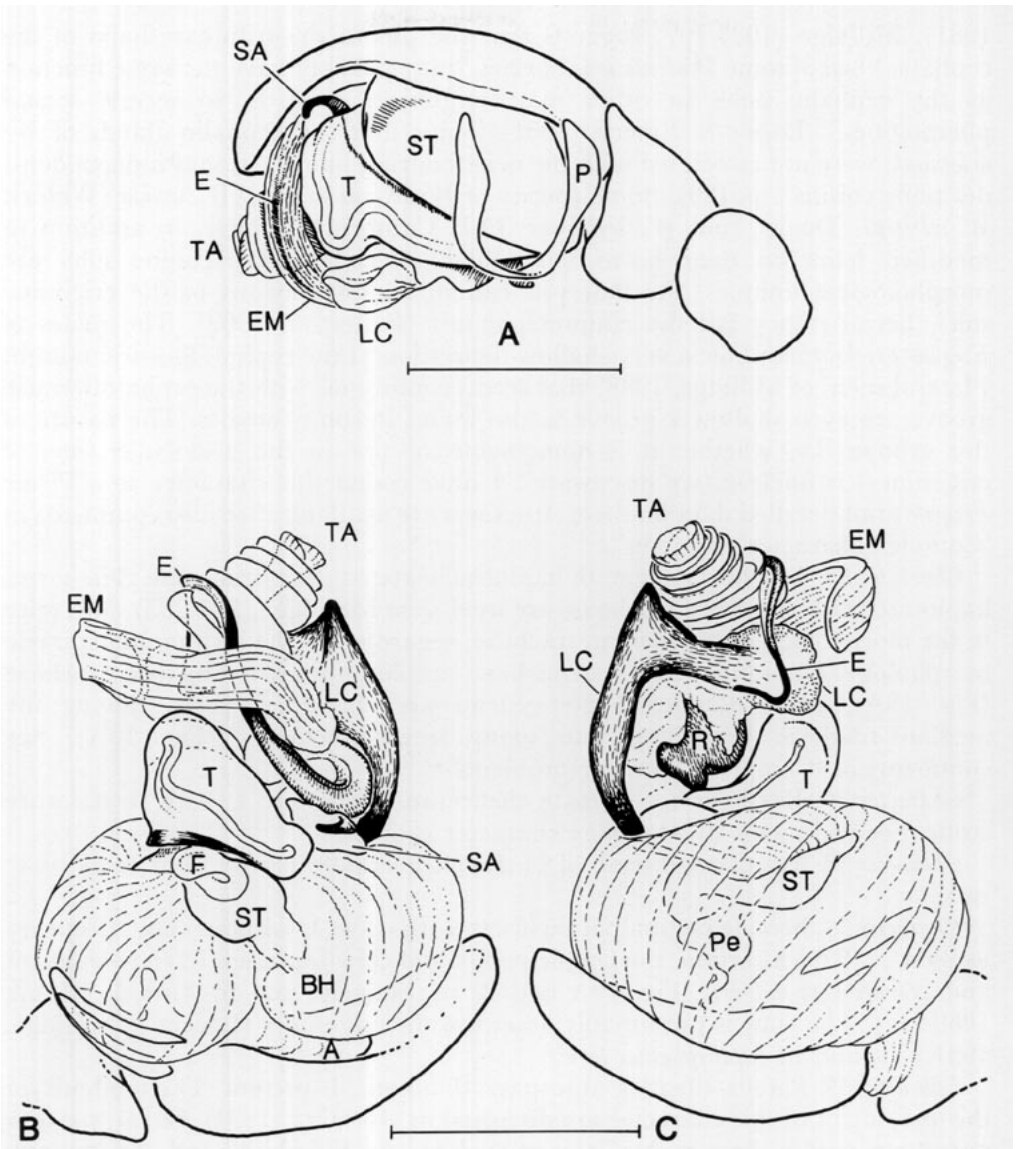


Figure 8. *Linyphia triangularis*, male palp morphology. A, Ectal. B, Expanded, ectal. C, Expanded, mesal (scale bars = 0.5 mm).

Somatic morphology

Character 34. Mynoglenine cephalic sulci. 0: absent; 1: present. The presence of sub-ocular cephalic sulci (Fig. 19H, I) with secretory cells that exhibit a unique strategy of membrane amplification (Blest & Taylor, 1977; Blest & Pomeroy, 1978; Blest, 1979) is a putative synapomorphy for mynoglenine linyphiids (Millidge 1984). Under the dissecting microscope *Walckenaeria directa* shows no sulci; scanning electron microscopy is needed to assess the presence of cuticular openings. Cuticular pores and their associated gland have been described for the cephalic lobe (tigella) of *Walckenaeria acuminata* Blackwall (Lopez & Emerit,

1981). Millidge (1983:107) suggests that the pits of the trifurcate hairs of the cephalic horn of some *Walckenaeria* species "may possibly have the same function as the cephalic holes in other male erigonines, that is, to secrete sexual pheromones." Lopez & Emerit (1981) found that the cephalic glands of *W. acuminata* were not associated with the neighbouring hairs ("ils sont indépendents des poils voisins", p. 129). Some species of *Walckenaeria* (e.g. *W. antica* (Wider), *W. alticeps* (Denis), and *W. stylifrons* (O.P.-Cambridge)) have, in addition to modified hairs on their horns, postocular sulci. If the erigonine sulci are morphological uniques, the hair pits cannot be homologous to the erigonine sulci, because they fail the conjunction test (Patterson, 1982). The males of *Erigone psychrophila* show a very shallow depression at the cephalothoracic margin ('lateral sulci' of Millidge, 1988) that seems continuous with the cephalothoracic groove; an even shallower groove is also found in some females. The nature of this groove (i.e. whether it is homologous or not to the postocular sulci of erigonines) is unclear (see discussion). I have coded this character as a '?' for *Erigone* until detailed data on these structures are available. See also comments in 'Complex character problems'.

Character 35. Tracheal system. 0: haplotracheate; 1: desmitracheate. The terms haplotracheate and desmitracheate are used *sensu* Millidge (1984:233), and refer to the morphology of the median tracheae, regardless of the atrium and spiracle morphology. Haplotracheate systems have simple unbranched median tracheae (Fig. 15A), while desmitracheate systems are characterized by having the median tracheae branching into many small tracheoles (Fig. 18A). See comments in 'Complex character problems'.

Character 36. Ectal surface of male chelicerae. 0: smooth; 1: with stridulatory striae. See comments in 'Complex character problems'.

Character 37. Retrolateral teeth of female chelicera. 0: three; 1: four or more; 2: two.

Character 38. Female pedipalpal tarsus. 0: with claw; 1: without claw. Contrary to Blest's (1979) assertion, the female pedipalpal claw is present in *Haplinis diloris* and *Novafroneta vulgaris*, Fig. 19A and B, respectively, and in *Afroneta* (Holm, 1968:21)). The claw is presumably absent in the erigonines (Locket & Millidge, 1951:173) and in *Lepthyphantes tenuis*.

Character 39. Patella-tibia leg autospasy. 0: absent; 1: present. The methods for the assessment of this character are discussed in Hormiga (1994). So far, patellar autospasy within Araneoidea is restricted to the linyphiids and the pimoids (Roth & Roth, 1984:142; Hormiga, 1994). Outside of Araneoidea, Roth & Roth report patella-tibia detachment in the families Filistatidae, Leptonetidae, and Hersiliidae. I have recorded it in several species of African hersiliids, in both live and alcohol specimens.

Character 40. Trichobothrium on metatarsus IV. 0: present; 1: absent. The presence of a metatarsal trichobothrium on the fourth leg has often been used in linyphiid systematics (Lehtinen & Saaristo, 1970:157). In the present sample the metatarsus IV trichobothria are absent in *Linyphia*, *Microlinyphia*, *Bolyphantes*, and *Lepthyphantes*, and in *Tetragnatha*.

Spinneret spigot morphology

Character 41. PMS. 0: with anterior aciniform brush; 1: without brush. The PMS anterior aciniform brush, found in most araneids and cribellate orb

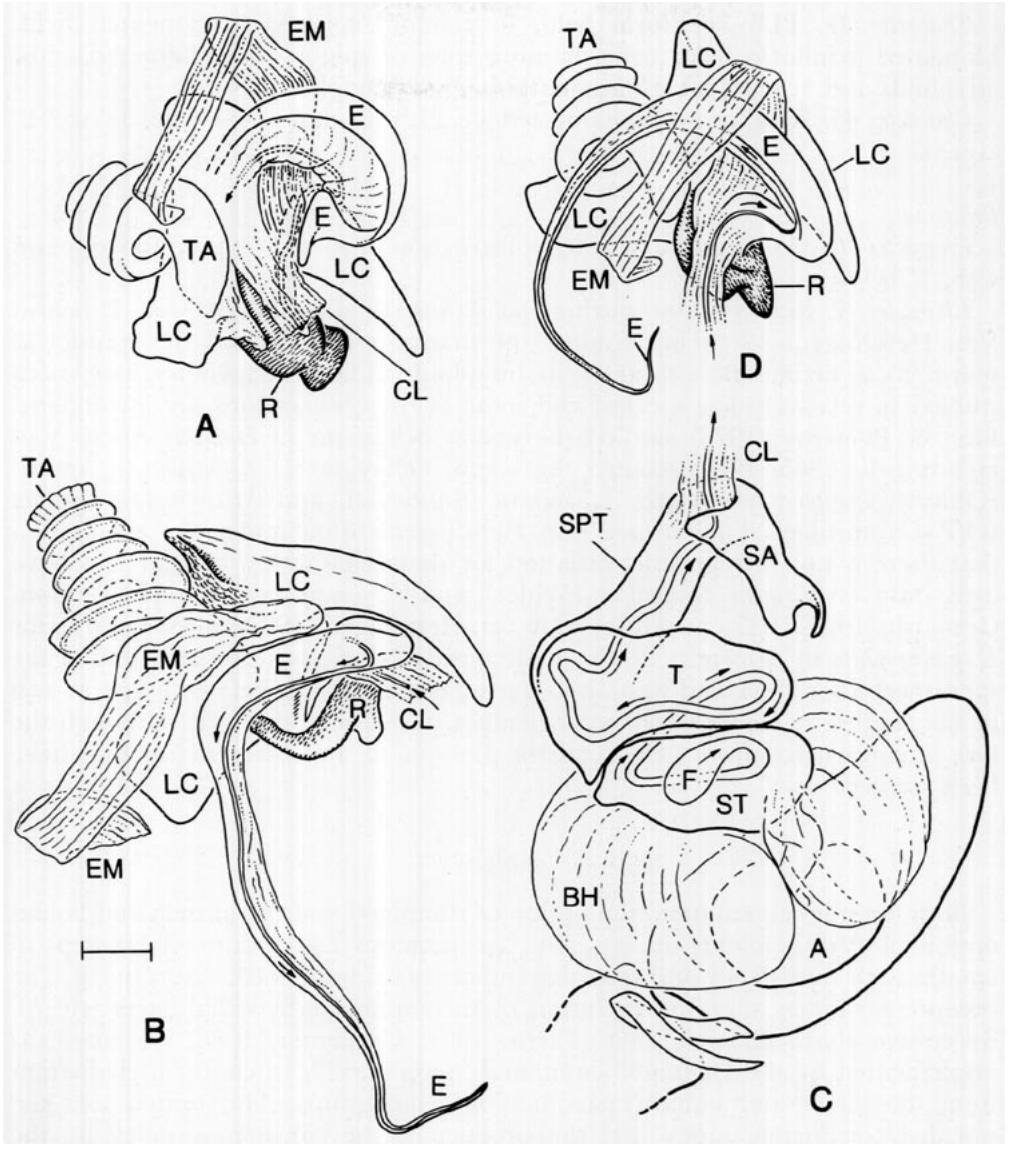


Figure 9. *Linyphia triangularis*, male palp morphology. A, Embolic division, schematic (distal half of the embolus not drawn). B, Embolic division. C, D, Schematic, embolic division excised (scale bar = 0.1 mm).

weavers (Coddington, 1989:89), is absent in the pimoid-linyphiid clade and in *Tetragnatha*.

Character 42. Aciniform spigots on female PMS. 0: more than one; 1: one; 2: absent. Aciniform gland spigots, on both PMS and PLS, are poorly developed in linyphiids (Peters & Kovoor, 1991). In pimoids the aciniform fields are reduced to one or no spigots. *Stemonyphantes blauveltae* also lacks aciniform spigots.

Character 43. PLS mesal cylindrical spigot base. 0: same size; 1: enlarged. Linyphiids, as well as some tetragnathids (see discussion), have the mesal cylindrical spigot with an enlarged base (Fig. 28D).

Character 44. PLS aciniform field. 0: random spigots; 1: elongated field. Elongated aciniform fields (one or more rows of spigots) are characteristic of linyphiids and at least some tetragnathids (Coddington, 1989).

Character 45. Aciniform spigots on female PLS. 0: more than one; 1: one; 2: absent.

Behaviour

Character 46. Male position during construction of sperm web. 0: above sperm web; 1: below.

Character 47. Male position during ejaculation. 0: above sperm web; 1: below. Van Helsdingen (1983) has studied the mating sequence and the transfer of sperm as a taxonomic character in linyphiids. These behaviours have been studied in relatively few species, and some of the observations are incomplete. Blest & Pomeroy (1978) studied the sexual behaviour of *Haplinis diloris*. Van Helsdingen (1965, 1969) studied the sexual behaviour of *Lepthyphantes leprosus* (Ohlert), *Linyphia triangularis*, *L. hortensis* Sundevall, and *Microlinyphia impigra* (O.P.-Cambridge). I have used van Helsdingen's data under the assumption that there is not intrageneric variation for these characters. Similarly, I have used data on *Erigone dentipalpis* (Wider) and *E. longipalpis* (Sundevall) from Gerhardt (1923, 1927), as published in van Helsdingen (1983), for the entries for *E. psychrophila* in Appendix 2. The male position during the construction of the sperm web (both fork and web), and during ejaculation, is below the sperm web in the studied erigonines and mynoglenines, and above the web (although the fork is constructed from below) in the Linyphiini and Micronetini that have been studied.

Analysis

Both the implicit enumeration option of Hennig86 and the branch and bound option of PAUP found four equally parsimonious cladograms of 80 steps of length, with consistency and retention indices of 0.73 and 0.81, respectively. The consistency index after the exclusion of the uninformative characters is 0.70. Successive character weighting (Farris, 1969; Carpenter, 1988) was used, as implemented by the Hennig86 command "ie;xs w;cc;", to choose a cladogram from the set of four equally parsimonious cladograms. This option uses the rescaled consistency index (i.e. the product of the consistency index by the retention index) as a weighting function, which reaches 0 when the character has as much homoplasy as possible (Farris, 1989). A single iteration resulted in one cladogram of minimal length (Fig. 31), which corresponds to one of the original set of four trees from the unweighted data. This result is stable in a second iteration.

The four minimal length cladograms resulting from the analysis of the unweighted data differ in the interrelationships of the species of *Pimoa* and in the position of *Stemonyphantes*. Three of the four cladograms agree in the linyphiid groupings as depicted in Fig. 31 but provide three different resolutions for *P. rupicola*, *P. crispa*, and *P. altioculata*. In the fourth topology *Stemonyphantes* is sister to *Pimoa*. Only the loss, presumably in parallel, of the aciniform gland spigots in the PMS and PLS in both genera (characters 42 and 45, respectively) unambiguously supports the clustering of *Stemonyphantes* with *Pimoa*. To study the

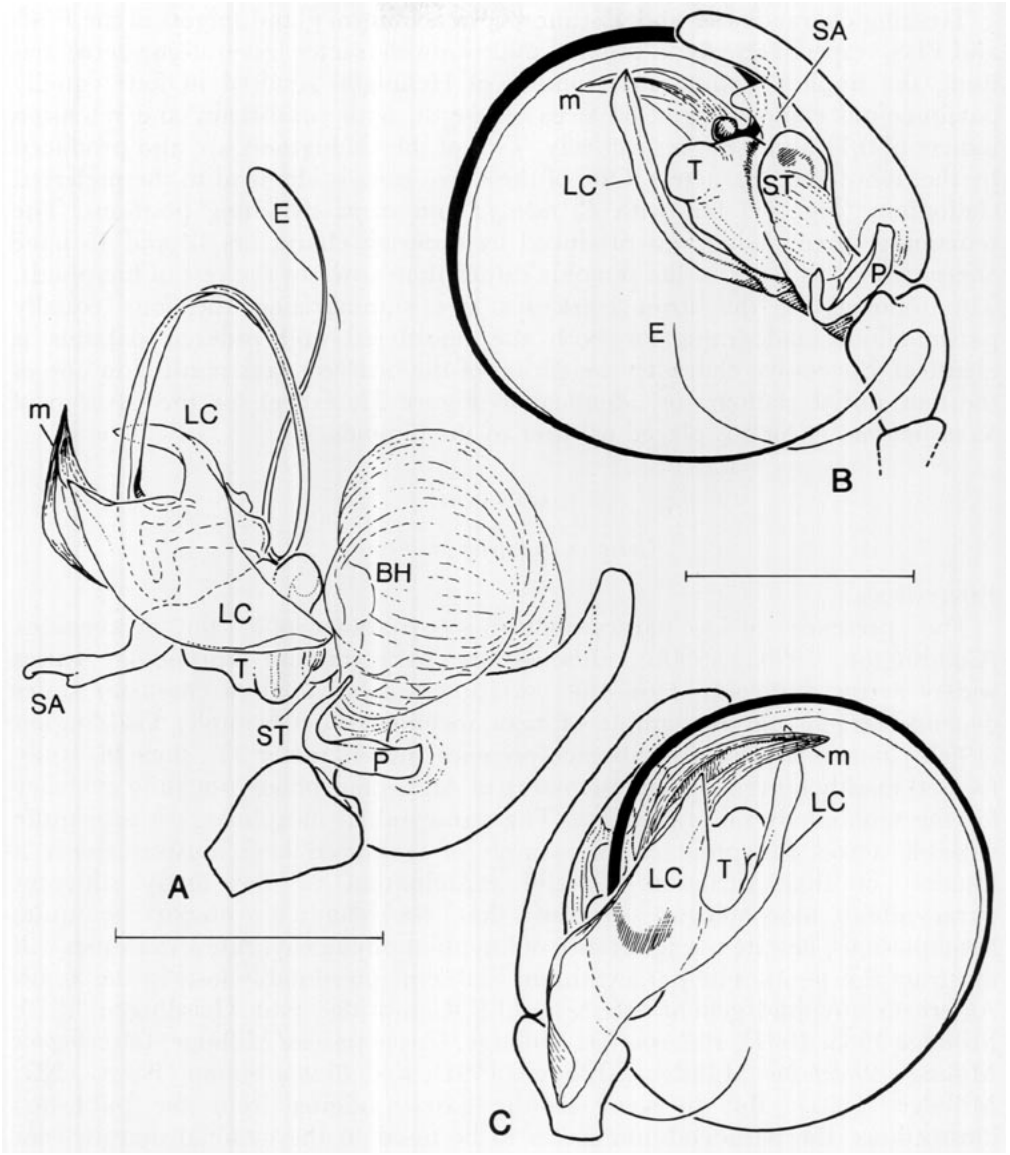


Figure 10. *Microlinyphia dana*, male palp morphology. A, Expanded, ectal. B, Ectal. C, Mesal (scale bar = 0.5 mm).

effects of these two characters on the placement of *Stemonyphantes* I analysed the dataset after excluding characters 42 and 45. For this modified dataset the implicit enumeration option produced three cladograms, which correspond to the same initial topologies, with the exclusion of the cladogram that groups pimoids with *Stemonyphantes*. The cladogram selected by the successive character weighting analysis (Fig. 31) is preferred as a hypothesis to explain the phylogenetic relationships of this sample of taxa, because it is based on the most consistent characters. These results are congruent with those from a similar data matrix in which a total of 20 species of *Pimoa* were analysed together with the same sample of linyphiids (Hormiga, 1994).

Treating characters 42 and 45 (number of aciniform gland spigots in the PMS and PLS, respectively) as an ordered multistate character (several-one-zero) and using the implicit enumeration option of Hennig86 resulted in four equally parsimonious cladograms of 82 steps of length, with consistency and retention indices of 0.71 and 0.80, respectively. Two of the cladograms are also produced by the unordered characters. One of these two trees is identical to the preferred cladogram (Fig. 31) but with *P. rupicola* and *crispa* switching positions. The remaining three cladograms produced by ordering characters 42 and 45 have *Stemonyphantes* as sister to the pimoids rather than sister to the rest of linyphiids. The topology of the strict consensus tree summarizing the four equally parsimonious cladograms for both the unordered and ordered datasets is identical. Successive character weighting of the ordered data resulted in one of the four initial cladograms, identical to Figure 31, except for the position of *Stemonyphantes,* which is placed as sister to the pimoids.

DISCUSSION

Complex character problems

Paracymbium

The presence of a paracymbium is synapomorphic for Araneoidea (Coddington, 1990a, 1990b), although the paracymbium morphology varies widely across araneoids. How this variation is subdivided in character states depends largely on the sample of taxa included. For example, Coddington (1990b) simply coded for its absence/presence (his character 33), since his study focused mainly on the higher systematics of Araneomorphae, providing evidence for the monophyly of Araneoidea. The paracymbial morphology is also quite variable across Linyphiidae. The sample of taxa used here illustrates only a fraction of that variation. Careful examination of the many different paracymbial morphologies suggests that the character might be quite homoplasious, despite our ignorance of linyphiid phylogeny. A few examples will illustrate this point. The paracymbium is absent (presumably lost) in the South American linyphiid genera *Sphecozone* O.P.-Cambridge (van Helsdingen, 1979; Millidge 1985, 1991), *Psilocymbium* Millidge, *Gymnocymbium* Millidge, *Gonatoraphis* Millidge, *Dolabritor* Millidge (Millidge, 1991), and *Brattia* Simon (Baert, 1987; Millidge, 1991). But in some of the cases, judging from the published illustrations, the paracymbium seems to be fused to the cymbial margin (not intersegmental), rather than absent (e.g. in the genera *Gonatoraphis* and *Dolabritor*, figs 808, 815, 818, 820 and 823 in Millidge, 1991). In the genus *Eurymorion* Millidge the paracymbium is reduced to a very small sclerite (Millidge, 1991: figs 236 and 238). In the Hawaiian species currently placed in *Labulla* Simon (which are not congeneric with the type species *L. thoracica* (Wider) and probably will require a new genus) the paracymbium is a small sclerite, heavily sclerotized, continuous with the base of the cymbium, with its attachment point surrounded by a less sclerotized region (Hormiga, unpublished). *Stemonyphantes* is considered by Millidge (1988) to have a paracymbium intermediate between the integral and the intersegmental types (Figs 2A and 3C).

