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Web-construction Behaviour in Australian *Phonognatha* and the Phylogeny of Nephiline and Tetragnathid Spiders (Araneae : Tetragnathidae)

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Abstract

Details of web-construction behaviour and morphology support the monophyly of nephiline spiders with *Phonognatha* as the sister-group to the remaining nephiline genera examined in this study. Phylogenetic analysis of the behavioural data suggests that specialisations in nephiline building behaviour and web architecture did not evolve concurrently, and that some preceded the female giantism (not male dwarfism) for which nephiline spiders are well-known. Cladistic analysis of 60 characters supports the monophyly of both Tetragnathidae and Tetragnathinae. New data from spinneret silk gland spigots, combined with other morphological and behavioural characters, provide the first concrete evidence that 'metine' genera, occasionally regarded as either a distinct family or subfamily, are a paraphyletic assemblage.

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Introduction

The family Tetragnathidae includes some of the most common and intensively studied spider genera, such as *Tetragnatha, Leucauge* and *Nephila*. Several species in this family have been the subjects of numerous biological studies (e.g. Robinson and Robinson 1973, 1976, 1978, 1980; Austin and Anderson 1978; LeSar and Unzicker 1978; Christenson and Goist 1979; Eberhard 1982, 1987*a*, 1987*b*, 1988*a*, 1988*b*, 1990; Gillespie 1986, 1987*a*, 1987*b*, 1992; Higgins 1987, 1988, 1989, 1990, 1991, 1992; Cohn 1990; Croom *et al.* 1991; Vollrath and Parker 1992; Stauffer *et al.* 1994). In all, 51 genera and more than 900 species are included in the family Tetragnathidae as currently delimited (Platnick 1993).

Despite a long taxonomic history, the limits of the family Tetragnathidae have never been firmly established. The taxonomic position of the Australian genus *Phonognatha* within Tetragnathidae has also been controversial. The presence of an intact temporary spiral in the finished orb and the long carapace led some workers to suggest placing *Phonognatha* within Nephilinae (e.g. Simon 1892), but the position of the male palpal sclerites, the long palpal tibia and the similar size of male and females have led others to propose a placement within the metines (Davies 1988). Since orb-construction behaviour of 'true nephilines' (*Nephila, Nephilengys* and *Herennia*, at least) is distinctive with respect to both radius construction and sticky spiral localisation (Eberhard 1982), observations of these behaviours in *Phonognatha* could help to resolve its taxonomic position and to clarify the evolution of web-building behaviour in nephiline spiders.

Taxonomic opinion on the separation of Araneidae and Tetragnathidae has varied widely. Tetragnathidae was first treated as a family by Menge in 1866 (Levi 1986: 93). In Simon's (1892) classification, tetragnathid genera were included in the argiopid subfamilies Tetragnathinae and Nephilinae, the latter with four groups (Phonognatheae, Nephileae, Herennieae and Clitaetreae). In Roewer's (1942) catalog, tetragnathids were treated as a separate family except that metines and nephilines were subfamilies within the Araneidae. Kaston (1948) distinguished Tetragnathidae from Araneidae, but included the genus *Meta* in the latter. Bonnet (1956, 1957, 1958, 1959) included all tetragnathids in Argiopidae. Locket *et al.* (1974) included European metine genera in tetragnathids. Brignoli (1983) ranked Metidae and Tetragnathidae as separate families, but left Nephilinae in Araneidae.

Although Levi (1980, 1981, 1986) initially followed the views of Kaston and Gertsch, as he gathered information on the systematics of the group he recognised the existence of Tetragnathidae as a separate family, rather than as an araneid subfamily. The cladogram in Levi (1980) shows araneines as a clade within what are currently recognised as tetragnathid genera, which would render tetragnathids polyphyletic. Levi (1986) found no clear distinction between metines and the remaining tetragnathids and nephilines. Most recently, Levi and Von Eickstedt (1989) continued to place nephilines in Tetragnathidae and provided a list of tetragnathid synapomorphies, but did not hypothesise any cladistic structure for the family.

Coddington (1990*a*) presented a cladogram that supported tetragnathid monophyly by four apomorphies (there were six tetragnathid genera in the matrix, out of a total of 15 araneoid genera): paracymbium morphology, sperm reservoir switchback in the tegulum, palp conformation, and loss of the median apophysis. However, the paracymbia of metines, nephilines and tetragnathines are disparate, and optimisation of this character as a family apomorphy presumed that all the disparate paracymbia morphologies are homologous as tetragnathid paracymbia. Secondly, a switchback in the sperm reservoir is also found in theridiosomatids (Coddington 1986), pimoids (Hormiga 1994*a*) and cyatholipids (Davies 1978; Coddington 1990*a*; Griswold, personal communication), although the detailed morphology and pattern of the various switchbacks differ. Tetragnathid monophyly would therefore depend on the tetragnathid state being autapomorphic. In the current study, it appears that if the presence of a switchback is optimised to the basal node of Tetragnathidae, it must reverse to the primitive simple spiral condition in *Phonognatha, Chrysometa, Metellina* and the tetragnathine node (*Tetragnatha, Pachygnatha* and *Glenognatha*), although the tetragnathine sperm reservoir is greatly enlarged in diameter. Thus, two of the four cladistic apomorphies suggested by Coddington are not present in all members of Tetragnathidae, and their status as apomorphies depended on assumptions about character optimisation. His results also suggested that nephilines (represented by two genera in his sample) were monophyletic and sister to the rest of the tetragnathid lineages considered in that data set.

In this paper we provide new data on orb-web construction behaviour in *Phonognatha* and investigate its phylogenetic position in the light of this and other character information. We study and reassess the morphological and behavioural evidence for the monophyly of Tetragnathidae and its main lineages, including the subfamily Nephilinae. We also present new information on the comparative morphology of the spinneret silk spigot of tetragnathids. We present a more detailed cladistic analysis of tetragnathid monophyly and phylogeny than any published to date.

Methods

Abbreviations

The following is a list of anatomical abbreviations used in the text and Figures.

A	alveolus
AC	aciniform gland spigot(s)
AG	aggregate gland spigot(s)
ALS	anterior lateral spinneret
AME	anterior median eyes
BH	basal hematodocha
C	conductor
CB	cymbium
CD	copulatory duct
CO	copulatory opening
CY	cylindrical gland spigot(s)
E	embolus
EB	embolus base
ETm	embolus–tegulum membrane
ED	ejaculatory duct
F	fundus
FD	fertilisation duct
FL	flagelliform gland spigot(s)
g	groove of conductor
m	membrane (or membranous)
MEA	metine embolic apophysis
MAP	major ampullate gland spigot(s)
mAP	minor ampullate gland spigot(s)
P	paracymbium
PI	piriform gland spigot(s)
PLE	posterior lateral eyes
PLS	posterior lateral spinneret
PME	posterior median eyes
PMS	posterior median spinneret
S	spermatheca
SP	secondary process of paracymbium
ST	subtegulum
T	tegulum

Behaviour

Behavioural observations on *Phonognatha* spp. were made by one of us (W. G. E.) in an open, low eucalyptus and casuarina forest at the northern edge of Tinaroo Lake at Tinaroo Falls, Queensland, Australia, in July 1992. Unfortunately, no mature individuals were found in this area or nearby, so species identification is not possible. This species is called *Phonognatha* sp. 1 in the descriptions below. In addition, one fresh web of an immature *P. graeffei* (Keyserling)(identified by R. Raven) was observed at Canungra, Queensland, and a web of an immature *P.* sp. 2 (perhaps a different species) was photographed in forest just behind the beach at Cape Tribulation, Queensland. Voucher specimens of *P.* sp. 1 (Nos 3726, 3728 and 3739) and of *P.* sp. 2 (No. 3710) have been deposited in the Museum of Comparative Zoology, Cambridge, MA 02138, USA.

In the behavioural descriptions, legs are designated as inside (i) or outside (o) in accord with their position with respect to the hub (i = the side nearest the hub). First, second, third and fourth legs are designated as I, II, III and IV, respectively.

The entries of the behavioural characters for the rest of taxa in Table 1 have been extracted from Levi (1980), Eberhard (1982) and Coddington (1986, 1990*a*).

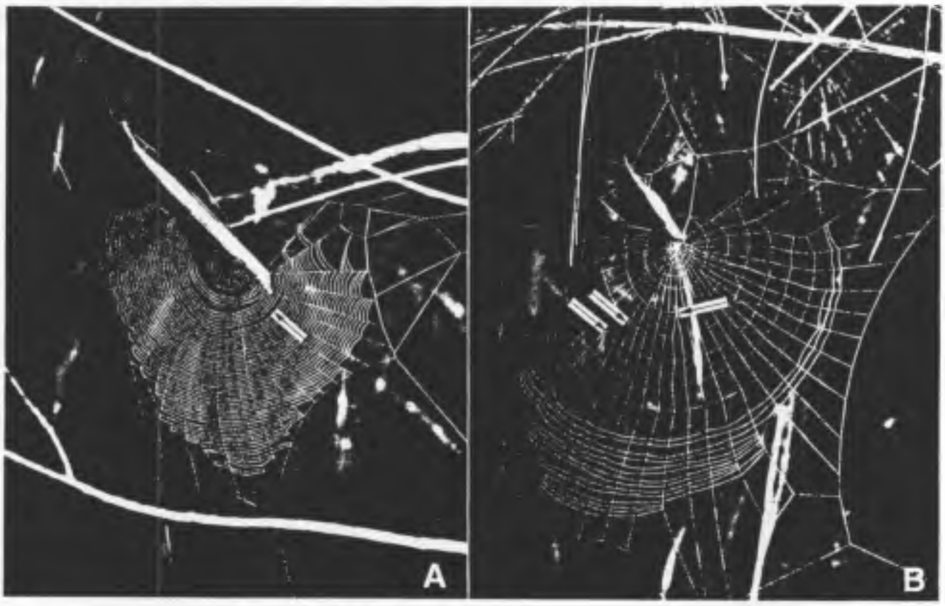


Fig. 1. Webs of immature *Phonognatha* sp. 1. A, Finished orb (arrow indicates intact temporary spiral); B, orb with incomplete sticky spiral (arrows indicate 'split' radii).

Morphology

A good fraction of the characters in this study have already been used in the taxonomic literature [e.g. Levi's revisions (Levi 1980, 1981, 1986; Levi and Von Eickstedt 1989) and other sources (e.g. Davies 1988; Coddington 1989, 1990*a*, 1990*b*; Hormiga 1994*a*, 1994*b*)]. Because many of these features were merely mentioned in passing or only tentatively proposed as phylogenetically informative, this study assesses their congruence with other comparative data. Characters from the literature were critically assessed before inclusion in the data matrix, and were rechecked using museum specimens and illustrated when necessary (e.g. paracymbium morphology). Some of the data on spinneret silk spigot morphology have already been published elsewhere (Kovoor 1986; Coddington 1989; Hormiga 1994*a*, 1994*b*), the rest are presented here for the first time. The methods of study of the morphological features follow those of Coddington (1989) and Hormiga (1994*a*). We used adult females as study animals for all characters except those that concern male genitalic or secondary sex characters (Characters 1, 3, 14, 15, 19–39 in Table 1).

Taxon Sampling

We selected the taxa in this study to investigate the phylogenetic position of *Phonognatha* within Tetragnathidae and to investigate in greater detail the monophyly and phylogenetic relationships of the

Table 1. Characters and taxon codings for Fig. 30

The character description format is 'Character name: first state; second state; third state.' A '0' in the matrix codes for the first state, a '1' for the second and so on. (see text for details). Taxon abbreviations in the matrix from left to right are *Uloborus* (Ul), *Araneus* (Ar), *Argiope* (Ag), *Linyphia* (Li), *Pimoa* (Pi), *Steatoda* (St), *Nesticus* (Ne), *Epeirotypus* (Ep), *Phonognatha* (Ph), *Clitaetra* (Cl), *Nephila* (Na), *Herennia* (He), *Nephilengys* (Ng), *Azilia* (Az), *Dolichognatha* (Do), *Meta* (Me), *Chrysometa* (Ch), *Metellina* (Mt), *Leucauge* (Le), *Tetragnatha* (Te), *Glenognatha* (Gl), *Pachygnatha* (Pa)

		No. of steps	Consistency index	Retention index	Weight
	UAALPSNEPCNHNADMCMLTGP lrgiitephlaegzoehteela				
Somatic characters					
1. Dorsal abdominal scutum of ♂: absent; present	0000000000111000000000	1	1·00	1·00	10
2. Cheliceral stridulatory striae: absent; present	0001100000000000000000	1	1·00	1·00	10
3. Lateral eyes of ♂: separate; touching	0111111110111001111011	4	0·25	0·25	0
4. PME tapeta: absent; present	011111111?111001111000	3	0·33	0·60	2
5. PLE tapeta: absent; present	011111111?1??001111011	3	0·33	0·33	1
6. Clypeus: < AME diameter; ≥ AME diameter	0011111100111001111111	4	0·25	0·40	1
7. Dorsal femoral trichobothria: present; absent	0111111111111111110000	2	0·50	0·25	3
8. Patella–tibia autospasy: absent; present	0001100000000000000000	1	1·00	1·00	10
9. Sustentaculum: absent; present	0110000000000000000000	1	1·00	1·00	10
10. Theridiid tarsal comb: absent; present	0000011000000000000000	1	1·00	1·00	10
11. Caudal gut caeca: absent; present	?000???????????0??11?1	1	1·00	1·00	10
12. Booklung cover: smooth; grooved	0110001010111001000000	5	0·20	0·24	0
13. Spiracle: post; advanced	0000000000000000000011	1	1·00	1·00	10
14. Size of ♂: > 0·5♀; < 0·4♀	0010000000111000000000	2	0·50	0·66	3
15. ♂ *v*. ♀ cheliceral size: same; larger; smaller	0201000010000010110111	6	0·33	0·42	1
16. Cheliceral boss: smooth; striae	-000-00-01111000000000	1	1·00	1·00	10
17. Chel boss striae: < 20; > 25	---------0111---------	1	1·00	1·00	10
18. Cheliceral denticles: absent; present	1110001111111000000000	3	0·33	0·77	2
Characters of the male					
19. Palpal patella macrosetae: 1; 0; 2	0200000100000010000011	4	0·50	0·33	1
20. Cymbium: entire; constricted	0000000000000000000111	1	1·00	1·00	10
21. Cymbium: dorsal; mesal	0110000000000000000000	1	1·00	1·00	10
22. Paracymbium: absent; integral; intersegmental; articulated	0112101111111111111333	4	0·75	0·66	5

Table 1 continued.

		No. of steps	Consistency index	Retention index	Weight
	UAALPSNEPCNHNADMCMLTGP lrgiitephlaegzoehteela				
23. Paracymbium base: sclerotised like cymbium; less so	-00-0-0001111000100---	2	0·50	0·75	3
24. Paracymbium morphology: 0; 1; 2; 3; 4; 5; 6	-0035-6042222000000111	6	1·00	1·00	10
25. Paracymbium secondary process: absent; procurved; complex	00000-0000000012210000	3	0·66	0·50	3
26. Paracymbium apophysis: absent; anterior; folding; basal; several	-0000-4022222000400111	4	0·75	0·85	6
27. Tegular sclerites: subterminal; apical	0001000001111111111111	3	0·33	0·71	2
28. Reservoir: normal; enlarged	0000000000000000000111	1	1·00	1·00	10
29. Reservoir: spiralled; switchback	0000101101111111001000	6	0·16	0·50	0
30. Median apophysis: present; absent	0001000001111111111111	2	0·50	0·83	4
31. Conductor + embolus: separate; conductor wraps embolus	000-000011111?11111111	1	1·00	1·00	10
32. Conductor with sigmoid distal end: absent; present	000-0000000110000000000	1	1·00	1·00	10
33. Embolus-tegulum orientation: parallel; 90°	0000000001111000000000	1	1·00	1·00	10
34. Araneid radix: absent; present	0110000000000000000000	1	1·00	1·00	10
35. Stipes: absent; present	0110000000000000000000	1	1·00	1·00	10
36. Distal hematodocha: absent; present	0100000000000000000000	1	1·00	1·00	10
37. Metine embolic apophysis: absent; present	0000000000000011110000	2	0·50	0·66	3
38. Embolus-tegulum membrane: absent; present	0111000001111111111111	3	0·33	0·50	1
39. Theridiid tegular apophysis: absent; present	0000011000000000000000	1	1·00	1·00	10
Genitalia of the female					
40. Epigynum: present; lost	0000000000000000000111	1	1·00	1·00	10
41. Fertilisation ducts; present; absent	0000000000000000000111	1	1·00	1·00	10
Behaviour					
42. Web posture: extended; L12s flexed	011111111?11101010?00?	4	0·25	0·40	1
43. Web architecture: orb; sheet; gum foot	000112200?000000000000	2	1·00	1·00	10
44. Hub against substrate: absent; present	000----011011000000000	2	0·50	0·66	3
45. Hub bite-out: absent; present	011----10?000111111101	3	0·33	0·60	2

Table 1 continued.

		No. of steps	Consistency index	Retention index	Weight
	UAALPSNEPCNHNADMCMLTGP lrgiitephlaegzoehteela				
46. Hub: closed; open	-00----0-?---0011111-1	1	1·00	1·00	10
47. Hub loop-no sticky spiral shift: gradual; abrupt	000----10?0001111111-?	2	0·50	0·83	4
48. Radii construction: singly attached; twice	000----00?1110000?000?	1	1·00	1·00	10
49. Radii construction: not cut and reeled; cut and reeled	011----1??0001111?111?	2	0·50	0·66	3
50. Non-sticky spiral: removed; remains	000----01?1110000?000?	1	1·00	1·00	10
51. Non-sticky contact in 1st sticky spiral construction: present; absent	000----10???1?111?11-?	2	0·50	0·66	3
52. Sticky spiral location: oL1; iL1; oL4	000----12?2221111?111?	2	1·00	1·00	10
53. Wrap-bite attack: present; absent	000111?1??1?1??0??01??	3	0·33	0·50	1
Spinnerets					
54. ALS piriform gland spigot bases: normal; reduced	0001111110000000000000	1	1·00	1·00	10
55. PMS nubbin: present; absent	1001110000000000000001	4	0·25	0·25	0
56. PMS aciniforms: extensive; reduced	0001111111111101111111	2	0·50	0·66	3
57. PLS CY size: same; enlarged	0001100000000000000011	2	0·50	0·66	3
58. PLS base CY position: central; peripheral	0001111111111111111111	1	1·00	1·00	10
59. PLS triad: separate; embrace flagel	-110000000111100000000	2	0·50	0·80	4
60. PLS aggregate spigot: normal; widened	0000011000000000000000	1	1·00	1·00	10

tetragnathid subfamilies. Phylogenetic analysis is necessarily a pragmatic compromise between total taxonomic representation (all taxa) and complete knowledge (for very few taxa are all relevant characters known). Inclusion of relatively unstudied taxa means an increase in missing entries, which often increases instability and ambiguity of results (Platnick *et al.* 1991). Limiting taxa only to those that are well-known biases the results because critical character combinations might not appear in those taxa. In our experience, bias due to under-representation of taxa has a greater effect than ambiguity created by missing data. Our selection is intended to be large enough to represent the clades we discuss and yet complete enough to make analysis and the results both stable and feasible to report. Inclusion of a taxon depended heavily, among other things, on whether sufficient specimens and behavioural information were available. Among tetragnathids we included the five classical nephiline genera (*Phonognatha*, *Nephila*, *Nephilengys*, *Herennia* and *Clitaetra*), three tetragnathine genera in the strict sense (*Tetragnatha*, *Glenognatha* and *Pachygnatha*), and a diverse selection of 'metine' genera (*Meta*, *Leucauge*, *Chrysometa*, *Dolichognatha*, *Metellina* and *Azilia*). Clearly, many more 'metine' genera could have been included (and should be in future studies). We included as outgroup taxa one deinopoid (*Uloborus*, Uloboridae), two basal araneoids (*Araneus* and *Argiope*, Araneidae), *Epeirotypus* [Theridiosomatidae, to represent symphytognathoids (Eberhard 1982; Coddington 1986)], and *Steatoda*

Fig. 2. Web of an immature *Phonognatha* sp. 1. Arrows mark loop of sticky spiral that was made without the spider making contact with the inner loop of sticky spiral.

(Theridiidae) and *Nesticus* (Nesticidae) to represent the theridioid lineage. Finally, we included both *Linyphia* and *Pimoa* to test again whether *Pimoa* could be more closely related to 'metines' rather than linyphiids (Hormiga 1994*a*). The linyphiid–pimoid clade represents a large and diverse clade that may be closely related to tetragnathids (e.g. Coddington and Levi 1991) and therefore potentially important to assess homologies and polarities of characters.

Our first concern was to resolve the controversy over the placement of *Phonognatha* and to further study the evidence for the monophyly of Tetragnathidae and Nephilinae. The study was not designed to imply anything about Araneidae or the placement of the Linyphiidae–Pimoidae clade in Araneoidea, or unequivocally to resolve debates over the validity of the 'metines' as a family or monophyletic subgroup within Tetragnathidae, especially as about 30 genera (that is, more than half of the currently recognised tetragnathid genera) are informally considered to be'metines' (*sensu* Brignoli 1983). Although this is the most comprehensive and focused attempt to examine tetragnathid phylogeny to date and our results bear on these admittedly interesting questions, they should be interpreted with caution.

Cladistic Analysis

We analysed the data of Table 1 using Hennig86 (Farris 1988) and PAUP 3.1.1 (Swofford 1993). With Hennig86, we used the exact solution option 'ie'. The resulting trees were then submitted to successive character weighting (Farris 1969; Carpenter 1988) to assess the internal consistency of the data and the cladistic reliability of the results (Carpenter *et al.* 1993). In PAUP we used the branch and bound option, again submitting the resulting tree to successive approximations (using the maximum value of the rescaled consistency index to provide the new character weights). Multistate characters (7 out of 60 characters; Table 1) were treated as non-additive (unordered). A justification for our preference for non-additive coding can be found in Hormiga (1994*b*). We used MacClade 3.0 (Maddison and Maddison 1992) to optimise characters on the tree. If optimisations were ambiguous, we usually resolved them using the ACCTRAN option (Farris optimisation), which maximises homology by favouring

Fig. 3. Web of an immature *Phonognatha* sp. 2. Arrows mark an intact temporary spiral.

secondary loss over convergence, as an explanation for homoplasy. In a few cases, ACCTRAN was not sufficient to specify the location of changes, in which case we chose how to allocate steps on the basis of our knowledge of the character and intuition about how it was likely to have evolved.

Results

Characters

We considered but finally omitted a number of characters mentioned in the literature because they either were variable or were impossible for us to define and code clearly. These include the size of the tarsal organ on the cymbium (tiny versus prominent; Levi 1986: 94), silvery or white coloration on the abdomen (Levi 1986), shape of the median ocular area, and the 'distinctive' male palpal tibial morphology (Levi 1986: 95, table 2). These characters may turn out to be informative when more rigorously defined or for different sets of taxa. In the descriptions that follow, if a character seems weak, ambiguous, or so complex that our coding may not fairly represent reality, we note what effect excluding the character from the analysis had on the results, if any. Characters 2, 7–12, 13, 30–37 and 40–41 have been discussed elsewhere (Levi 1986; Wunderlich 1986; Coddington 1989, 1990*a*, 1990*b*; Forster *et al.* 1990; Hormiga 1993, 1994*a*, 1994*b*).

