

Morphology and relationships within the spider family Filistatidae (Araneae: Araneomorphae)

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Abstract – The morphology and generic relationships of the filistatid spiders are discussed, with emphasis upon genitalic and silk spinning structures. A cladistic analysis of generic relationships is presented and two new subfamily groupings are recognised. These are the Filistatinae (*Filistata*, *Kukulcania*, *Sahastata* and, provisionally, *Zaituna*), and the Prithinae, subfam. nov. (*Pritha*, *Wandella*, *Yardiella*, *Andoharano*, *Afrofilistata*, *Pikelinia*, *Filistatoides*, *Filistatinella*). The taxonomic validity of the prithine genera *Malalistata* and *Tricalamus* are questioned. The affinities of the enigmatic central Asian genus *Microfilistata* remain obscure.

INTRODUCTION

The Filistatidae are cribellate haplogyne spiders possessing an intriguing mixture of primitive and specialised characters. Despite their extensive circum-tropical/warm temperate distribution they comprise a relatively small group of 14 genera, including two recently described from Australia (Gray 1994).

The peculiar structural features of the filistatid spiders have made elucidation of their family relationships difficult. Their silk spinning structures are particularly striking – the peculiar annulate sculpturing of the spinneret spigot shafts (Fig. 12), the claviform cribellum spigots (Fig. 13), and the presence of three rows of calamistrum setae (Figs 2, 4) are unique among spiders. Their possession of a cheliceral lamina and a fused tegulum/subtegulum has usually associated the Filistatidae with or near the Scytodoidea, a grouping of haplogyne families (Brignoli 1978; Lehtinen 1986; Coddington 1990). A more radical proposal was made by Eskov and Zonshtein (1990). They give the Filistatidae infraordinal status within the Orthognatha as sister group to the Theraphosomorphae. However, this interesting hypothesis ignores many important characters that link the filistatids to the Araneomorphae. A better supported hypothesis is that of Forster *et al.* (1987), which places the filistatids within the araneomorph group Neocribellatae. Platnick *et al.* (1991) included a survey of spinneret morphology as part of a study of haplogyne spider phylogeny. Their analysis suggests that the classical Haplogynae (inclusive of Filistatidae) does represent a monophyletic group. This is placed at the base of the Araneoclada, with the Filistatidae as the

cribellate sister group of the remaining ecribellate haplogyne families.

This paper is dedicated to Dr Barbara York Main, in recognition of her remarkable contribution to arachnological research in Australia. Through her research, her encouragement of the work of students and colleagues and her promotion of the importance of arachnological studies, she has greatly enhanced the reputation of Australian arachnology.

TAXONOMY

Generic relationships within the Filistatidae have received little attention. The only review of filistatid genera and generic characters is that of Lehtinen (1967), but no analysis of relationships has been presented. The present study relies strongly on new characters derived from the spinning organs and genitalia. The morphological data and phylogenetic analysis presented below separate the filistatid genera into two major groups which are given subfamilial status.

Subfamily Filistatinae Simon

Diagnosis

Large-medium sized spiders. Fovea present, pit-like. Legs spined, including tarsal spines. Plumose hairs absent. Palpal cymbium long, cylindrical. Calamistrum placed on metatarsal crest. Number of calamistrum rows variable, setae sinuous and strongly ribbed, combing teeth absent. Cribellum spigots strongly claviform. Spinneret spigots numerous. Respiratory system with a single wide posterior spiracle.

Included genera

Filistata Latreille, 1810, *Kukulcania* Lehtinen, 1967, *Sahastata* Benoit, 1968. *Zaituna* Lehtinen, 1967 is provisionally included here.

Subfamily Prithinae, subfam. nov.**Diagnosis**

Small-medium sized spiders. Fovea absent. Leg spines few to absent, tarsal spines never present. Plumose hairs present or absent. Palpal cymbium short, shape variable. Calamistrum typically with 3 rows of toothed setae. Cribellum spigots weakly claviform. Spinneret spigot density low, especially on PLS and PMS. Spinneret field with large claviform setae. Respiratory system typically with two posterior spiracles.