Most linyphiids seem to have a more or less J- (e.g. *Trichopterna thorelli* (Westring)) or U-shaped paracymbium (e.g. *Linyphia triangularis*, Fig. 8A), but

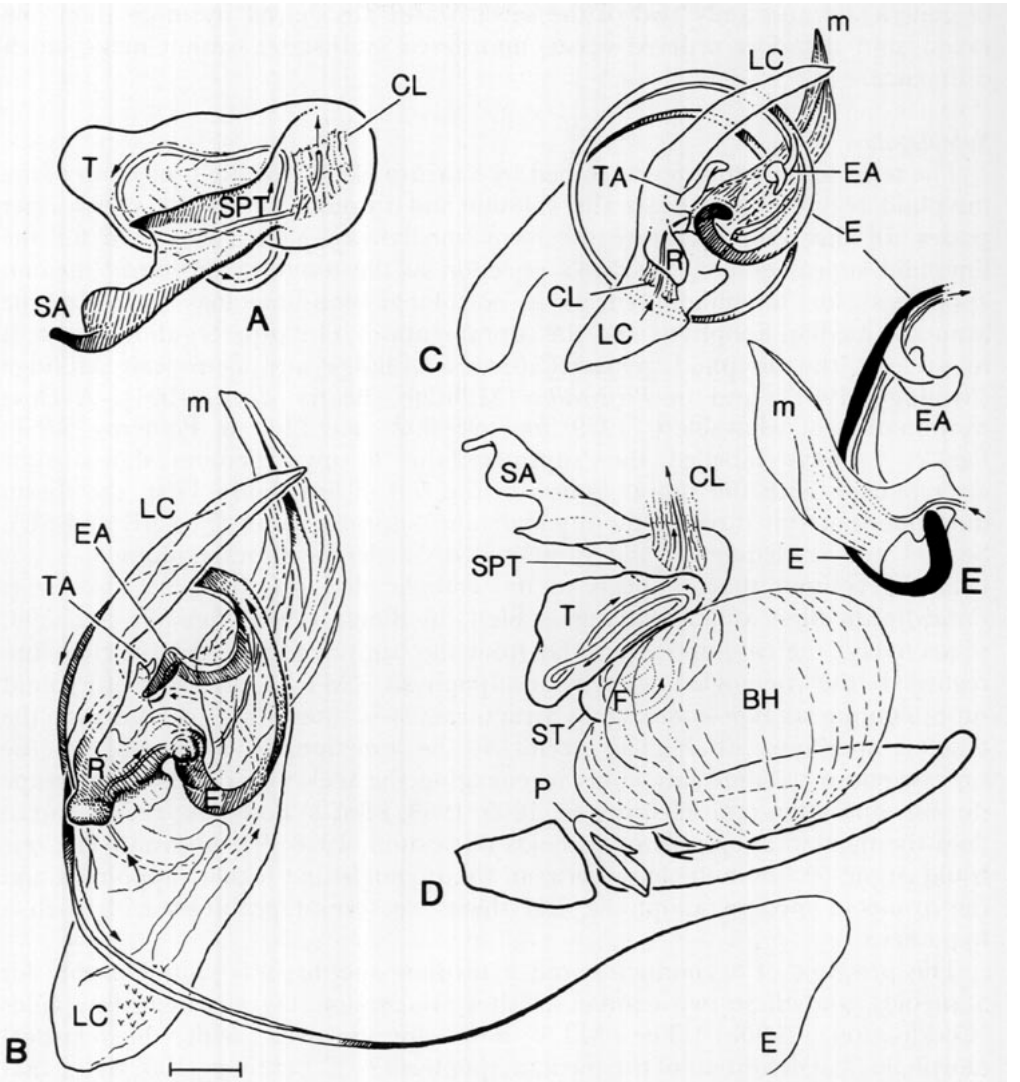


Figure 11. *Microlinyphia dana*, male palp morphology. A, Tegulum and suprategulum, schematic. B, Embolic division (scale bar = 0.1 mm). C, D, Schematic, embolic division excised. E, Embolus base (modified from van Helsdingen, 1970).

there is a continuum of intermediates. It has been argued (Blest, 1979; Wunderlich, 1986) that erigonines and mynoglenines share a common type of 'simple' paracymbium, as opposed to the more 'complex' linyphiine paracymbium, but this view has been rebutted by van Helsdingen (1986:122), who points out that many linyphiine genera also have the so-called 'simple' paracymbium. Apart from a semantic problem (i.e. defining simplicity and complexity in the context of the paracymbium), breaking down paracymbium morphology to character states is a difficult task. I have followed a conservative approach by subdividing it into seven character states, although all the linyphiids, with the exception of *Stemonyphantes*, are coded as having the same state (2). This coding provides little grouping information in the present sample

of genera, because only two of the seven states are shared by more than one taxon, and therefore ordered versus unordered multistates cannot make much difference.

Suprategulum

The term suprategulum was coined by Saaristo (1971) for the projection of the linyphiid tegulum that bears the column and through which the sperm duct passes. In the prior literature the term 'median apophysis' was used for the linyphiid suprategulum. Saaristo's rejection of the usage of the term 'median apophysis' for linyphiids reflects a postulated non-homology between the araneoid median apophysis and the suprategulum. The suprategulum is absent in at least the linyphiid genera *Caleurema* Millidge and *Diechomma* Millidge (Millidge, 1991), and in *Priscipalpus* Millidge (Beatty *et al.*, 1991). A close examination of what Blest (1979: figs 596–602) and Blest & Pomeroy (1978: figs 2, 4) have labelled the 'suprategulum' in mynoglenines shows some discrepancies with the suprategulum of the rest of linyphiids. First, the sperm duct does not run through the mynoglenine 'suprategulum' (Figs 4E and 5E). Second and consequently, this presumed mynoglenine suprategulum does not bear the column that connects to the embolic division. In some cases (e.g. *Pseudafroneta* Blest and *Promynoglenes* Blest, in Blest's (1979) figs 597 and 598, respectively) the column is quite far from the 'suprategulum'. I have therefore regarded the mynoglenine tegular apophysis (MTA) and the linyphiid suprategulum as non-homologous structures. It is interesting to note that the tegular apophysis of *Haplinis* seems to be functionally analogous to the suprategulum in some linyphiids in engaging the socket of the epigynal scape during copulation (van Helsdingen, 1965, 1969; Blest & Pomeroy, 1978), and so does the median apophysis in araneids (Grasshoff, 1968:49). Alternatively, one could argue for the homology between the mynoglenine tegular apophysis and the araneoid median apophysis, but there are several problems with such a hypothesis.

The presence of a conductor and a median apophysis is plesiomorphic for araneoids, and these two tegular sclerites are presumably absent in linyphiids (Coddington, 1990a). The MTA does not fit well with the classical morphological definition of the median apophysis (e.g. Lehtinen, 1967:412), that is, a sclerite joined to the tegulum by means of a membranous region. The MTA is a large tegular projection, widest at its base which is not a membranous (or lightly sclerotized) joint (Figs 4A–E, 5A–E; figs 596–603 in Blest (1979)). The examination of the tegular apophyses in the outgroups does not provide an unambiguous solution to this problem. In pimoids the median apophysis, when present, is reduced to a small hook which in some cases shares a common base with the membranous conductor (Hormiga, 1994: figs 171, 215 and 321). In tetragnathids the median apophysis is lacking (Coddington, 1990a), and in araneids the median apophysis conforms to the classical definition (i.e. a sclerite with a membranous joint). The MTA could be a modified araneoid median apophysis or a new sclerite, autapomorphic for mynoglenines.

The morphological data do not discriminate between these two hypotheses, but suggest that the MTA is not homologous to the suprategulum and that the MTA is quite different from the typical araneoid median apophysis. Congruence with other characters argues against the MTA-MA homology hypothesis.

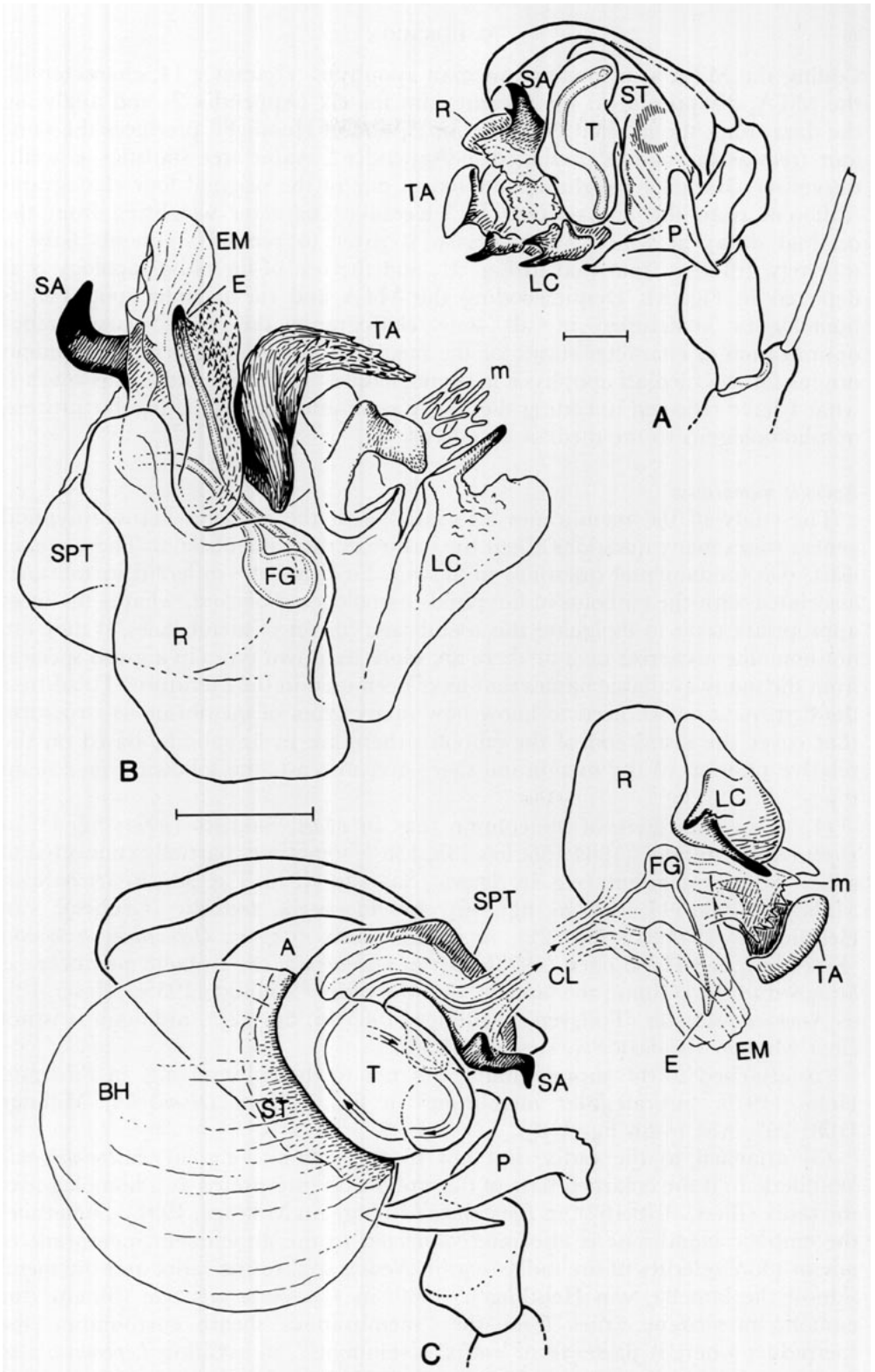


Figure 12. *Bolyphantes luteolus*, male palp morphology. A, Ectal. B, Embolic division. C, Schematic, embolic division excised (scale bars = 0.1 mm).

Coding the MTA as a modified median apophysis (character 14; character 12, the MTA, disappears) in the present data matrix (Appendix 2) and analysing the data using the implicit enumeration option of Hennig86 produces the same four trees as the matrix presented in Appendix 2 (same tree statistics as well). Successive character weighting resulted in one of the original four cladograms (different from the one selected by successive character weighting from the original data) in which *Stemonyphantes* is sister to pimoids; pimoids have a topology different from that in Fig. 31, and the rest of linyphiid topology is as depicted in Fig. 31. Despite coding the MTA and the median apophysis as homologous structures, in all four cladograms the most parsimonious optimization of character states for the median apophysis requires independent origins for the median apophysis in mynoglenines and in pimoids. This result is what I have reflected in coding the MTA as an autapomorphic tegular process, non-homologous to the median apophysis.

Embolic membranes

The study of the membranes associated with the embolus across linyphiid genera raises many questions about the nature of these membranes. There are, at least, two fundamental questions to answer. First, are the different membranes associated with the embolus in linyphiids homologous? Second, what is the most appropriate term to designate this membrane (or set of membranes, if they are not homologous across taxa or there are more than two types in a given species) from the many available names that have been used in the literature? To address the first question we need to know how many types of membranous structures that cover the distal end of the embolus there are in linyphiids. Based on the relative position of the membrane there are, at least, the following four main types:

(1) as an outgrowth of the column (e.g. in *Maro*, Saaristo (1971: fig. 1); in *Diplocentria*, Millidge (1984:156, figs 135, 136)), sometimes partially connected to either the suprategulum (e.g. in *Agyneta*, Saaristo (1973: Fig. 38), in *Spirembolus*, Millidge (1980:111, SA in fig. 46), in *Allomengea dentisetis* (Gruber), van Helsdingen (1974:314, fig. 21), or to the radix (e.g. in *Oreonetides recurvatus* (Emerton), van Helsdingen (1973b:59); in *Dubiaranea*, the embolic membrane is attached to the column, the lamella, and the radix (Millidge (1985:3, figs 5, 12); in *Neomaso pollicatus* (Tullgren) (Millidge, 1985:46, fig. 227), although it is not clear whether this latter species has a radix).

(2) attached to the suprategulum, but not to the column (e.g. in *Pelecopsis*, Holm (1979, 'suprategular membrane' in figs 1–3; in *Disembolus*, Millidge (1981:265, AM in his figs 4–8)).

(3) attached to the radix, but not to the column (e.g. in *Australolinyphia* Wunderlich, if the enlarged base of the embolus is interpreted as a homologue of the radix (Blest, 1979:162); in *Epiwubana* Millidge, in Millidge, 1991). Sometimes the embolic membrane is also interconnected to the attachment membrane of one or more sclerites of the radix (e.g. in *Neriene* spp. to the radix and the mesal side of the lamella, van Helsdingen, 1969; in *Laperousea cupidinea* (Simon) the embolic membrane arises from the "membranous sheath surrounding the spermduct where it passes from 'radix' to embolus", in addition *Laperousea* also has a tegular membrane (van Helsdingen, 1972:376, figs 2–4)).

(4) tegular outgrowth (e.g. in *Microbathyphantes asiaticus* van Helsdingen and

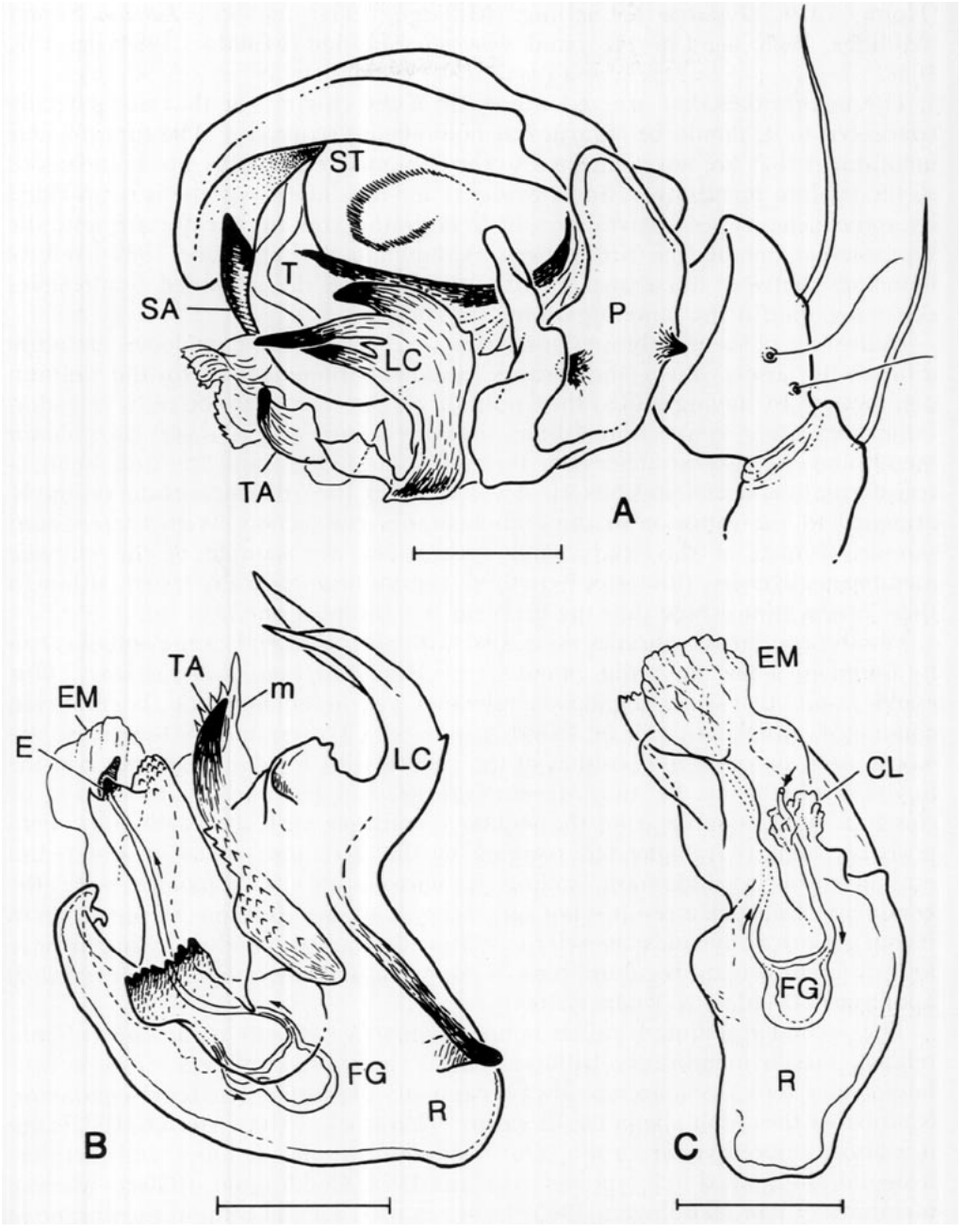


Figure 13. *Lepthyphantes tenuis*, male palp morphology. A, Ectal. B, C, Embolic division (scale bars = 0.1 mm).

Emenista bisinuosa Simon (van Helsdingen, 1985)). *Tunagyna* Chamberlin & Ivie has, in addition to the tegular membrane, a column membrane (van Helsdingen, 1973a:42; Millidge, 1984, figs 87, 89).

Some genera have both a suprategular membrane and a column membrane, for example: *Pelecopsis* Simon, *Trichopterna* Kulczyński, and *Tybaertiella* Jocqué

(Holm, 1979), *Phanetta* Keyserling (Millidge, 1984: fig. 95), *Laetesia* Simon (Millidge, 1988: figs 146–148), and *Annapolis* Millidge (Millidge, 1984: figs 107, 108).

The membranes that are an outgrowth of the column, or that are partially connected to it, should be regarded as homologous structures. The suprategular membranes that are not connected to the column are probably not homologous to the column membranes. Some evidence for this latter hypothesis is provided by some genera (see above) in which both the column membrane and the suprategular membrane are present. Conjunction (Patterson, 1982) refutes homology between these two membranes, because the supposed homologues occur together in the same organism.

In the case of the membranes or sclerites on the radix the homologies are more difficult to assess. Such membranes could be homologous to the column membranes, by having shifted their position on the column to the radix or radix-radical sclerite(s) connection. In fact, in some genera (e.g. *Neriene*) the column membrane is also attached to the radix and the lamella, and such a transformation seems possible. However in other taxa the membrane is simply attached to the radix or to the embolus-radix connection. With the reduced sample of taxa of this study, and with a reduced sample of the embolic membrane diversity, this latter hypothesis cannot be empirically tested, although these observations show that the problem is a complex one.

Finally, tegular membranes associated with the distal end of the embolus can be found in a few linyphiid genera (e.g. *Microbathyphants* and *Emenista*). One could argue that such tegular membranes are homologues of the araneoid conductor, which can still be found in pimoids. To test such a hypothesis we would need to know the position of the genera with tegular membranes in the linyphiid phylogeny. Because *Microbathyphantes* and *Emenista* do not seem to be closely related, homologizing the tegular membrane with the conductor would probably require independent origins of this structure when mapped and optimized on a cladogram, failing to corroborate its homology with the conductor. But such a result is not surprising at all. For example, in the northern North American lycosids the sclerite classically named 'conductor' might have four different origins: tegulum, base of the palea, median apophysis, or terminal apophysis (Dondale & Redner, 1990).

The second question I raised concerns how we should name the column-related embolic membranes. Different authors have used different terms, but the homologies across taxa are not always explicitly discussed. The term 'conductor' is probably the oldest one in the literature (Comstock, 1910; Osterloh, 1922), but it is also commonly used for a tegular conductor in other families, and therefore it should not be used in linyphiids (Saaristo, 1971; Coddington, 1990a). 'Median membrane' (van Helsdingen, 1965) has been used for the column membrane in linyphiids. Subsequently, it was argued (Saaristo, 1971) that the tegular projection of the linyphiids is not a homologue of the araneoid median apophysis, but an autapomorphic structure of linyphiids (the suprategulum). In that sense it seems more appropriate to use a term like 'suprategular membrane', rather than 'median membrane', since linyphiids lack the median apophysis. However, the term 'suprategular membrane' has already been used by Holm (1979) for a membrane that is not connected to the column, and that in fact seems not homologous to the column membranes. Holm uses the term 'radical

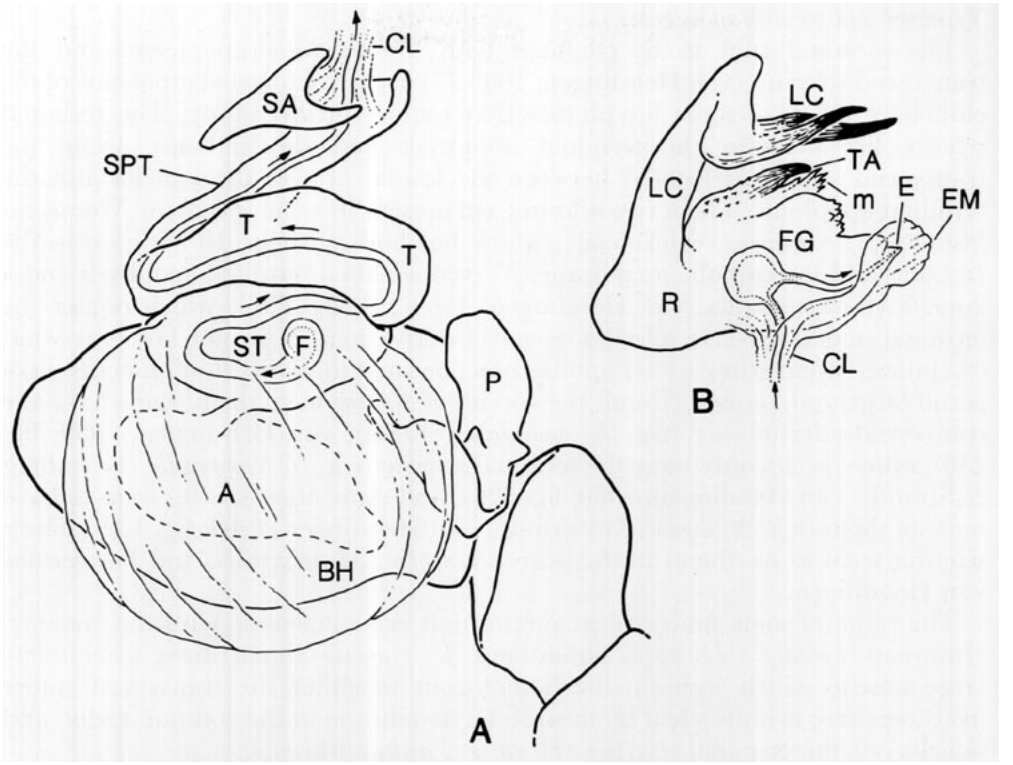


Figure 14. *Lepthyphantes tenuis*, male palp morphology. A, B, Schematic, embolic division excised.

membrane' for the column membranes, but not all the column membranes are partially fused to the radix, and the use of such a term for all linyphiids might be misleading. Holm's (1979) term 'conductor membranes', for the column or suprategular membranes in general, is not acceptable for the same reasons that render inappropriate the use of the name 'conductor' in linyphiids.