Somatic morphology

Character 1. Male dorsal abdominal scutum. 0: absent; 1: present. This scutum is characteristic of the males of higher nephilines. Its presence in *Clitaetra* species varies. It is present in *C. episinoides* Simon, but the scutum of this species differs from the rest of nephiline scuta in being very lightly sclerotised. In a different undetermined species of *Clitaetra* from Cameroon the scutum is absent. Coding this character in the matrix as

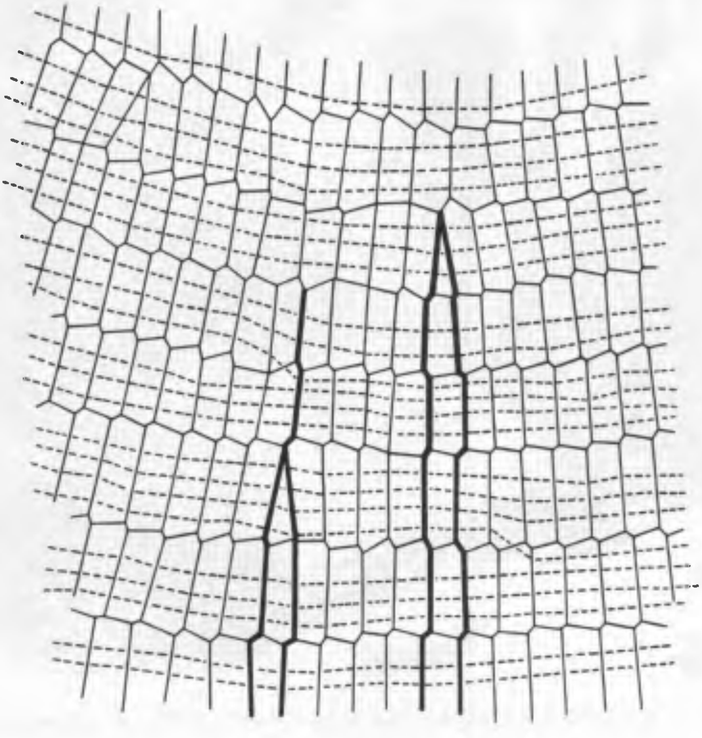


Fig. 4. A portion of the web of an adult *Nephila clavipes* (traced from a photograph) showing radii and the temporary spiral (solid thin lines) and the sticky spiral (dashed lines). Two pairs of radii that were added while the spider laid the temporary spiral are shown as solid thick lines. The origin on the temporary spiral of the pair of the right is clear. The pair on the left also originated on the temporary spiral (one loop farther outward), but the two lines were then attached to each other by the next two loops of the temporary spiral. During the loops of the temporary spiral that followed they remained apart.

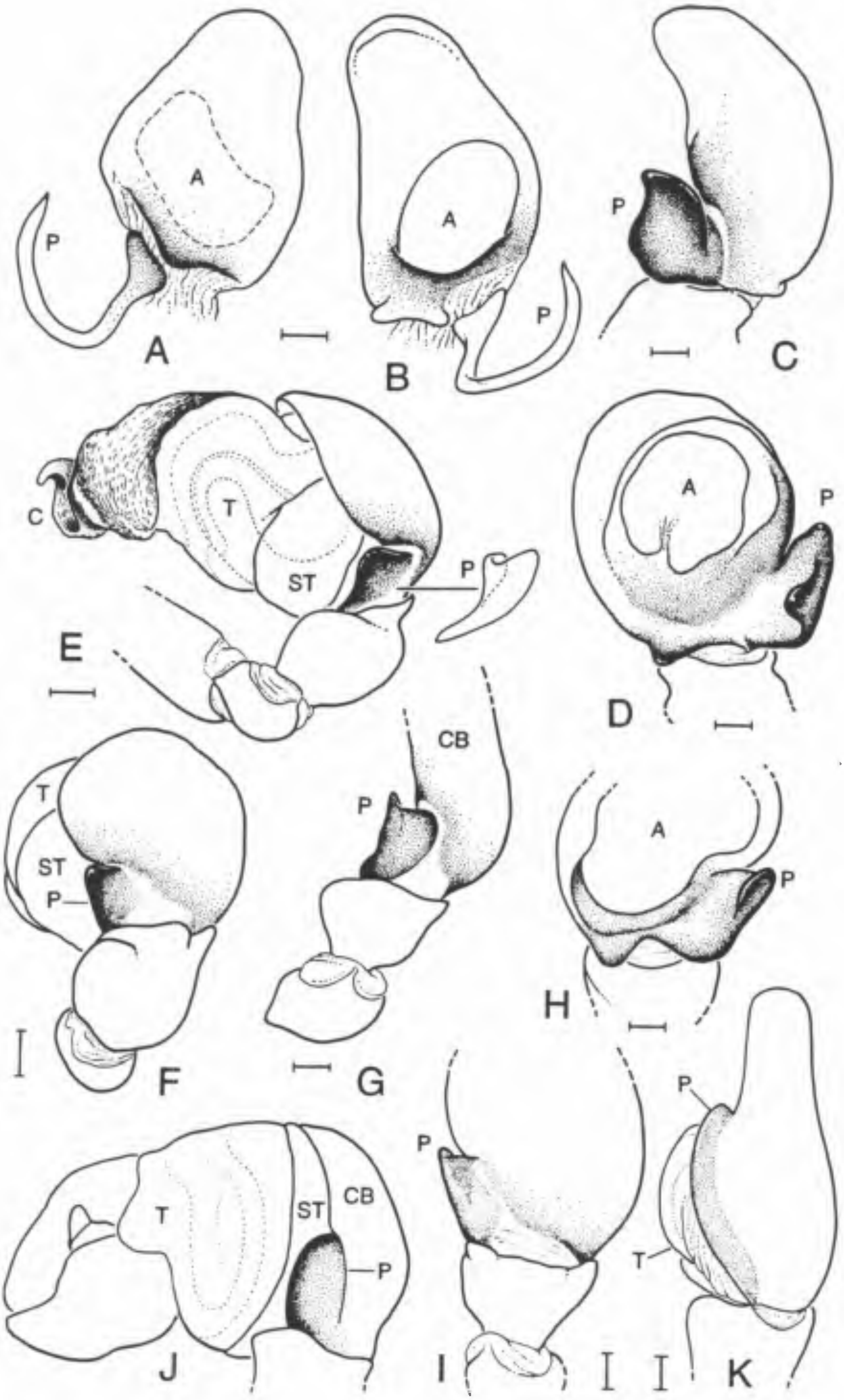


Fig. 5. Paracymbium morphology. A, *Linyphia triangularis* (Clerck), dorsal; B, *Linyphia triangularis* (Clerck), ventral; C, *Zygiella x-notata* (Clerck), retrolateral; D, *Zygiella x-notata* (Clerck), ventral; E, *Nephilengys cruentata* (Fabricius), retrolateral; F, *Nephilengys cruentata* (Fabricius), dorsal; G, *Nephila clavipes*, retrolateral; H, *Nephila clavipes*, ventral; I, *Nephila clavipes*, dorsal; J, *Herennia* sp. (Australia), retrolateral (redrawn from Davies 1988); K, *Phonognatha graeffei*, retrolateral. Scale bars 0·1 mm.

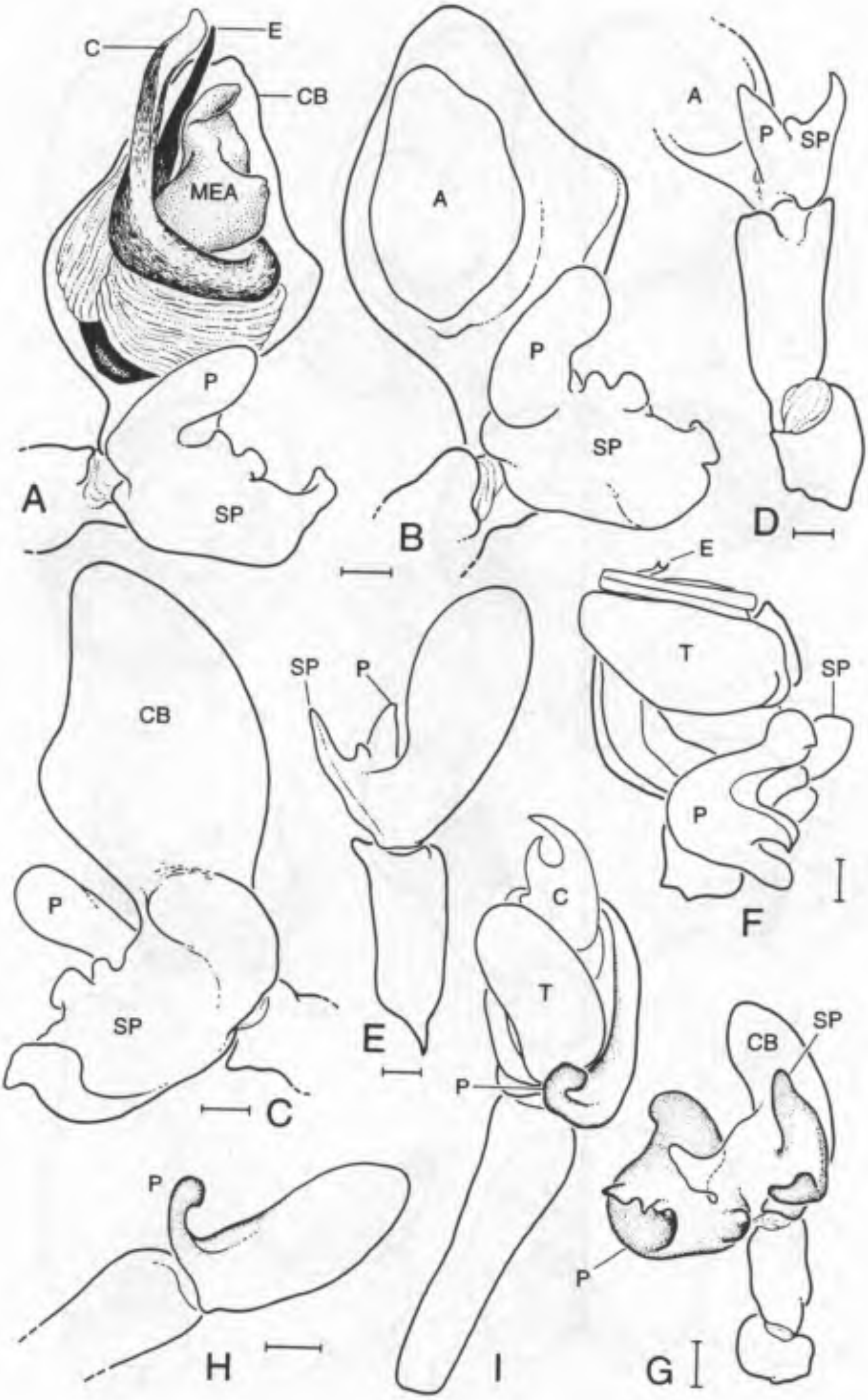


Fig. 6. Paracymbium morphology. A, *Meta americana* (Marusik & Koponen), ventral; B, *Meta americana*, ventral; C, *Meta americana*, dorsoectal; D, *Metellina curtisi* (McCook), ventral; E, *Metellina curtisi* (McCook), dorsal; F, *Chrysometa alboguttata* (O.P.-C.), ventral (redrawn from Levi 1986); G, *Chrysometa alboguttata* (O.P.-C.),, retrolateral; H, *Leucauge venusta* (Walck.), retrolateral; I, *Leucauge venusta* (Walck.), retroventral. Scale bars 0·1 mm, except A–C, 0·2 mm.

'present' for *Clitaetra* or excluding it altogether from the analysis produces no changes in the cladogram topology.

Character 2. Cheliceral stridulatory striae. 0: absent. 1: present. The presence of stridulatory striae is a synapomorphy of linyphiids plus pimoids (see Hormiga 1994*b*: 36).

Character 3. Lateral eyes of the male. 0: separate. 1: touching. Levi (1981: 275) suggested that lateral eye separation correlates with the 'metine' resting position (Character 38) due to natural selection to improve vision around the juxtaposed legs. However, the correlation is imperfect at best, as neither the nephilines nor *Dolichognatha pentagona* (Hentz), which have separated lateral eyes, use the metine resting posture (however, we have studied a probably undescribed species of *Dolichognatha* from Peru in which both sexes have juxtaposed lateral eyes). Some tetragnathine taxa and others such as *Azilia* do support the correlation. The well-separated lateral eyes found in some tetragnathids appear to have evolved from ancestors with juxtaposed lateral eyes (an araneoid synapomorphy) and therefore are different from the primitively separated eyes of uloborids and deinopids. This character is difficult to define and code, is highly variable at intrageneric level (and therefore it is prone to errors derived from taxonomic sampling), can exhibit some degree of sexual dimorphism, is highly homoplasious (has both a low consistency and retention index), and at this level it provides little phylogenetic information.

Character 4. PME tapeta. 0: absent. 1: present.

Character 5. PLE tapeta. 0: absent. 1: present. Presence of tapeta in secondary eyes is generally plesiomorphic in spiders. Deinopoids lack tapeta altogether, but most araneoids have tapeta in some of their eyes. Among tetragnathids, some genera lack tapeta in median eyes and some in both posterior and median (Levi 1980, 1981, 1986).

Character 6. Clypeus height. 0: smaller than one AME diameter. 1: equal or larger than one AME diameter. A high clypeus (state 1) was used in Coddington (1990*b*) as a synapomorphy of higher araneoids.

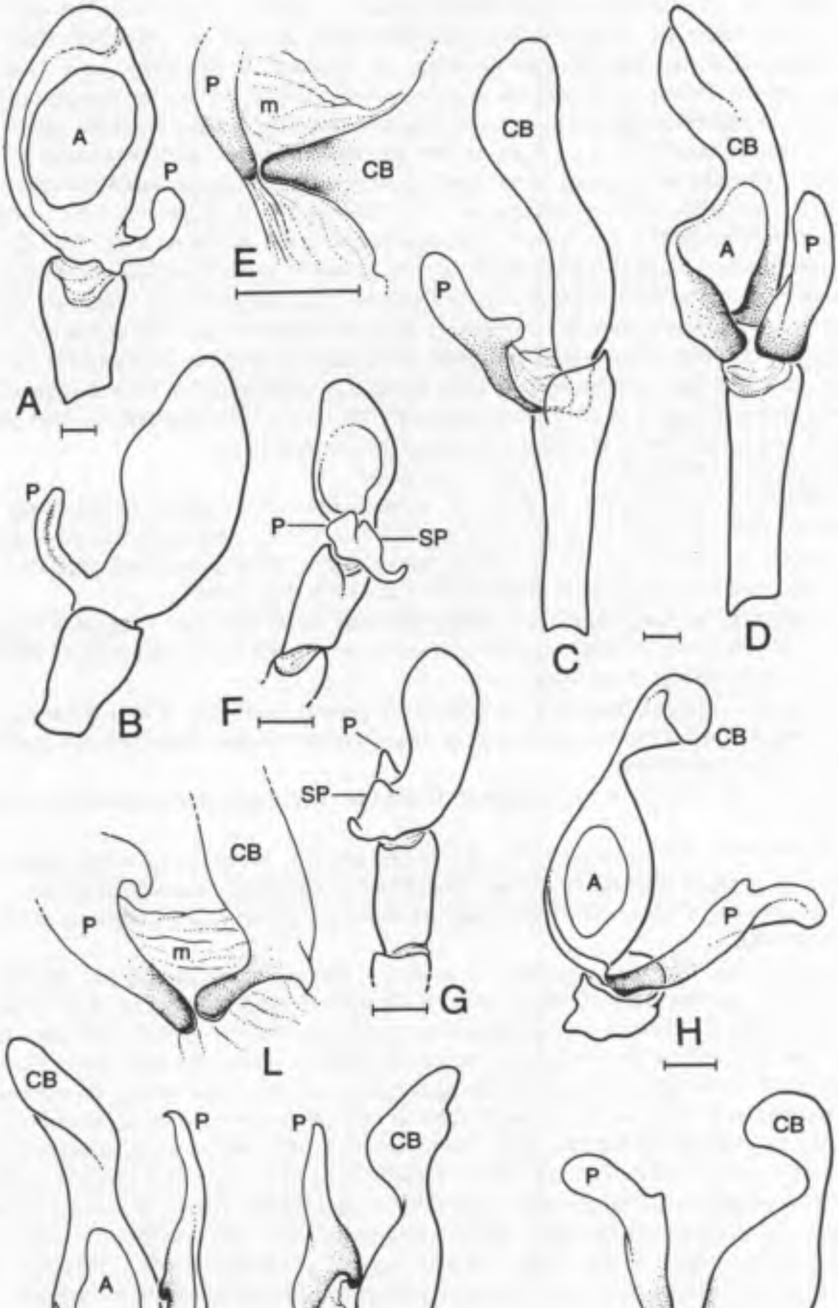
Character 7. Dorsal femoral trichobothria. 0: present. 1: absent. Within the tetragnathids dorsal femoral trichobothria are found in *Leucauge* and in the tetragnathines (Levi 1980, 1981; Coddington 1990*a*).

Character 8. Patella–tibia autospasy. 0: absent. 1: present (see comments in Hormiga 1994*b*).

Character 9. Sustentaculum. 0: absent. 1: present. Presence of a sustentaculum is probably synapomorphic for Araneidae (Scharff and Coddington, unpublished data).

Character 10. Tarsus IV theridiid comb. 0: absent. 1: present. See comments in Forster *et al.* (1990: 97).

Character 11. Posterior gut caeca. 0: absent. 1: present. Palmgren (1978*a*, 1978*b*) found differences in the arrangement of the intestinal caeca between Araneidae and Tetragnathidae. *Tetragnatha* and *Pachygnatha* have much bulkier ventral caeca than those of Araneidae that extend into the chelicerae and pedipalpal coxae. He also found a posterior, unpaired dorsal caecum occupying the space between the tergo-dorsal muscles and the dorsal apodeme in these two genera. The dorsal posterior caecum is absent in *Meta*, probably suppressed by the extremely bulky poison glands, and in all 62 species of the 24 European families that Palmgren (1978*a*) studied. The absence of such a caecum (probably a symplesiomorphy) suggested to Palmgren (1978*b*) that the controversial genus *Meta* was an araneid, rather than a tetragnathid, but our data place *Meta* firmly within the latter family. The intestinal caeca of *Leucauge* are also typical of tetragnathids (Palmgren 1979). Exclusion of this character from the matrix results in 12 minimal length cladograms of 129 steps, with consistency and retention indices of 0·56 and 0·72, respectively. All these 12 cladograms agree on the monophyly of Tetragnathidae, Nephilinae (including *Phonognatha*), Tetragnathinae, and *Metellina* plus *Chrysometa* (included among these 12 cladograms are the three minimal length trees that result from the analysis of the complete data set). The monophyly of the mentioned groups persists in the three cladograms that result from successive character weighting.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Character 12. Booklung cover. 0: smooth. 1: grooved. The presence of grooves on the abdominal booklung covers is a classic morphological character in diagnoses of higher araneid and araneoid groups (e.g. Simon 1895; Kaston 1948). Here the feature serves as a synapomorphy for Nephilinae, with homoplasious occurrences in *Clitaetra* (reversal), *Meta*, *Nesticus* and the two araneid genera.

Character 13. Tracheal spiracle. 0: posterior. 1: advanced. An advanced spiracle is typical of higher tetragnathines.

Character 14. Size of the male. 0: > 0·5 female. 1: < 0·4 female. The definition of sexual size dimorphism will vary with the intent of the study, but here we have chosen to regard body length of the male that is about 0·4 or less of the body length of the female as 'dimorphic.' Total body length measurements were taken from the descriptive taxonomy literature. As defined, the condition occurs in *Argiope*, *Nephila*, *Herennia* and *Nephilengys*. *Phonognatha* (male : female ≈ 0·64) and *Clitaetra* (male : female ≈ 0·62) are not markedly more dimorphic than other genera, e.g. *Uloborus* (≈ 0·68) or *Leucauge* (≈ 0·69). Although *Phonognatha* and *Clitaetra* are the most 'dimorphic' of the genera we scored as non-dimorphic, there is a much bigger difference between *Argiope*, *Nephila*, *Herennia*, and *Nephilengys* and all the other genera in this study than between *Phonognatha* and *Clitaetra* and the rest. Excluding this character from the analysis makes no difference to the cladogram topology.

Character 15. Cheliceral size of the male versus that of the female. 0: same. 1: larger. 2: smaller. Levi (1986) suggested that large chelicerae of males typified several tetragnathid genera. We found that this character was a synapomorphy for the tetragnathines and for *Chrysometa* plus *Metellina*, but elsewhere was homoplasious.

Character 16. Cheliceral boss. 0: smooth. 1: striated. The cuticle of the cheliceral boss of tetragnathids is primitively smooth (Fig. 27A, B). In distal nephilines this cuticle has been modified into a striated pattern (Figs 27C, D, 28A–29B).

Character 17. Cheliceral boss striae. 0: few (<20). 1: numerous (>25). While most distal nephilines have numerous striae on the cheliceral boss (e.g. Fig. 28A, B), *Clitaetra* has few striae (composed of relatively larger cuticular protuberances, Fig. 27C, D). While in our taxonomic sample this character is not phylogenetically informative, it might be informative when the other nephiline genera (namely *Perilla* and *Deliochus*) are studied.

Character 18. Cheliceral denticles. 0: absent. 1: present. Denticles between the anterior and posterior rows of cheliceral teeth are found in araneids (at least several species of *Araneus*, *Zygiella* and *Argiope*), uloborids (see Peters 1982, fig. 2A for *Uloborus walckenaerius* Latreille), theridiosomatids (Coddington 1986) and nephilines (Fig. 26C, D), including *Phonognatha*.

Genitalia of the male

Character 19. Palpal patella macrosetae of the male. 0: one. 1: none. 2: two. Two macrosetae on the pedipalpal patella of the males are characteristic of many araneid genera. Most of the tetragnathids studied here, as well as linyphiids, pimoids, theridiids, nesticids and uloborids, have one patellar macroseta in the male pedipalp. This seta apparently has been lost at least three times, once each in *Dolichognatha* and *Epeirotypus*, and in the common ancestor of *Pachygnatha* and *Glenognatha* (or, alternatively, regained in

Fig. 7. Paracymbium morphology. A, *Azilia affinis* O.P.-C., ventral; B, *Azilia affinis* O.P.-C., retrolateral; C, *Tetragnatha versicolor* Walck., dorsoectal, D, *Tetragnatha versicolor* Walck., ventral; E, *Tetragnatha versicolor* Walck., detail of paracymbium attachment; F, *Dolichognatha pentagona* (Hentz), ventral; G, *Dolichognatha pentagona* (Hentz), dorsal; H, *Glenognatha heleios* Hormiga, ventral; I, *Glenognatha heleios* Hormiga, retrolateral; J, *Pachygnatha autumnalis* Keyserling, ventral; K, *Pachygnatha autumnalis* Keyserling, retrolateral; L, *Pachygnatha autumnalis* Keyserling, detail of paracymbium attachment (schematic). Scale bars 0·1 mm.