Included genera

Afrofilistata Benoit, 1968, *Andoharano* Lehtinen, 1967, *Filistatinella* Gertsch and Ivie, 1936, *Filistatoides* F.O.P.-Cambridge, 1899, *Pikelinia* Mello-Leitão, 1946, *Pritha* Lehtinen, 1967, *Wandella* Gray, 1994, *Yardiella* Gray, 1994. *Malalistata* Mello-Leitão, 1946 and *Tricalamus* Wang, 1987 also belong here but, as noted below, their taxonomic validity is uncertain.

Remarks

Representatives of the genera *Malalistata*, *Tricalamus*, *Zaituna*, and *Microfilistata* Zonshtein 1990 have not been seen by the author. However, the validity of the first two genera require confirmation. *Tricalamus* from southern China, as described by Wang (1987a), seems identical to *Pritha* species described from the same region (Wang 1987b) except for its supposedly unique possession of a triseriate calamistrum. However, as discussed below, the possession of a triseriate calamistrum is characteristic of many species within both *Pritha* and other filistatid genera, and cannot be used as a primary definer of generic status.

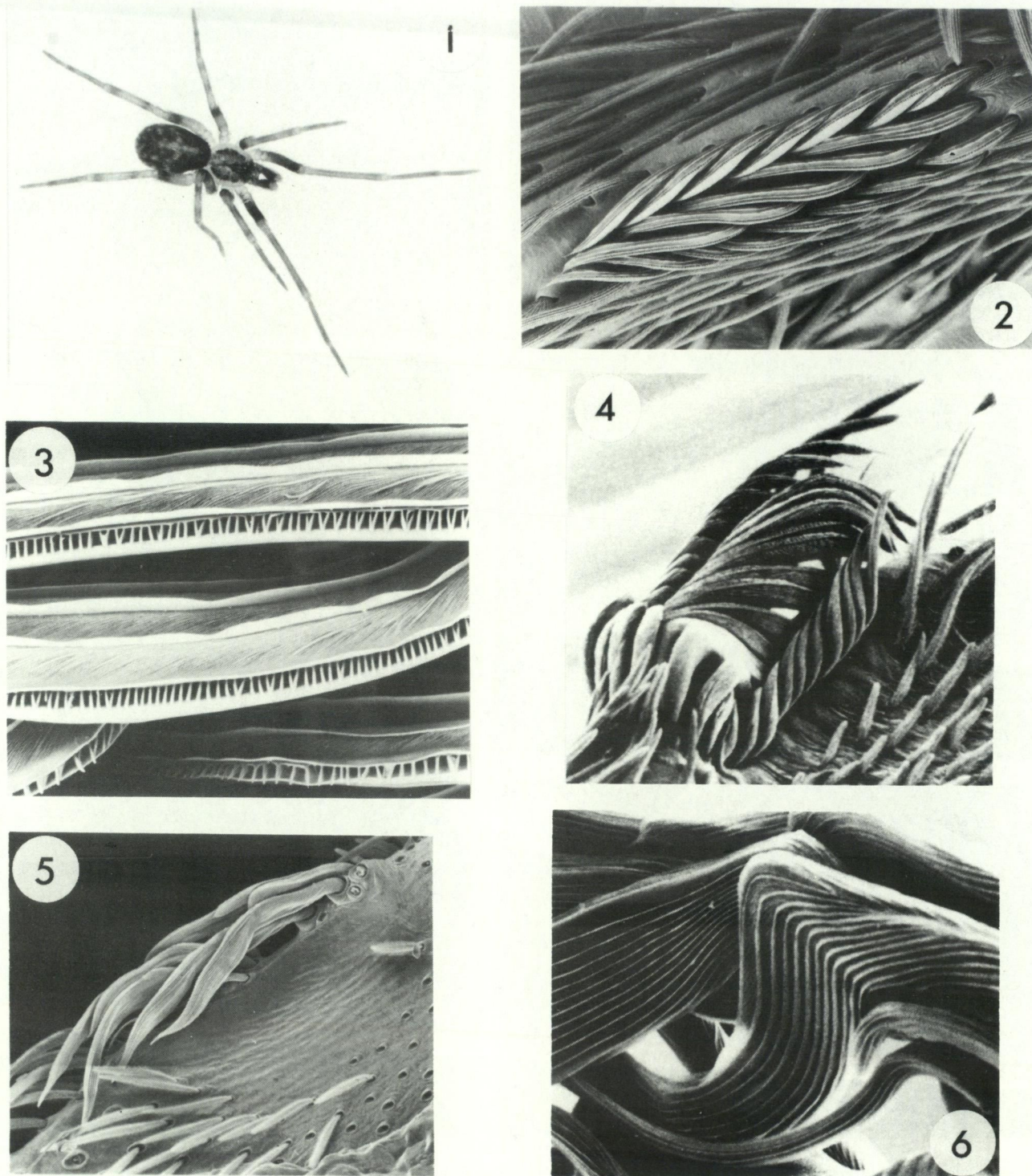
The monotypic South American genus *Malalistata* is based upon female type specimens from Argentina. No additional material has been collected. In the description of Mello-Leitão (1946) the complete absence of tarsal claws is the most striking characteristic, a state found nowhere else among the spiders. Examination of preserved material of *Pikelinia*, a genus whose distribution overlaps that of *Malalistata*, revealed many specimens lacking tarsal claws. However, detached claws were located in the residual material at the bottom of the specimen vials. Consequently, *Malalistata* may represent a misidentified species of *Pikelinia*, its erection owing more to anomalous preservation than to biological reality.