One of the most widely used terms in linyphiid taxonomy during the recent years for such a membrane has been 'embolic membrane'. Although it was first used in *Linyphia* and its relatives (*Neriene*, *Microlinyphia*, etc.; van Helsdingen, 1969), its usage extended to many other linyphiid genera. However, the so-called embolic membrane in *Linyphia*, *Neriene*, *Microlinyphia*, and close relatives, and the column embolic membrane of other linyphiids might not be homologous (Saaristo, 1973:389; see discussion above), and one could argue that the use of 'embolic membrane' should be restricted to the former taxa. Alternatively, a new name could be coined for the column membranes of linyphiids, but I think that it might add more confusion to this already confusing problem. I suggest continuing with the use of the term 'embolic membrane', despite the doubts on its homology in certain taxa, but redefining it to refer only to the column related membranes (and excluding the tegular, suprategular, etc. membranes); this embolic membrane might be interconnected to other sclerites. In the future, if the homology between the column embolic membranes and the embolic membrane in *Linyphia* and relatives is not corroborated by the phylogeny, a new term could be coined for the embolic membrane in the latter taxa.

Terminal and transversal sclerites

The terminal (not to be confused with the terminal apophysis) and the transversal sclerites (van Helsdingen, 1969:77) are two radical components of the embolic division of some linyphiines that require further study. The terminal sclerite lies between the terminal apophysis and the embolus, while the transversal sclerite is located between the lateral arm of the lamella and the terminal apophysis. These two sclerites are present in some species of *Neriene*, for instance *N. emphana* (Walckenaer), which has both of them. In addition to the embolus and the embolic membrane, *N. emphana* has a terminal apophysis and a lamella characteristica (van Helsdingen, 1969:213, fig. 296), which render the terminal and transverse sclerites as novel derivations. I do not know at what level these two sclerites are synapomorphic, because their distribution across taxa is still largely unknown. Not all the species of *Neriene* have them: some have the transversal sclerite only (e.g. *N. amiculata* (Simon); van Helsdingen, 1969: fig. 279), other species only have the terminal sclerite (e.g. *N. longipedella* (Bösenberg & Strand); van Helsdingen, 1969: fig. 328), and some other species seem to have none of them (e.g. *N. digna* (Keyserling); van Helsdingen, 1969: fig. 109). These sclerites seem to be absent in the genera *Linyphia*, *Microlinyphia*, and *Frontinellina* van Helsdingen.

The radix of some undescribed species that are congeneric with the endemic Hawaiian '*Labulla*' ('*L*'. *torosa* Simon and '*L*'. *graphica* Simon) have a relatively large sclerite which seems to be homologous to either the transversal (more likely, because it is attached by means of a membrane to the column, radix, and lamella) or the terminal sclerites (Hormiga, unpublished).

Cephalic sulci

Cephalic sulci are also found in many male erigonines (Fig. 19G), which raises the question of whether the erigonine sulci are homologous or not to the mynoglenine sub-ocular sulci (Fig. 19H, I; for a summary on the similarities and differences between erigoninae and mynogleninae sulci, see Blest, 1979:165). The sub-ocular sulci of mynoglenines are found in both male and females, being very similar in both sexes. The juvenile mynoglenines also have functional sulci, at least in the species of *Haplinis* that have been studied so far (Blest & Taylor, 1977). The mynoglenine sulci do not play any active role during courtship (at least in the species studied by Blest & Pomeroy, 1978), and might elaborate defensive secretions, because the unique ultrastructure of the clypeal secretory cells is consistent with the synthesis of a toxic product (Blest & Taylor, 1977). On the other hand, erigonine post-ocular sulci (Fig. 19G), as well as the cephalic elevations, are found only in adult males. Erigonine sulci usually have pores associated with glands that are cytologically different from those of the mynoglenine sulci (Blest & Taylor, 1977; Schaible *et al.*, 1986; Schaible & Gack; 1987), and the sulci play an active mechanical role during the courtship: the sulci are gripped by the female cheliceral fangs, as first noted by Bristowe (1931).

Nevertheless, these glands are not always associated with cephalic specializations (*contra* Blest & Taylor 1977:491). Clypeal glands have been reported for the male of *Ceratinopsis penicillatus* (Westring) (Lopez, 1976; Lopez & Emerit, 1981), an erigonine with an unmodified cephalic region and little sexual dimorphism in the carapace morphology. Millidge (1988:256) considers two different forms of linyphiid cephalic sulci: the 'ocular sulci' (below or behind the

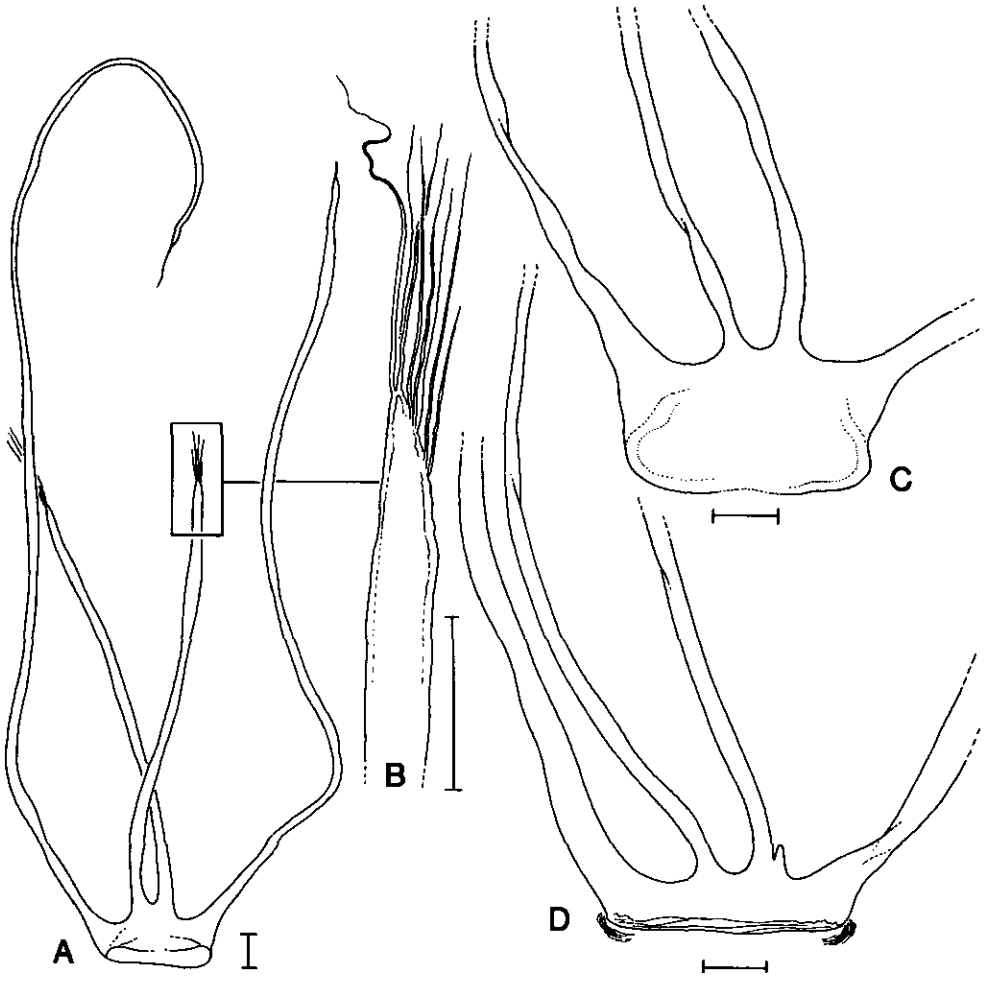


Figure 15. Tracheal system morphology of *Pimoa* (dorsal view of females). A, *P. altioculata*. B, Ditto, detail of the distal end of the median trunk. C, *P. cthulhu*. D, *P. breuili* (scale bars = 0.1 mm).

eyes) and the 'marginal sulci' (near the carapace margin). As an example of the latter he cites the case of *Erigone atra* (Blackwall), in which both sexes have a cuticular depression that parallels the carapace margin, although there are no data on the presence of cuticular openings/glands in the mentioned sulci. Similar sulci, according to Millidge, are also found in the erigonine *Troxochrus scabriculus* (Westring). These erigonine sulci, as well as the mynoglenine sulci and other sulci found in some dionychans (e.g. *Thanatus*) and lycosoids (e.g. *Hygrolycosa*), are proposed to be homologous structures by Millidge (1988).

The homology of the 'lateral sulci' of some erigonine genera with the typical erigonine 'ocular sulci' is, at best, doubtful. *Troxochrus scabriculus* has, according to Millidge, lateral sulci, but it *also* has conspicuous postocular sulci with a small anterior pit (see Roberts, 1987:74, figs 31a, b). Thus *T. scabriculus* fails the homology conjunction test, and at least in this case the lateral sulci and the postocular sulci cannot be homologous structures. Similarly, the male of *Baryphyma gowerense* (Locket) has well marked postocular sulci (Kronestedt, 1979:

figs 1, 2). Judging from Kronestedt's micrographs, the male (and the female) also has a very shallow lateral depression that would fall into Millidge's category of 'lateral sulci'. Once more conjunction argues against the homology of these two structures.

Millidge (1993a) has recently redescribed an erigonine species, *Blestia sarcocuon* (Crosby & Bishop), in which the males have sulci located on both sides of the clypeus, under the lateral eyes. The sulci are found on both sides of a conspicuous transverse groove (Fig. 19C, D) that has its anterior and posterior margins in intimate contact in its central part (Crosby & Bishop, 1927:149; Millidge, 1933a; Hormiga, personal observation). The sulci have groups of cuticular pores and spines on the margins (Millidge, 1933a). Because of their position and association with a clypeal groove it is not clear whether the sulci of *Blestia* are homologous to the post-ocular sulci found in other erigonines. A clypeal groove with similar 'sulci' can be found in the males of the erigonine *Floricomus praedesignatus* Bishop & Crosby (Fig. 19E, I), although it is not known whether there are any cuticular pores in the groove. This groove seems to be the result of the close contact between a cephalic lobe and a large clypeal lobe (Bishop & Crosby, 1935: figs 22, 23; Hormiga, personal observation), which leave a fissure between the lobes (Fig. 19E).

Although *Floricomus* species lack post-ocular sulci, the morphology and position of the 'sulci' of *F. praedesignatus* do not suggest homology to the erigonine post-ocular sulci. According to Millidge (1933a:127) the sulci of *Blestia sarcocuon* resemble the sulci found in some mynoglenines (particularly those of *Protoerigone* females, although nothing is known about the nature of the clypeal glands of *Blestia*) and this resemblance, in his opinion, "gives support to the suggestion (Blest & Taylor, 1977; Blest & Pomeroy, 1978; Blest, 1979) that the post-ocular sulci of the erigonines may be homologous with the clypeal sulci of the mynoglenine". As Millidge admits, if this is a "relict erigonine character", it has been retained *only* in *B. sarcocuon*. As I will argue later on, Millidge's hypothesis of homology cannot be tested without some notion of the phylogeny of the erigonines (and the phylogenetic placement of *Blestia*), because the implications of any homology hypothesis have to be assessed against the rest of the observations (i.e. characters and their distribution across taxa) in order to either corroborate or refute it.

Mynoglenine and erigonine ocular sulci can be interpreted as homologues (i.e. with a single origin) or as two independent developments. The available evidence is not easily interpreted in either way. The mynoglenine and erigonine sulci differ in their position, in the cytological structure of their associated glands, and, as far as it is known, in their behavioural role. Therefore, the homology hypothesis does not fit well with the classical homology criteria of position and special similarity. Nevertheless, Blest (1979:169) argues in favour of the homology of the mynoglenine and erigonine sulci. He proposed a seven-step "hypothetical, linear evolutionary sequence" in which the mynoglenine conditions give rise to the (presumably more 'advanced') erigonine condition. Because the interpretation of the sulci is critical for the study of the phylogeny of linyphiids, I shall examine Blest's hypothesis in detail.

A cornerstone in Blest's hypothesis is his interpretation of the sulci morphology and sexual dimorphism of the New Zealand mynoglenine genus *Protoerigone* Blest (Blest, 1979:168, figs 606–609). The males of *Protoerigone* have their sulci more

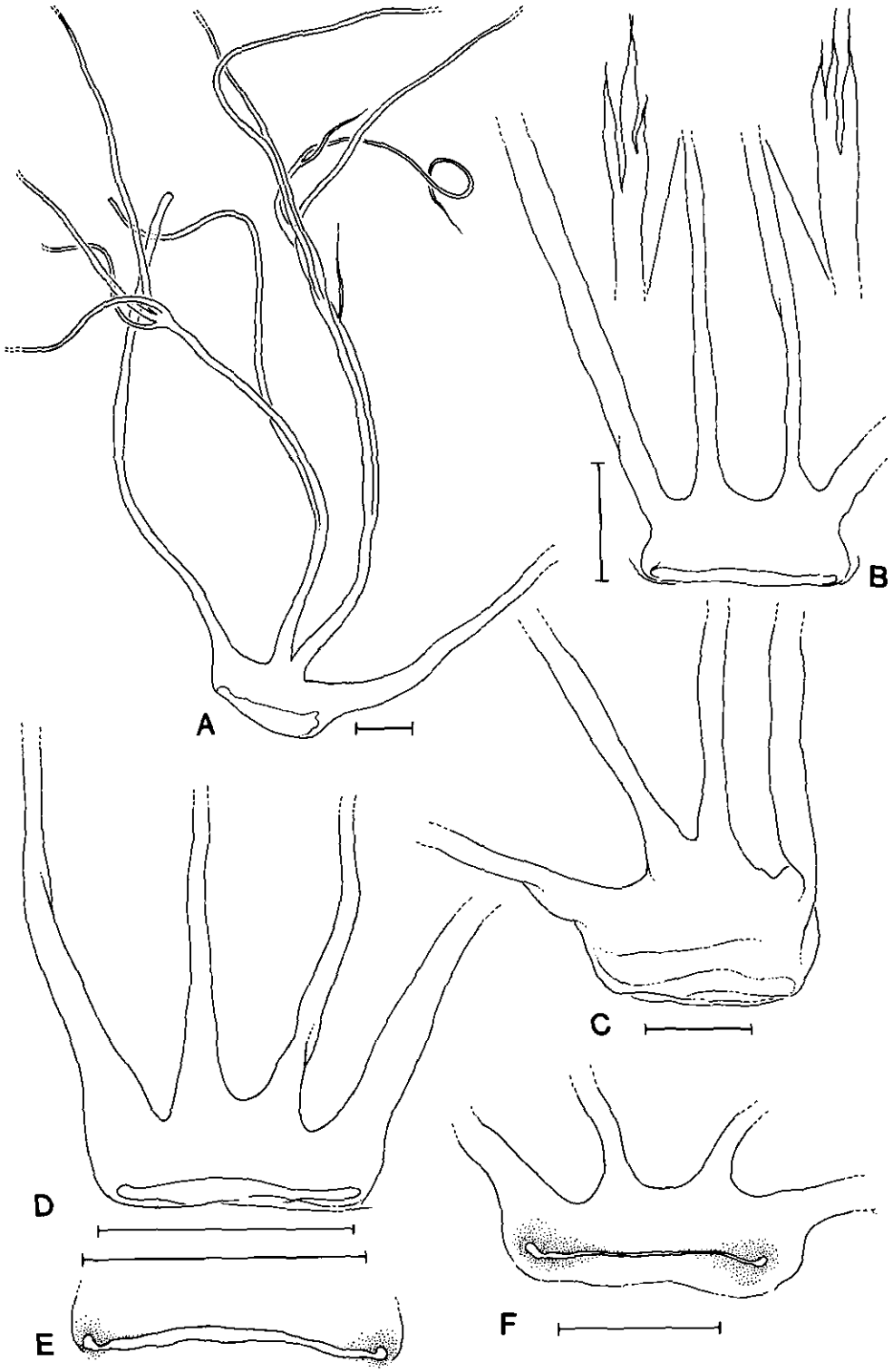


Figure 16. Tracheal system morphology (females). A, *Allomengea dentisetis*, dorsal. B, *Drapetisca alteranda*, ventral. C, *Stemonyphantes blauveltae*, ventral. D, *Lepthyphantes flavipes*, dorsal. E, *L. tenuis*, spiracle, dorsal. F, *Centromerus sylvaticus*, spiracle, dorsal (scale bars = 0.1 mm).

deeply invaginated than the females, and directed more laterally than in the rest of the mynoglenine genera. The female sulci are like those of the typical mynoglenines. The sulci of *Protoerigone* are not equipped internally with spines, as erigonine sulci usually are, although they have secretory pores and a few stout spines in the outer posterior region of the sulcus. This morphology is interpreted by Blest (1979:168) as an "elaboration towards the erigonine condition", and furthermore, he assumes that "in *Protoerigone* the female grips the males' head in the same manner (as erigonine females) during copulation". The latter assumption is critical, but has not been directly observed and it has not been studied whether the male and female secretory cells differ or if they elaborate different secretions. *Protoerigone* conveniently 'bridges' between the mynoglenine and the erigonine sulci morphology, in a hypothetical transformation series that attempts to explain the change from a secretory function of the sulci (mynoglenines) to a mechanical role during copulation (erigonines).

Although Blest's transformation series is a feasible one, many other different and equally reasonable orderings of the character states (i.e. other evolutionary sequences) are possible (see Mickevich & Weller, 1990 for a critique of the use of transmodal characters, that is, characters that incorporate either a general or specific theory of character evolution). His hypothesis is therefore dependent on the hopeful assumption that *Protoerigone* is some kind of 'missing link'; however this is highly speculative, since no data exist (other than the similarity of the sulcus morphology between the males of *Protoerigone* and the erigonine males) on either the secretions of the sulci glands, nor on the behavioural role of the glands of *Protoerigone*. Congruence with other character systems offers a powerful test to the homology hypothesis of the sulci. As we have seen, the preliminary data (position, special similarity) argue against the homology hypothesis. To build a hypothesis on the evolution of the sulci (which implicitly carries a phylogenetic scheme for those taxa) and then use it later on to hypothesize the phylogeny of the group is only valid when the hypothesis under test is tested against the rest of the characters, which might be or might not be congruent with it (failing to corroborate the hypothesis in the latter case).

Blest (1979:165) has argued that the most economical hypothesis (i.e. parsimonious) "would suggest that the sulci of the mynoglenine type gave rise directly to the kind found in Erigoninae." Mapping his hypothesis on his cladogram (*op. cit.*, p. 172, which in parenthetical notation can be summarized as: (Mynogleninae (Linyphiinae, Erigoninae)) requires the gain of the mynoglenine type of sulci in the common ancestor of all linyphiids, profound modifications (morphological, cytological, and behavioural) of the sulci to achieve the erigonine type of sulci (either in the ancestral erigonines or at the level of the linyphiine-erigonine ancestor) and finally the loss of the sulci (and its accompanying glands and behaviour) in the linyphiines. The alternative hypothesis (i.e. non homology of mynoglenine and erigonine sulci) maps on the mentioned cladogram as two independent origins of the two types of sulci. The evolution in parallel of the erigonine and mynoglenine sulci would then account for their numerous differences.

Although the latter hypothesis is more parsimonious (in both Blest's and my cladogram of Fig. 31) this question cannot be powerfully tested until more data (taxa, particularly those with any type of sulci and/or glands, and information on the glands) are included in the data set. This is due to the effect that

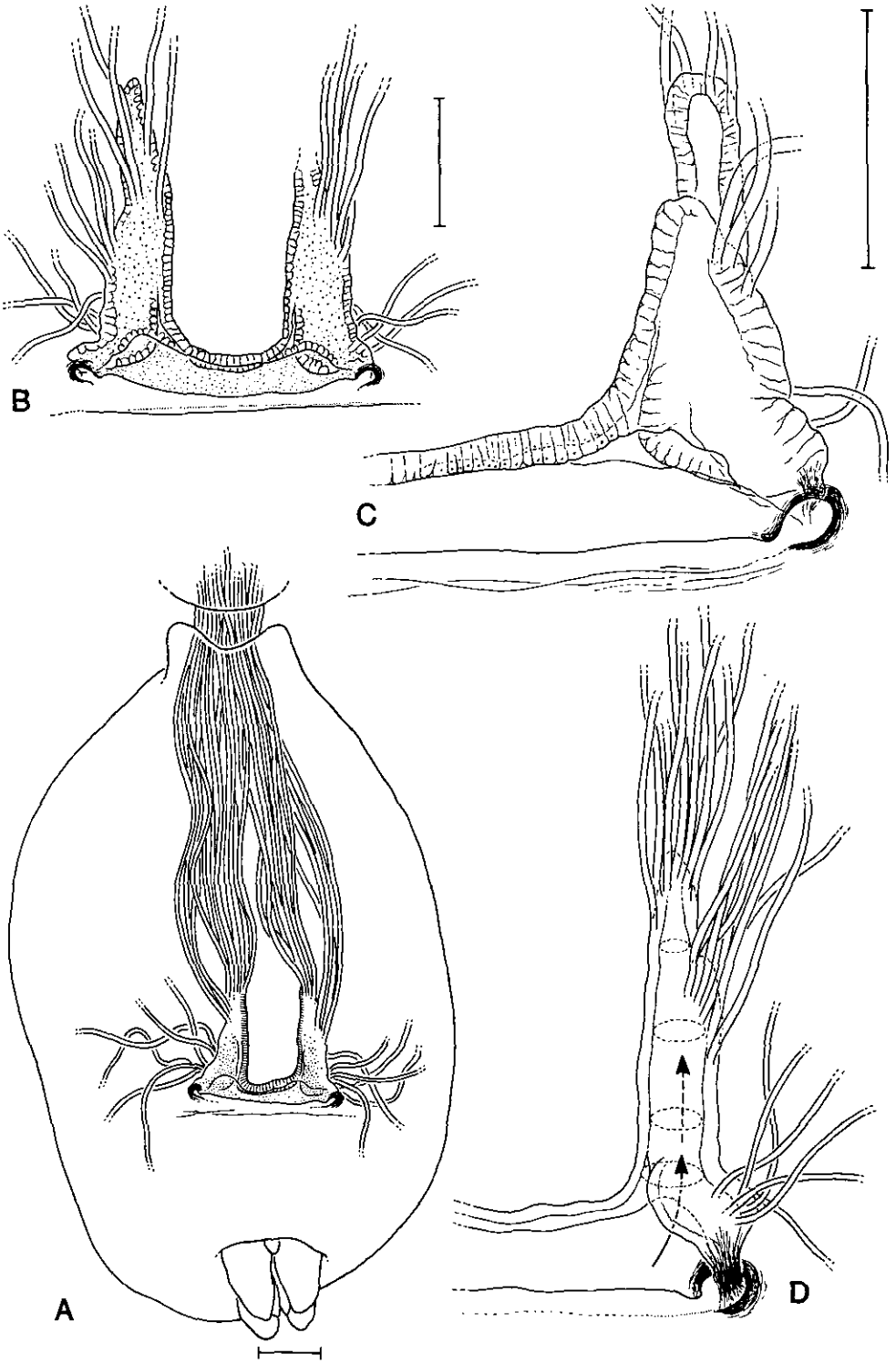


Figure 17. *Tennesseellum formicum* (male), tracheal system morphology. A, Ventral. B, Ventral, some of the median trunk tracheoles have not been drawn. C, Ditto. D, Schematic, dorsal (scale bars = 0.1 mm).

mynoglenine and erigonine cladogram topologies might have on the optimization of the character(s) on the linyphiid cladogram. When more data become available, gland topography and cytology, sulcus morphology, and the behavioural role of the glandular-sulcal complex should be coded as different characters. Only then will we be able to assess alternative hypotheses on the evolution of these cephalothoracic specializations.