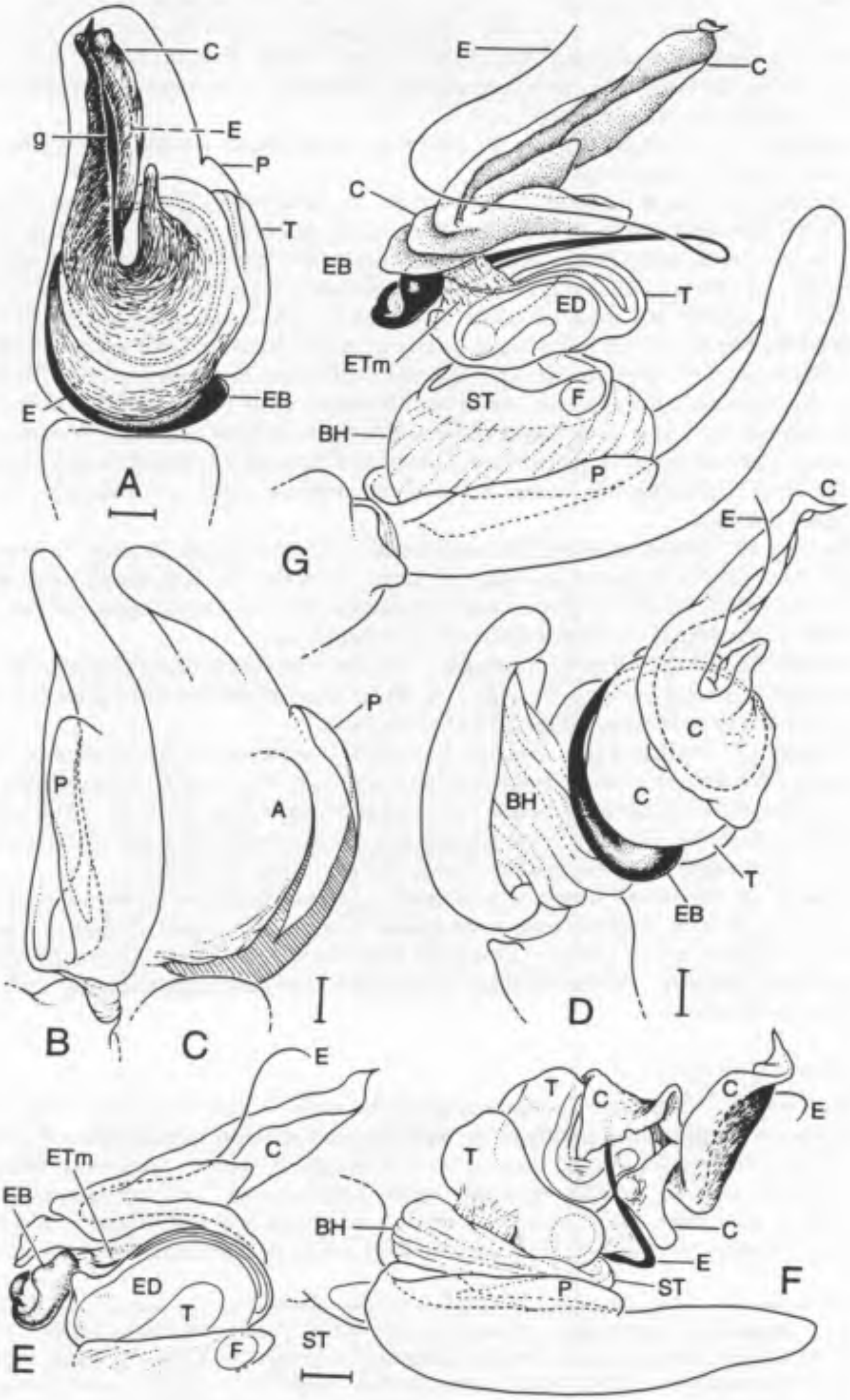


Fig. 8. *Phonognatha graeffei*, palp morphology. A, ventral; B, cymbium, ectal; C, detail of cymbium, ventral; D, partially expanded, mesal; E, partially expanded, retrolateral; F, partially expanded, ectal; G, expanded palp (schematic), retrolateral. Scale bars 0·1 mm.

Tetragnatha). The coding of this character for *Pachygnatha* is problematic because of intrageneric variation. *P. autumnalis* Keyserling lacks macrostae in the patella and *P. clerckii* Sundevall and *P. degeeri* Sundevall have one. *P. brevis* Keyserling and *P. furcillata* Keyserling have one seta that by size is smaller than macrosetae and indistinguishable from the rest of the setae of the palp articles. Recoding this character as 0 (one macroseta) for *Pachygnatha* produces no change in the cladogram topology (in fact such recoding renders the character phylogenetically uninformative).

Character 20. Cymbium. 0: entire. 1: constricted. The presence of a constricted cymbium (with the mid-region substantially narrower than either end) is characteristic of true tetragnathine genera. Although Levi (1986; character b in his table 1; see also his figures 736, 739 and 745) coded *Homalometa* as having the same kind of modified cymbium as the tetragnathines, its cymbium is less constricted than in the tetragnathine lineage, and perhaps it should receive a different, intermediate coding (Hormiga, personal observation).

Character 22. Cymbium orientation. 0: dorsal. 1: mesal. In araneids the cymbium takes a mesal position and the palpal sclerites are oriented ectally and ventrally (Levi 1983: 251, fig. 8). Most spiders outside Araneidae exhibit the plesiomorphic state (dorsal orientation of the cymbium with sclerites facing ventrally).

Character 22. Paracymbium. 0: absent. 1: integral. 2: intersegmental. 3: articulated (for paracymbial characters see also comments in Hormiga 1994*b*).

Character 23. Degree of sclerotisation of the paracymbium base. 0: sclerotised like the cymbium. 1: less sclerotised.

Character 24. Paracymbium morphology. 0: short basal structure, more or less hook-shaped. 1: longer than wider and finger-like. 2: flat and roughly rectangular. 3: U-shaped. 4: long projection of the basal half of the cymbium, continuous with the retrolateral margin. 5: flat and roughly triangular. 6: very large and broader than width of cymbium, the paracymbium base is directed towards the tibia and then curves towards the distal end of the cymbium (see Gertsch 1984).

Character 25. Paracymbium secondary process. 0: absent. 1: procurved. 2: complex.

Character 26. Paracymbial apophysis. 0: absent. 1: anterior. 2: folding of margin. 3: basal. 4: several apophyses. An anteroventral fold is found in the paracymbium of the nephiline genera (Figs 5E, G–I, 8B–C, 9B, 11F, 12E). In the tetragnathines the paracymbium presents an apophysis in the anterior margin (Fig. 7C, H–K).

The simplest interpretation of the paracymbium (Figs 5, 6 and 7) is as a synapomorphy of Araneoidea, but it is a very diverse structure that is quite difficult to code (Coddington 1986, 1990*a*, 1990*b*; Hormiga 1994*a*, 1994*b*). For example, the paracymbium may be absent, flexibly attached to the cymbium, or fixed, and, if flexible, where it inserts can vary (Character 22). As expected, the fixed condition is primitive for Araneoidea and variants on this theme are mostly autapomorphic. An articulated paracymbium is synapomorphic for tetragnathines. The degree of sclerotisation of the paracymbium base (Character 23) also varies among the taxa considered here. Most taxa have the same overall degree of sclerotisation of the paracymbium as the cymbium, but in some taxa the base is only weakly sclerotised, almost membranous [e.g. *Nephila clavipes* (L.), Fig. 5I]. This state apparently evolved at least two times, in *Chrysometa* (Fig. 6G) and in the nephilines (with exception of *Phonognatha*). A weakly sclerotised paracymbium base is also found in some araneids, like *Zygiella x-notata* (Fig. 5C).

Paracymbium morphology (Character 24) varies widely across taxa. The paracymbium has been independently lost in several instances (e.g. in the tetragnathid genus *Homalometa*, among symphytognathoids, and in several linyphiid genera, like *Sphecozone*). The coding of variable characters tends to require many character states to adequately represent their diversity, but as the number of states increases, the cladistic value of the character decreases (if fewer states are shared among taxa). Hormiga (1993, 1994*b*) coded the morphological diversity of the paracymbium of a relatively small sample of linyphiid genera (plus the

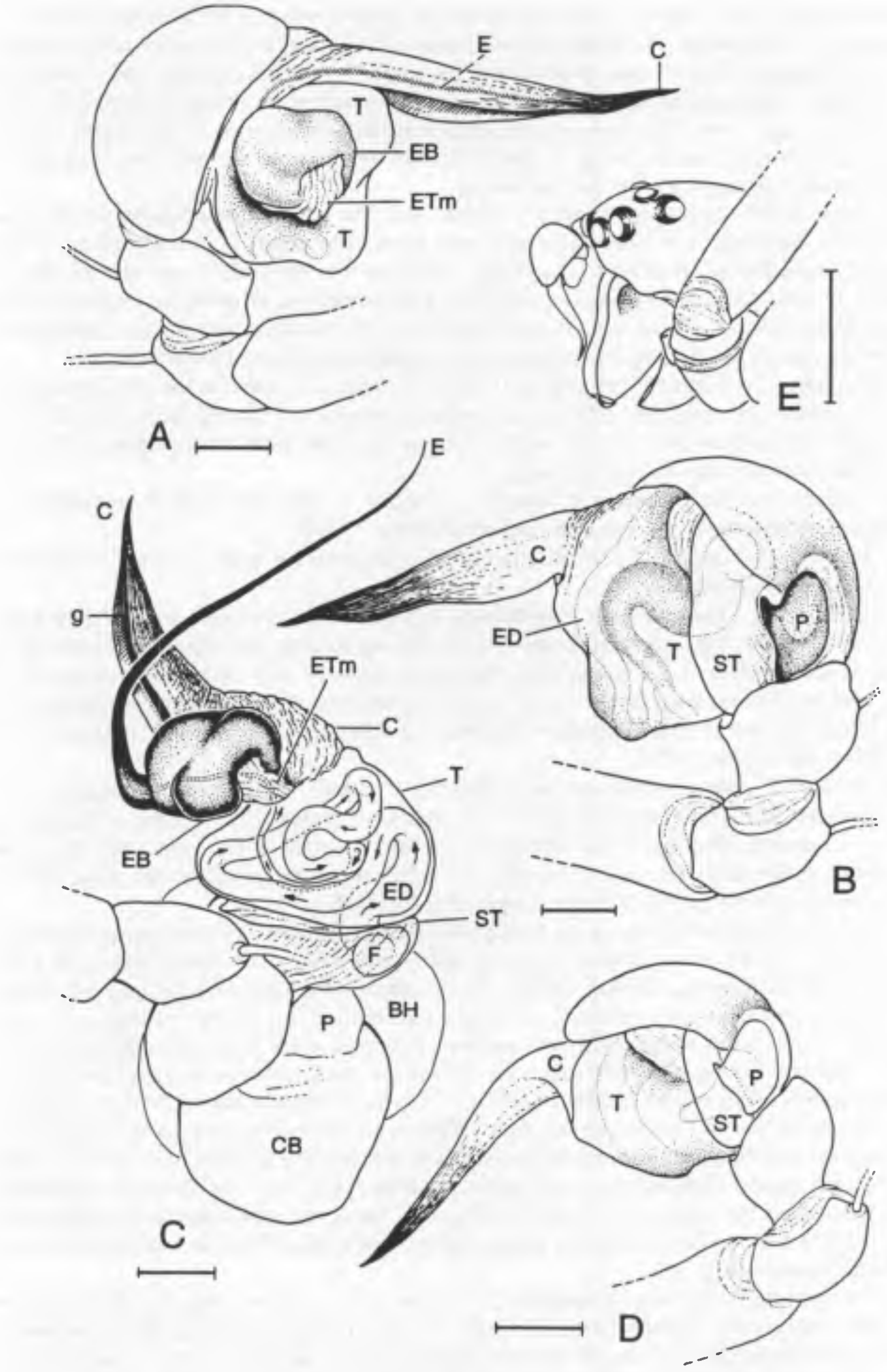


Fig. 9. *Clitaetra* spp., palp morphology. A–C, *C.* sp. (Cameroon); D–E, *C. episinoides* Simon. A, mesal; B, ectal; C, expanded, anterodorsal; D, ectal; E, male cephalothorax. Scale bars 0·1 mm, except E, 0·5 mm.

appropriate outgroups) into seven character states, but most of the diversity was allocated to the outgroups (a sample of five pimoids, *Tetragnatha* and *Zygiella*). For the taxa of the present study the morphology of the paracymbium has been divided into seven character states: state 0 (short and hook-like, Fig. 13H) is found in some tetragnathids and in *Araneus* and *Epeirotypus*. States 1 (paracymbium longer than wide and finger-like, Fig. 7C, D, H–L) and 2 (flat and roughly rectangular, Fig. 5E–J) are found in other Tetragnathidae (tetragnathines and distal nephilines, respectively). States 3 (U-shaped, Fig. 5A, B) and 5 (flat and roughly triangular; Hormiga (1994*a*, fig. 11), are autapomorphies of some of the outgroups (*Linyphia* and *Pimoa*, respectively). State 4 (long projection of the cymbial margin, Figs 5K, 8C and B) is an autapomorphy of *Phonognatha*. State 6 is an autapomorphy of *Nesticus* (Gertsch 1984, figs 1C, 50–57).

This analysis suggests that the plesiomorphic paracymbium morphology in tetragnathids is a short basal structure, more or less hook shaped (state 0), as found in *Azilia* (Figs 7B, 13A), *Leucauge* (Figs 6H, 13H), *Araneus* and *Epeirotypus*. Tetragnathines have a characteristic elongate, narrow paracymbium (state 1; Fig. 7C, D, H–K). The nephilines (except *Phonognatha*) have a flat and roughly rectangular paracymbium (state 2; Fig. 5G–J). The paracymbium morphology of *Phonognatha* seems to be unique within the tetragnathids, being a long projection of the basal half of the cymbium, continuous with the retrolateral margin (state 4; Figs 5K, 8B and 8C). Exclusion of Character 24 does not produce any changes in cladogram topology.

Complex paracymbia can also have secondary processes (Character 25; e.g. Fig. 6B) or not, although, in the context of this data set, this character is not especially informative. In many instances the paracymbium has one or several apophyses whose position varies (Character 26). Absence of paracymbial apophyses is the plesiomorphic condition, occurring in all the outgroups of this study. If the paracymbial characters (Characters 22–26) are excluded from the analysis nine minimal-length cladograms of 111 steps result. These nine trees differ from those resulting from the complete data set (Fig. 30) only in the interrelationships of the metines (although in all the nine topologies *Azilia* remains sister to *Dolichognatha* and *Chrysometa* to *Metellina*). Successive character weighting this partial data set results in the same three trees than the complete data set.

Character 27. Tegular sclerites. 0: subterminal. 1: apical. Coddington (1990*a*) used Millidge's (1977) concept of 'palp conformation' to define the 'metine palp conformation'. It now seems clearer to avoid such ensemble characters and instead to reduce complex descriptions as nearly as possible to elemental comparisons. Tegular sclerites vary in their insertion on the tegulum. In most tetragnathids (and in linyphiids), the tegular sclerites are grouped together and terminal on the tegulum. In other taxa various sclerites insert subterminally. Therefore, the apical insertion of the tegular sclerites is a synapomorphy of Tetragnathidae.

Character 28. Sperm reservoir. 0: normal. 1: enlarged. The reservoir of the ejaculatory duct typically is thin or narrow with an obvious space between its spirals (Fig. 12D), but in tetragnathines it is rather fat so that adjacent spirals seem nearly to touch, a derived condition.

Character 29. Reservoir course. 0: spiralled. 1: with a switchback. The primitive course of the reservoir within the tegulum seems to be a simple spiral (Coddington 1990*a*). In various taxa, especially theridiosomatids (Coddington 1986), abrupt bends or switchbacks in the course of the reservoir can be homologised and are phylogenetically informative. Nephilines usually have complex routings with switchbacks (e.g. Figs 9C and 12D), but several 'metine' genera also have switchbacks (e.g. Fig. 13A). In the context of this study this feature emerges as a synapomorphy for higher araneoids (i.e. all araneoids except Araneidae), although it requires four reversals under Farris' optimisation.

Character 30. Median apophysis. 0: present. 1: absent (see comments in Coddington 1990*a*; Hormiga 1994*b*).

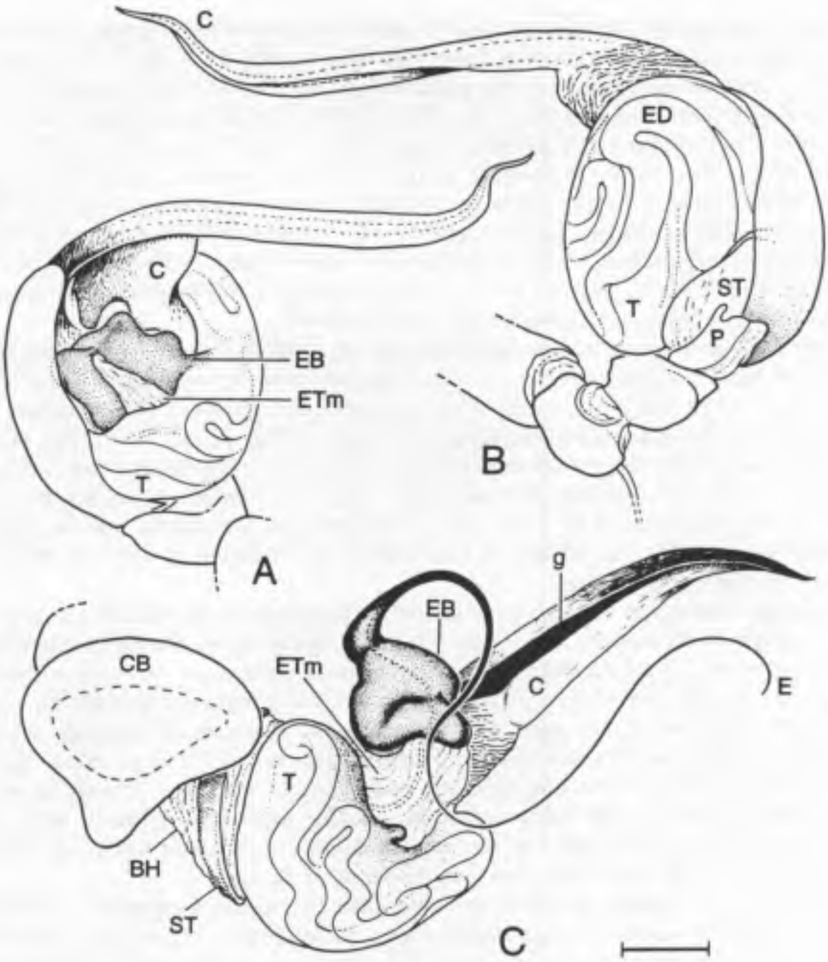


Fig. 10. *Nephila clavipes*, palp morphology. A, ectal; B, proventral; C, expanded, anterodorsal. Scale bars 0·2 mm.

Character 31. Conductor and embolus. 0: separate. 1: conductor wraps embolus. The presence of a close association between the embolus and the conductor, closely coiling together, is characteristic of tetragnathids (Levi 1986: 94; Figs 6A, 8A, 9A and so on). This tetragnathid synapomorphy is perhaps the most conspicuous diagnostic character of the family. Only *Azilia* lacks this mentioned condition (Fig. 13A), chiefly because it is debatable whether *Azilia* has a conductor or not. The small sclerotised tegular lobe next to the embolus base could be homologised to the araneoid conductor (e.g. Levi 1980, fig. 305). If the homology is accepted it is admittedly a highly modified conductor and Character 28 should be coded as 'non-applicable' for *Azilia* because although the embolus shows some degree of coiling, it is impossible for such a conductor to wrap the embolus. Coding this character as either 'absent' or 'non-applicable' produces no change in the cladogram topology. Given the uncertainty about the nature of *Azilia*'s tegular lobe we have coded it as '?'.

Character 32. Sigmoid distal end of conductor. 0: absent. 1: present. This feature occurs only in *Herennia* and *Nephilengys* (Figs 11C and 12C). In *Herennia* the distal end of the conductor fits the epigynal cavity where the copulatory duct opens (Fig. 11G–I). It is fairly common in museum specimens to find adult females with the epigynum (one or both sides) plugged by the conductor–embolus complex (Levi *in litt.*; personal observation; see also Robinson and Robinson 1978, 1980); in these cases the distal end of the embolus, where the ejaculatory pore is presumably located, is placed within the spermatheca (Fig. 11J). The presence of 'eunuchs' (Robinson and Robinson 1978; Robinson and Lubin 1979) is an additional synapomorphy for *Herennia* plus *Nephilengys*.

Character 33. Embolus–tegulum orientation. 0: parallel. 1: 90°. Right-angle orientation of the embolus–conductor in relation to the longitudinal axis of the pedipalp (e.g. Fig. 9A) is a characteristic apomorphy of higher nephilines.

Character 34. Araneid radix. 0: absent. 1: present.

Character 35. Stipes. 0: absent. 1: present. The stipes is a sclerite found between the embolus and the radix in some araneids. In the context of our data set the stipes is a synapomorphy of Araneidae, but not all araneids have a stipes.

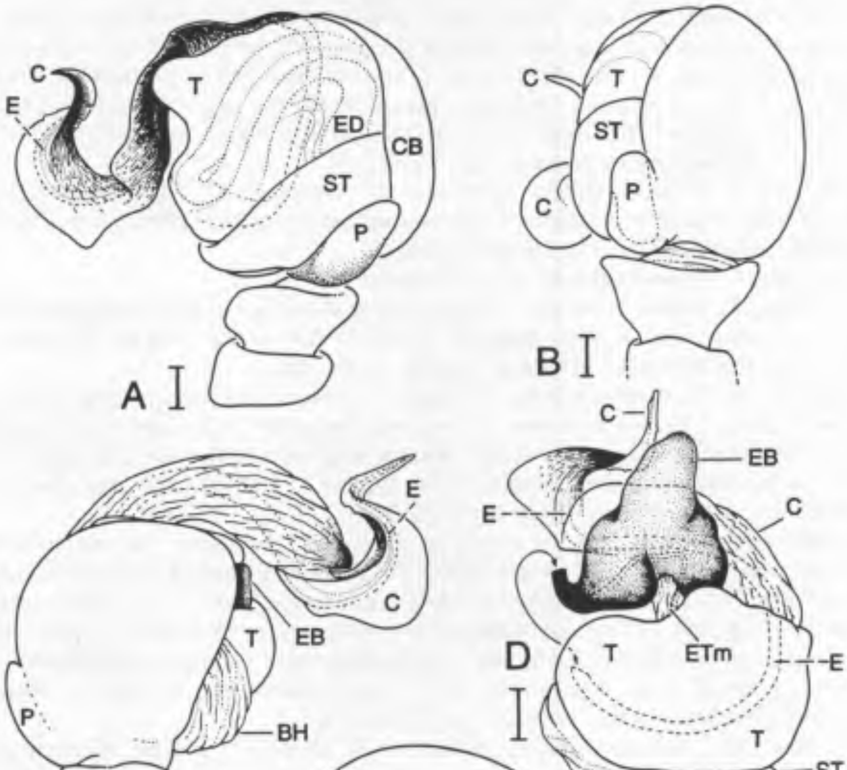
Character 36. Distal hematodocha. 0: absent. 1: present. The distal hematodocha, *sensu* Comstock (1910: 177), is a membranous structure between the radix-stipes and the embolus of some araneids. In our taxonomic sample this character is not phylogenetically informative.

The radix, stipes and distal hematodocha, typical of araneid palps, are absent from tetragnathids (see Coddington 1990*a*; Hormiga 1994*b*).

Character 37. Metine embolic apophysis. 0: absent. 1: present. The metine embolic apophysis (Levi 1986: 94, Coddington 1990*a*: 16) is a lobe extending from the base of the embolus (Fig. 13A–G); in the unexpanded palp it can be seen next to the embolus, distal to the tegulum (Fig. 6A). In *Dolichognatha pentagona* (Hentz) the base of the apophysis seems to fuse with both the embolus and the tegulum (Hormiga and Coddington, unpublished data). However, in the Peruvian species (Fig. 13B, C) the embolus plus the embolic apophysis form a distinct sclerite, similar to the case of other metines.

Character 38. Embolus–tegulum membrane. 0: absent. 1: present. A membranous connection between the base of the embolus and the tegulum is present in all the tetragnathids that we have examined (Figs 8G, 9C, 10C, 13A, E–H). Schult and Sellenschlo (1983) incorrectly homologised the embolus–tegulum membrane with the araneid distal hematodocha. The latter membrane is distal to the radix (a sclerite that is absent in tetragnathids), and connects it to the stipes (also absent in tetragnathids). The embolus–tegulum membrane could be synapomorphic for Tetragnathidae, but equally parsimonious alternative interpretations exist. It could be argued that the tetragnathid embolus–tegulum membrane is homologous to the linyphiid column (the membrane that connects the suprategulum to the linyphiid radix; see Hormiga 1994*b*) and to the araneid membrane that connects the tegulum to the radix. This latter alternative is the one we have coded in our matrix. The most parsimonious optimisation of this character on the cladogram presented in Fig. 30 unambiguously suggests an independent origin for the linyphiid column, questioning therefore its homology with the araneid and tetragnathid membranes. Only if the pimoid–linyphiid clade is sister to the clade composed of theridioids plus symphytognathoids could the linyphiid column be parsimoniously considered to be a homolog of the araneid and tetragnathid membranes. As for the homology of this membrane between the araneids and the tetragnathids two equally parsimonious alternatives exist. In Fig. 30 we have mapped these changes as a single origin for the latter mentioned two taxa, being secondarily lost in the pimoids, theridioids and symphytognathoids. However, the same number of steps is required to map the changes as an independent origin in araneids and tetragnathids.

Character 39. Theridiid tegular apophysis. 0: absent. 1: present. Theridiids and nesticids have an outgrowth of the tegulum that contains a portion of the sperm duct reservoir (Coddington 1990*a*: 17, 18). This apomorphy provides further evidence of the sister-group relationship between these two families.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Genitalia of the female

Character 40. Epigynum. 0: present. 1: lost.

Character 41. Fertilisation ducts. 0: present. 1: absent. In the tetragnathines both the epigynum and the fertilisation ducts are lost.

Behaviour

The behavioural characters are treated in detail in Eberhard (1982) and Coddington (1986, 1990*a*).

Character 42. Web posture. 0: extended legs. 1: legs I and II flexed.

Character 43. Web architecture. 0: orb. 1: sheet. 2: gum foot.

Character 44. Hub against substrate. 0: absent. 1: present. A photograph of the web of an unidentified species of *Clitaetra* (Preston-Mafham 1991: 117) shows the hub built against a tree trunk. This is consistent with other nephilines, and we have coded *Clitatetra* as having a hub against substrate.

Character 45. Hub bite-out. 0: absent. 1: present.

Character 46. Hub. 0: closed. 1: open.

Character 47. Hub loop – no sticky spiral shift. 0: gradual. 1: abrupt.

Character 48. Radii construction. 0: radii singly attached. 1: radii attached twice.

Character 49. Radii construction. 0: radii not cut and reeled. 1: radii cut and reeled.

Character 50. Non-sticky spiral. 0: removed from finished web. 1: remains in finished web.

Character 51. Non-sticky contact in 1st sticky spiral construction. 0: present. 1: absent.

Character 52. Sticky spiral location. 0: oL1. 1: iL1. 2: oL4.

Character 53. Wrap-bite attack. 0: present. 1: absent.

Spinnerets

Character 54. ALS piriform gland spigot bases. 0: normal. 1: reduced. The presence of reduced ALS piriform spigot bases is a synapomorphy of the linyphioid–theridioid–symphytognathoid clade (Griswold *et al.* 1994).

Character 55. PMS nubbin. 0: present. 1: absent. Yu and Coddington (1990) hypothesised that the PMS nubbin was the vestige of a juvenile minor ampullate spigot that is never functional in araneoid adults. The nubbin (Figs 15C, 16C) may persist in adults of some taxa (e.g. nesticids, araneids and theridiosomatids) but it is entirely lost in linyphiids, pimoids, theridiids, cyatholipids, some synotaxids, and *Pachygnatha* among the tetragnathids. Its absence in uloborids is probably primitive rather than a secondary loss. The exclusion of this character from the analysis produces no change in cladogram topology.

Character 56. PMS aciniform gland spigots. 0: extensive. 1: reduced. Primitively, orbicularians have numerous PMS aciniform spigots (more than 20; Coddington 1989, figs 4, 8, 12), but among higher araneoids they are often reduced in number (Coddington 1989; Fig. 24C). Among the tetragnathids studied here *Azilia affinis* O. P.-Cambridge has the largest number of PMS aciniform spigots (*c.* 40 spigots; Fig. 23C) and has been coded as

Fig. 11. *Herennia* spp. genitalic morphology. A, B, E, F, *H. ornatissima* (Doleschall); C, D, *H.* sp. (India); G–J, *H.* sp. (Luzon, Philippines). A, palp, ectal; B, palp, dorsoectal; C, partially expanded palp, dorsal; D, detail of partially expanded palp, ventral (during specimen manipulation the embolus was broken near its base; the broken distal part can be seen under the tegulum and the conductor); E, cymbium, dorsal; F, paracymbium (schematic), ventral; G, epigynum, ventral (both epigynal sides are plugged with the conductor–embolus complex that has been removed from the right side); H, detail of the conductor–embolus complex as oriented in the epigynum of the previous figure (the distal end of the embolus and the conductor are broken off); I–J, epigynum with conductor–embolus complex in left side; I, ventral (fertilisation ducts and spermathecae are shown with dashed lines); J, dorsal (the conductor–embolus complex is shown inside the epigynum as dashed). Scale bars 0·1 mm.

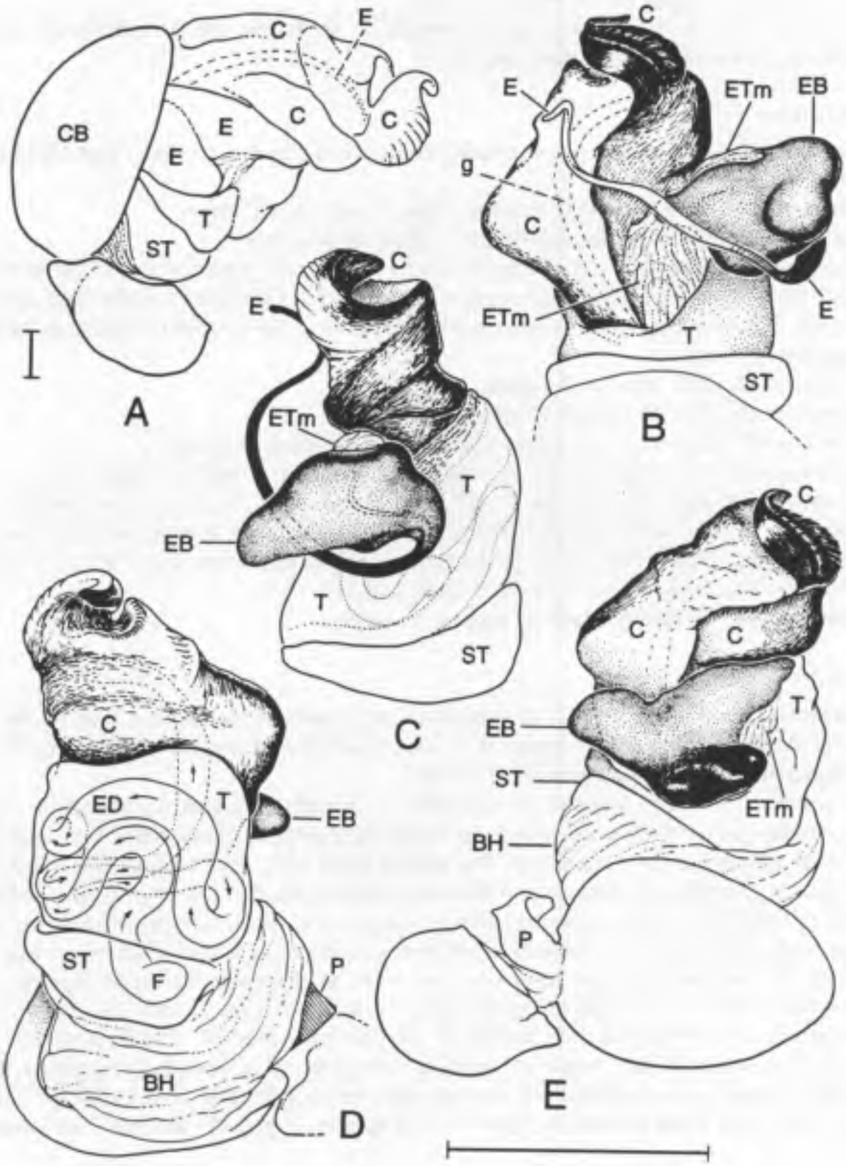

Fig. 12. *Nephilengys cruentata* palp morphology. A, mesal; B, expanded, dorsal (the embolus has been displaced from the conductor groove); C, expanded, anterior; D, expanded, ventral; E, expanded, dorsal. Scale bars 0·5 mm, except A, 0·1 mm.

having an extensive aciniform field (state 0, the plesiomorphic condition). *Meta americana* Marusik and Koponen has about 20 PMS aciniform spigots (a relatively high number in the context provided by most of the tetragnathids studied here), but we have interpreted it as having a reduced field because it is clearly smaller than the aciniform fields found in deinopoids and araneids (e.g. Coddington 1989, fig. 12). Coding *Meta* as having the

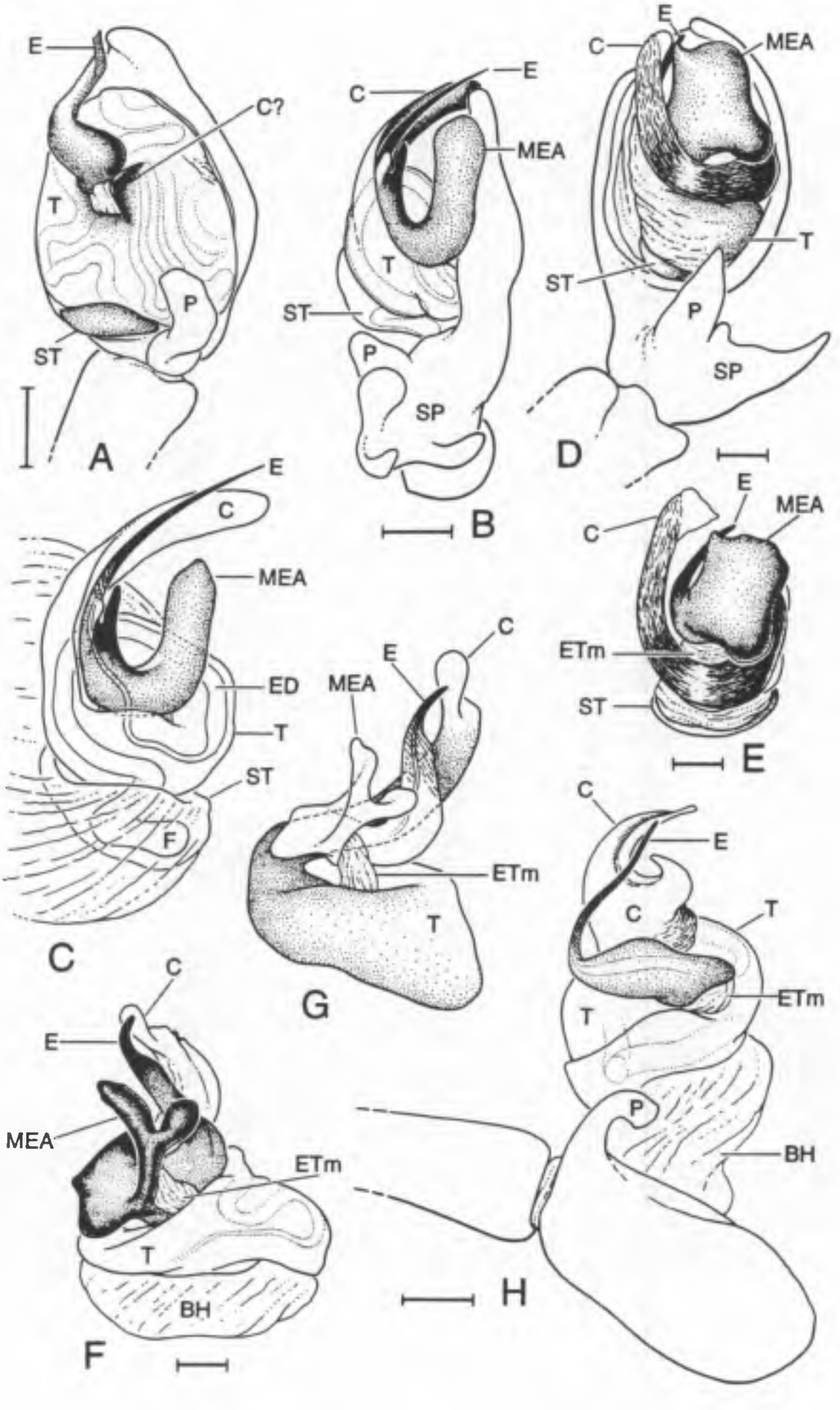

Fig. 13. Palp morphology of 'metines'. A, *Azilia affinis*, ventral; B, *Dolichognatha* sp. (Peru), dorsolateral; C, *Dolichognatha* sp. (Peru), expanded, schematic; D, *Metellina curtisi*, ventral; E, *Metellina curtisi*, expanded, detail; F, *Meta menardi* (Latr.), expanded, detail; G, *Meta menardi* (Latr.), expanded, schematic; H, *Leucauge venusta*, expanded, retrolateral. Scale bars 0·1 mm, except A and F, 0·2 mm.

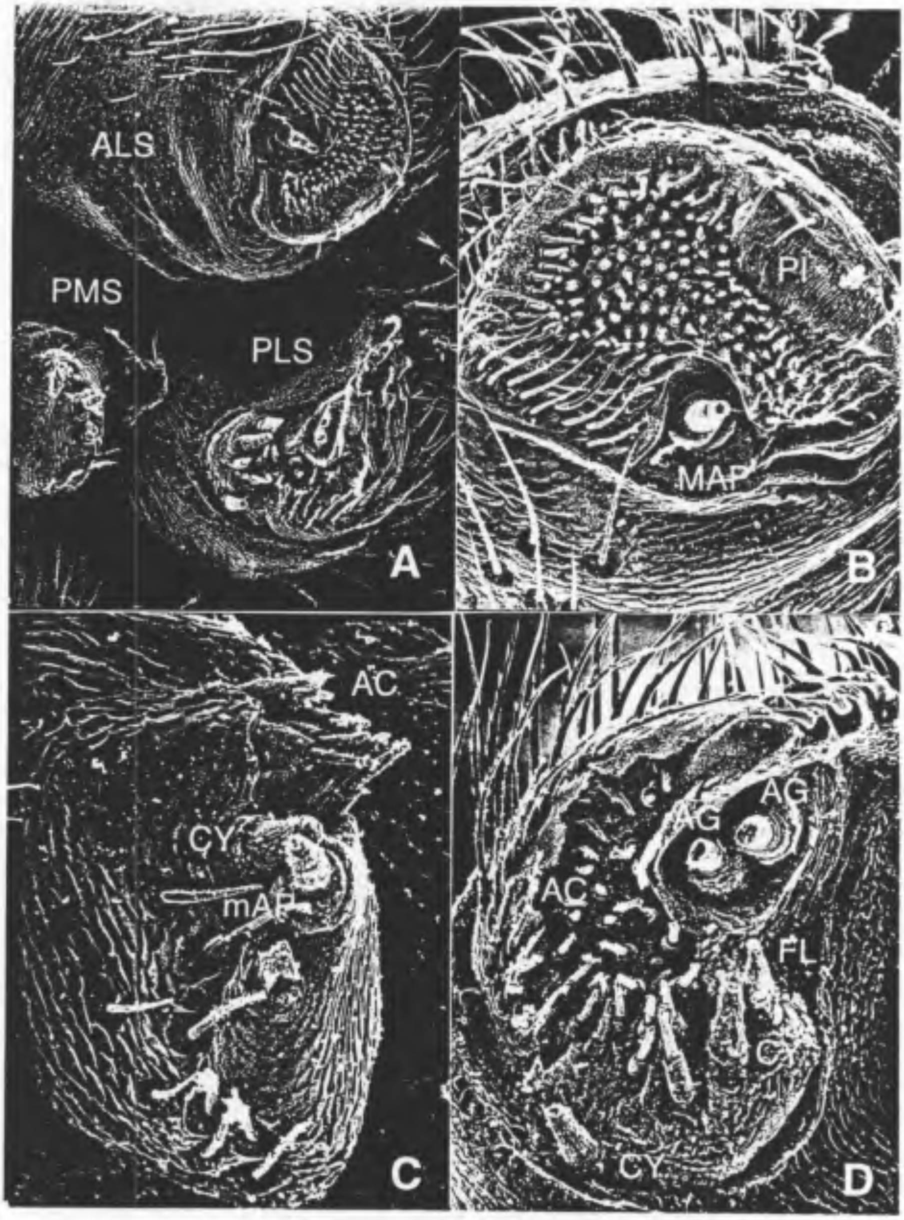

Fig. 14. *Phonognatha graeffei*, spinnerets of female. A, left spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

plesiomorphic condition (state 0) instead produces no changes in the cladogram topology.

Character 57. PLS mesal cylindrical gland spigot base. 0: same size as the other PLS cylindrical spigot. 1: enlarged. The PLS mesal cylindrical spigot is usually about the same

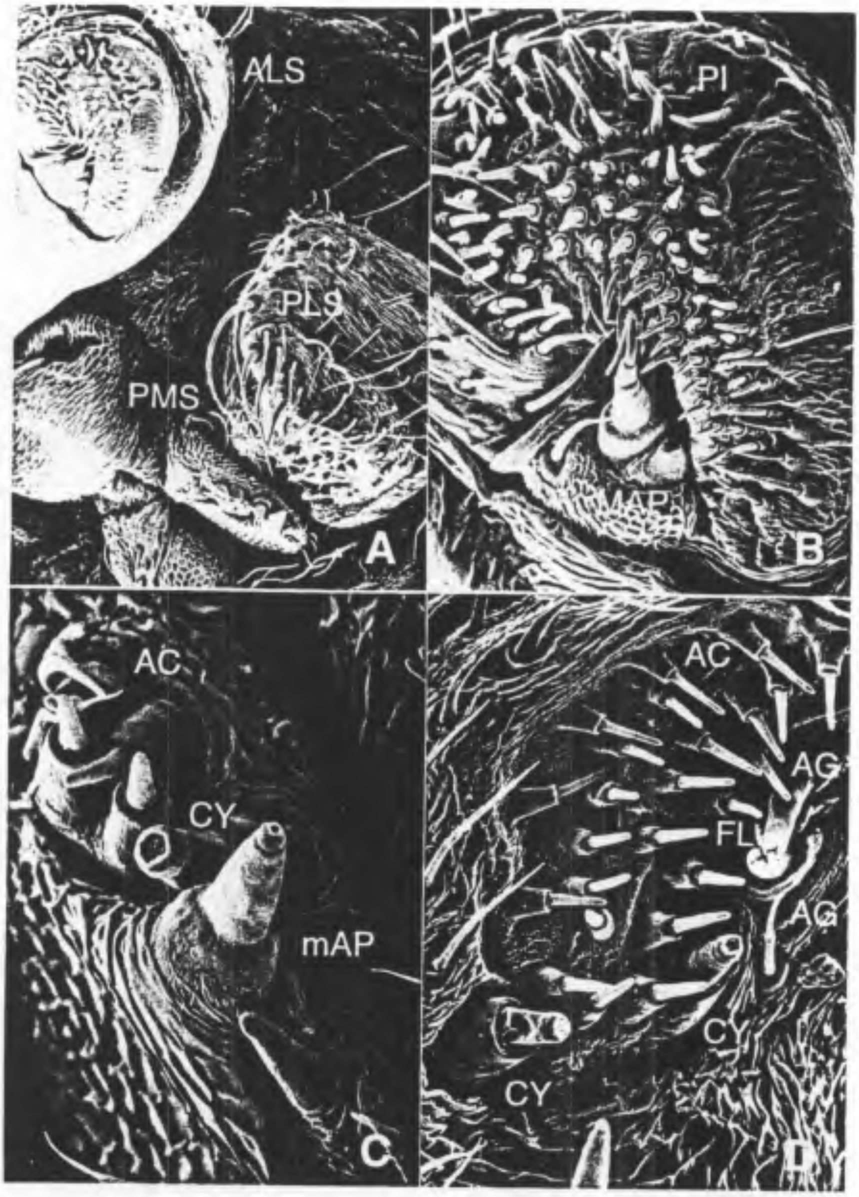

Fig. 15. *Clitaetra* sp. (South Africa), spinnerets of female. A, left spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

size as the ectal one (on the PLS) or that on the PMS (Fig. 24D), but in a few taxa it is obviously larger and longer (Fig. 25D; Hormiga 1994*b*, figs 21D, 23D, 26D). This feature has apparently evolved in parallel in the linyphiid–pimoid clade (Hormiga 1993, 1994*b*) and in *Glenognatha–Pachygnatha*.

Character 58. PLS mesal cylindrical gland spigot position. 0: central. 1: peripheral. In most primitive orbicularians and other spiders, the PLS mesal cylindrical spigot (which is

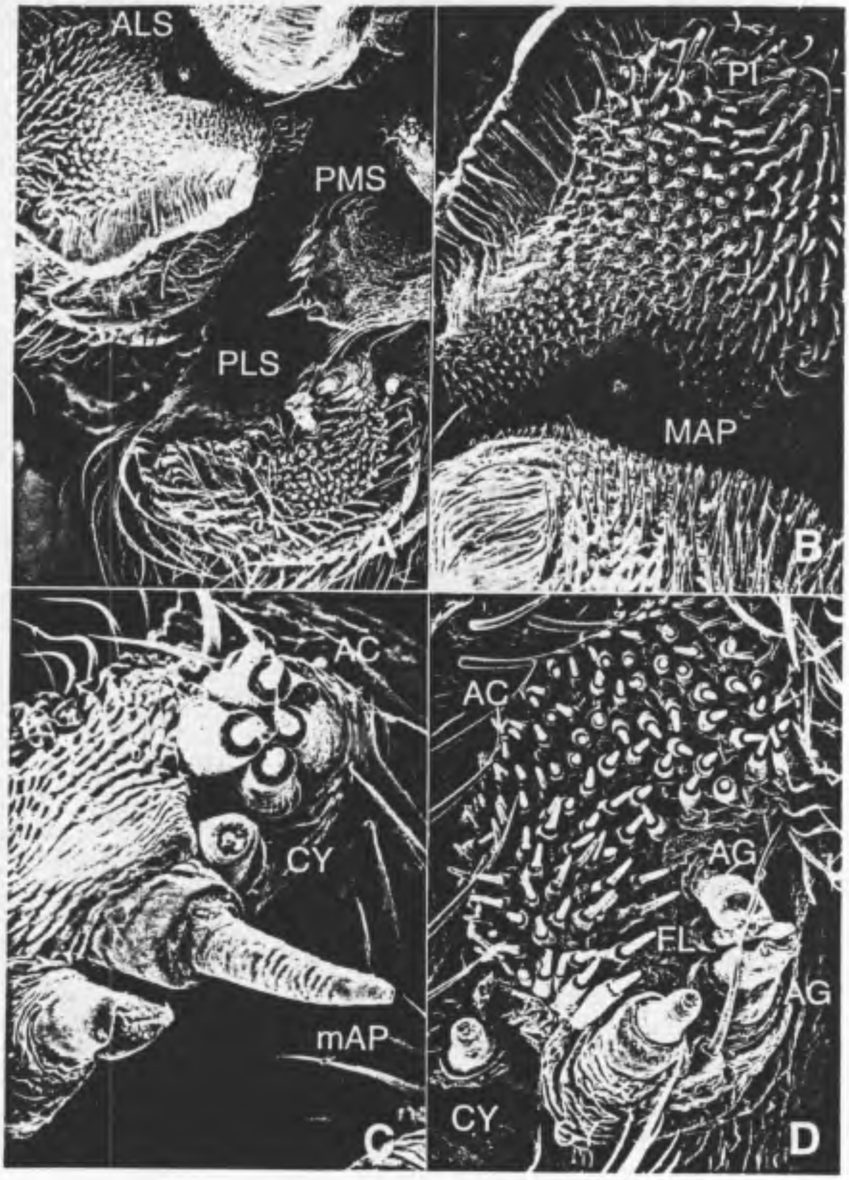

Fig. 16. *Nephila clavipes*, spinnerets of female. A, right spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

usually anterior to the other PLS cylindrical spigot) is contained within the PLS aciniform spinning field (Coddington 1989, figs 17, 21). In higher araneoids (and in the araneid *Zygiella*) it is peripheral (Hormiga 1994*b*: 48; Fig. 16D).