Cheliceral stridulatory striae

Stridulatory striae on the ectal side of the chelicerae are found in most pimoids and linyphiids, but not all (e.g. *Centromerus*; van Helsdingen, 1973a:6). Presumably, sound is produced by friction of enlarged setal bases in the proximal part of the mesal side of the pedipalpal femur (plectron) against the cheliceral striae (pars stridens). In the studied linyphiid species the cheliceral striae and the plectrons are similar (Starck, 1985), except in the case of some *Stemonyphantes* species, which have the plectron composed by a series of cuticular protuberances or warts, rather than by enlarged setal bases (van Helsdingen, 1968; Starck, 1985). Similar cheliceral striae have also evolved in several distantly related araneomorphs: some Archaeidae, Mecysmaucheniidae, and Pararchaeidae (Forster & Platnick, 1984); Mimetidae (*Ero*, Machado, 1941); Hahniidae (*Hahnia*, Jocqué & Bosmans, 1982); Austrochilidae and Gradungulidae (Forster *et al.*, 1987); Tetragnathidae (*Meta*) and Spatiatoridae (fossil) (Wunderlich, 1986); Gasteracanthidae (*Thelacantha*, Scharff personal communication); and in some Sicariidae, Scytodidae, Diguetidae, Ochyroceratidae, Pholcidae, and Caponiidae (Jocqué & Bosmans, 1982, citing several authors, *q.v.*; see also Starck, 1985). Structurally similar striae are also found in some caddis-fly larvae (Trichoptera, Hydropsychidae; Jansson & Vuoristo, 1979) in which the stridulatory organ illustrates a remarkable convergence with the organ found in linyphiids and other spider groups. The most parsimonious hypothesis to explain the available data is to postulate a single origin for the cheliceral striae of linyphiids and pimoids, and to regard the striae in other spider lineages as independently evolved. Similarly, plectrons across linyphiids and pimoids are probably homologous, including the autapomorphic plectron of *Stemonyphantes*.

The stridulatory organ might have intrageneric variation; for instance, within the linyphiid genus *Callitrichia* Fage the cheliceral striae are present only in some species (Holm, 1962:126). Data from the literature about the sexual dimorphism of this organ are scarce and often inconclusive. In pimoid species the striae are more conspicuous and common in males than in females (Hormiga, 1994). Legendre (1963:378) points out the presence of such stridulatory organ (which he terms 'Organe de Campbell', after F. M. Campbell, who first described it in 1881) in the males of *Lepthyphantes* and describes the female organ as "similaire mais très imparfait et fort vraisemblablement non fonctionnel."

Van Helsdingen (1968:119) reported that in *Stemonyphantes* the stridulating files are present in the males of some species, but never in the females. Saaristo (1971:470) reports the female cheliceral stridulatory organ of *Maro minutus* O.P.-Cambridge as less developed than in the male, although in other species of the same genus (e.g. *M. sublestus* Falconer, p. 472) there seems to be no sexual dimorphism in this respect. In *Walckenaeria furcillata* (Menge) the female cheliceral striae are weaker than in the male (Holm, 1984:138). However, Locket & Millidge (1951:42) and van Helsdingen (1963:143) regard the

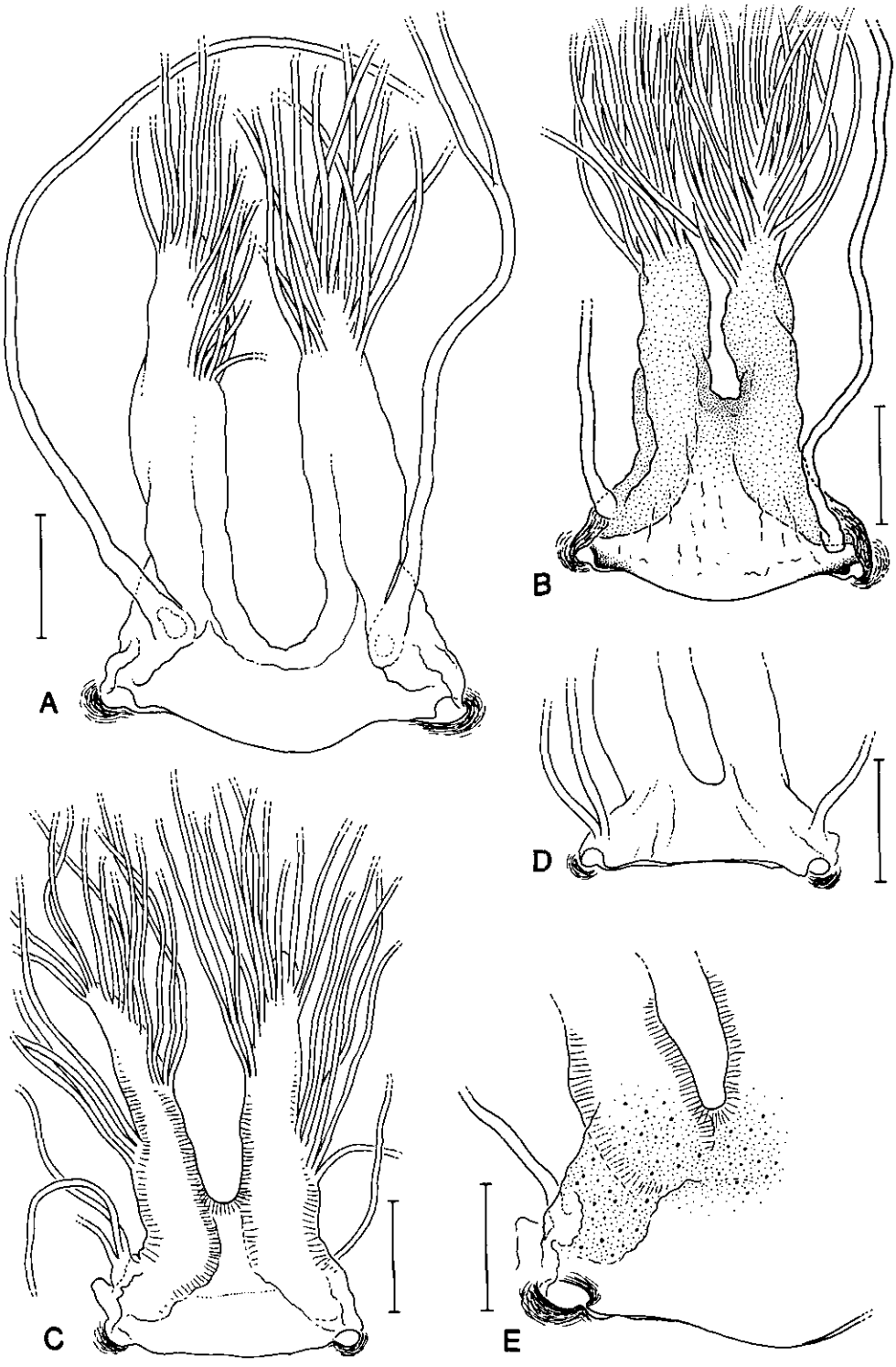


Figure 18. Tracheal system morphology of erigonines. A, *Gonatium rubens*, female, dorsal. B, *Hypselistes florens*, female, dorsal. C, *Erigone aletris*, female, ventral. D, Ditto. E, Ditto, male, ventral (scale bars = 0.1 mm).

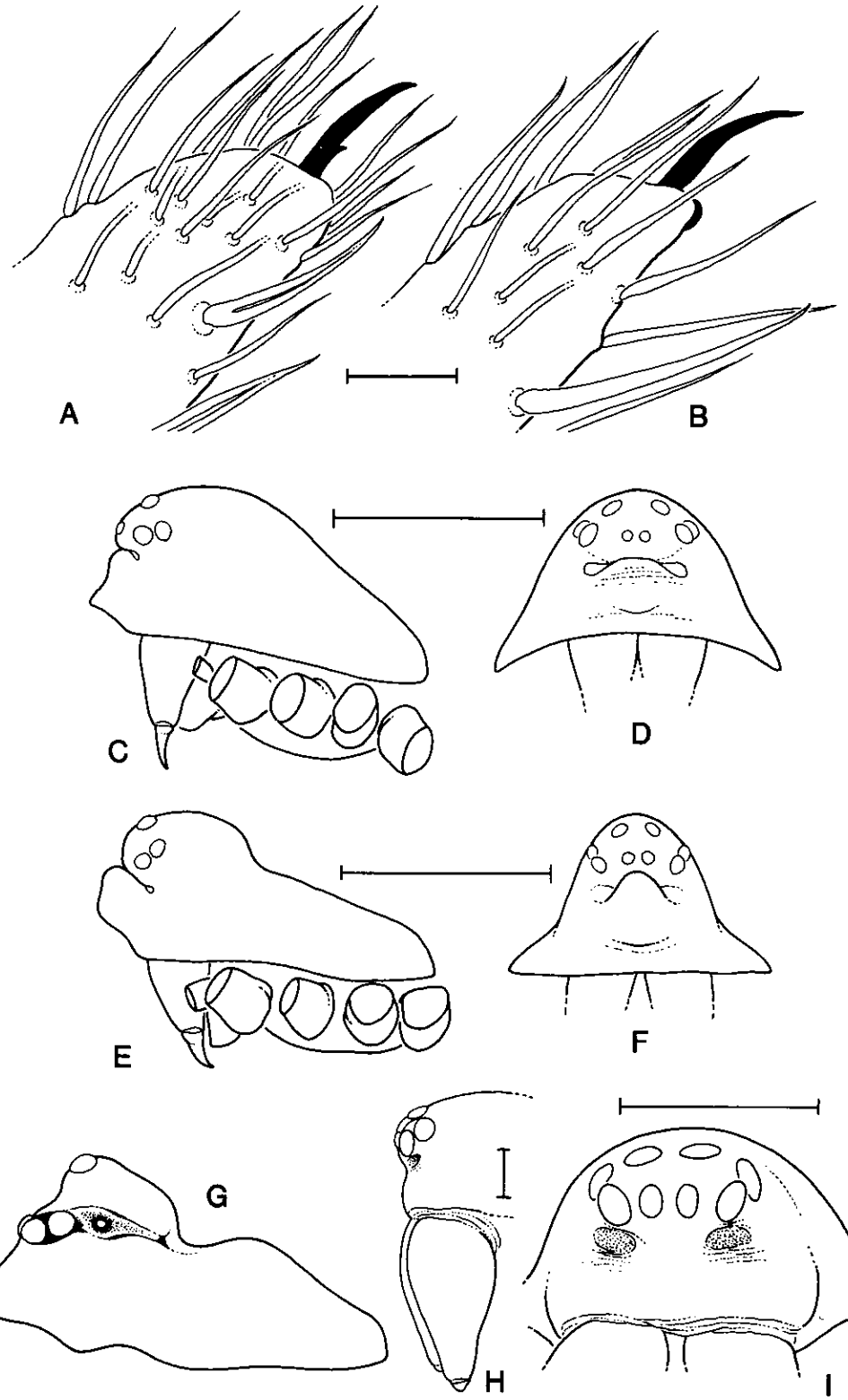
stridulatory striae as more common in female than in male linyphiid species. Starck (1985) describes three patterns of sexual dimorphism of the cheliceral stridulatory organ in linyphiids: females with striae and plectron less developed than in males (e.g. *Lepthyphantes tenuis* and *Drapetisca socialis*), females without stridulatory organ (but present in males; e.g. several species of *Centromerus*), and organ present in both sexes, but without any sexual dimorphism (e.g. *Meioneta rurestris* (C. L. Koch)). Intraspecific variation (within sexes) has been documented only in a few instances (e.g. van Helsdingen *et al.*, 1977: fig. 3), although its ranges across the family are very poorly known.

There are little data on the role of stridulation in linyphiids. It has been suggested as a mechanism for the recognition of conspecifics (van Helsdingen *et al.*, 1977). Acoustic communication may allow the male to approach the female without triggering aggression or flight (Krafft, 1982) and/or prevent hybridization with closely related species, as in Stratton & Uetz (1986) studies of reproductive isolation in two species of the lycosid *Schizocosa* (which uses a different type of stridulatory organ). The aforementioned hypotheses fail to explain the presence of this organ in the females. The stridulation in females could be interpreted as a rejection signal, i.e. 'unwillingness' of the female to mate in response to male courtship. Similar signals have been found in several species of insects, in which the rejection signals were similar in several closely related species in contrast with the species-specific male courtship signals (Ewing, 1989). The detailed studies of van Helsdingen (1965) on the mating behaviour of *Lepthyphantes leprosus* suggested that stridulation might play an important role during the male approach to the female, and perhaps during the female rejection of the male after the copula, but it has not been empirically tested. At least four alternative hypotheses can be formulated to explain stridulation in linyphiids: the defensive mechanism, the reproductive isolation, the aggressive behaviour inhibitor, and the male threat display hypothesis.

According to the defensive mechanism hypothesis, stridulatory signals are used as a defensive mechanism (e.g. defence from predators), the stridulatory organ should be present in both sexes, as well as in the juveniles. Little variation is expected in the acoustic pattern of the signals between sexes and age classes. These predictions can be tested by studying the distribution of the stridulatory organ (males, females, and several moulting stages of juveniles), and also comparing the acoustic patterns they produce. Additionally, it can be predicted that when threatened or disturbed (as in the Jansson & Vuoristo study) these animals would stridulate.

The reproductive isolation hypothesis postulates that stridulation functions as a reproductive isolating mechanism through mate recognition. It predicts that different species will have a different acoustic pattern (at least in the males) when reproductively active in the same place at the same time (Alexander, 1967). The stridulatory striae of the male are predicted to be different for each species, although it is not a *sine qua non* condition, because different acoustic

Figure 19. Female palpal claw of mynoglenines: A, *Haplinis diloris*. B, *Novafroneta vulgaris*. Male cephalothorax and sulci: C, *Blestia sarcocuon* (Erigoninae), lateral. D, Ditto, anterior. E, *Floricomus praedesignatus* (Erigoninae), lateral. F, Ditto, anterior. G, *Walckenaeria incisa* (Wider) (Erigoninae), lateral (redrawn from Roberts, 1987). H, *Afroneta* sp. (Mynogleninae), lateral. I, Ditto, anterior (scale bars, A, B = 0.05 mm, H = 0.2 mm, C–G and I = 0.5 mm).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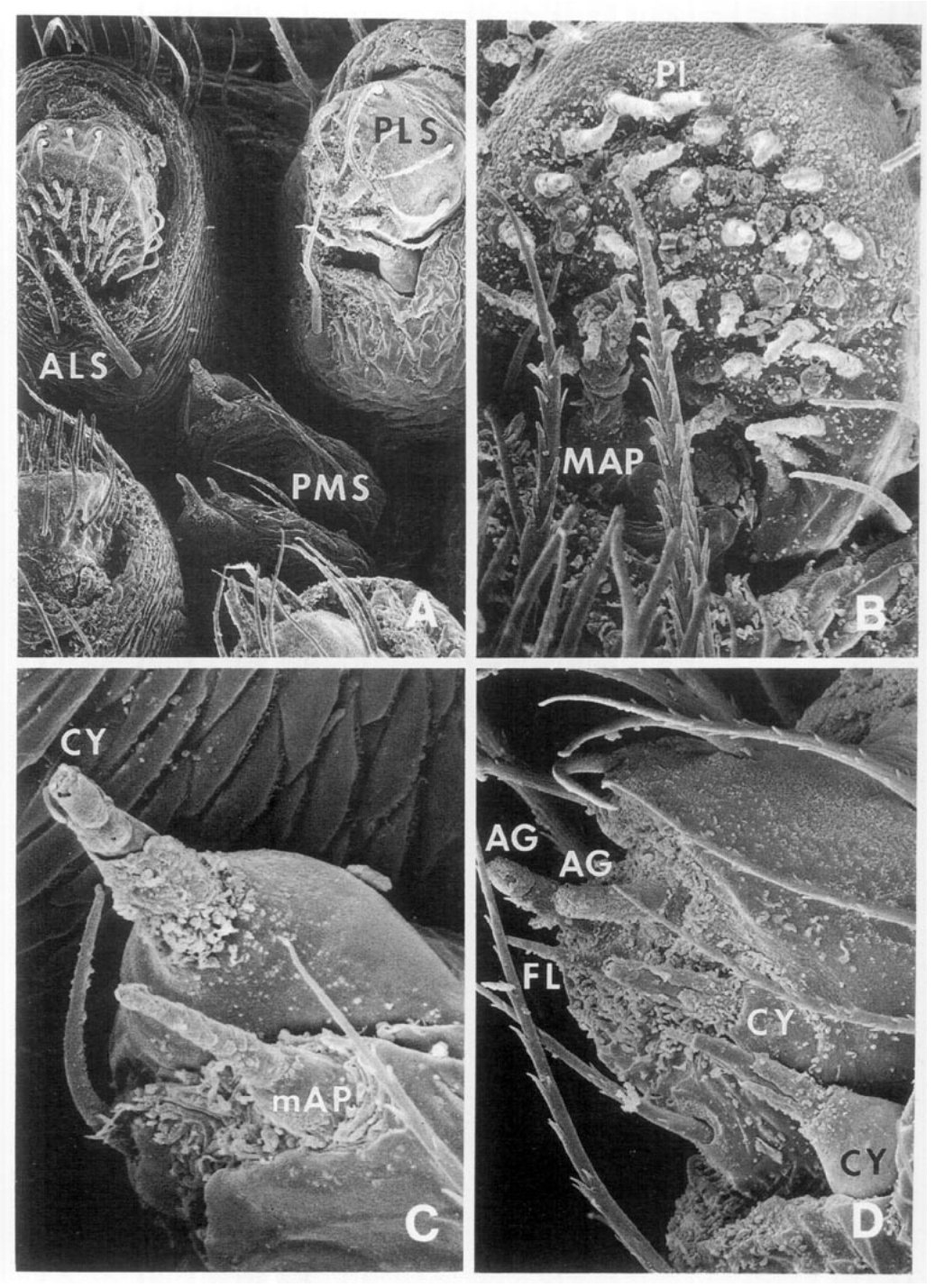

Figure 20. *Stemonyphantes blauveltae*, female spinnerets. A, Left spinneret group. B, Anterior lateral spinneret, close-up. C, Posterior median spinneret, close-up. D, Posterior lateral spinneret, close-up.

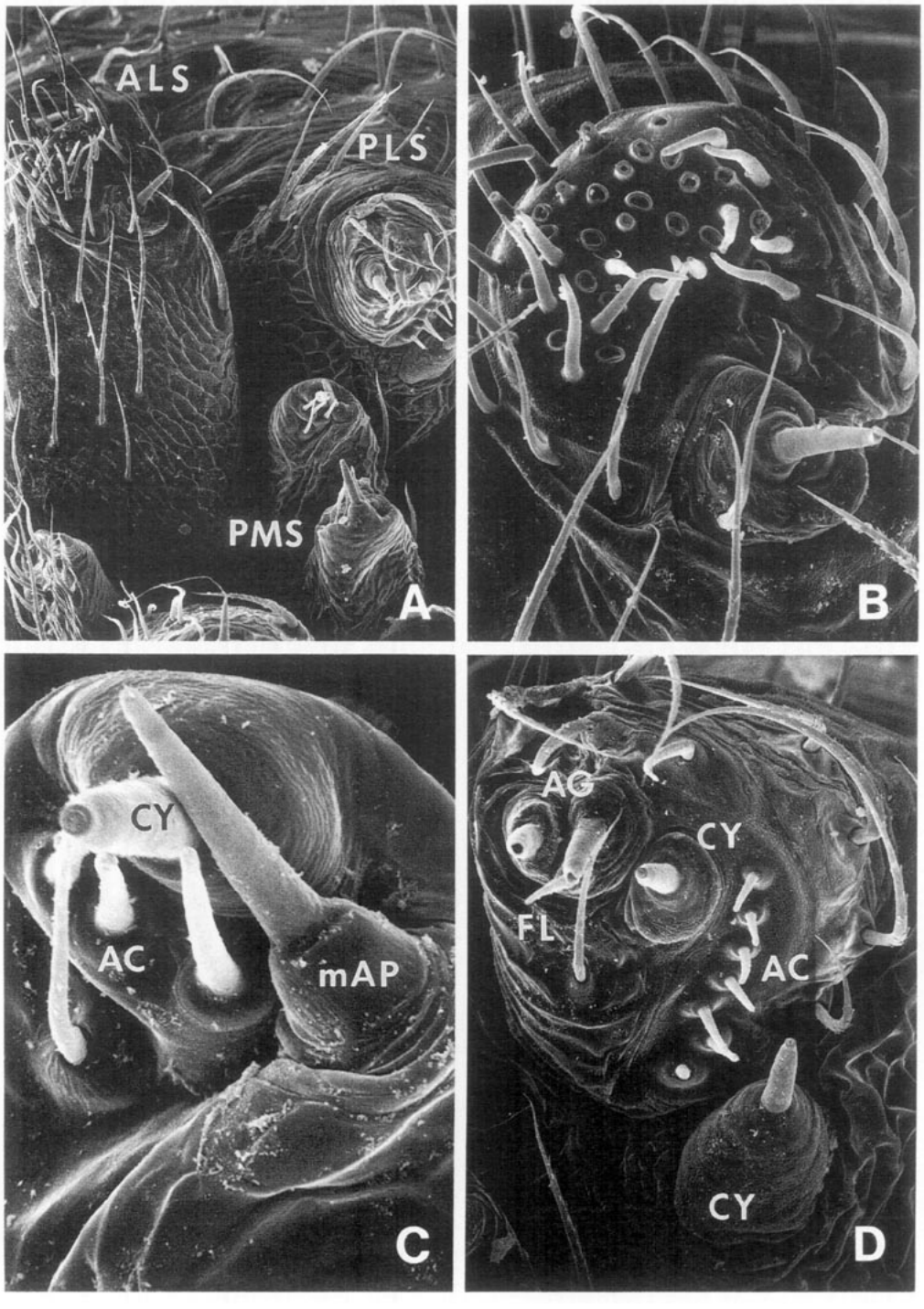

Figure 21. *Novafroneta vulgaris*, female spinnerets. A, Left spinneret group. B, Anterior lateral spinneret, close-up. C, Posterior median spinneret, close-up. D, Posterior lateral spinneret, close-up.

patterns can be obtained with the same stridulatory striae. This hypothesis also predicts that virgin females should recognize the stridulatory signals of conspecific males, and therefore respond receptively to male courting behaviour. On the other hand a female should display some kind of 'rejection' behaviour towards a heterospecific male displaying courtship behaviour. It also predicts that altering the stridulation pattern (e.g. by artificially modifying the striae) in the males would result in unsuccessful courtship and/or copula, as happened in Gwinner-Hanke's study (1970).