Character 59. PLS aggregate-flagelliform triad. 0: Aggregate spigots apart from flagelliform spigot (Figs 14D, 24D and 25D). 1: distal end of aggregate spigots embrace the

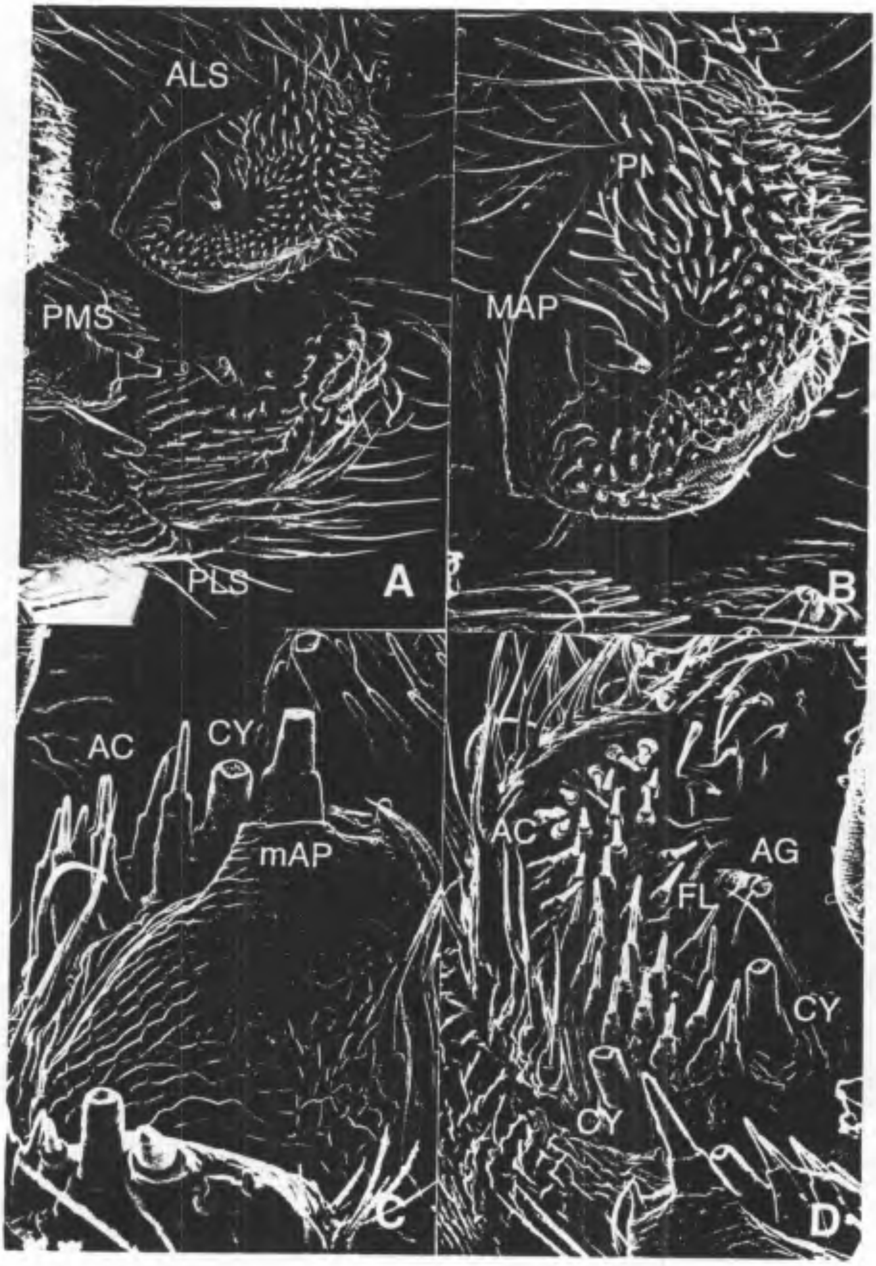

Fig. 17. *Herennia* sp. (Philippines), spinnerets of female. A, left spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

distal end of the flagelliform spigot (Figs 15D, 26A and 26B). We have found the apomorphic condition (state 1) in all nephilines we have examined, with the exception of

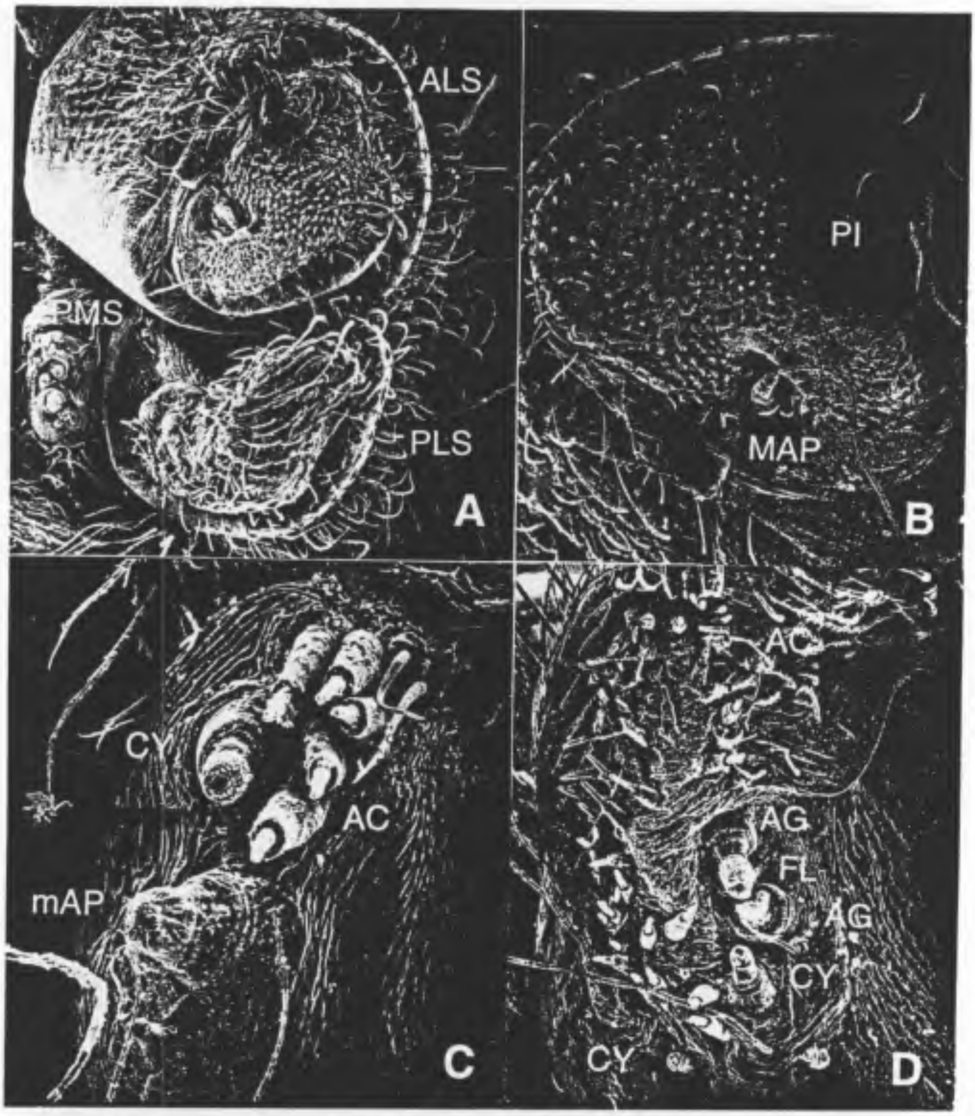

Fig. 18. *Nephilengys cruentata*, spinnerets of female. A, left spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

Phonognatha. State 1 is also found in *Araneus* and in some other araneids [e.g. *Gasteracantha cancriformis* (L.)].

Character 60. PLS aggregate gland spigot. 0: normal. 1: enlarged. The PLS of theridiids and nesticids have highly modified aggregate gland spigots (wider than any other spigots on any of the spinnerets). Typically, theridiids have a much greater spigot width than that of nesticids, but at least one aggeregate spigot is enlarged in nesticids (Coddington 1989, figs 29, 33, 37; Forster *et al*. 1990).

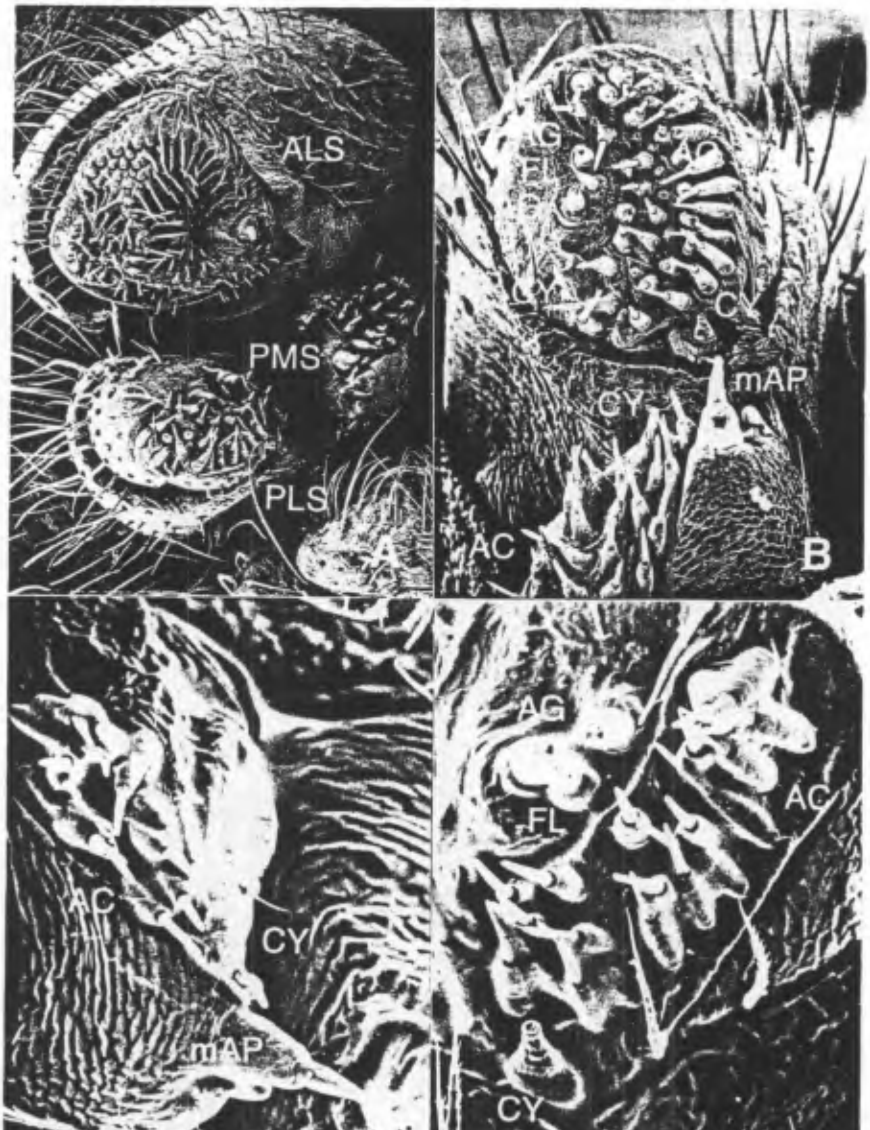

Fig. 19. *Meta americana*, spinnerets of female. A, right spinneret group; B, posterior median spinneret and posterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

Web-construction Behaviour in Phonognatha *spp.*

Phonognatha sp. 1

Of nine spiders located during one morning, one built an orb between 1200 and 1800 hours, none built between 1800 and 2200 hours (although most did lay one or more lines attached to the curled leaf retreat soon after sundown, presumably anchoring it against the persistent wind), four (including the individual that had built in the afternoon) built new orbs before arrival again at 0400 hours, two built between 0500 and 0600 hours, and the other three did not build orbs that day. Portions of two web constructions were observed. The

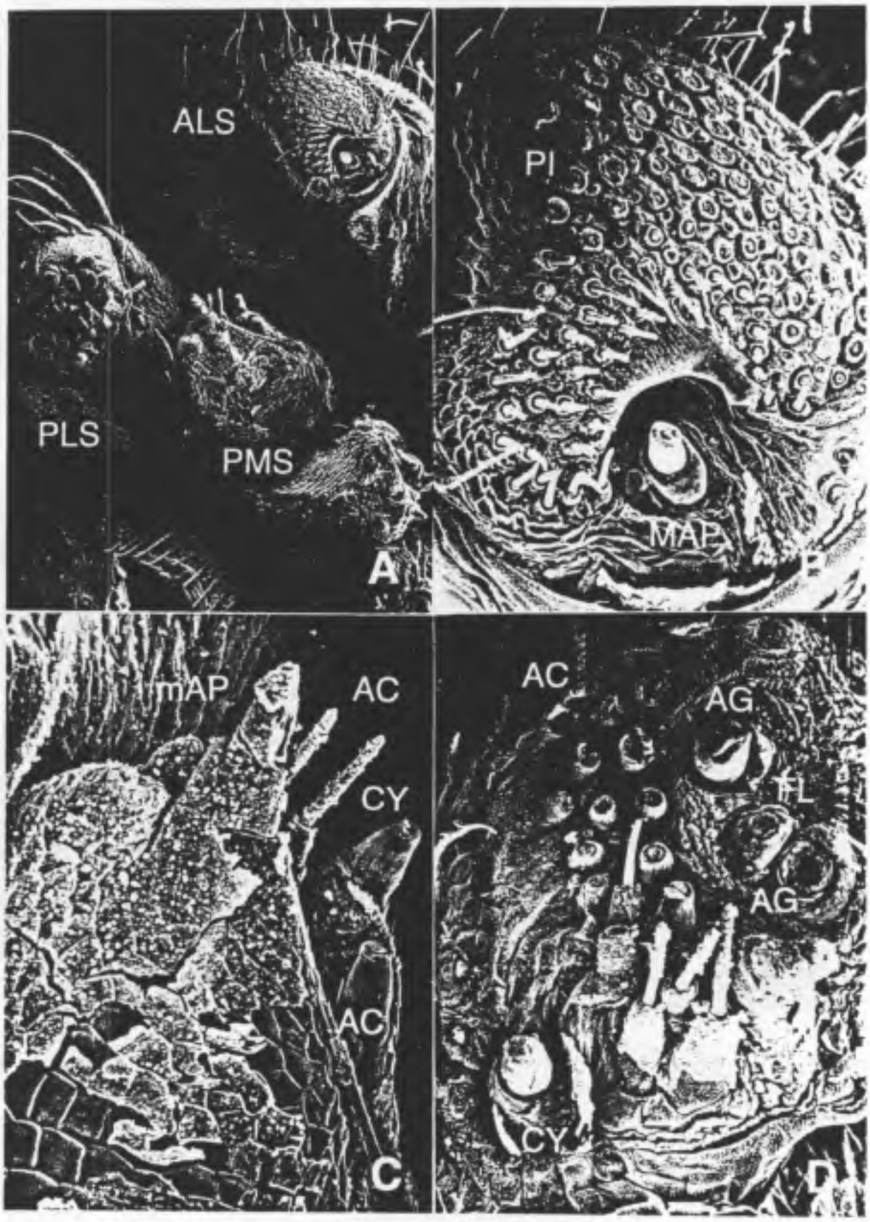

Fig. 20. *Chrysometa flava* (O.P.-C.), spinnerets of female. A, right spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

spiders were apparently disturbed by the headlamp used to observe them, and both terminated web construction when the sticky spiral was only partly finished.

Radius construction behaviour (Characters 44 and 45) clearly differed from that of all nephilines observed to date. Only a single new radius (instead of two) was laid with each trip away from the hub. It could not be ascertained whether the line laid on the way out was

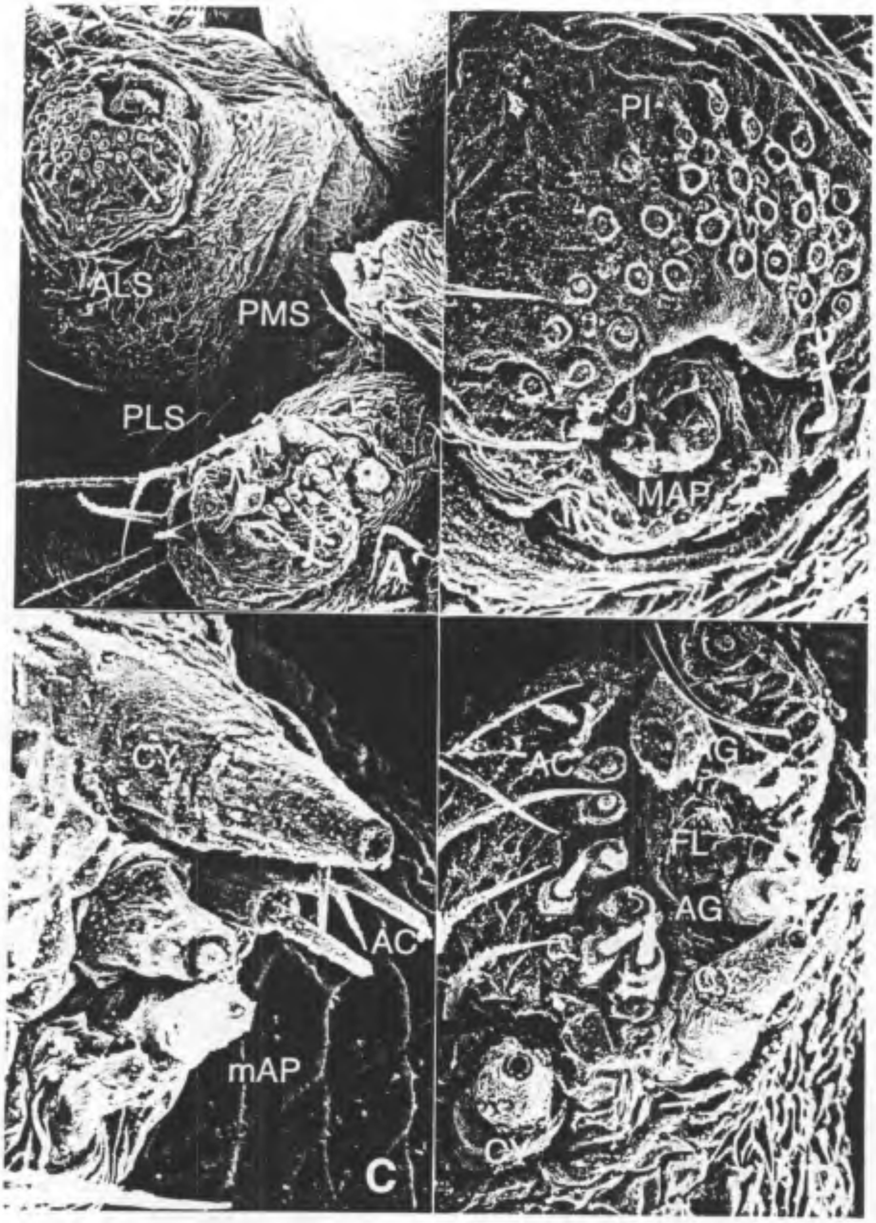

Fig. 21. *Metellina curtisi*, spinnerets of female. A, right spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

broken and reeled up on the way back to the hub, so the behaviour corresponded to either F1 or F4 of Eberhard (1982). Hub loop construction occurred between trips away from the hub to lay radii, at least during the last 5–10 radii. Each radius was held with oIII and oIV as the hub line was attached to it, with one leg on each side of the attachment. Temporary spiral construction began with a gradual widening of the spacing of the hub spiral, and included

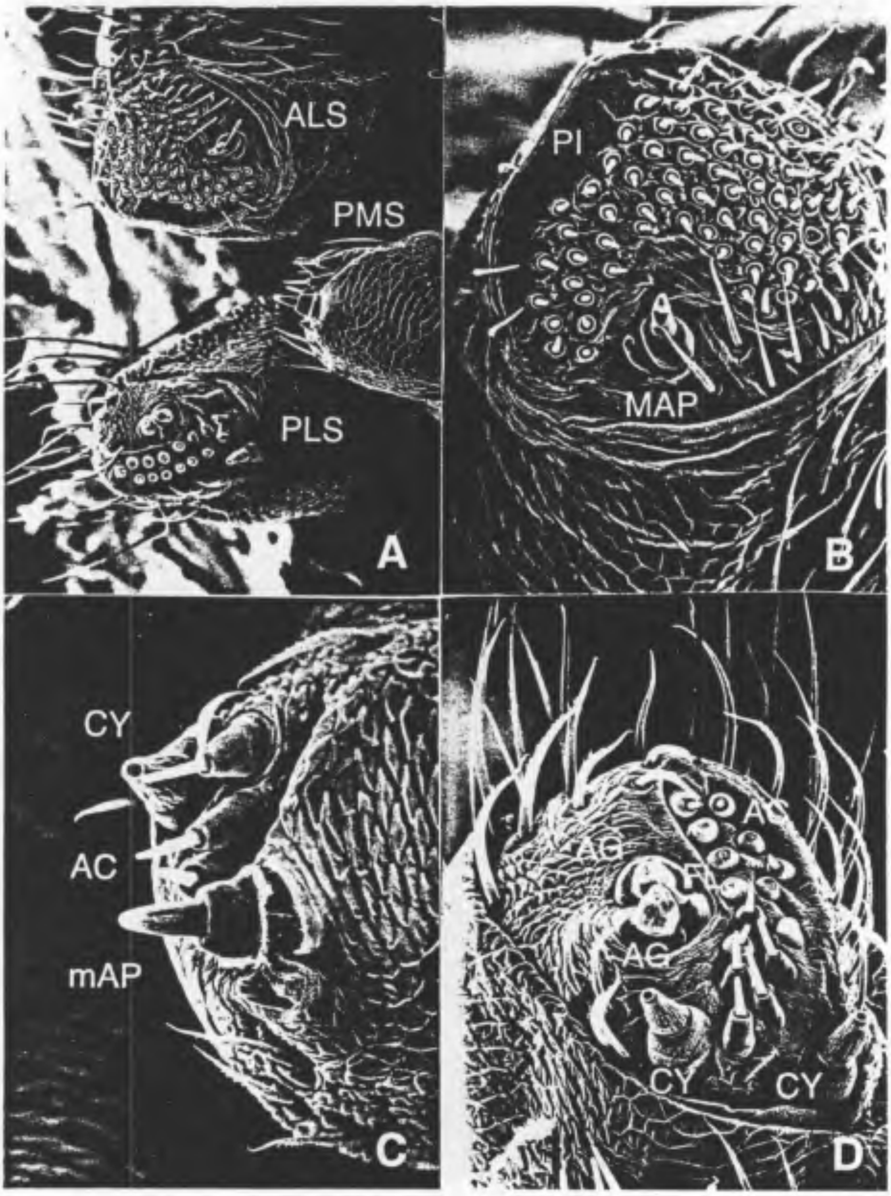

Fig. 22. *Leucauge venusta*, spinnerets of female. A, right spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

several switchbacks in the lower portion of the web (Figs 1, 2) (Character H1 of Eberhard 1982). During temporary spiral construction the spider was never out of contact with the preceding loop of temporary spiral. After a short pause at the end of temporary spiral construction, the spider began laying sticky spiral. Its front legs maintained contact with the outer loop of temporary spiral as it laid the outermost loop of sticky spiral (Character D2 of Eberhard 1982).

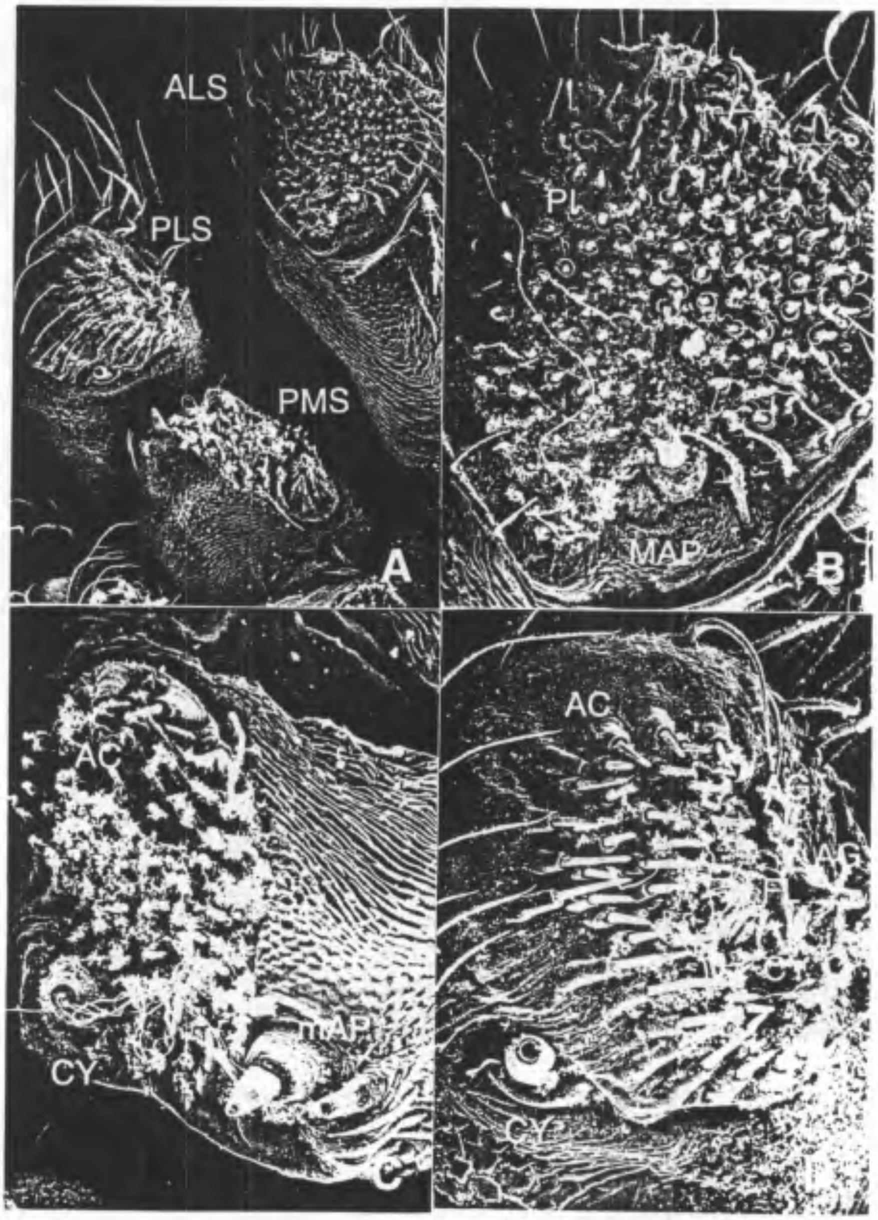

Fig. 23. *Azilia affinis*, spinnerets of female. A, right spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

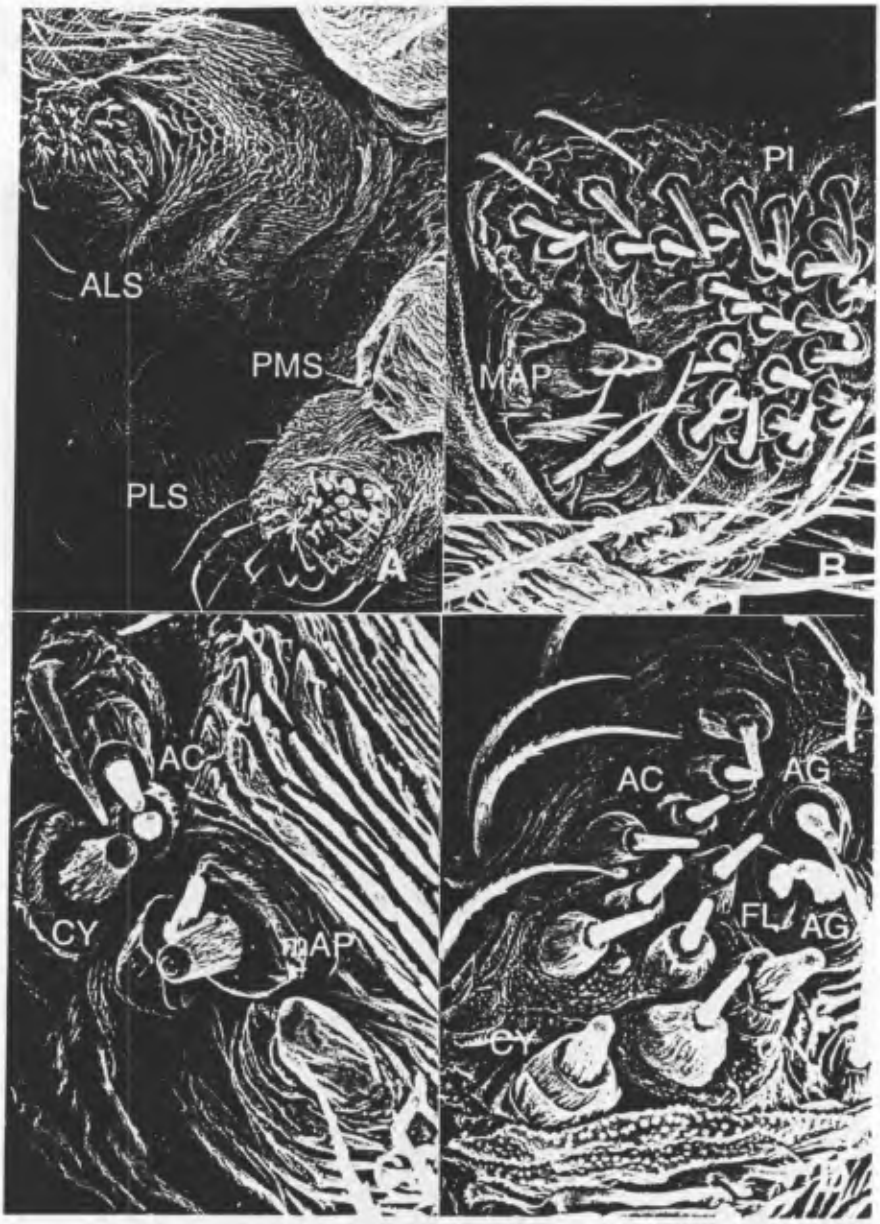

Fig. 24. *Dolichognatha pentagona*, spinnerets of female. A, right spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

As the spider laid subsequent loops of sticky spiral, the behaviour used to locate the innermost loop already laid (Character 48) was somewhat variable. Several lines of evidence indicate that it was similar to the behaviour of *Nephila* (Character A3 of Eberhard 1982).

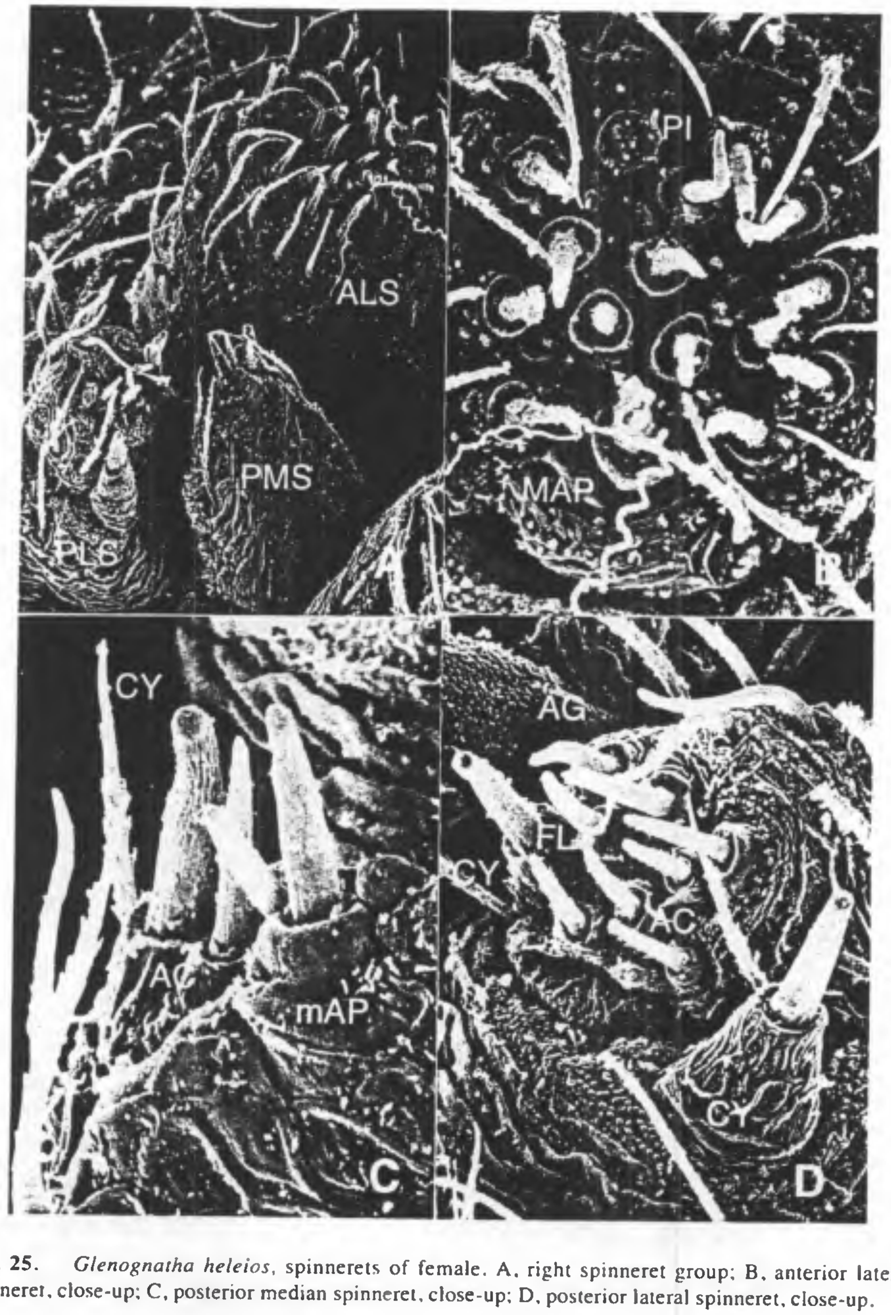

Fig. 25. *Glenognatha heleios*, spinnerets of female. A, right spinneret group; B, anterior lateral spinneret, close-up; C, posterior median spinneret, close-up; D, posterior lateral spinneret, close-up.

Leg oI sometimes tapped briefly preceding an attachment of the sticky spiral to a radius, but in about two thirds of the attachments did not move to touch the inner loop (i.e. the last loop laid) of sticky spiral. Thus, the behaviour did not conform to that of many araneids (A2 of Eberhard 1982). The tapping movements of leg oI were directed laterally rather than by forward extensions as in metines (Character A1 of Eberhard 1982). Leg iI (the leg used by nearly all the metines we studied to locate the inner loop of sticky spiral – A1 of Eberhard 1982) never made any movements toward the sticky spiral, and instead walked along the temporary spiral. Leg oII seemed not to tap in an exploratory fashion, but rather stepped directly from radius to radius, perhaps following leg oI (Eberhard 1982).

The movements of leg oIV (the leg apparently used by all studied nephilines to locate the

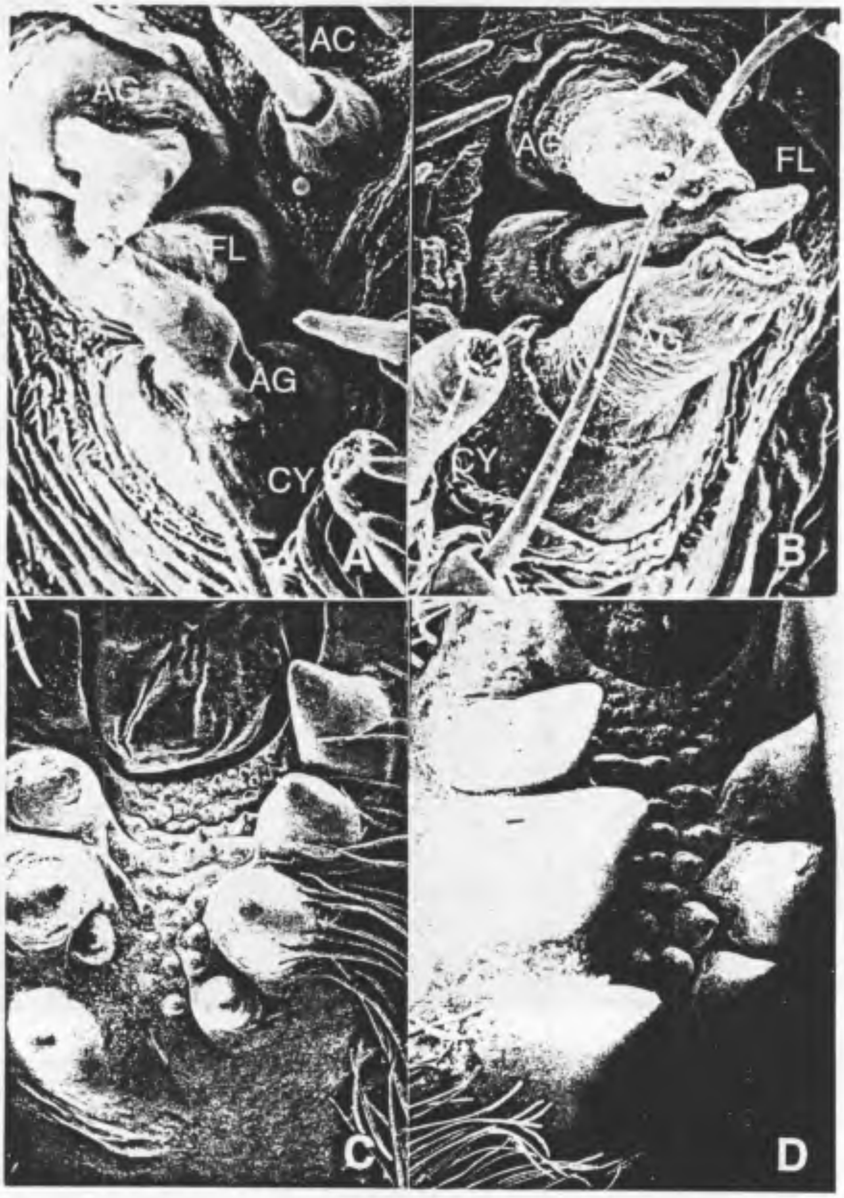

Fig. 26. PLS triad (A and B) and cheliceral denticles (C and D). A, *Clitaetra* sp. (South Africa); B, D, *Nephila clavipes;* C, *Herennia* sp. (Philippines).

inner loop – A3 of Eberhard 1982) were too rapid to follow in detail. At the moment of attachment of the sticky spiral, oIV grasped the radius just outside the point of attachment, leg oIII grasped the radius just inside this point, and leg iIV pushed the new segment of sticky spiral (Characters B2 and C1 of Eberhard 1982). In one series of 10–20 attachments in which the inner loop and the oIV could be seen clearly, the tarsus of leg oIV was just outside the inner loop of sticky spiral, and apparently grasped the radius at the point where the inner loop was attached, as in nephilines (Eberhard 1982). Since no other legs consistently contacted the inner loop of sticky-spiral preceding attachments, this apparent

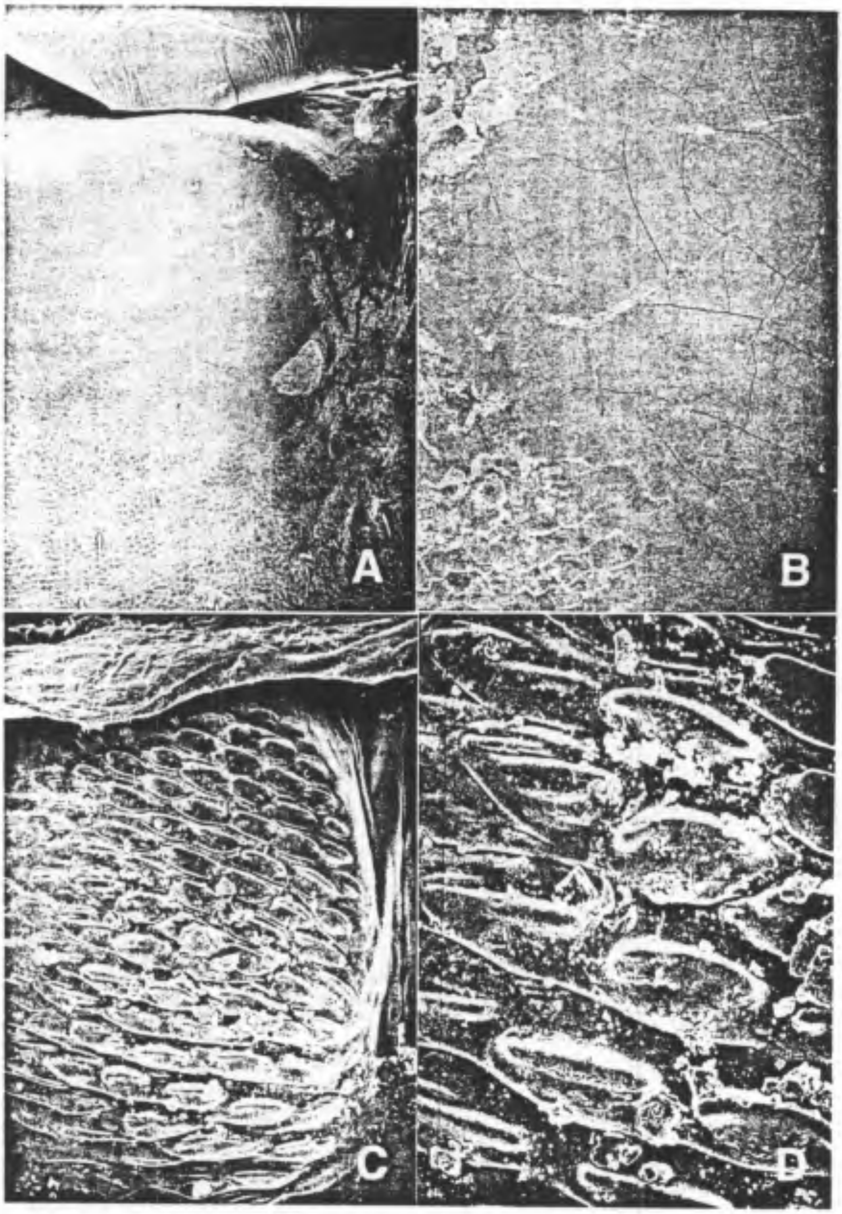

Fig. 27. Cheliceral boss. A, B, *Phonognatha graeffei;* C, D, *Clitaetra* sp. (Cameroon).

precision suggests that leg oIV may have made exploratory movements, as in nephilines (A3 of Eberhard 1982), locating the inner loop of sticky spiral as it reached toward and slid along the next radius.

It appeared that, as in other orb weavers (e.g. *Leucauge mariana* – Eberhard, unpublished data; see also Eberhard 1982), *P.* sp. 1 also used an alternative set of cues (probably involving the distance from the temporary spiral) to determine where to attach the sticky spiral. Thus, when the spider made the next to last loop in the web in Fig. 2 (arrows), it did not appear to touch the previous loop of sticky spiral at any time with any legs. The resulting space between the two sticky lines was relatively uniform, but greater than that of previous loops.

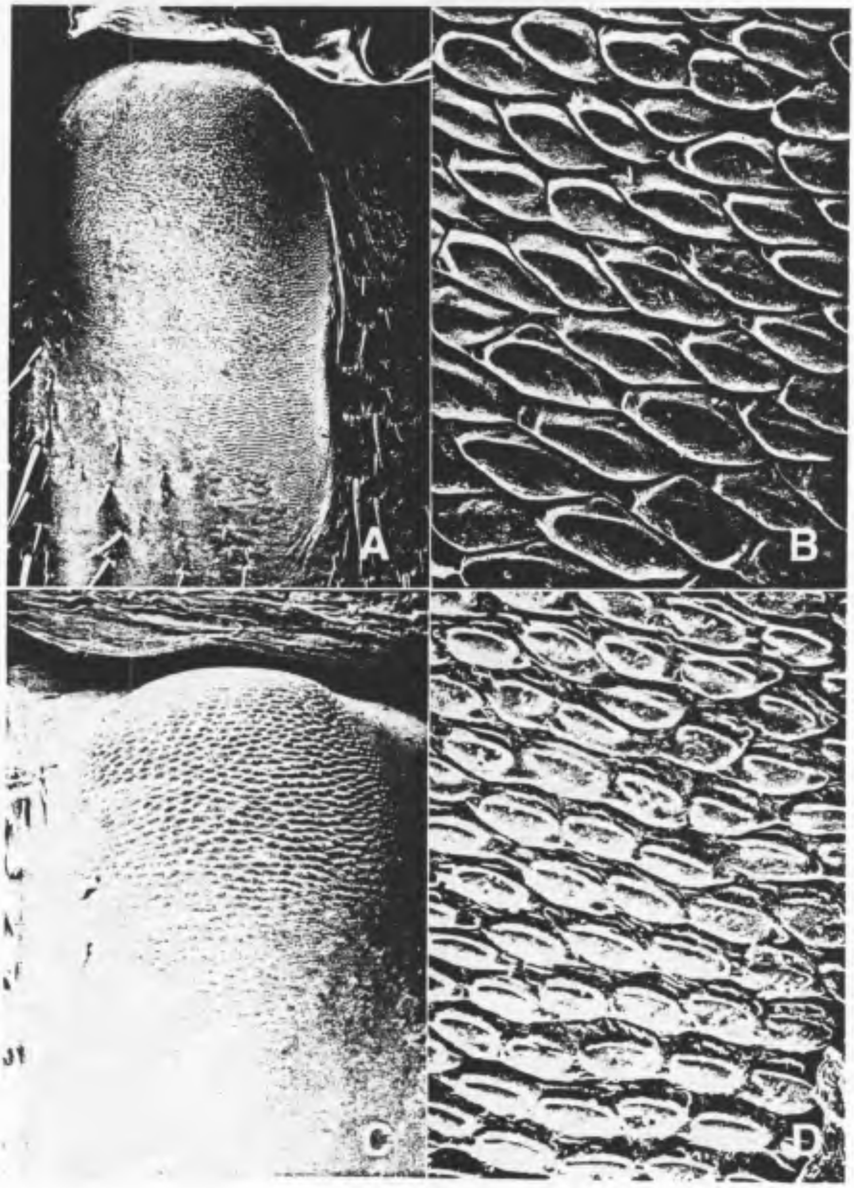

Fig. 28. Cheliceral boss. A, B, *Nephila clavipes*; C, D, *Herennia* sp. (Philippines).