An alternative (but not mutually exclusive) explanation is provided by the aggressive behaviour inhibitor hypothesis, which assigns to the male stridulatory signals an inhibitory function on (conspecific) female aggressive behaviour, allowing the male to remain in the virgin female's web and start courtship. Because this mechanism would be a barrier for heterospecific matings it would also function as a reproductive isolating mechanism. It differs from the previous hypothesis in that it requires an inhibitory function for the stridulatory signals, while the former does not have this requirement. This hypothesis predicts that a conspecific male unable to stridulate could not inhibit the female aggressive behaviour towards him, and that heterospecific males would also fail to do so (given that females are virgin, and therefore willing to mate).

According to the male threat displays hypothesis stridulatory signals could be used in male-male agonistic interactions. Although it is not clear in what situations it would be used, territoriality would be one aspect to consider. If that is the case, the stridulatory signals would be used between males contesting for a resource (e.g. the web) and would contribute in deciding the outcome of the contest (at this point and without any preliminary data it is difficult to hypothesize how). An initial testable prediction would be that we should expect stridulation to occur when one adult male is introduced into another male web.

Tracheal system

I did not intend to survey linyphiid tracheal morphology, since this has already been done for roughly 25% of the then known genera, mainly by Blest (1976) and Millidge (1984, 1986). However differences in my observations, as well as in those described by Lamy (1902), from those reported by Millidge (1986) prompted me to reexamine some of the morphologies described by Millidge. Overall this dataset relies on Blest's and Millidge's tracheal descriptions, except for the issue of the presence/absence of a spiracular atrium and the way in which the atrium opens to the outside (one versus two spiracles).

For the erigonine species I examined (see Appendix 1) I found no evidence of the median tracheae opening directly to separate spiracles, as Millidge (1986) reported. Furthermore, I found they possess a spiracular atrium, which stains similarly to the rest of the system. The spiracle is most visible at its ends, where it is wider and rounded, but there is a slit connecting both ends (Fig. 18A–E). The end is not a closed circle, as Millidge's illustrations seem to suggest, since it is open at its inner part to the interconnecting slit (Fig. 18D). The slit can be clearly seen in the SEM micrographs of *Walckenaeria directa* (Fig. 29C, D). The median tracheal trunks do not start at the rounded end of the spiracle (what Millidge describes as independent spiracles), as one should expect if they were to open directly to the 'two spiracles'. The chitinous reinforcements on the lateral wall of the atrium can be clearly seen in *Hypselistes florens* (O.P.-Cambridge),

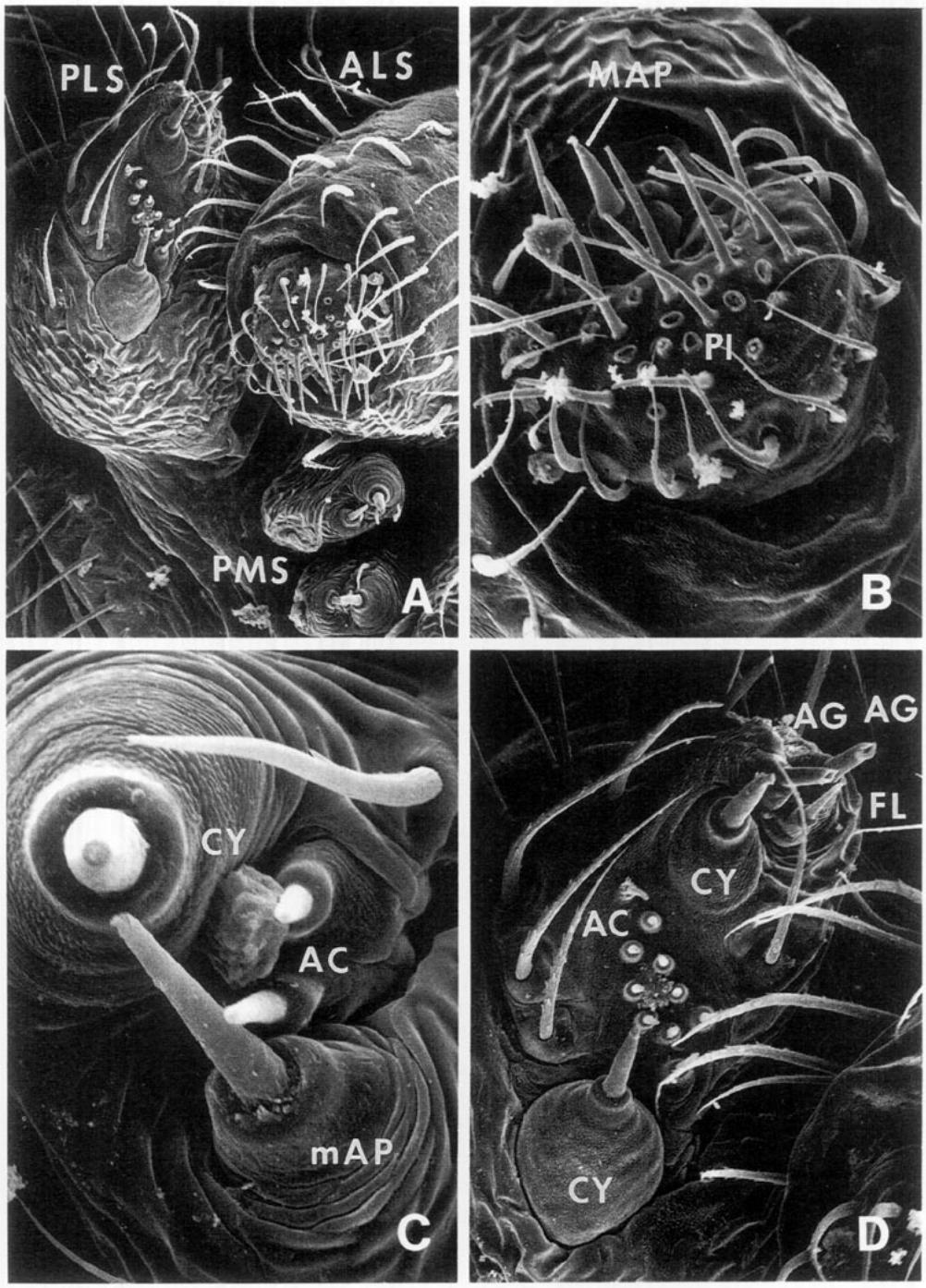

Figure 22. *Haplinis diloris*, female spinnerets. A, Right spinneret group. B, Anterior lateral spinneret, close-up. C, Posterior median spinneret, close-up. D, Posterior lateral spinneret, close-up.

between the base of the median and lateral trunks and the ends of the spiracle (Fig. 18B); they are hypothesized to be homologous to what Lamy (1902:153, 160; plate VI, figs 1, 2) calls 'piliers de renforcement' or 'piliers latéraux du vestibule' in *Araneus diadematus* Clerck. The median tracheal trunks are interconnected close to their base, which is enclosed in the atrium. The connection between the median trunks has the same kind of spiculated lining (the 'petites épines chitineuses' of Lamy (1902:155; plate VI, fig. 2 and plate VIII, fig. 5) as the trunks do (Figs 18B, E). Therefore, the connection is not a 'duct'.

Confusion may arise from the fact that the anterior part of the atrium, between the median trunks, is lined like the median trunks. In other words, there is a continuum between the median tracheal trunks and the anterior part of the atrium, which corresponds to what Millidge calls the 'connecting duct'. I have not found any interruption between the median trunks, as Millidge reports, since these share a common atrium. This general atrial/spiracular pattern was observed in the erigonines *Erigone aletris* Crosby & Bishop, *E. psychrophila*, *Gonatium rubens* (Blackwall), *Grammonota angusta* Dondale, and *Hypselistes florens* (see Fig. 18A–E). These are not new data at all. A detailed, good description of the tracheal system of *Erigone dentipalpis* (Wider) can be found in Lamy (1902:196, figs 38, 40–42; apparently overlooked by Millidge):

> "le stigmate, situé devant les filières et constitué par une fente dilatée à ses extrémités en deux bordés extérieurement d'un bourrelet chitineux, conduit dans une chambre d'où partent deux tubes latéraux grêles et non ramifiés et deux larges troncs médians courts émettant des petits tubules, surtout à leur sommet, òu ceux-ci forment deux fascieaux pénétrant dans le céphalothorax."

However, Lamy's figures might be misleading beause he depicts the median trunks in such a way that they seem to open via independent spiracles; I found no evidence for this.

Erigone aletris and *E. psychorophila* are reported to have several lateral tracheae (compare to *Gonatium rubens* and *Hypselistes florens*, which have only a single lateral tracheal trunk, Fig. 18A, B, respectively). Lamy (1902:197, figs 40–42) describes a similar variation for *Erigone dentipalpis*.

Stemonyphantes blauveltae and *Allomengea dentisetis* (Grube) (Fig. 16C, A, respectively) have atria opening through a single spiracle, contrary to Millidge's (1986) assertion that in both genera the atrium opens via two spiracles. An atrium opening via a single spiracle was also found in *Drapetisca alteranda* Chamberlin, *Centromerus sylvaticus* (Blackwall), *Lepthyphantes flavipes* (Blackwall), *L. tenuis* (Fig. 16B, F, D, E, respectively), and *L. intricatus* (Emerton). These latter genera were also reported by Millidge (the first one only implicitly) to have the atrium opening via two spiracles. In the latter two species the slit is very similar to the one reported here for the erigonines, with markedly wider round ends. This fact might have caused them to be taken as having two separate spiracles.

Meioneta rurestris (C.L. Koch) has an atrium that opens via a single spiracle, very similar to what I have described here for erigonines, although the single specimen I was able to examine has a small number of tracheoles at the base of the dorsum of the medial trunks, anterior to the atrium, as well as the distal bundle. This contrasts with what Millidge (1986, fig. 2) reported for *Meioneta*

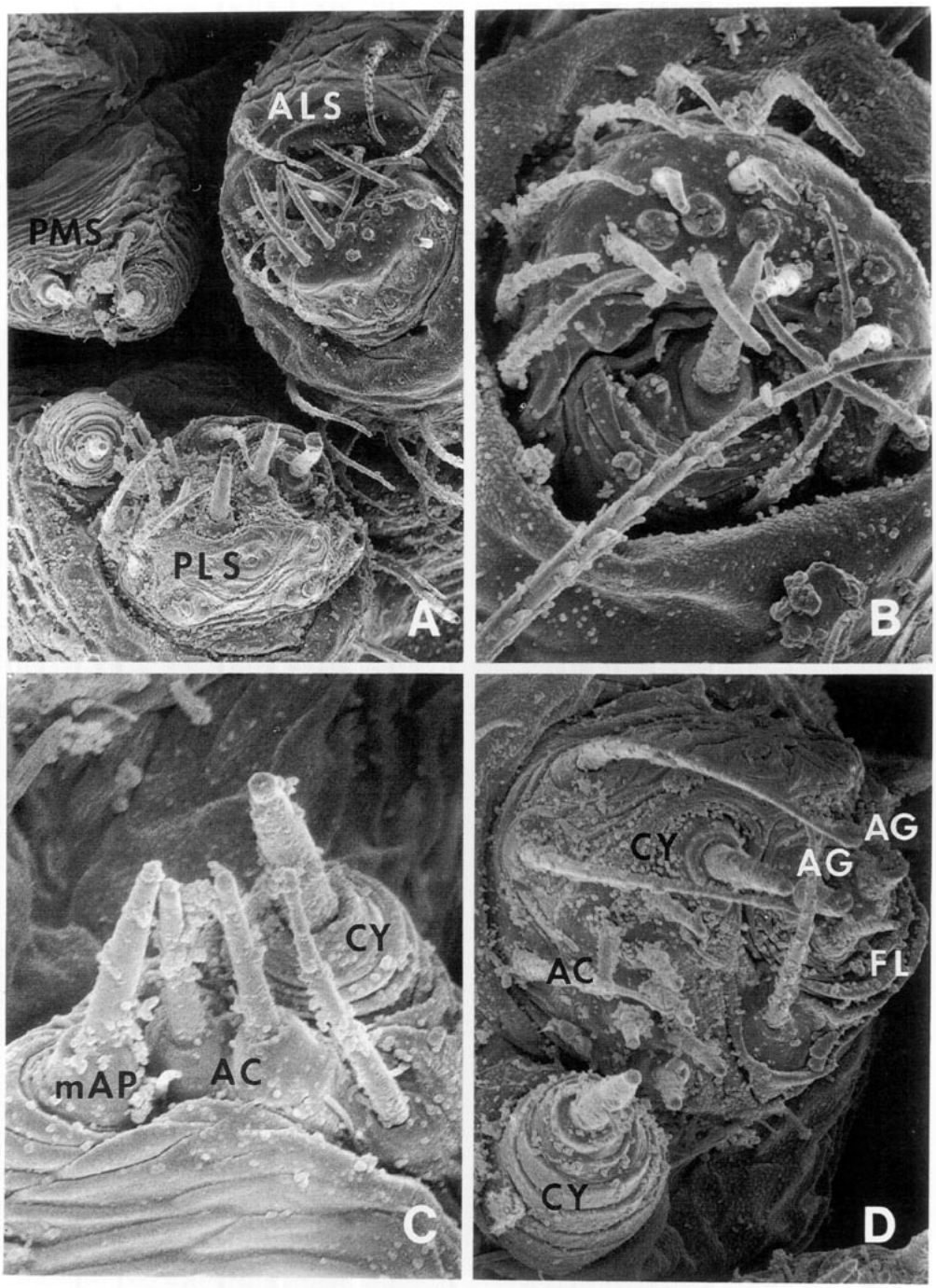

Figure 23. *Walckenaeria directa*, female spinnerets. A, Left spinneret group. B, Anterior lateral spinneret, close-up. C, Posterior median spinneret, close-up. D, Posterior lateral spinneret, close-up.

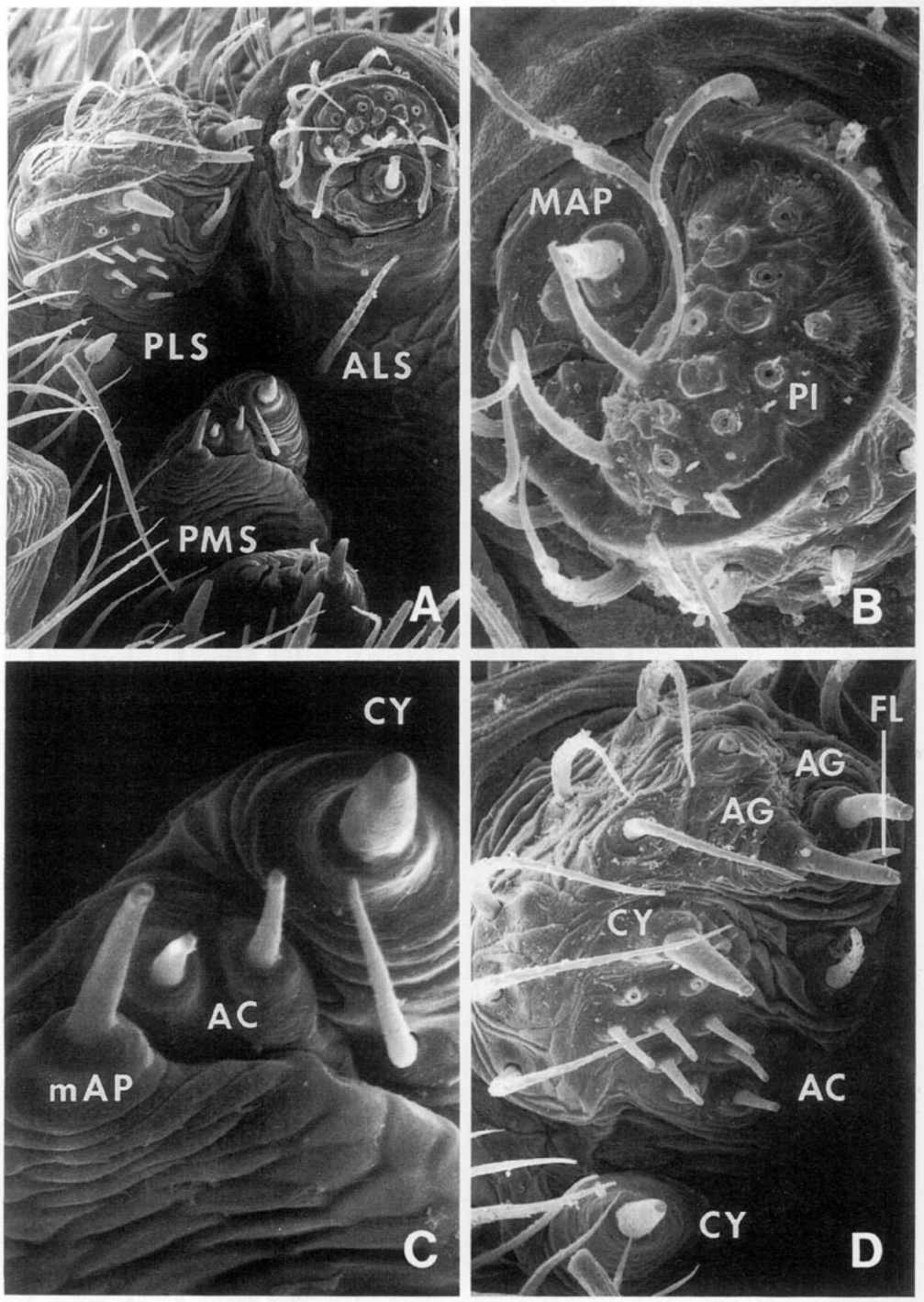

Figure 24. *Erigone psychrophila*, female spinnerets. A, Right spinneret group. B, Anterior lateral spinneret, close-up. C, Posterior median spinneret, close-up. D, Posterior lateral spinneret, close-up.

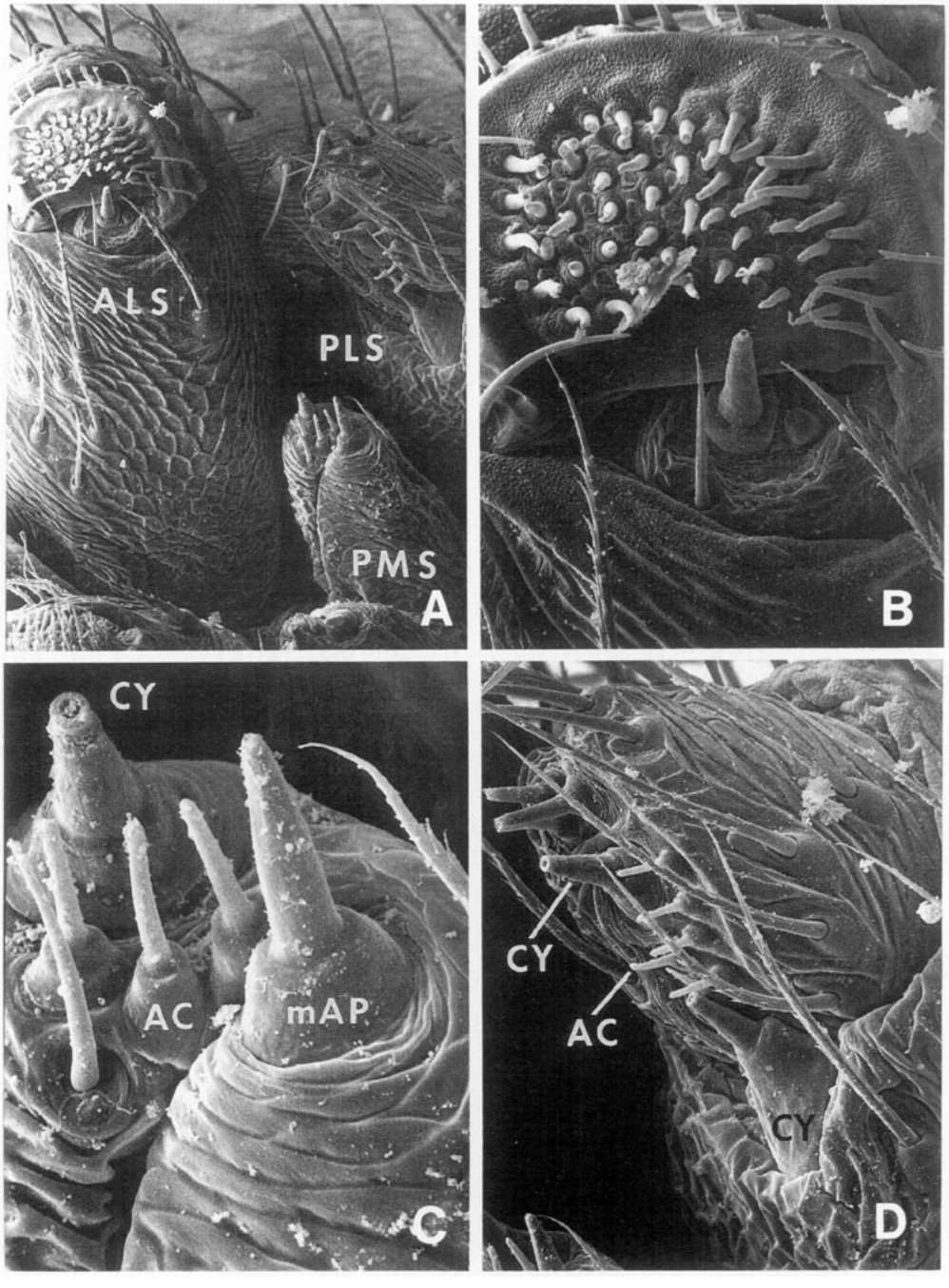

Figure 25. *Linyphia triangularis*, female spinnerets. A, Left spinneret group. B, Anterior lateral spinneret, close-up. C, Posterior median spinneret, close-up. D, Posterior lateral spinneret, close-up.

nigripes Simon (i.e. two spiracles and no atrium). The tracheal morphology of *Tennesseellum formicum* (Emerton) is similar to that of *Meioneta*, but the tracheal spiracle is positioned at some distance from the spinnerets (Fig. 17A–D). *Tennesseellum* has an atrium which stains similarly to the rest of the tracheal system. I found no evidence of two separate spiracles, nor did I find a transverse duct joining the median trunks, as Millidge (1986:57) had reported. The Pimoidae have a haplotracheate pattern (Hormiga, 1994; Fig. 15A–D).