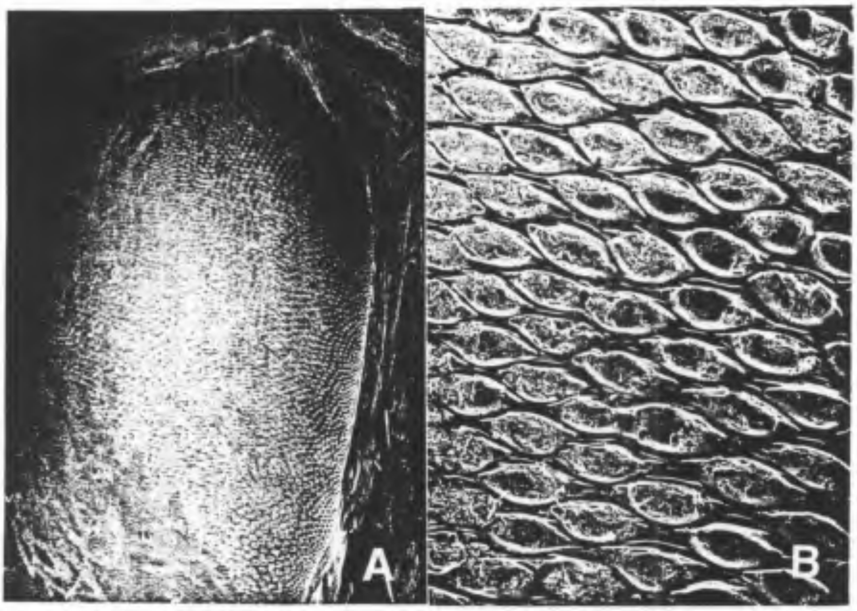

Fig. 29. Cheliceral boss. A, B, *Nephilengys cruentata.*

Most segments of temporary spiral were broken during sticky spiral construction, as in other orb weavers. In finished webs only a few short segments of temporary spiral remained (Fig. 1).

Other Phonognatha *species*

A finished web of *P.* sp. 2 (Fig. 3) and of *P. graeffei* offered some information about construction behaviour in these species. Portions of the sticky spiral were apparently intact in the *P.* sp. 2 web (arrow in Fig. 3), and most or all of the temporary spiral was intact in the *P. graeffei* web. In addition, the pattern of apparent splitting of radii in these webs suggested that radii were not laid in the nephiline fashion. None of the apparently split radii originated in pairs on the temporary spiral, as often, but not always, occurs in the webs of nephilines (compare Figs 1–3 with Fig. 4).

Cladistic Analysis

Using the exact solution both Hennig86 and PAUP 3.1.1 yielded three most parsimonious cladograms of 130 steps of length, with consistency and retention indices of 0·56 and 0·72, respectively. This result is stable under successive character weighting in Hennig86 and PAUP using the rescaled consistency index to set the new character weights (see Table 1 for weights).

The three resulting cladograms differ only in the inter-relationships among the outgroups: while these trees agree on the monophyly of threridioids plus linyphiioids plus symphythognathoids, the three possibles resolutions of this three-taxon statement are equally parsimonious. On the basis of our research in progress on orbicularian inter-relationships (Griswold *et al.* 1994) we have selected the topology in which theridiosomatids are sister to threridioids plus linyphiioids to map and study character evolution (Fig. 30).

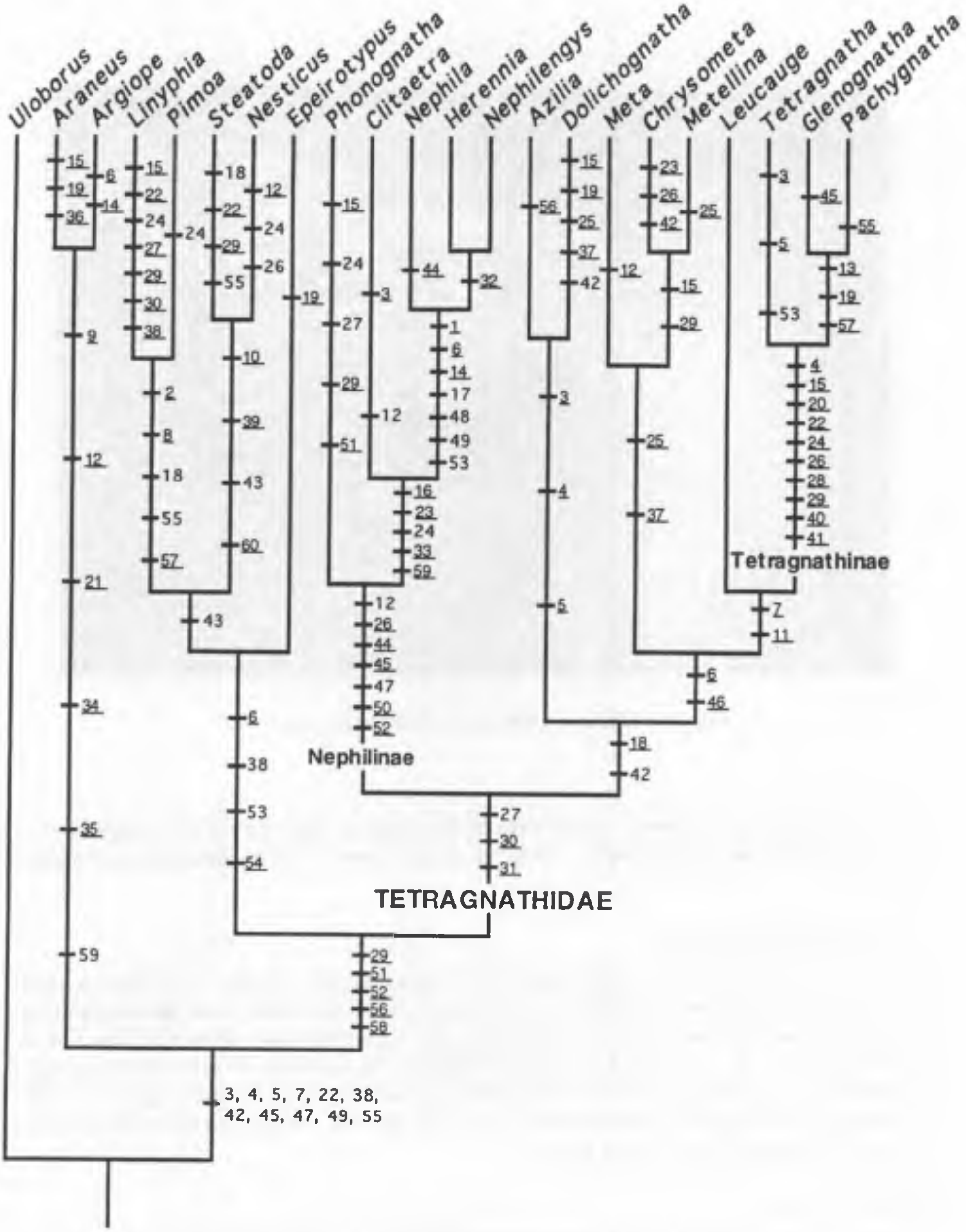

Fig. 30. One of the three minimal-length cladograms for the taxa and characters in Table 1 (the other two alternative most parsimonious cladograms differ only in the inter-relationships of the linyphioid–theridioid–symphythognathoid clade). The cladogram length is 130 steps; the consistency and retention indices are 0·56 and 0·72, respectively. Unambiguous character optimisations are underlined. Most of the ambiguous character optimisations have been resolved favouring reversals over parallelisms and convergences (see text for details).

Tetragnathidae as a whole, the nephilines (*Phonognatha*, (*Clitaetra*, (*Nephila*, (*Herennia*, *Nephilengys*)))), a core set of metine genera (*Meta* (*Chrysometa*, *Metellina*)) and the tetragnathines (*Tetragnatha* (*Glenognatha*, *Pachygnatha*)), and the doublet *Azilia–Dolichognatha* are monophyletic (Fig. 30). The nephiline clade is sister to the remaining tetragnathids and *Leucauge* is sister to the tetragnathine lineage. The monophyletic group composed of *Epeirotypus* (Theridosomatidae), the linyphiid–pimoid clade and the nesticid–theridiid clade is the sister-group of Tetragnathidae. Tetragnathidae plus the latter-mentioned clade are sister to Araneidae. In previous versions of the data that differed by minor variations in coding schemes, inclusion or exclusion of apparently labile characters, or taxa missing many entries, a variety of metine topologies resulted, but Nephilinae and Tetragnathinae remained monophyletic with metines falling between.

Discussion

Behaviour

The behavioural characters discussed here are summarised in Table 1. The radius construction behaviour of *P.* sp. 1 clearly differed from that of all studied nephilines (four species in the genera *Nephila*, *Nephilengys* and *Herennia*) (Hingston 1922*a*, 1922*b*; Wiehle 1931; Peters 1954; Eberhard 1982). The sticky-spiral localisation behaviour of *P.* sp. 1, however, was probably the same as that in nephilines, and clearly did not resemble that of any other studied tetragnathid. *Phonognatha* also differed from non-nephiline tetragnathids in maintaining contact with the temporary spiral while laying the first loop of sticky spiral 1982). Maintaining contact with the non-sticky spiral is probably plesiomorphic for araneoids. Additional similarities in web construction with nephilines are suggested by behavioural details that were deduced from finished webs of this and other species of *Phonognatha*. The temporary spiral was left at least partially intact in the finished webs of *P.* sp. 1 and *P.* sp. 2, and, as in nephilines, was completely intact in the orb of *P. graeffei*. Davies (1988, citing a personal communication from F. Vollrath) noted that the temporary spiral is also left intact in the web of an unspecified species of *Phonognatha*. In both *P.* sp. 1 and *P. graeffei* the sticky spiral was spaced away from temporary spiral lines at the same distances from sticky spiral lines, as occurs in the nephilines (Wiehle 1931; Robinson 1973; Fig. 4). Hub construction occurred during at least the later stages of radius construction in *P.* sp. 1, and (deduced from a web photograph) in *P.* sp. 2, as in nephilines. Also, as in nephilines, the central portion of the hub was not removed in *P.* sp. 1 (Characters 45 and 46), in contrast with nearly all other tetragnathids (Character state G1 of Eberhard 1982).

By optimising and mapping on the minimal length cladogram the behavioural characters reported here a possible sequence in the evolution of some of the distinctive web building behaviour of nephilines can be suggested. Nephiline sexual size dimorphism (arbitrarily defined here as males less than 0·4 times the female size, Character 14) evolves at the node subtending *Nephila*, *Herennia* and *Nephilengys*. *Phonognatha* and *Clitaetra* males are roughly 0·6 the size of females, whereas derived nephilines are approximately 0·4 or less. Males in more distant outgroups to the nephiline clade are also about 0·6 times the size of females. Sexual size dimorphism in nephilines is more correctly thought of as female giantism, not male dwarfism (*contra* the traditional view, e.g. Vollrath 1980; Vollrath and Parker 1992), because size of males in nephilines is either comparable to or larger than size of males in tetragnathid outgroups (Coddington 1994). At the same node, one of the three behavioural features classically associated with nephiline sexual size dimorphism may have also evolved: the habit of attaching radii twice to the frame, so that two radial lines result per cycle of radius construction (Character 48, Eberhard 1982). This behaviour results in a web 'rich' in strong radial lines and is presumably more efficient in terms of effort and silk expended (unfortunately, the web-building behaviour of *Clitaetra* has not been described). It makes biological sense that this increase in radii should evolve at roughly the same time as a large increase in size of females in *Nephila*, *Nephilengys* and *Herennia*, because the increase in radii results in a stronger web, and the double attachment of the radii spreads the stress of a frame–radius junction over a larger area.

On the other hand, the persistence of the temporary spiral (Character 50) probably evolved at the node that subtends *Phonognatha*. This feature should also strengthen the web. The origin of the use of the outside fourth leg to locate the previous sticky spiral segment during stick silk attachment is ambiguous because *Phonognatha* is intermediate in its behaviour. By the node subtending *Nephila*, however, this behaviour is clearly present and it allows an animal that is large compared with its mesh size to spin more efficiently. *Phonognatha* females are not much larger than other tetragnathids. Taken together, these features could be read as suggesting that a normal-proportioned lineage gained behavioural apomorphies that helped to stop larger prey (via the persistent non-sticky spiral), and that feature may have permitted females to grow to a large size (perhaps by fecundity-based selection given increased prey resources), and that further apomorphies in building behaviour (how sticky spirals are located) may have accommodated the increase in size of females. Even if sexual size dimorphism in nephilines is presumed to be adaptive, it seems unnecessary to hypothesise a novel selective regime exclusively on males to explain size of males in the Nephilinae. If size of males prior to the node subtending *Nephila*, *Herennia* and *Nephilengys* was selectively determined, the same selective regime presumably continued to act (and to explain) size of males after the increase in size of females. Prior to the evolution of female giantism, size of males presumably was well adjusted to its selective regime. After females increased in size, males apparently remained at their plesiomorphic size or possibly increased. An hypothesis of novel selective factors promoting male dwarfism thus seems unnecessarily complex to explain size of nephiline males. On the other hand, selection on females would be required to explain the apomorphic increase in size of females documented in Fig. 30.

Lack of hub removal (Character 45), a further point of similarity with nephilines, may have evolved in the *Phonognatha* line of descent in association with the use of a leaf retreat. A convergent lack of hub removal occurs in at least one (Eberhard 1986) and probably several species of *Tetragnatha* in which a twig runs through the centre of the web (W. G. E. has seen *Tetragnatha* webs of this type in India, Costa Rica and Australia; in other *Tetragnatha* species the centre of the hub is consistently removed (Eberhard 1982). Hub removal is also lacking in the araneine *Spilasma artifer* Simon (Eberhard 1982), which suspends a large retreat made of detritus at the centre of its orb, similar in size to the curled leaf of *Phonognatha* (Eberhard 1982, 1986). Thus, the evolutionary origin of lack of hub destruction in nephilines may have been associated with the inclusion of leaves or other objects at the hub, which were later abandoned in the nephiline lineage. However, juvenile *Nephila clavipes* (L.) and, more rarely *N. pilipes* (Fabricius), and sometimes adults, arrange 'garbage' at the hub (L. Higgins, personal communication), suggesting perhaps that early ontogenetic stages of (at least some species of) *Nephila* still exhibit the plesiomorphic behaviour (i.e. having some type of foreign matter at the hub). *Nephilengys* and *Herennia* both spin hubs against substrate, which is not dissimilar, albeit extremely exaggerated and modified. We have coded the nephilines, with the exception of *Nephila*, as spinning their hubs against a substrate (Character 44), although the case of *Phonognatha* differs in that the substrate is a leaf. Coding *Phonognatha* as not spinning the hub against a substrate (Character 44, state 0) produces no changes in cladogram topology.

Tetragnathid Phylogeny

Our behavioural and morphological data suggest that nephilines are monophyletic and include *Phonognatha*, which is sister to the (*Clitaetra* (*Nephila* (*Herennia*, *Nephilengys*))) clade. Because of *Phonognatha*'s basal position some of its features may represent the plesiomorphic condition for Nephilinae. The placement of *Phonognatha* as a nephiline is unambiguously supported by the five following nephiline synapomorphies: presence of a folded paracymbial apophysis, presence of a hub established against a substrate, absence of hub removal during web construction, persistence of an intact temporary spiral in the finished orb, and the use of fourth legs to locate the previous sticky loop during sticky spiral construction. Additional but ambiguous support (that is, that the character changes can be assigned to other parts of the cladogram without increasing the cladogram length) is offered by grooved booklung covers (convergent in the araneids, *Nesticus* and *Meta*), and possibly the reversion to a gradual shift from the hub loops to the temporary spiral. Seven synapomorphies support the monophyly of *Nephila*, *Herennia* and *Nephilengys*. Three of these synapomorphies offer unambiguous support: the presence of a dorsal abdominal scutum in the males (but see our comments under the description of Character 1), presence of a high clypeus, and an increase in the body size of females. The other four have alternative most parsimonious optimisations on the cladogram: highly striated cheliceral boss; doubly attached radii in the web; radii construction lacking the cut and reel behaviour; and absence of wrap-bite attack. The presence in these three genera of partial web-renewal behaviour (Nentwig and Spiegel 1986) adds additional support for their monophyly. Of course, adding additional data or taxa to the matrix may alter some of these results. In particular, we could not include the two remaining nephiline genera (*Deliochus*, known from eastern and south-western Australia and Tasmania and *Perilla*, known from South-east Asia) because of insufficient preserved material and the lack of behavioural observations. However, both genera have been suggested as part of the nephiline lineage (Simon 1892, Roewer 1942). Addition of potential nephiline taxa should be a high priority for future work because it is mainly by taxon addition that a more detailed understanding of the sequence of events in web evolution will be obtained.

Our analysis also corroborates other previous results. Tetragnathidae, and tetragnathines, are monophyletic, the nephiline clade is sister to the rest of the family, and 'metines' in any broad sense are ill-defined and probably paraphyletic (certainly paraphyletic in the present taxonomic sample). Whichever metine genera are included, they usually fall compactly between the well-defined nephilines and tetragnathines, rather than basal in the family (*contra* Levi 1981: 276). On the other hand, metines never emerged as a monophyletic group in any versions or treatments of our data, and relationships were always highly unstable. Fig. 30 summarises knowledge of tetragnathid phylogenetic relationships as discussed here, and we regard it as a reasonable and testable working hypothesis.

The case for tetragnathid monophyly remains much the same. Two characters are unambiguously synapomorphic in the context of this data set: the loss of the median apophysis (Character 30) paralleled in linyphiids and in some pimoids, although the median apophysis is presumably present in the basal pimoid lineages (Hormiga 1994*a*) and the presence of a conductor and embolus spiralling with each other (Character 31), which is unique to tetragnathids within araneoids. Additional support for the monophyly of Tetragnathidae is provided by the presence of apical tegular sclerites (Character 27), although this character can be alternatively optimised as having two origins within the tetragnathids. As discussed earlier, if the tetragnathid embolus–tegulum membrane (Character 38) is not homologous to the membrane found between the tegulum (suprategulum in the case of linyphiids) and the radix in linyphiids and araneids, the presence of such membranous connection could provide additional support for the monophyly of Tetragnathidae. The presence of palpal sclerites in theridiids and nesticids that could be median apophysis homologs is obviously relevant to the lack of such a structure in tetragnathids, but its implications can only be determined in the context of a much larger analysis. Among symphytognathoids, only theridiosomatids have a median apophysis, but the structure is convincingly similar to the araneid condition (Coddington 1986). The inference that tetragnathids lost the median apophysis independently therefore depends critically on the cladistic position of theridiosomatids. In sum, the best argument for tetragnathid monophyly remains the peculiar conformation of the bulb and its distal sclerites.

The linyphiid clade is similar to tetragnathids in lacking the median apophysis and in having relatively derived spigot morphology. However, neither the linyphiid–pimoid clade nor the theridiid–nesticid clade can be coded for the building behaviour characters because they have modified orb-building behaviour and architecture and the homologous behaviours, if they exist, remain unstudied.

We tried several variant analytical approaches to deal with the absence of behavioural data for linyphiids, pimoids, nesticids and theridiids. The simplest option is to exclude from the analysis the characters that describe the orb-web building behaviour (Characters 43–52). Under this approach, the linyphioid–theridioid–symphythognathoid clade remains sister to the monophyletic Tetragnathidae, although relationships within tetragnathids might change and the cladistic resolution within metines and nephilines suffers (however, the following tetragnathid clades remain supported in the strict consensus cladogram: the nephilines, excluding *Phonognatha* in some topologies; the tetragnathines; *Meta* sister to *Chrysometa* plus *Metellina*; and the monophyly of the tetragnathid genera outside the Nephilinae). A second approach is to code both linyphiids and pimoids as primitively lacking all orb-web building behaviours, rather than as 'unknown' for these features. Given how Characters 43–52 are coded, one would have to add about six web architectural characters to the matrix, such as absence or presence of the hub, temporary spiral, frames, radii and sticky spirals, as well as a few additional behavioural features. Such a change does not affect the results for this matrix, although it probably would if we included non-orb-weaving taxa outside Orbiculariae.

Tetragnathinae (i.e. the group including at least the genera *Tetragnatha*, *Glenognatha* and *Pachygnatha*) is monophyletic, based on the following ten synapomorphies: loss of PME tapeta; enlarged chelicerae of males; constricted cymbium of males; presence of a cymbium–paracymbium articulation, which evolved independently, and therefore is not homologous to the linyphiid intersegmental paracymbium; elongated paracymbium; presence of an anterior apophysis on the paracymbium; enlarged sperm reservoir in the tegulum; loss of the epigynum; and loss of the fertilisation ducts in the genitalia of females. The reversal in tetragnathines to the spiral condition of the sperm reservoir in the tegulum provides further support for their monophyly.

Leucauge (classically regarded as a 'metine' genus) appears more closely related to the tetragnathines than to other tetragnathid lineages, based on two synapomorphies, the presence of dorsal femoral trichobothria (convergent in uloborids) and of posterior gut caeca, although for the latter character data on many taxa are not available (Palmgren 1978*a*, 1978*b*, 1979). R. R. Forster was perhaps the first to argue that *Leucauge* and relatives are a lineage apart from the 'metines,' and may merit family status (personal communication; *in litt.* G. H.). Our analysis supports separation of 'leucaugids' and 'metines.' However, Forster also suggested that leucaugids, together with the metines and the eryciniolid lineage, form a monophyletic group. Our results do not corroborate such a clade (although we did not include *Eryciniolia*), since according to our results any group that includes *Meta* and *Leucauge* ought to include the tetragnathines as well.

The last result is more negative than positive, and concerns the identity of 'metines', Metinae, or even Metidae. The monophyly of the classical Metidae (e.g. as delimited by Brignoli 1983) is a well-known old problem. Our results suggest that Metinae (six genera in this sample) are paraphyletic. More typical metine genera (*Meta*, *Metellina* and *Chrysometa*) may form a monophyletic group, and additional genera may belong to this lineage. But the same might be said of *Leucauge* and its relatives, as Foster has pointed out (*in litt.*), and for *Dolichognatha* and *Azilia*, which, according to our data, form another distinct lineage. At face value the results suggest the existence of at least three 'metine' lineages. These results were, however, so sensitive to inclusion and exclusion of taxa and changes in coding that we have little confidence that much of the 'metine' region of the cladogram presented here will survive future work (mainly in the form of addition of new taxa). We are doubtful that any taxa or characters can be added to support the monophyly of Metinae or Metidae. In all of the former versions of this data set (more than three dozen) 'metine' genera were consistently unstable, but tetragnathines and nephilines remained monophyletic. This cladistic instability of the 'metine' genera is due to serious homoplasy in almost every classical morphological character system used to characterise metines (cf. Levi 1980 and 1986 for further discussion of characters), and in retrospect it is no surprise that tetragnathid relationships and limits should have been a vexing problem. Perhaps the most reliable feature for the mentioned monophyletic group of metine genera is the metine embolic apophysis (Character 37), with homoplasy in *Dolichognatha*. Exclusion of Character 37 from the analysis results in 21 minimal-length cladograms that are similar to the tree depicted in Fig. 30 and differ only in the relationships of the metines. The successive character-weighting analysis of such reduced data set results in the same three cladograms that are obtained from the analysis of the complete data set.