Spinneret spigot morphology

The comparative morphology of the spinning apparatus of linyphiids has been relatively little studied. Hopfmann (1935) examined *Neriene montana* (Clerck), Wasowska (1966) and Peters & Kovoor (1991) examined *Linyphia triangularis*, and Coddington (1989) studied *Frontinella pyramitela* (Walckenaer). Only the last two studies provided detailed scanning electron micrographs of the spinnerets and its associated spigots, although Hopfmann's drawings (1935: figs 5–7) are sufficient to distinguish the different spigot types and their relative positions. The genera presented here confirm some previous hypotheses which were based on only one or a few linyphiid species. The linyphiid spigot morphology fits well in the araneoid groundplan, as Coddington (1989, 1990) and Peters & Kovoor (1991) had already pointed out. Although Peters & Kovoor (1991:15) claim that "the spinning apparatus of *Linyphia triangularis* corresponds to the *araneid* pattern" (italics mine), it is more accurate to state that it corresponds to the *araneoid* pattern, since the alleged points of similarity (e.g. the araneoid PLS triad) are also shared by other areneoid families (e.g. Tetragnathidae). The data presented here agree with Peters & Kovoor's hypothesis on the small number of aciniform glands as a familial characteristic of linyphiids. However, such reduction of the aciniform spigots is found in other derived araneoids and it may be correlated with the lack of aciniform A glands (Coddington, 1989:90).

Pimoids and linyphiids have in common the position of the mesal cylindrical spigot in the periphery of the PLS spinning field, which is also found in *Zygiella x-notata* (personal observation) and in some other tetragnathids (Coddington, personal communication; Kovoor, 1990; Platnick *et al.*, 1991; Wasowska, 1966). This peripheral cylindrical spigot, which Millidge (1988:263) incorrectly classifies as an 'additional or extra spigot', is present in the erigonines studied here as well as in *Diplocentria bidentata* (Emerton), and probably in most of the erigonines, contrary to Millidge's assertion of the absence of this cylindrical spigot in all the erigonines.

This pattern of peripheral cylindrical spigots might be a synapomorphy for pimoids, linyphiids, and tetragnathids, but more evidence is needed. Linyphiids share with pimoids the enlargement of the peripheral cylindrical spigot base (e.g. *Microlinyphia* in Fig. 26D). I have been able to examine unpublished SEM micrographs of the spigot morphology of *Helophora insignis* (Blackwall) and *Drapetisca* sp., taken by Jonathan Coddington. *Helophora insignis* is very similar to the linyphiids described here: it has two aciniform spigots in the PMS and an elongated aciniform field with ten spigots, between the two distantly separated cylindrical spigots of the PLS. *Drapetisca* is unusual in that the PLS triad has been reduced to a single spigot, either the flagelliform or one of the two aggregate gland spigot. The remaining PLS spigots are typical.

It is unlikely that this species (or at least the adult females), has any sticky silk

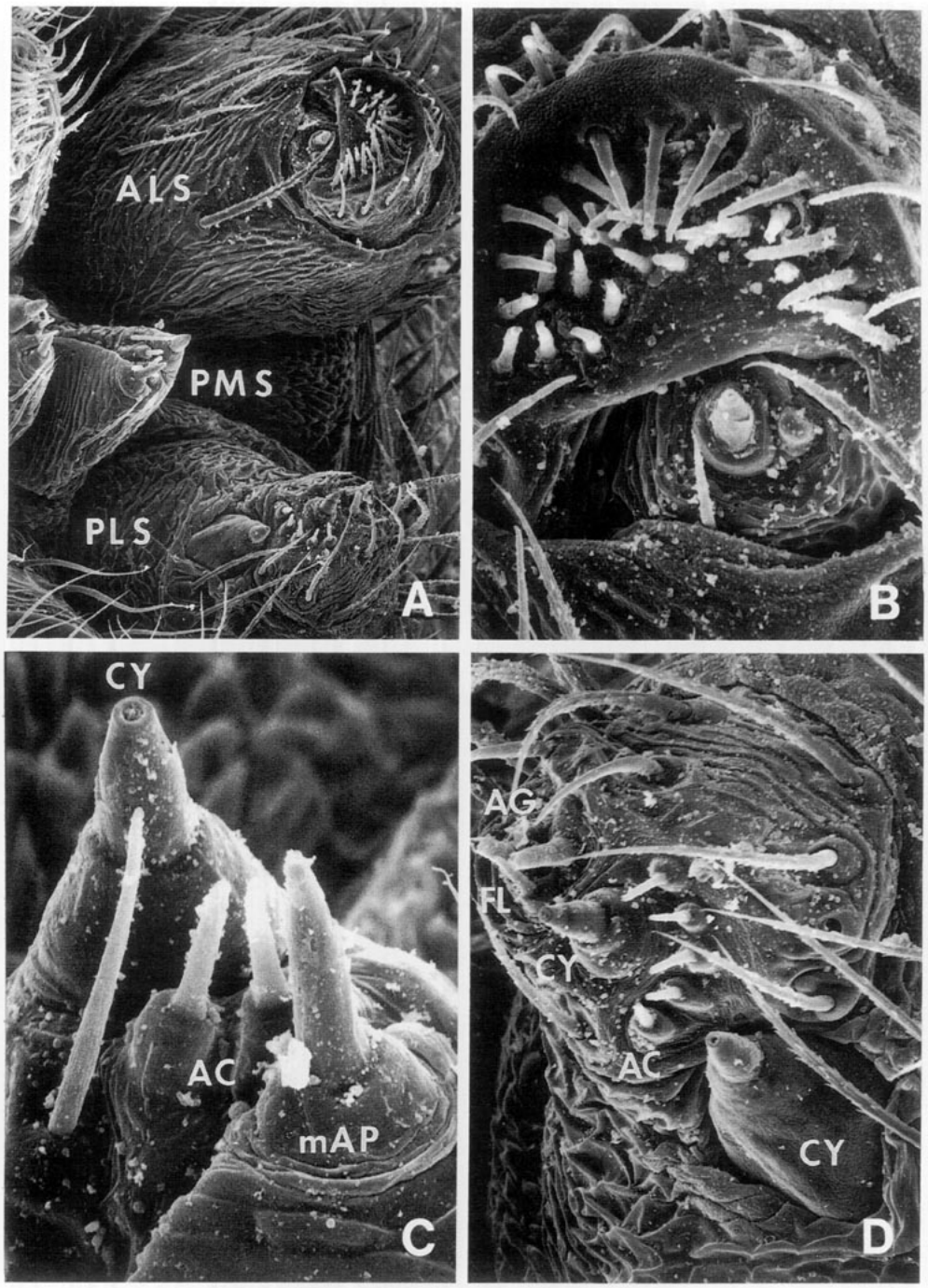

Figure 26. *Microlinyphia dana*, female spinnerets. A, Left spinneret group. B, Anterior lateral spinneret, close-up. C, Posterior median spinneret, close-up. D, Posterior lateral spinneret, close-up.

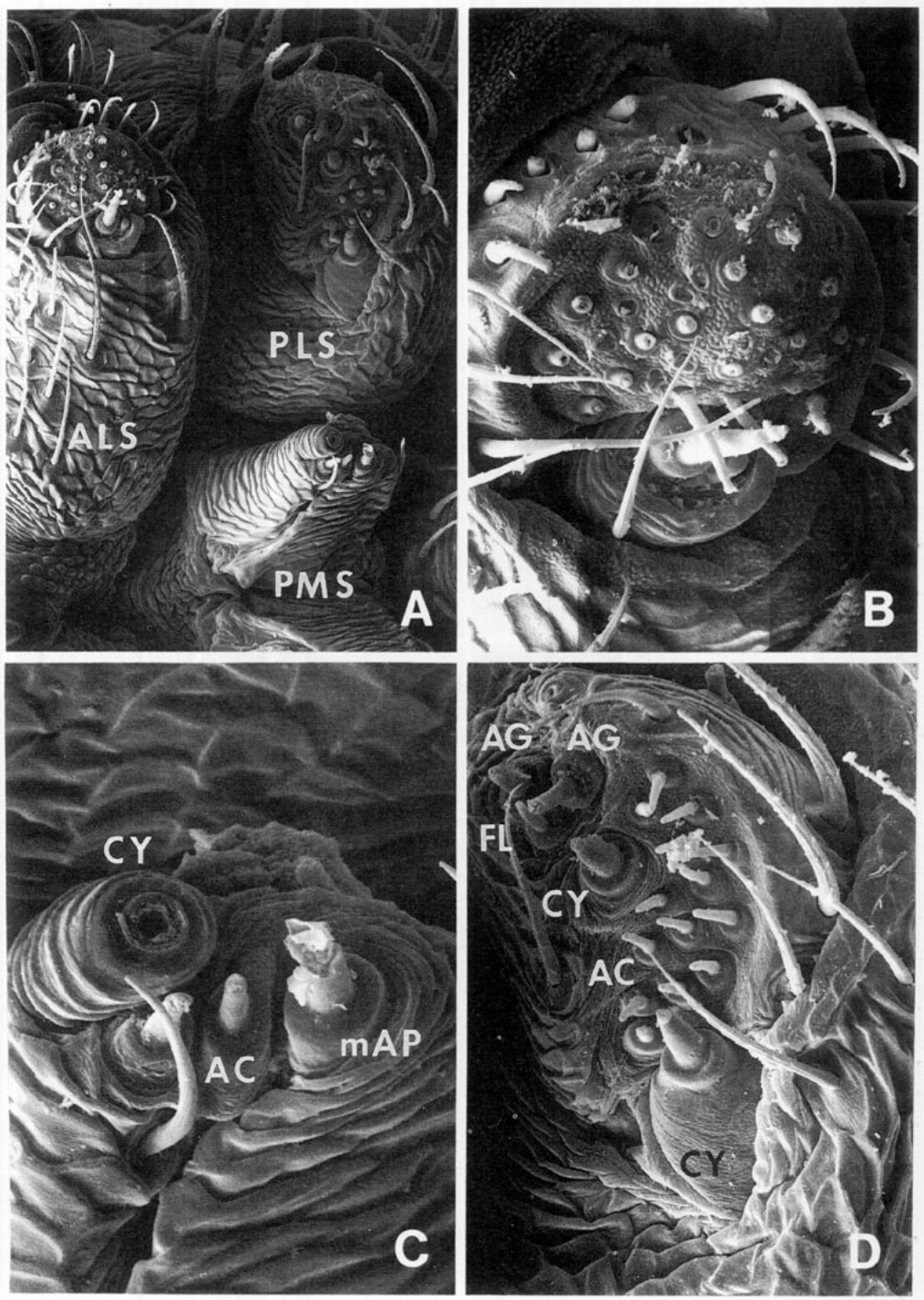

Figure 27. *Bolyphantes luteolus*, female spinnerets. A, Left spinneret group. B, Anterior lateral spinneret, close-up. C, Posterior median spinneret, close-up. D, Posterior lateral spinneret, close-up.

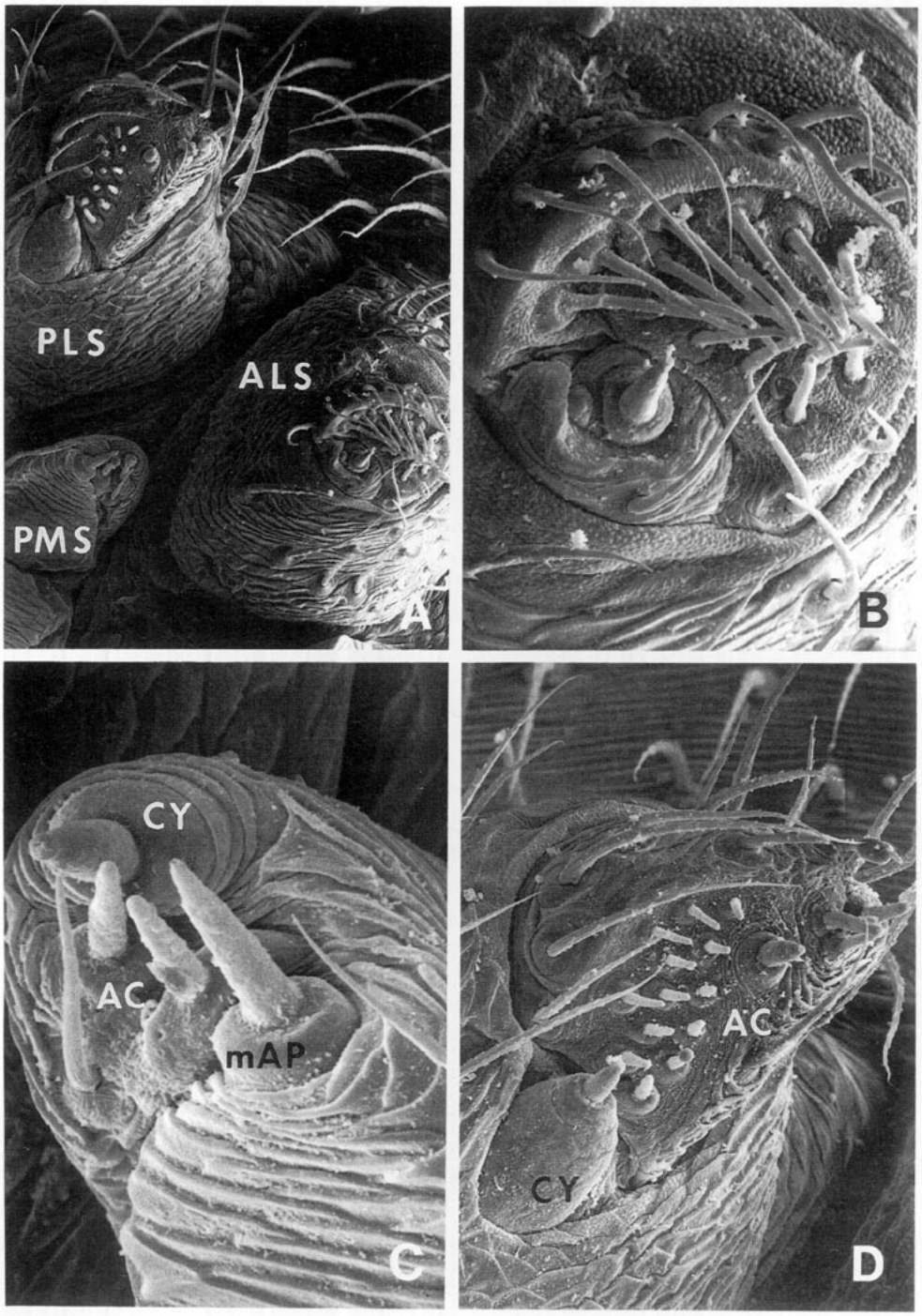

Figure 28. *Lepthyphantes tenuis*, female spinnerets. A, Right spinneret group. B, Anterior lateral spinneret, close-up. C, Posterior median spinneret, close-up. D, Posterior lateral spinneret, close-up.

in its web. Early natural history observations indicated that the European species *D. socialis* (Sundevall), which is usually found on tree trunks, had abandoned web construction (Bristowe, 1958:267; Nielsen, 1932:203), although the latter author pointed out that "(*D. socialis*) may occur so abundantly on the same stem that the tree is entirely covered with silk from the securing-threads and glitters in the sun". The fine web of *D. socialis* was finally documented by Kullmann (1961). The North American species *D. alteranda* Chamberlin also builds a web, which "is a sheet closely appressed to the tree trunk, hence difficult to see" (Kaston, 1978:117)". However, until more explicit and detailed information on the web building behaviour of *Drapetisca* is provided it is not possible to determine the biological significance of the reduced triads.

So far, all the linyphiid genera I have examined, plus those reported in the literature, show the mesal cylindrical base enlargement, which seems to be less pronounced in the pimoids (Hormiga, 1994). This synapomorphy, together with the patella-tibia autospasy and the cheliceral stridulating files, support the monophyly of pimoids plus linyphiids. There seems to be little variation in spinneret spigot morphology of the linyphiids described here. The loss of all the aciniform gland spigots seen in *Stemonyphantes blauveltae* has also occurred in some of the pimoids (Hormiga, 1993, 1994). I have mapped (Fig. 31) the loss of the PMS aciniforms as independent events occurring in parallel in *Stemonyphantes* and in the pimoids (Hormiga, 1994). The PLS aciniform spigots are lost in parallel in the higher pimoids and in *Stemonyphantes*. It will be interesting to know if this absence of aciniform spigots is shared by other species of *Stemonyphantes*. Charles Griswold and I have examined specimens of a west African species of the mynoglenine genus *Afroneta* in which all the aciniform spigots have also been lost, and on the PMS only the minor ampullate gland spigot remains. The male has no spigots on either the PMS or the PLS. The New Zealand mynoglenines studied so far have aciniform spigots on both the PMS (2–3 spigots) and the PLS (7–9 spigots). The study of more linyphiid taxa might reveal more instances of, presumably, independent losses of the aciniform fields. While I have examined the implications of additively coding the number of aciniform spigots (several-one-zero), there is no strong biological evidence to support this gradualistic coding scheme. Furthermore, in a cladistic analysis of the species of *Pimoa*, Hormiga (1994) has found that none of the 15 most parsimonious cladograms could explain the data without re-appearance of the aciniform spigots, at one point or another, after being lost in the nearest ancestor.

Monophyly of Linyphiidae

The monophyly of the linyphioid clade (pimoids plus linyphiids) has already been treated in detail in Hormiga (1993, 1994). Linyphiids and pimoids share the following four apomorphies: loss of paracymbial apophyses, presence of cheliceral stridulatory striae, autospasy at the patella-tibia junction, and the enlargement of the peripheral cylindrical spigot base of the PLS. The presence of sheet capture webs in both groups offers additional support for their sister-group relationship.

In the present data set, linyphiid monophyly is supported by eight synapomorphies (but only characters 15 and 29 can be unambiguously optimized). Two of them might be 'artifacts' due to the small taxon sample size:

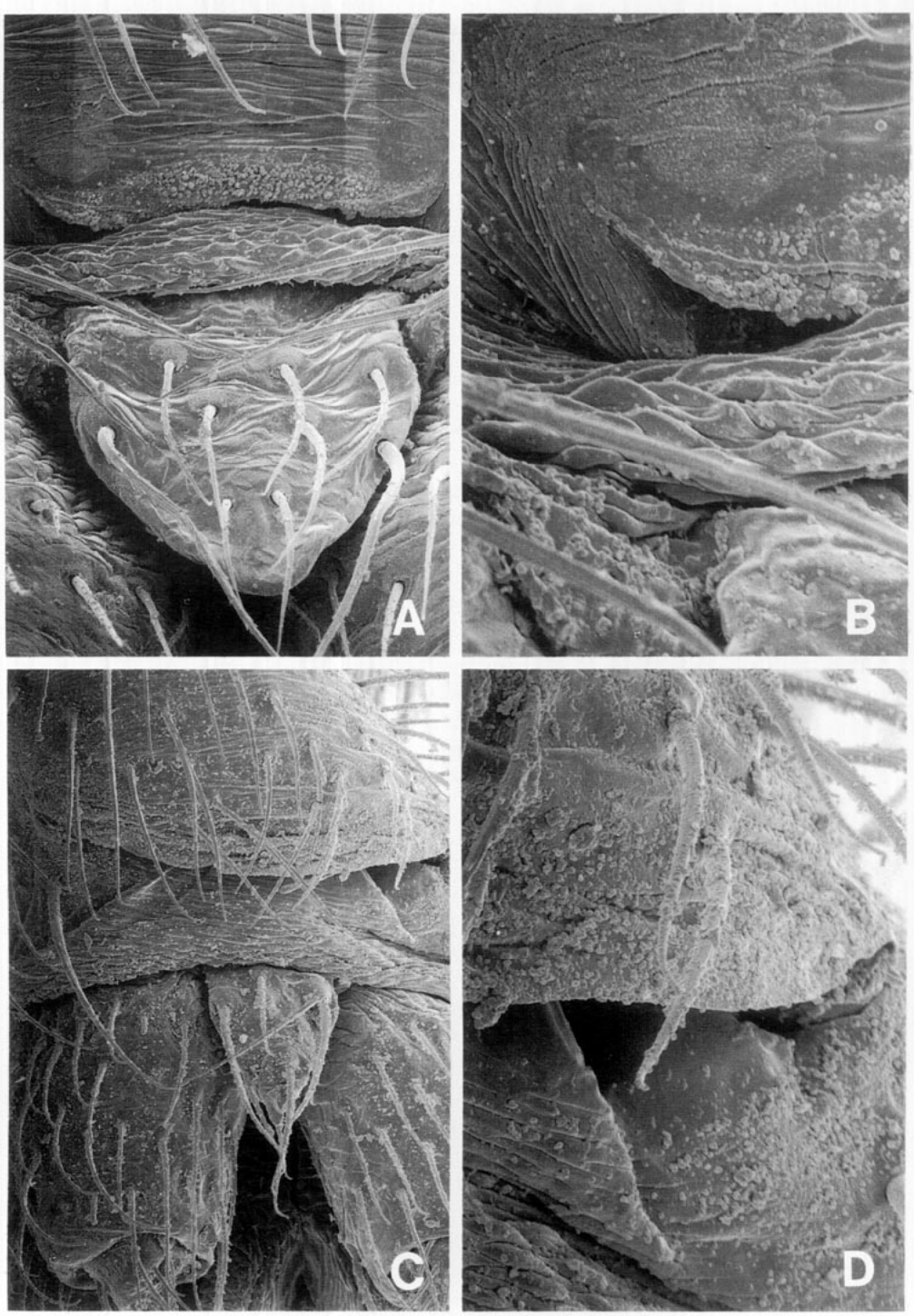

Figure 29. Respiratory spiracle, A, B, *Stemonyphantes blauveltae*, female. C, D, *Walckenaeria directa*, female.

the number of prolateral trichobothria in the male pedipalpal tibia (character 29, one trichobothrium in the present sample of linyphiids, except in *Haplinis*) and the number of retrolateral teeth in the female chelicerae (character 37, four or more teeth). These two synapomorphies might not be corroborated with a data matrix that includes a larger number of linyphiid genera. The remaining six synapomorphies provide stronger support for the monophyly of linyphiids, although homoplasy exists. All known linyphiids lack the araneoid median apophysis and conductor (characters 14 and 15, respectively), which are still present, although reduced in size, in their closest relatives, the pimoids, as well as in other orbicularian families. These two linyphiid synapomorphies had already been suggested by Coddington (1990a). The presence of an intersegmental paracymbium is another synapomorphy for linyphiids. Some tetragnathids have similar intersegmental paracymbia (Levi, 1981), but 'paracymbium intersegmentality' might not be homologous in tetragnathids and linyphiids (i.e. might have two independent origins).

Millidge (1988) regards the intersegmental condition of the paracymbium in linyphiids and in some tetragnathids as different, because in the tetragnathids the paracymbium is "not attached to the (cymbium-tibia) joint membrane, and must be regarded as integral". It is conceivable that these two intersegmental attachments represent different states within the same transformation series, but the possibility of independent origins exists too. I have taken the conservative approach of coding them, at least initially, as the same manifestation of a single character. Congruence with other characters will test this hypothesis. In his speculations on the origin of the intersegmental paracymbium Millidge (1988) argues that some linyphiids (*Neomaso* Forster, *Floronia* Simon, and *Drapetisca* Menge) "have an integral paracymbium in addition to the intersegmental one", which may indicate that "in the Linyphiidae the latter paracymbial type was not derived from the former". I agree that it is logical to conclude that the intersegmental paracymbium of the mentioned genera cannot be derived from their ectal cymbial apophysis ('integral paracymbium'). However, the generalization of this particular case to a higher level (linyphiids and the rest of araneoids) is based on the assumption that the integral 'paracymbium' of *Neomaso* and other genera is homologous to the integral paracymbium of araneoids.

Such assumptions seem quite unrealistic, since they require independent origins of the paracymbium in linyphiids and the rest of araneoids, and the loss in all linyphiids (with exception of the 'missing link' genera like *Neomaso*) of the araneoid paracymbium. If there are two types of paracymbia in these taxa it is clear that they are non-homologous structures: "if two structures are supposed to be homologous, that hypothesis can be conclusively refuted by finding both structures in one organism" (Patterson, 1982:38). Since they are non-homologous structures, only one of them can be correctly called the paracymbium. The logical candidate is the intersegmental one, since it is the one that almost all the linyphiids have.

The radix and the column (characters 22 and 23, respectively) are potential synapomorphies of Linyphiidae that need the resolution of the pimoid-linyphiid clade position in Araneoidea to be fully assessed. Coddington (1990a:14) has suggested that linyphiids and araneids are sister groups. If that is the case the linyphiid radix could be a homolog of its homonym in araneids. Similarly, the

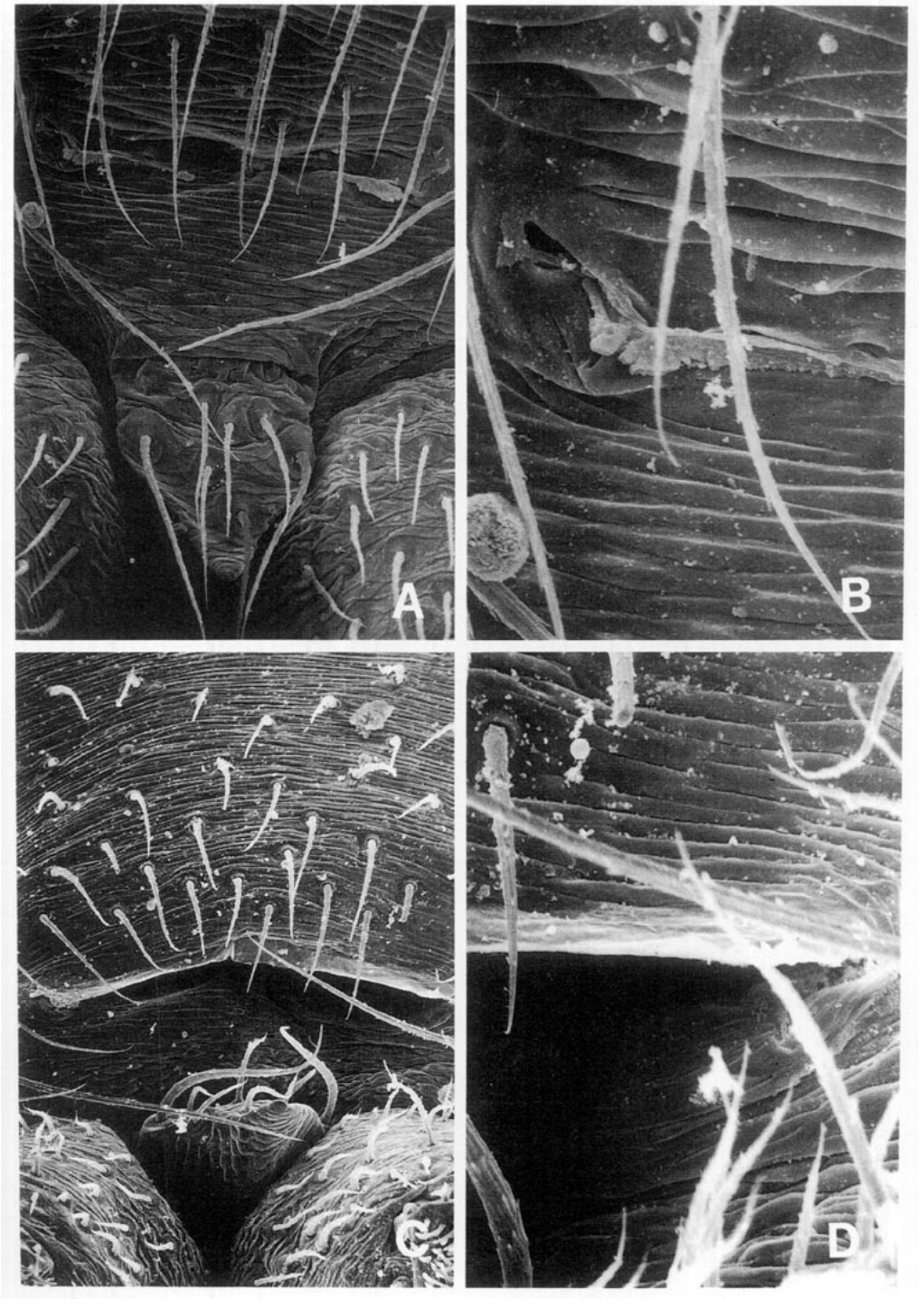

Figure 30. Respiratory spiracle. A, B, *Lepthyphantes tenuis*, female. C, D, *Microlinyphia dana*, female.

column could be homologous to the araneid distal haematodocha (the membrane between tegulum and embolic division; see fig. 8 in Coddington, 1990a). However, Comstock's (1910:177, 179) original use of the term 'distal haematodocha' was for the membrane between the radix-stipes and the embolus (N. Scharff *in litt.*). Recent preliminary results on the phylogeny of araneids and relatives (N. Scharff and J. Coddington, personal communication) suggest that Tetragnathidae, and not Araneidae, is the sister group of the pimoid-linyphiid clade, but that result might be an artifact resulting from their limited taxon sample size. If that is the case, the linyphiid and the araneid radix have evolved independently, refuting therefore their homology, despite sharing the same name (this is the hypothesis that I have mapped in the cladogram of Fig. 31). Another

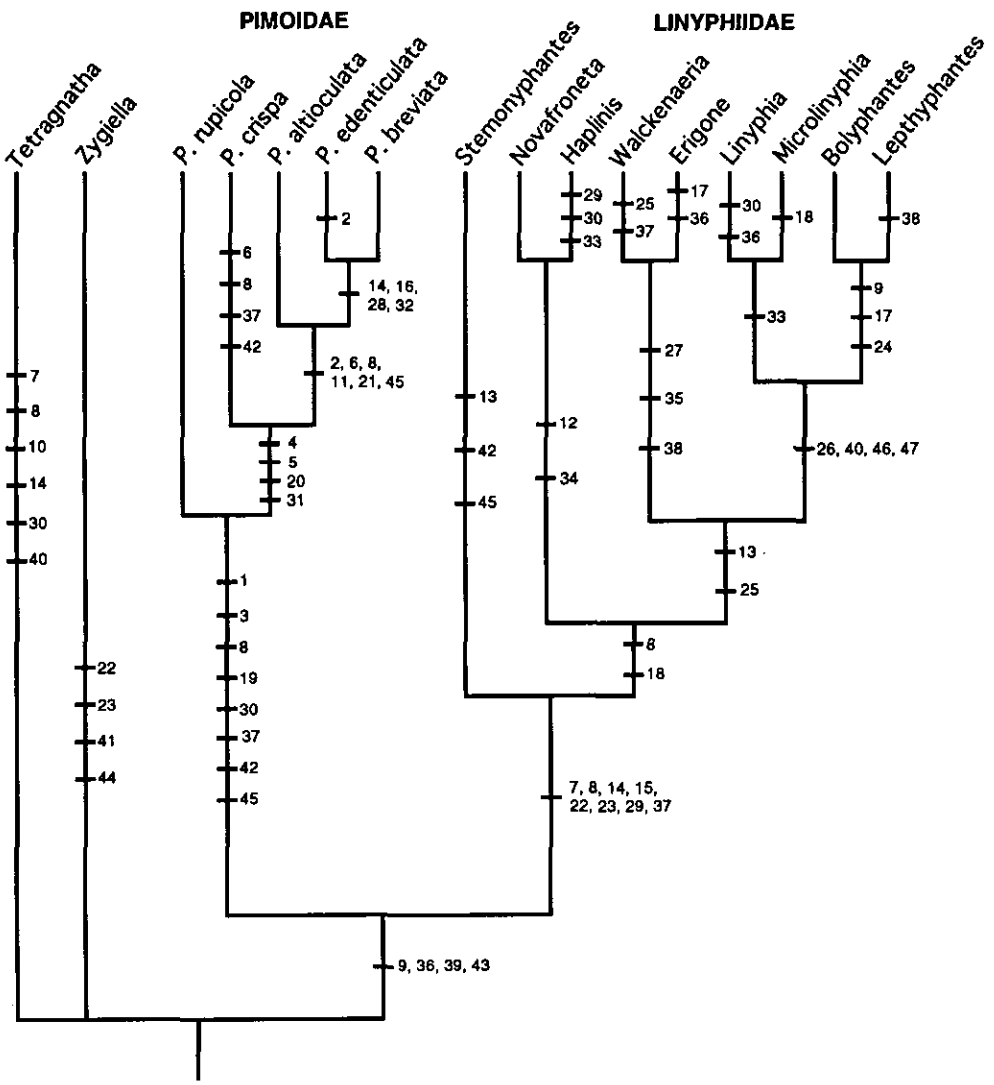

Figure 31. Preferred minimum length cladogram for the taxa and characters in Appendix 2. Three equally parsimonious alternative topologies exist (see text). The cladogram length is 80 steps; the consistency and retention indices are 0.73 and 0.81, respectively.

implication of Scharff and Coddington's results is that complex embolic divisions have probably evolved independently in araneids and linyphiids, which might suggest that basal linyphiids (*Stemonyphantes* and mynoglenines in my cladogram) have primitively simple, rather than secondarily simplified, embolic divisions.

Linyphiid clades

The linyphiid genera of this study can be divided into four terminal clades plus the genus *Stemonyphantes*. Two synapomorphies group all the linyphiid genera, with the exclusion of *Stemonyphantes:* the presence of a 'U'- or 'J'-shaped paracymbium and the embolic membrane (characters 8 and 18, respectively). The paracymbium in *Stemonyphantes* is attached to both the cymbium and the tibia-cymbium intersegmental membrane (Fig. 3C), and for this reason Millidge (1988) considers it to be intermediate between the integral and intersegmental types. The *Stemonyphantes* type of paracymbium is hypothesized to have been present in the common ancestor of all linyphiids (therefore, it would be synapomorphic for the family), derived from either the araneid or the tetragnathid type of paracymbium. The presence of an embolic membrane is also synapomorphic for all the linyphiid genera, excluding *Stemonyphantes* (but it is lost in *Microlinyphia*).

The genus *Stemonyphantes* is peculiar on several counts. I have already discussed its paracymbium morphology and the absence of aciniform spigots in at least *S. blauveltae*, which have been lost independently of the pimoids. Its male palp morphology, particularly the embolic division, is very different from the rest of linyphiids. Several authors have already pointed out the difficulties of homologizing the elements of the embolic division (Blauvelt, 1936; Merrett, 1963; van Helsdingen, 1968). The suprategulum (character 13) of *Stemonyphantes* is articulated to the tegulum by means of a membranous hinge (van Helsdingen, 1968; 'a' in Figs 2C and 3B), while in the rest of linyphiids the suprategulum is continuous with the tegulum (not articulated). While my initial hypothesis was to regard these two types of suprategula (articulated and not articulated) as homologous, the most parsimonious optimization of this character suggests the possibility of independent origins for these two types. A monophyletic origin of the suprategulum in the common ancestor of all linyphiids (which implies secondary absence of the suprategulum in the mynoglenines) requires one additional step in the cladogram of Fig. 31. Position and detailed similarity suggest independent origins (i.e. non-homology) for the tibial apophyses of erigonines (retrolateral and heavily sclerotized), *Stemonyphantes* (ventral and hook-like) and pimoids (dorsal and rounded).

Two synapomorphies support the monophyly of mynoglenines: the tegular apophysis (character 12) and the cephalic sulci (character 34). The mynoglenine tegular apophysis is not homologous to the linyphiid suprategulum, as I have already discussed, and it seems to be an autapomorphic development of this group. In addition to this apophysis some mynoglenines (e.g. *Haplinis diloris*, Fig. 5A, B, E) have a small tegular process ('tegular prominence' in Blest, 1979). Holm (1979:256) has argued that the tegular process of *Haplinis* might be homologous to the protegulum found in erigonines. While Holm (1979, 1984) has described the erigonine protegulum as having membranous integument, the mynoglenine tegular process appears quite sclerotized. Other than the fact that

both structures are positioned on the tegulum, I do not see much evidence in support of such claim. A second mynoglenine synapomorphy is the presence of characteristic cephalic sulci (character 34), which I have already discussed.

Another classical question in linyphiid evolution is whether the 'simplicity' in many erigonine male palps is primitive or derived. Simple or complex embolic divisions (*sensu* Merrett, 1963) allude to the absence (simple, e.g. *Haplinis* or *Walckenaeria*) or presence of radical sclerites (complex, e.g. *Erigone* or *Linyphia*). However, this terminology does not provide a clearcut division, since intermediate levels of embolic division complexity exist. It seems more appropriate to address the radical sclerites independently, rather than the embolic division as a whole. While some of the cases of simple embolic divisions might be the result of simplification (i.e. loss of sclerites), it is less likely, but not impossible, that complex divisions have evolved more than once within linyphiids. In the cladogram depicted in Fig. 31 the pimoid clade and the two most basal linyphiid clades have simple embolic divisions, which suggests that the radical component of *Stemonyphantes* is primitively simple, not simplified. Erigonines and linyphiines share the presence of a suprategulum continuous with the tegulum (i.e. not articulated) and of a terminal apophysis in the embolic division. The terminal apophysis (which in erigonines could also be homologized with the lamella characteristica) is absent in many erigonine genera which have very simple embolic divisions, like *Walckenaeria*. A larger sample of taxa, particularly erigonines, is needed to test this latter synapomorphy, because of the diversity of erigonine embolic divisions.

Erigonine monophyly is supported by the presence of a retrolateral tibial apophysis in the male palp (character 27), a desmitracheate tracheal system (character 35), and the loss of the female pedipalpal claw (character 38). As we have seen, position and detailed similarity do not suggest a single origin for the tibial apophyses of erigonines, *Stemonyphantes*, and pimoids. In general, orbicularians lack male palpal tibial processes, except the mentioned cases, but there are some sporadic exceptions, like some anapids (Griswold, 1990:14). The presence of a retrolateral palpal tibial apophysis defines the so called 'RTA clade' (Coddington & Levi, 1991), a putatively monophyletic assemblage of families, sister to the Orbiculariae, which contains, among others, the lycosoids, dictynoids, dionychans, and amaurobiids (although the 'RTA clade' is based on little evidence and almost no quantitative analysis; Coddington, personal communication).

Within the linyphiids the presence of medial tracheal trunks branched into multiple tracheoles that go into the prosoma (desmitracheate pattern) is characteristic of erigonines, and as Millidge (1984:233) has suggested, it provides evidence for the monophyly of erigonines. However Millidge (1984:233, see also p. 258) misunderstands parsimony when he claims that this latter hypothesis on the monophyly of erigonines "is of course dependent on the assumption (based on the principle of Occam's Razor, or parsimony, Nelson & Platnick, 1981:37) that within the Linyphiidae the desmitracheate system evolved only once from the primitive haplotracheate system". The principle of parsimony involves only the preference for simpler hypotheses over more complex ones (Nelson & Platnick, 1981:37), that is, preference for those hypotheses that minimize the number of *ad hoc* statements necessary to explain our observations. The parsimony criterion is a reasoning tool to choose among competing alternative

hypotheses, and not an assumption on the evolutionary process. However, the desmitracheate pattern is homoplasious, since similar medial trunks are also found, at least, in the linyphiines *Tennesseellum formicum*, *Meioneta*, and *Agyneta* (Millidge, 1986). It also suggests a synapomorphy that groups the genera *Tennesseellum*, *Meioneta*, and *Agyneta* which also have similar male genitalia (Saaristo, 1973; Millidge, 1977).

The linyphiid tracheal system needs reevaluation. As I have discussed earlier, some of the published observations on the tracheal system anatomy are not accurate. Most of the inaccuracies refer to the presence or absence of a tracheal atrium and its opening spiracle. I have found no evidence of atria opening via two independent spiracles in the linyphiids that I examined (see Appendix 1), which is in disagreement with some of Millidge's (1986) morphological data. In the absence of a bispiraculated tracheal system (or tracheal systems without atrium) Millidge's (1986) hypothesis on the evolution of the linyphiid tracheal system collapses due to lack of evidence for his hypothetical ancestral stages (A and B in Millidge's fig. 12) as well as for four out of his five terminal morphologies (D–F and H in the same figure).

Within the Linyphiidae the presence of the female palpal claw is plesiomorphic, and therefore its absence in erigonines is synapomorphic. The palpal claw has been independently lost in *Lepthyphantes tenuis*. Detailed examination of many other linyphiid genera will probably bring other cases of secondary absence of the claw, which is also absent in some other araneoids, like theridiosomatids (Coddington, 1986). Future studies will probably discover other synapomorphies that corroborate the monophyly of erigonines.

Two characters that need further study are the protegulum and the male cephalic modifications. I have briefly discussed earlier in this paper the latter character. Similar, and independently derived, cephalic modifications can be found in some male theridiids (e.g. *Argyrodes* Simon, Levi & Levi, 1962; Lopez, 1977; Lopez & Emerit, 1979, 1981). The protegulum (Holm, 1979; 'bezel' in Crosby & Bishop, 1925:6) is a protruding membranous projection arising from the apical side of the tegulum (Fig. 6C). According to Holm (1984:140) the protegulum is present in all erigonine spiders, and "probably has a mechano and/or chemoreceptive function during copulation, then being always turned in the same direction as the embolus". More data are needed to corroborate the protegulum as an erigonine synapomorphy, particularly regarding its alleged presence in all erigonines, and its absence (or presence of a plesiomorphic homologue) in all or some of the rest of linyphiids.

The monophyly of linyphiines (Linyphiini plus Micronetini in Wunderlich, 1986) is supported by four synapomorphies: the presence of a lamella characteristica (character 26), the loss of the trichobothrium of metatarsus IV (character 40), and the position of the male above the sperm web during its construction and during ejaculation (characters 46 and 47, respectively). The latter two characters should be regarded as provisional, because of our limited knowledge of linyphiid behaviour. I have already treated the problems involved in assessing the homologies of the terminal apophysis and lamella characteristica in linyphiids. In the cladogram depicted in Fig. 31 the lamella is a linyphiine synapomorphy.

Alternatively, one could interpret erigonines as lacking the terminal apophysis, but having instead a lamella characteristica. The mapping of these

two synapomorphies would be then as follows: the lamella grouping erigonines plus linyphiines (secondarily absent in some erigonines) and the terminal apophysis would be a synapomorphy restricted to linyphiines. The epigynal atrium (character 33) is the only synapomorphy supporting the monophyly of Linyphiini. A similar atrium is found in *Haplinis* (Blest, 1979:100), but it is absent in *Novafroneta* (Millidge, 1984:241). Millidge (1984:255) has pointed out that the atrium is more highly developed in the Linyphiinae than in the Mynogleninae. Because the cladogram suggests independent origins for the atria in Mynogleninae and Linyphiini, its homology is questionable. The derivation of the epigynal atrium in the common ancestor of mynoglenines and erigonines plus linyphiines requires at least two additional steps in the cladogram. The presence of a scape in the dorsal plate of the epigynum might provide additional support for the monophyly of the Linyphiini (Millidge, 1984:241, 256). A study assessing the possible homology to the dorsal scape in other linyphiids (e.g. some mynoglenines) is needed to corroborate this latter putative synapomorphy.

The monophyly of Micronetini is supported by three synapomorphies: the presence of paracymbial apophyses, a short embolus (it also occurs in *Erigone*), and the presence of Fickert's gland in the radix (characters 9, 17 and 24, respectively). Paracymbial apophyses are present in both *Tetragnatha* and *Zygiella*, but absent in pimoids and linyphiids, with the exception of the micronetines, which suggest independent derivations (a single origin requires four extra steps in the cladogram). While most linyphiids, as well as the pimoids, have a more or less long and filiform embolus, the Micronetini (and some erigonines) have a short embolus, but this character when used for a large sample of linyphiid genera might have a poor fit to the cladogram. Another putative synapomorphy for this group has been postulated by Saaristo (1975:25), who suggests that the presence in the female genitalia of receptacles (spermathecae) divided into two semidetached compartments (which he has named 'receptaculae A and B', figs 11a and b) represents a derived (i.e. synapomorphic) feature of Micronetini (his Lepthyphantinae). Saaristo has studied the spermathecal chambers across a large number of Micronetini genera (e.g. *Maro*, *Agyneta*, *Anomalaria*, *Meioneta*, *Aprolagus*, *Syedrula*, etc.), as well as in *Araneus* (Araneidae), which has the presumably plesiomorphic condition (simple, undivided spermathecae). Surprisingly, Millidge (1984) does not discuss Saaristo's spermathecal character in his taxonomic study of the epigynal morphology in linyphiids. To confirm the validity of Saaristo's spermathecal synapomorphy we need a study evaluating the homologous condition of this character in linyphiid taxa outside the Micronetini. Finally, an additional synapomorphy for the micronetine genera of this study has been suggested by Millidge (1984:256). According to Millidge the presence of a sigmoid scape in the ventral plate of the epigynum is a synapomorphy for several genera in the Micronetinae, including *Lepthyphantes* and *Bolyphantes*.

CONCLUSIONS

Comparisons of linyphiids to their closest relatives, the pimoids, and to the possible sister groups of the pimoid-linyphiid clade (tetragnathids and araneids) allow discrimination between plesiomorphic and apomorphic features, and makes it possible to place linyphiid systematics into a phylogenetic perspective.