Future work on tetragnathid phylogeny should include taxa such as *Deliochus*, *Perilla*, *Metabus*, *Tylorida* and *Eryciniolia* in the matrix. It should also pursue Palmgren's work on gastric caeca, study the biological role of grooves on booklungs, investigate in more detail the spermophor routing, study the female genitalia (see Forster 1980) and fill in missing entries in behavioural data. In addition, we need to understand better the genital mechanics so as to explain the rather extraordinary changes in genitalia of tetragnathine males and females, and to continue studies on spinneret spigots (e.g. the biological significance of the peculiar aggregate–flagelliform spigots arrangement found in nephilines and some araneids, Character 59). In the absence even of photographs of webs and hubs of the above genera, however, adding these taxa could obscure rather than illuminate tetragnathid phylogeny. Behavioural characters have usually played decisive roles in quantitative studies of spider phylogeny (e.g. Coddington 1990*a*, 1990*b*). A promising morphological character system that is almost completely unstudied in spiders is the detailed pattern of rhabdoms in secondary eyes, or, alternatively, the pattern they make with the tapetum. This feature can be quite easily observed and photographed (with a microscope) in living animals or very fresh preserved specimens, and preliminary observations suggest that it will be phylogenetically informative.

Conclusions

The behavioural and morphological data support the placement of *Phonognatha* within the nephilines and the monophyly of the subfamily Nephilinae. The study of some of these characters within the context provided by the nephiline cladogram suggests that the different specialisations of nephiline web-building behaviour did not evolve concurrently, and that some preceded the female giantism (not male dwarfism) characteristic of distal nephiline genera like *Nephila* and *Herennia*. The cladistic analysis also supports the monophyly of both Tetragnathidae and Tetragnathinae and suggests that the nephiline clade is sister to the remaining tetragnathids. The status of the 'metines', sometimes regarded as either a distinct family or subfamily, remains controversial since the data suggest that they are a paraphyletic assemblage. In our opinion it is unlikely that this latter result is an artifact due to taxon sampling.

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References

Austin, A. D., and Anderson, D. T. (1978). Reproduction and development of the spider *Nephila edulis* (Koch) (Araneidae : Araneae). *Australian Journal of Zoology* **26**, 501–18.

Bonnet, P. (1956). 'Bibliographia Araneorum.' Vol. 2, pp. 919–1926. (Toulouse.)

Bonnet, P. (1957). 'Bibliographia Araneorum.' Vol. 2, pp. 1927–3026. (Toulouse.)

Bonnet, P. (1958). 'Bibliographia Araneorum.' Vol. 2, pp. 3027–4230. (Toulouse.)

Bonnet, P. (1959). 'Bibliographia Araneorum.' Vol. 2, pp. 4231–5058. (Toulouse.)

Brignoli, P. M. (1983). 'A Catalogue of the Araneae Described between 1940 and 1981.' (Manchester University Press and British Arachnological Society: London.)

Carpenter, J. M. (1988). Choosing among multiple equally parsimonious cladograms. *Cladistics* **4**, 291–6.

Carpenter, J. M., Strassmann, J. E., Turillazzi, S., Hughes, C. R., Solís, C. R., and Cervo, R. (1993). Phylogenetic relationships among paper wasp social parasites and their hosts (Hymenoptera : Vespidae; Polistinae). *Cladistics* **9**, 129–46.

Christenson, T. E., and Goist, K. C. (1979). Cost and benefits of male–male competition in the orb weaving spider *Nephila clavipes*. *Behavioral Ecology and Sociobiology* **5**, 87–92.

Coddington, J. A. (1986). The genera of the spider family Theridiosomatidae. *Smithsonian Contributions to Zoology* **422**, 1–96.

Coddington, J. A. (1989). Spinneret silk spigot morphology: evidence for the monophyly of orb-weaving spiders, Cyrtophorinae (Araneidae), and the group Theridiidae–Nesticidae. *Journal of Arachnology* **17**, 71–95.

Coddington, J. A. (1990*a*). Ontogeny and homology in the male palpus of orb weaving spiders and their relatives, with comments on phylogeny (Araneoclada : Araneoidea, Deinopoidea). *Smithsonian Contributions to Zoology* **496**, 1–52.

Coddington, J. A. (1990*b*). Cladistics and spider classification: araneomorph phylogeny and the monophyly of orbweavers (Araneae : Araneomorphae; Orbiculariae). *Acta Zoologica Fennica* **190**, 75–87.

Coddington, J. A. (1994). The roles of homology and convergence in studies of adaptation. In 'Phylogenetics and Ecology'. (Eds R. Vane-Wright and P. Eggleton.) pp. 53–78. (Linnaean Society: London.)

Coddington, J. A., and Levi, H. W. (1991). Systematics and evolution of spiders (Araneae). *Annual Review of Ecology and Systematics* **22**, 565–92.

Cohn, J. (1990). Is the size that counts? Palp morphology, sperm storage, and egg hatching frequency in *Nephila clavipes* (Araneae, Araneidae). *Journal of Arachnology* **18**, 59–72.

Comstock, J. H. (1910). The palpi of male spiders. *Annals of the Entomological Society of America* **3**, 161–85.

Croom, H. B., Gillespie, R. G., and Palumbi, S. R. (1991). Mitochondrial DNA sequences coding for a portion of the RNA of the small ribosomal subunits of *Tetragnatha mandibulata* and *Tetragnatha hawaiensis* (Araneae, Tetragnathidae). *Journal of Arachnology* **19**, 210–14.

Davies, V. T. (1978). A new family of spiders (Araneae: Teemenaaridae). In 'Arachnology'. (Ed. P. Merrett.) pp. 293–302. (Symposia of the Zoological Society of London 42: London.)

Davies, V. T. (1988). An illustrated guide to the genera of orb-weaving spiders in Australia. *Memoirs of the Queensland Museum* **25**, 273–332.

Eberhard, W. G. (1982). Behavioural characters for the higher classification of orb-weaving spiders. *Evolution* **36**, 1067–95.

Eberhard, W. G. (1987*a*). Effects of gravity on temporary spiral construction by *Leucauge mariana* (Araneae : Araneidae). *Journal of Ethology* **5**, 29–36.

Eberhard, W. G. (1987*b*). Hub construction by *Leucauge mariana* (Araneae, Araneidae). *Bulletin of the British Arachnological Society* **7**, 128–32.

Eberhard, W. G. (1988*a*). Behavioral flexibility in orb web construction: effects of supplies in different silk glands and spider size and weight. *Journal of Arachnology* **16**, 295–302.

Eberhard, W. G. (1988*b*). Memory of distances and directions moved as cues during temporary spiral construction in the spider *Leucauge mariana* (Araneae : Araneidae). *Journal of Insect Behavior* **1**, 51–66.

Eberhard, W. G. (1990). Early stages of orb construction by *Philoponella vicina*, *Leucauge mariana*, and *Nephila clavipes* (Araneae, Uloboridae and Tetragnathidae), and their phylogenetic implications. *Journal of Arachnology* **18**, 205–34.

Farris, J. S. (1969). A successive approximations approach to character weighting. *Systematic Zoology* **18**, 374–85.

Farris, J. S. (1988). 'Hennig86, version 1·5.' Computer program distributed by A. G. Kluge, Museum of Zoology, The University of Michigan, Ann Arbor, Michigan 48109–1079, USA.

Forster, R. R. (1980). Evolution of the tarsal organ, the respiratory system and the female genitalia in spiders. *Verhandlungen Internationaler Arachnologen-Kongress* **8**, 269–84.

Forster, R. R., Platnick, N. I., and Coddington, J. A. (1990). A proposal and review of the spider family Synotaxidae (Araneae, Araneoidea), with notes on theridiid interrelationships. *Bulletin of the American Museum of Natural History* **193**, 1–116.

Gertsch, W. J. (1984). The spider family Nesticidae (Araneae) in North America, Central America, and the West Indies. *Bulletin of the Texas Memorial Museum* **31**, 1–91.

Gillespie, R. G. (1986). Between population comparison of resource acquisition in the long jawed orb weaving spider *Tetragnatha elongata*. Ph. D. Thesis, University of Tennessee, Knoxville.

Gillespie, R. G. (1987*a*). The mechanism of habitat selection in the long-jawed orb-weaving spider *Tetragnatha elongata* (Araneae, Araneidae). *Journal of Arachnology* **15**, 81–90.

Gillespie, R. G. (1987*b*). The role of prey availability in aggregative behaviour of the orb weaving spider *Tetragnatha elongata*. *Animal Behavior* **35**, 675–81.

Gillespie, R. G. (1992). Impaled prey. *Nature* **355**, 212–13.

Griswold, C. E., Coddington, J. A., Hormiga, G., and Scharff, N. (1994). Phylogeny of the orb web building spiders (Araneomorphae, Orbiculariae). *American Arachnology* **50**, 5 (Abstract).

Higgins, L. E (1987). Time budget and prey of *Nephila clavipes* (Linnaeus) (Araneae, Araneidae) in southern Texas. *Journal of Arachnology* **15**, 403–20.

Higgins, L. E. (1988). Variation in web structure in the orb-weaving spider *Nephila clavipes* and correlated changes in life history (Panama, Mexico, Texas). Ph. D. Thesis, University of Texas, Austin.

Higgins, L. E. (1989). Effect of insemination on the morphology of the internal female genitalia of the spider *Nephila clavipes* (Araneae : Araneidae). *Annals of the Entomological Society of America* **82**, 748–53.

Higgins, L. E. (1990). Variation in foraging investment during the intermolt interval and before egg-laying in the spider *Nephila clavipes* (Araneae : Araneidae). *Journal of Insect Behavior* **3**, 773–83.

Higgins, L. E. (1991). Response of *Nephila clavipes* to mock predation changes with the proximity of the molt. *Journal of Arachnology* **19**, 231–2.

Higgins, L. E. (1992). Developmental plasticity and fecundity in the orb-weaving spider *Nephila clavipes*. *Journal of Arachnology* **20**, 94–106.

Hingston, R. W. G. (1922*a*). The snare of the giant wood spider (*Nephila maculata*) Part II. The continuation of the snare. *Journal of the Bombay Natural History Society* **28**, 642–9.

Hingston, R. W. G. (1922*b*). The snare of the giant wood spider (*Nephila maculata*) Part III. Further lessons of the *Nephila*. *Journal of the Bombay Natural History Society* **28**, 911–23.

Hormiga, G. (1993). Implications of the phylogeny of Pimoidae (new rank) for the systematics of linyphiid spiders (Araneae, Araneoidea, Linyphiidae). *Memoirs of the Queensland Museum* **33**, 533–42.

Hormiga, G. (1994*a*). A revision and cladistic analysis of the spider family Pimoidae. *Smithsonian Contributions to Zoology* **549**, 1–104.

Hormiga, G. (1994*b*). Cladistics and the comparative morphology of linyphiid spiders and their relatives (Araneae, Araneoidea, Linyphiidae). *Zoological Journal of the Linnean Society* **111**, 1–71.

Kaston, B. J. (1948). 'The Spiders of Connecticut.' (Connecticut Geological and Natural History Survey: Hartford.)

Kovoor, J. (1986). L'appareil séricigène dans les genres *Nephila* Leach et *Nephilengys* Koch: anatomie microscopique, histochimie, affinités avec d'autres Araneidae. *Revue Arachnologique* **7**, 15–34.

LeSar, C. D., and Unzicker, J. D. (1978). Life history, habits, and prey preferences of *Tetragnatha laboriosa* (Araneae: Tetragnathidae). *Environmental Entomology* **7**, 879–84.

Levi, H. W. (1974). The orb-weaver genus *Zygiella* (Araneae, Araneidae). *Bulletin of the Museum of Comparative Zoology* **146**, 267–90.

Levi, H. W. (1980). The orb-weaver genus *Mecynogea*, the subfamily *Metinae* and the genera *Pachygnatha*, *Glenognatha* and *Azilia* of the subfamily Tetragnathinae north of Mexico (Araneae : Araneidae). *Bulletin of the Museum of Comparative Zoology* **149**, 1–75.

Levi, H. W. (1981). The American orb-weaver genera *Dolichognatha* and *Tetragnatha* north of Mexico (Araneae : Araneidae, Tetragnathinae). *Bulletin of the Museum of Comparative Zoology* **149**, 271–318.

Levi, H. W. (1983). The orb-weaver genera *Argiope*, *Gea*, and *Neogea* from the Western Pacific region (Araneae: Araneidae, Argiopinae). *Bulletin of the Museum of Comparative Zoology* **150**, 247–338.

Levi, H. W. (1986). The neotropical orb-weaver genera *Chrysometa* and *Homalometa* (Araneae: Tetragnathidae). *Bulletin of the Museum of Comparative Zoology* **151**, 91–215.

Levi, H. W., and Von Eickstedt, V. R. D. (1989). The Nephilinae spiders of the Neotropics (Araneae: Tetragnathidae). *Memorias del Instituto Butantan (Sao Paulo)* **51**, 43–56.

Locket, G. H., Millidge, A. F., and Merret, P. (1974). 'British Spiders.' Vol. 3. (Ray Society: London.)

Maddison, W. P., and Maddison, D. R. (1992). 'MacClade: Analysis of Phylogeny and Character Evolution, Version 3.0.' (Sinauer Associates: Sunderland, Massachussetts.)

Menge, A. (1866). Preussische Spinnen. *Schrifteb der Naturforschenden Gesellschaft in Danzig* **1**, 1–152.

Millidge, A. F. (1977). The conformation of the male palpal organs of Linyphiid spiders and its application to the taxonomic and phylogenetic analysis of the family (Araneae : Linyphiidae). *Bulletin of the British Arachnological Society* **4**, 1–60.

Nentwig, W., and Spiegel, H. (1986). The partial web renewal behaviour of *Nephila clavipes* (Araneae : Araneidae). *Zoologischer Anzeiger* **5/6**, 351–6.

Plamgren, P. (1978*a*). Taxonomic position of the genus *Meta* (Araneida). *Annales Zoologici Fennici* **15**, 241–2.

Palmgren, P. (1978*b*). On the muscular anatomy of spiders. *Acta Zoologica Fennica* **15**, 1–41.

Palmgren, P. (1979). On the internal taxonomic characters of the genus *Leucauge* White (Araneida). *Bulletin of the British Arachnological Society* **4**, 394–5.

Peters, H. M. (1954). Estudios adicionales sobre la estructura de la red concéntrica de las arañas. *Comunicaciones del Instituto Tropical de Investigaciones Científicas de la Universidad de El Salvador* **3**, 1–18.

Peters, H. M. (1982). Wie spinnen der Familie Uloboridae ihre beute einspinnen und verzehren. *Verhandlungen des Naturwissenschaftlichen Vereisn in Hamburg* **25**, 147–67.

Platnick, N. I. (1993). 'Advances in Spider Taxonomy 1988–1991.' (New York Entomological Society and American Museum of Natural History: New York.)

Platnick, N. I., Griswold, C. E., and Coddington, J. A. (1991). On missing entries in cladistic analysis. *Cladistics* **7**, 337–43.

Preston-Mafham, R. (1991). 'The Book of Spiders and Scorpions.' (Crescent Books: New York.)

Robinson, M. H., and Lubin, Y. D. (1979). Specialists and generalists: the ecology and behaviour of some web-building spiders from Papua New Guinea. 1. *Herennia ornatissima*, *Argiope ocylaoides* and *Arachnura melanura* (Araneae : Araneidae). *Pacific Insects* **21**, 97–132.

Robinson, M. H., and Robinson, B. (1973). Ecology and behavior of the giant wood spider *Nephila maculata* (Fabricius) in New Guinea. *Smithsonian Contributions to Zoology* **149**, 1–76.

Robinson, M. H., and Robinson, B. (1976). The ecology and behavior of *Nephila maculata:* a Supplement. *Smithsonian Contributions to Zoology* **218**, 1–22.

Robinson, M. H., and Robinson, B. (1978). The evolution of courtship systems in tropical araneid spiders. *Symposia of the Zoological Society of London* **42**, 17–29.

Robinson, M. H., and Robinson, B. (1980). Comparative studies of the courtship and mating behavior of tropical araneid spiders. *Pacific Insects* **36**, 1–218.

Roewer, C. F. (1942). 'Katalog der Araneae.' Vol. 1. pp. 1–1040. (Bremen.)

Schult, J., and Sellenschlo, U. (1983). Morphologie und funktion der genitalstrukturen bei *Nephila* (Arach., Aran., Araneidae). *Mitteilungen aus den Hamburgischen Zoologischen Museum und Institut* **80**, 221–30.

Simon, E. (1892). 'Histoire naturelle des Araignées.' (Librarie Encyclopedique de Roret: Paris.)

Stauffer, S. L., Coguill, S. L., and Lewis, R. V. (1994). Comparison of physical properties of three silks from *Nephila clavipes* and *Araneus gemmoides*. *Journal of Arachnology* **22**, 5–11.

Swofford, D. L. (1993). 'PAUP: Phylogenetic Analysis Using Parsimony, Version 3.1.1.' (Smithsonian Institution: Washington, DC.)

Vollrath, F. (1980). Why are spider males small? A discussion including observations on *Nephila clavipes*. In 'Proceedings of the 8th International Congress of Arachnology, Vienna'. (Ed. J. Gruber.) pp. 165–9. (Verlag H. Egermann: Vienna.)

Vollrath, F., and Parker, G. A. (1992). Sexual dimorphism and distorted sex ratios in spiders. *Nature* **360**, 156–9.

Wiehle, H. (1931). Neue beiträge zur kenntnis des fanggewebes der spinnen aus den familien Argiopidae, Uloboridae und Theridiidae. *Zeitschift für Morphologie un Ökologie der Tiere* **22**, 349–400.

Wunderlich, J. (1986). 'Spinnenfauna Gestern und Heute.' (Erich Bauer Verlag bei Quelle & Meyer: Wiesbaden.)

Yu, L., and J. A. Coddington. (1990). Ontogenetic changes in the spinning fields of *Nuctenea cornuta* and *Neoscona theisi* (Araneae; Araneidae). *Journal of Arachnology* **18**, 331–45.

Appendix. Material examined

Only those specimens that have been illustrated in this paper (or those which have been mentioned in the text in the context of character descriptions or discussions) are listed in this appendix. Specimens are listed alphabetically by family, genus and species. Localities are given as they are shown in the museum specimen labels. Specimens deposited at the Smithsonian Institute are labelled as USNM

Araneidae

Araneus cavaticus (Keyserling): USA: Maine: Washington Co.: Gouldsboro, 9.ix.1989 (J. Coddington, USNM).

Araneus diadematus Clerck: USA: Rhode I., Jamestown, 10.viii.1917 (J. H. Emerton, USNM); Oregon: Portland, Sep. 1934 (J. M. Pierson, USNM).

Araneus marmoreus Clerck: USA: Connecticut: Windham Co: Pomfret, Rt. 44, 1.ix.1974 (J. Coddington, USNM).

Argiope aurantia Lucas: USA: Texas: Bastrop Co.: 13 mi S-SE Elgin, 15.viii.1968 (B. Vogel, USNM).

Zygiella atrica (C. L. Koch): USA: Maine: Bar Harbor, 3.ix.1954 (B. J. Kaston, USNM).

Zygiella x-notata (Clerck): USA: Massachusetts: Wood's Hole, Aug. 1883 (J. H. Emerton, USNM); Washington: Jefferson Co.: Olympic N. P.: Kalaloch, 24.viii.1987 (Smith *et al.*, USNM); Denmark: Copenhagen, Tivoli Gardens, 15.viii.1989 (J. Coddington, USNM).

Linyphiidae

Linyphia triangularis (Clerck): Germany: between Deutzand and Siegen, 9.viii.1964 (R. Crabill, USNM); France: Manche, Quettehou, 27.vii.1956 (USNM).

Pimoidae

Pimoa altioculata (Keyserling): USA: Washington: Nahcotta, 23.viii.1955 (T. Kincaid, CAS); Canada: British Columbia: Wellington, Vancouver I., 1–20.xi.1950 (R. Guppy, AMNH).

Appendix. continued

Tetragnathidae

Ailia affinis O. P.-C.: USA: Georgia: Bryan Co.: Richmond Hill State Park, 1.viii.1985 (J. Coddington, USNM).

Azilia sp.: Peru: Tambopata Reserve, 8.vi.1988 (J. Coddington, USNM).

Chrysometa alboguttata (O. P.-C.): Colombia: San Pedro, S. N. de Sta. Marta, 3.iv.1975 (J. A. Kochalka, USNM).

Chrysometa flava (O.P.-C.). Costa Rica: Heredia: Est. Biol. La Selva, 22.iii.1979 (J. Coddington, USNM).

Clitaetra episinoides Simon: Madagascar: Dist. Fianaratsoa: Ambozotany, 15.vii.1992 (V. D. and B. Roth, MCZ).

Clitaetra sp.: Cameroon: SW Province: Fako Div.: Limbe Subdiv., 1·4 km NE of Etome, 13–19.i.1992 (J. Coddington *et al.*, USNM).

Clitaetra sp.: South Africa: Natal: St. Lucia Ntl Pk, Fanies Camp, 24.i.1991 (V. D. and B. Roth, CAS).

Dolichognatha pentagona (Hentz): USA: Alabama: Lee Co.: Chewacla State Forest, 23.vi.1980 (J. Coddington, USNM).

Dolichognatha sp.: Peru: Madre de Dios: P. N. Manu, 26–3.ix.1991 (D. Silva, USNM).

Glenognatha heleios Hormiga: USA: New Jersey: Ocean Co.: Tuckerton, 7.xi.1984 (H. Döbel, USNM).

Herennia ornatissima Doleschall: Philippines: Los Baños, Jul. 1909, No. 777-D (Ledyard, MCZ).

Herennia sp.: India: Tamil Nadu, 21 km NE of Madurai, 27–28.xii.1989 (V. D. and B. Roth, CAS).

Herennia sp.: Philippines: Luzon: Nueva Vizcaya, Imugam Sta. Fe, 31.v.1987 (C. K. Starr, USNM).

Leucauge venusta (Walckenaer): North America (no locality data, USNM).

Meta americana Marusik And Koponen: USA: New Hampshire: Woodsville, 18.ix.1954 (R. Andrews, USNM).

Meta menardi (Latreille): France: Pyrenees Orientales: Vernet-les-Bains 22.viii.1989 (J. Coddington, USNM).

Metellina curtisi (McCook): USA: Washington: Snohomish Co.: Crystal Creek, 24.x.1986 (R. Crawford, USNM); Oregon: Corvallis, no date (USNM).

Nephila clavipes (L.): Peru: Madre de Dios: Manu, 25.ix.1987 (J. Coddington and D. Silva, USNM). USA: Florida: Alachua Co.: University of Florida Campus, Medical Garden, 3–11.viii.1985 (J. Coddington, USNM).

Nephila sp.: Cameroon: SW Province: Fako Div.: Limbe Subdiv., 1·4 km NE of Etome, 13–19.i.1992 (J. Coddington *et al.*, USNM).

Nephilengys cruentata (Fabricius): Angola: Vila Salazar, 8.ix.1949 (B. Malkin, USNM); Brazil (USNM).

Pachygnatha autumnalis Keyserling: USA: Massachussets: Barnstable Co.: FCWMA (R. L. Edwards, USNM).

Phonognatha graeffei (Keyserling): Australia, Canberra, ACT, 15.v.1963 (C. R. MacLellan, AMNH); Queensland: nr Mt Tambourine, 18.vii.1992 (J. Coddington and G. Hormiga, USNM).

Tetragnatha versicolor Walckenaer: USA: California: Siskiyou Co.: Yreka-Sahasta R., 8 mi. N of Yreka, 17.viii.1964 (P. L. and U. F. Holt, USNM).

Uloboridae

Uloborus glomosus (Walckenaer): USA: Georgia: Gainesville, 30.vii.1942 (B J. Kaston, USNM). Connecticut: Farmington, 13.vi.1962 (J. F. A., USNM).

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