This study corroborates some of the previous phylogenetic hypotheses and it serves to highlight some areas which require further investigation. It also suggests that the vast amount of linyphiid morphological data that has been gathered during the long taxonomic history of the group has to be critically approached, and that in some cases published data are wrong. In many instances the data cannot be accurately retrieved from the literature (due to incomplete descriptions, 'iconographic' illustrations, etc.). In other cases the morphological descriptions are erroneous (e.g. some of the observations of the tracheal system).

Shortly after the acceptance of this paper for publication, a work by Millidge (1993b) appeared on linyphiid systematics based mainly on the study of the epigynal morphology. The author erected a new linyphiid subfamily, modified his former definitions of several of the remaining subfamilies, and once again suggested that linyphiids find their closest relatives among dictynoids and/or amaurobioids, especially the families Dictynidae and Titanoecidae. The author does not seem to pay any attention to shared derived traits as evidence of recency of common ancestry, and he ignores well-known (and published) character distributions that flatly contradict his hypotheses of relationship and homology. For example he rejects, once more, the placement of Linyphiidae in Araneoidea, but avoids confronting several recent studies that specifically addressed his proposals (e.g. Coddington, 1990a, b; Coddington & Levi, 1990; Peters & Kovoor, 1991). The available evidence clearly suggests that linyphiids are more closely related to araneoid families than to either dictynoids or amaurobioids, hence further hypotheses that depend on the latter notion face the same flaw. Until Millidge shows that the linyphiid-amaurobioid/dictynoid link has even a remote chance of being correct, ideas that depend on that notion are more like wishful thinking than hypotheses. His desultory enumeration of isolated instances of similarity between the morphology of linyphiids and amaurobioids and dictynoids is not sufficient to change the former into the latter.

The monophyly of the Linyphiidae is well supported (eight synapomorphies, although two of them might be methodological artifacts). The most parsimonious hypotheses (i.e. cladograms) to account for the distribution of characters presented in this study (Appendix 2) largely agree with the cladogram proposed by Wunderlich (1986) but suggest a different placement for the mynoglenines. Whereas Wunderlich suggested that mynoglenines as sister to the erigonines (Fig. 32A), here the former subfamily is considered as a relatively basal linyphiid clade, sister to erigonines plus linyphiines (Figs 31 and 32B). One extra step on this dataset is required by Wunderlich's hypothesis of mynoglenines plus erigonines monophyly.

The following characters, according to Wunderlich (1986:106), provide support for the monophyly of erigonines plus mynoglenines: female pedipalp without claw, pedipalpal femur with only one stridulating tooth, simple paracymbium and bulb structure, and perhaps the building of the sperm web from below. At least three of these characters do not provide evidence of monophyly when examined in detail. The female pedipalpal claw is present in at least all the mynoglenine genera that I have examined in this study. Aside from the problem of defining what 'simple' is intended to mean (perhaps without apophyses?), the presumably 'simple' paracymbium is not unique to erigonines and mynoglenines, since similar paracymbia are also found in many linyphiines

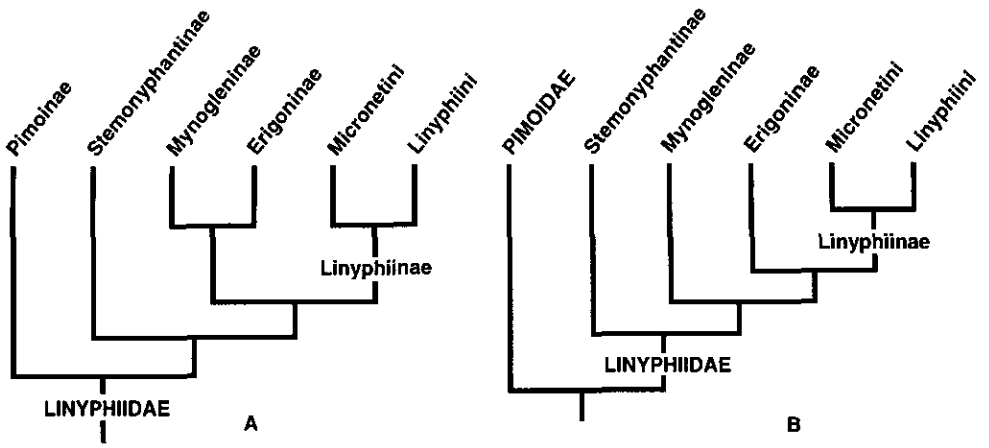

Figure 32. Cladograms for the subfamilies of Linyphiidae. A, Wunderlich (1986). B, this study.

(van Helsdingen, 1986:122). The similarities in palp (bulb) structure between mynoglenines and erigonines either do not stand close examination (i.e. homologous comparisons of every sclerite) or are not unique to these two groups. The rest of the characters (stridulating teeth and sperm web building behaviour) are poorly known and at present do not provide strong support for either of the two hypotheses. The presence of a fused suprategulum and a terminal apophysis in the male palp provide evidence for the monophyly of linyphiines plus erigonines, with the exclusion of mynoglenines (which lack both structures).

Both Wunderlich's and this study agree on considering the pimoids and *Stemonyphantes* as the most basal linyphiid lineages, and on the monophyly of the Micronetini plus the Linyphiini. However, it would be premature to use either of these two cladograms as a classification. Certainly the study of the linyphiid phylogeny is in its very early stages. Advances in the study of linyphiid phylogeny will require the identification of the closest relatives of the linyphiid-pimoid clade, and the addition of more linyphiid taxa and characters.

While the last decade has witnessed a significant increase in our knowledge on araneoid phylogeny (references in Coddington & Levi, 1991), the question of the placement of the linyphiid-pimoid clade in Araneoidea remains unsolved. Araneids and tetragnathids as sister taxa to linyphiids are two potential candidates. The poorly known family Cyatholipidae has also been suggested as a potential sister group to the linyphioid lineage. While many cyatholipids spin sheet webs similar to those of linyphiids, there are no morphological apomorphies that clearly link these two groups. A detailed study of cyatholipids may provide such evidence. Preliminary analysis of data on cyatholipid phylogeny suggests instead a close relationship to some taxa currently placed in the theridioid family Synotaxidae (C. Griswold, personal communication). The resolution of the placement of these derived araneoid lineages (the sheet weavers), together with the theridioid lineage, is essential for understanding the evolution of web architecture.

This study sample lacks representatives of the endemic genera from South America, Africa, Asia and Australia, which might be critical for understanding the phylogeny of Linyphiidae. Let us try to imagine for a moment what our knowledge of mammal phylogeny would be if we were to exclude the Australian

fauna. The monotremes, which bridge between other amniotes and the therians, would be out of the picture, and so would be a large fraction of the phylogenetically important marsupials. It is evident that the absence from any study of such pivotal groups would be critical for the formulation of phylogenetic hypotheses. But despite a few recent contributions (e.g. Millidge, 1985, 1991; Scharff, 1990; Millidge & Russell-Smith, 1992) the southern hemisphere linyphiid faunas remain largely unknown.

Our notion and knowledge of linyphiid phylogeny, including this study, are highly biased towards the Holarctic fauna. Very often these newly described taxa hardly fit in the current linyphiid classification. A detailed study of some of these taxa will be necessary before any robust hypotheses on linyphiid phylogeny and character evolution are produced. Apart from the southern hemisphere fauna, several taxa of uncertain affinities in Linyphiidae can be found in Millidge's (1984) *Stemonyphantes* group. This admittedly artificial assemblage was characterized exclusively by the female genitalia. The problems posed by some of the taxa assigned to this assemblage will be resolved using a strategy more rigorous than the flawed single character approach (e.g. the case of *Microlinyphia*, formerly included in the *Stemonyphantes* group). Other linyphiid taxa will need to be critically studied within a larger character context. To uncover trends in linyphiid character evolution a much more refined hypothesis on their phylogeny is needed. The basal linyphiid lineages (*Stemonyphantes* and its close relatives and the mynoglenines) need to be represented by a larger taxonomic sample to confirm some of the homology hypotheses discussed in this paper. Nevertheless, the linyphiids studied here permit the assessment of hypotheses of homology (and therefore of genealogy) for a relatively wide range of taxa.

Typically, linyphiid higher level classification has focused very extensively on genitalic characters. A close examination of the male palp morphology of some of the southern hemisphere genera should suffice to illustrate to what extent we need to reevaluate some of these character hypotheses. For example, the classical notion of linyphiids being readily diagnosed by the presence of a U-shaped free paracymbium does not work in numerous cases, especially outside the Holarctic region. The study of new and poorly known character systems (e.g. tracheal system, spinneret spigot morphology, functional aspects of genitalia, etc.) is greatly needed to improve our poor knowledge of linyphiid phylogeny.

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de Barcelona, Department de Biologia Animal, Barcelona, Spain, Dr C. Ribera. USNM National Museum of Natural History, Washington, D.C., Dr J. A. Coddington and Mr S. Larcher. UW Burke Memorial Washington State Museum, Seattle, Dr R. Crawford.

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ANATOMICAL ABBREVIATIONS USED IN THE TEXT AND FIGURES

A	alveolus	MA	median apophysis
AC	aciniform gland spigot(s)	MAP	major ampullate gland spigot(s)
AG	aggregate gland spigot(s)	mAP	minor ampullate gland spigot(s)
ALS	anterior lateral spinneret	MTA	mynoglenine tegular apophysis
BH	basal haematodocha	MTP	mynoglenine tegular process
C	conductor	P	paracymbium
CB	cymbium	PCS	pimoid cymbial sclerite
CDP	cymbial denticulate process	Pe	petiole
CL	column (stalk)	PEP	pimoid embolic-tegular process
CY	cylindrical gland spigot(s)	PI	piriform gland spigot(s)
E	embolus	PLS	posterior lateral spinneret
EA	embolic apophysis	PMS	posterior median spinneret
ED	ejaculatory duct	R	radix
EM	embolic membrane	SA	suprategular apophysis
F	fundus	SPT	suprategulum
FG	Fickert's gland	ST	subtegulum
FL	flagelliform gland spigot(s)	T	tegulum
m	membrane (or membranous)	TA	terminal apophysis
LC	lamella characteristica		

APPENDIX 1

Material examined

Specimens are listed alphabetically by family and species. An asterisk after the species name denotes that the tracheal system was dissected and examined. A plus sign after the species name denotes that the tracheal spiracle was examined by SEM.

Linyphiidae
Afroneta sp.: Cameroon: Northwest Province: Menchum Division, near Lake Oku, *c.* 2150 m., 7–13.II.1992 (Griswold, Larcher, Scharff & Wanzie, USNM, CAS).
Alomengea dentisetis (Gruber) (*): Canada: NW Territories, McKenzie, 5 mi. SE Ft. Providence, 15.VIII.1965 (J. & W. Ivie, USNM).
Blestia sarcocuon Crosby & Bishop: USA: West Virginia: Preston Co., W.V. University Forest, Chestnut Ridge, Pitfall trap, 15–22.V.1989 (D.T. Jennings, USNM).
Bolyphantes luteolus (Blackwall): Spain: Huesca: Jaca, San Juan de la Peña, 19.XII.1977 (C. Pedrocchi-Renault *et al.*, USNM).
Centromerus sylvaticus (Blackwall) (*): Spain: Huesca: Jaca, San Juan de la Peña, 17.X.1977 (C. Pedrocchi-Renault *et al.*, USNM).
Drapetisca alteranda Chamberlin (*): USA: Massachusetts: Barnstable Co.: Hatchville, FCWMA, 31.VII.1989 (R.L. Edwards, USNM).
Erigone aletris Crosby & Bishop (*): USA: Washington: Clallam Co.: Cape Alava, Olympic N.P., 17.VII.1984 (W. Maddison, USNM).
Erigone psychrophila Thorell (*+): USA: Alaska: Pt. Barrow, 23.VI.1963 (R.F. Ashley, AMNH).
Floricomus praedesignatus Bishop & Crosby: USA: West Virginia: Preston Co., W. V. University Forest, Chestnut Ridge, Pitfall trap, 30.V–5.VI.1989 (D.T. Jennings, USNM).
Gonatium rubens (Blackwall) (*): USA: Massachusetts: Barnstable Co.: Hatchville, FCWMA, 5.IX.1989 (R.L. Edwards, USNM).
Grammonota angusta Dondale (*): USA: Maine: Piscataquis Co.: NW of Soubunge Mtn., 24.VII.1984 (J. Collins, USNM).
Haplinis diloris (Urquhart): New Zealand: Fiordland Cascade, 16.I.1975 (A.D. Blest, OM).
Hypselistes florens (O.P.-Cambridge) (*): USA: Connecticut: Abington, 7.VIII.1974 (J.A. Coddington, USNM).

Lepthyphantes flavipes (Blackwall) (*): Spain: Huesca: Jaca, San Juan de la Peña, 2.I.1978 (C. Pedrocchi-Renault *et al.*, USNM).
Lepthyphantes intricatus (Emerton) (*): USA: Maine: Piscataquis Co.: Wels, 2.7 km. NE of Soubunge Mtn., 13.VII.1978 (D.T. Jennings & M.W. Houseweart, USNM).
Lepthyphantes tenuis (Blackwall) (*+): Spain: Huesca: Jaca, San Juan de la Peña, 8.VIII.1977 (C. Pedrocchi-Renault *et al.*, USNM).
Linyphia triangularis (Clerck): Germany: between Deutzand and Siegen, 9.VIII.1964 (R. Crabill, USNM); France: Manche, Quettehou, 27.VII.1956 (USNM).
Meioneta rurestris (C.L. Koch) (*): Spain: Huesca: Jaca, San Juan de la Peña, 27.VIII.1977 (C. Pedrocchi-Renault *et al.*, USNM).
Microlinyphia dana (Chamberlin & Ivie) (+): USA: Washington: Clallam Co.: Elwha river near Altaire campground, Olympic N.P., 2.VIII.1990 (G. Hormiga, USNM); Island Co.: Lake Pondilla, 16.VI.1987 (R. Crawford, UW).
Novafroneta vulgaris Blest: New Zealand: S of Brighton, 17.VII.1974 (A.D. Blest, OM).
Stemonyphantes blauveltae Gertsch (*+): USA: New York: Ithaca (USNM); Montana: Callaway Co.: Tucker Prairie, 22.III.1985, ♀ (J.C. Weaver, USNM).
Tennesseellum formicum (Emerton) (*): USA: Oklahoma: nr. Stillwater, Jun–Sep. 1966, sorghum field (C. Bailey, CAS); Texas: Austin, May 1948 (H. Exline-Frizzell, CAS).
Walckenaeria directa (O.P.-Cambridge (+): Canada: British Columbia: Terrace, III.1933, ♀ (Hippisley, AMNH).

Pimoidae
Pimoa altioculata (Keyserling) (*): USA: Washington: Nahcotta, 23.VIII.1955 (T. Kincaid, CAS); Canada: British Columbia: Wellington, Vancouver Is., 1–20.XI.1950 (R. Guppy, AMNH).
Pimoa breuili (Fage) (*): Spain: Asturias: Babia de Abajo, Cueva Pruneda, 5.IX.1987 (Ribera, Serra & Dominguez, UB); Teverga, Cueva de la Huerta, 1.IX.1987 (Ribera, Serra & Dominguez, UB).
Pimoa breviata Chamberlin & Ivie (*): USA: Oregon: Curry Co.: Brookings, Azalea St. Pk., 16.VII.1990 (G. Hormiga & L. Garcia de Mendoza, USNM).
Pimoa crispa (Fage): India: Dehra Dun District: Chakrata (syntypes; E.A. Glennie, MNHN).
Pimoa cthulhu Hormiga (*+): USA: California: Sonoma Co.: Salt Point St. Pk., 22.IX.1991 (D. Ubick, V. Vukasin & S. Lee, CAS); Mendocino Co.: Tranquility, 1.5 mi. S of Caspar, 19.IX.1990, ♀ (D. Ubick & J. Helfer, CAS).
Pimoa edenticulata Hormiga: USA: California: Trinity Co.: 13 mi N of Weaverville, near Tanbark picnic ground, off Route 3, Sahasta-Trinity National Forest, 30 Jul 1990 (G. Hormiga, USNM).
Pimoa jellisoni (Gertsch & Ivie) (*): USA: Idaho: Lost Lake, 20.VIII.1936 (W. Ivie, AMNH).
Pimoa rupicola (Simon): Italy: Alpi Apuane, 16.X.1975, 500 m (IZUI).

Other families
Tetragnatha versicolor Walckenaer: USA: California: Siskiyou Co.: Yreka-Sahasta River, 8 mi. N. of Yreka, 17.VIII.1964 (P.L. & U.F. Holt, USNM).
Zygiella x-notata (Clerck): USA: Massachusetts: Wood's Hole, VIII.1883 (J.H. Emerton, USNM); Washington: Jefferson Co.: Olympic N.P.: Kalaloch, 24.VIII.1987 (Smith, Craspey, Nitzberg, Kaltenthaler & Banks, USNM).

APPENDIX 2

Character state matrix

Rows represent characters and columns taxa. The first state is 'state 0', the second is 'state 1', etc. '?' represents missing data, and '—' non-applicable states. The last two columns give the consistency index (CI) and the weight (WE) assigned to the character in the successive character weighting analysis (see text). A = *Tetragnatha versicolor*, B = *Zygiella x-notata*, C = *Linyphia triangularis*, D = *Microlinyphia dana*, E = *Bolyphantes luteolus*, F = *Lepthyphantes tenuis*, G = *Erigone psychrophila*, H = *Walckenaeria directa*, I = *Haplinis diloris*, J = *Novafroneta vulgaris*, K = *Stemonyphantes blauveltae*. The remaining taxa are species of *Pimoa*: L = *P. rupicola*, M = *P. crispa*, N = *P. altioculata*, O = *P. breviata*, and P = *P. edenticulata*.

		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	CI	WE
Male genitalia																			
1.	Cymbium morphology: no cymbial denticulate process (CDP); with CDP;	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
2.	CDP denticles: numerous (> 20); few (< 20); dentiles lost	–	–	–	–	–	–	–	–	–	–	–	0	0	1	1	2	1.00	10
3.	Pimoid cymbial sclerite (PCS); absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
4.	PCS-cymbium connection: sclerotized and rigid; membranous and flexible	–	–	–	–	–	–	–	–	–	–	–	0	1	1	1	1	1.00	10
5.	PCS membranous ridge; absent; present	–	–	–	–	–	–	–	–	–	–	–	1	0	0	0	0	1.00	10
6.	PCS conformation: U; elongated anteroposteriorly; reversed J	–	–	–	–	–	–	–	–	–	–	–	0	2	1	1	1	1.00	10
7.	Paracymbium attachment; integral; intersegmental	1	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
8.	Paracymbium morphology: straight; large-pointed apex; U or J; linguiform-fused to PCS; triangular; short-procurved; *St* type;	0	1	2	2	2	2	2	2	2	2	6	3	5	4	4	4	1.00	10
9.	Paracymbium apophyses: present; absent	0	0	1	1	0	0	1	1	1	1	1	1	1	1	1	1	0.50	3
10.	Petiole: otherwise; fused to subtegulum	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
11.	Tegular suture: conspicuous; subtle or absent	–	–	–	–	–	–	–	–	–	–	–	0	0	1	1	1	1.00	10
12.	Mynoglenine tegular apophysis: absent; present	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	1.00	10
13.	Suprategulum: absent; continuous with tegulum; articulated	0	0	1	1	1	1	1	1	0	0	2	0	0	0	0	0	1.00	10
14.	Median apophysis: present; absent	1	0	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0.33	3
15.	Conductor: present; absent	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	1.00	10
16.	Conductor form: small and undivided; large and bilobate	0	0	–	–	–	–	–	–	–	–	–	0	0	0	1	1	1.00	10
17.	Embolus length: long and filiform; short	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0.50	2
18.	Embolic membrane: absent; present	–	0	1	0	1	1	1	1	1	1	0	–	–	–	–	–	0.50	2
19.	Pimoid embolic process (PEP): absent; present	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1.00	10
20.	PEP conformation: undivided; divided	–	–	–	–	–	–	–	–	–	–	–	1	0	0	0	0	1.00	10
21.	PEP base: narrow; wide and lamelliform	–	–	–	–	–	–	–	–	–	–	–	0	0	1	1	1	1.00	10
22.	Radix: absent; present	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
23.	Column (distal haematodocha): absent; present	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0.50	4
24.	Fickert's gland; absent; present	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1.00	10

		A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	CI	WE
25.	Terminal apophysis: absent; present	–	0	1	1	1	1	1	0	0	0	0	–	–	–	–	–	0.50	3
26.	Lamella characteristica: absent; present	–	0	1	1	1	1	0	0	0	0	0	–	–	–	–	–	1.00	10
27.	Male pedipalpal retrolateral tibial apophysis: absent; present	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1.00	10
28.	Male pedipalp tibial spines: scattered; distal row	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1.00	10
29.	Prolateral trichobothria in male palpal tibia: two; one	0	0	1	1	1	1	1	1	0	1	1	0	0	0	0	0	0.50	4
30.	Retrolateral trichobothria in male palpal tibia: two; four; three	1	0	2	0	0	0	0	0	2	0	0	2	2	2	2	2	0.50	3
	Female genitalia																		
31.	Epigynum form: protruding less than its width; protruding more	–	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1.00	10
32.	Dorsal plate of the epigynum: without projections; with projections	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1.00	10
33.	Atrium: absent; present	–	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0.50	2
	Somatic morphology																		
34.	Mynoglenine cephalic sulci: absent; present	0	0	0	0	0	0	?	0	1	1	0	0	0	0	0	0	1.00	10
35.	Tracheal system: haplotracheate; desmitracheate	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	1.00	10
36.	Ectal surface male chelicerae: smooth; with stridulatory striae	0	0	0	1	1	1	0	1	1	1	1	1	1	1	1	1	0.33	1
37.	Retrolateral teeth female chelicera: three; four or more; two	0	0	1	1	1	1	1	0	1	1	?	2	0	?	2	2	0.50	5
38.	Female pedipalpal tarsus: with claw; without claw	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0.50	2
39.	Patella leg autospasy: absent; present	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
40.	Trichobothrium metatarsus IV: present; absent	1	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0.50	3
	Spinneret spigot morphology																		
41.	PMS: with anterior aciniform brush; without	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
42.	Aciniform spigots in female PMS: more than one; one; absent	0	0	0	0	0	0	0	0	0	0	0	2	2	1	2	2	0.66	10
43.	PLS mesal cylindrical spigot base: same size; enlarged	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1.00	10
44.	PLS aciniform field random spigots; elongated field	1	0	1	1	1	1	1	1	1	1	1	–	–	–	–	–	1.00	10
45.	Aciniform spigots in female PLS: more than one; one; absent	0	0	0	0	0	0	0	0	0	0	0	2	1	1	2	2	0.66	10
	Behaviour																		
46.	Male position during construction of sperm web: above sperm web; below	?	?	0	0	?	0	1	?	1	?	?	?	?	?	?	?	1.00	10
47.	Male position during ejaculation: above sperm web; below	?	?	0	0	?	0	1	?	1	?	?	?	?	?	?	?	1.00	10