The affinities of *Zaituna* and *Microfilistata* are difficult to determine on the data available (primarily in Lehtinen (1967) and Brignoli (1982); and Zonshtein (1990) respectively). The provisional placement of *Zaituna* in the Filistatinae is based upon its possession of tarsal spines (Brignoli 1981) and a strongly coiled bulbal structure with a cylindrical cymbium (Lehtinen 1967), but additional characters are needed to confirm this placement. Interestingly, the highly derived male palp of *Microfilistata*, where the palpal bulb (with "a distinct conductor") is deeply recessed within the open apex of a cylindrical cymbium (Zonshtein 1990), has some resemblance to the palpal morphology seen in filistatine spiders. However, the generic relationships of *Microfilistata* remain unresolved.

MORPHOLOGY**Silk spinning structures***Calamistrum*

There has been considerable confusion about the structure of the filistatid calamistrum, placed near the base of metatarsus IV. Previous studies by Zapfe (1961), Lehtinen (1967), Patel (1978), Benoit (1968), Legendre (1971), Ledoux (1977), Brignoli (1982) and Coddington (1990) record the calamistrum as consisting of one or two rows of setae. Eskov and Zonshtein (1990) interpret the filistatid calamistrum, specifically including a triseriate structure reported for *Tricalamus* (Wang 1987a), as 'a single zig-zag row'. Scanning E. M. examination of calamistra in most filistatid genera has established the presence of three discrete rows of setae (Fig. 2) in representatives of all prithine genera. Reductive trends can be seen in some *Wandella* and *Pritha* species where the middle setal row is short or absent. In *Filistatinella* the outer setal row lacks the combing teeth of the other two rows. Importantly, one member of the Filistatinae, the north African genus *Sahastata*, also possesses a triseriate calamistrum (Fig. 4), though this is a more elaborate structure than those of the prithine genera. Brignoli (1982) figured a biseriata calamistrum for his *S. sabaea*, but the generic attribution of this species is uncertain. The triseriate calamistrum is not known outside the family Filistatidae. Given its wide distribution within the family this calamistrum structure can be regarded as a filistatid synapomorphy showing secondary reduction in a few genera.

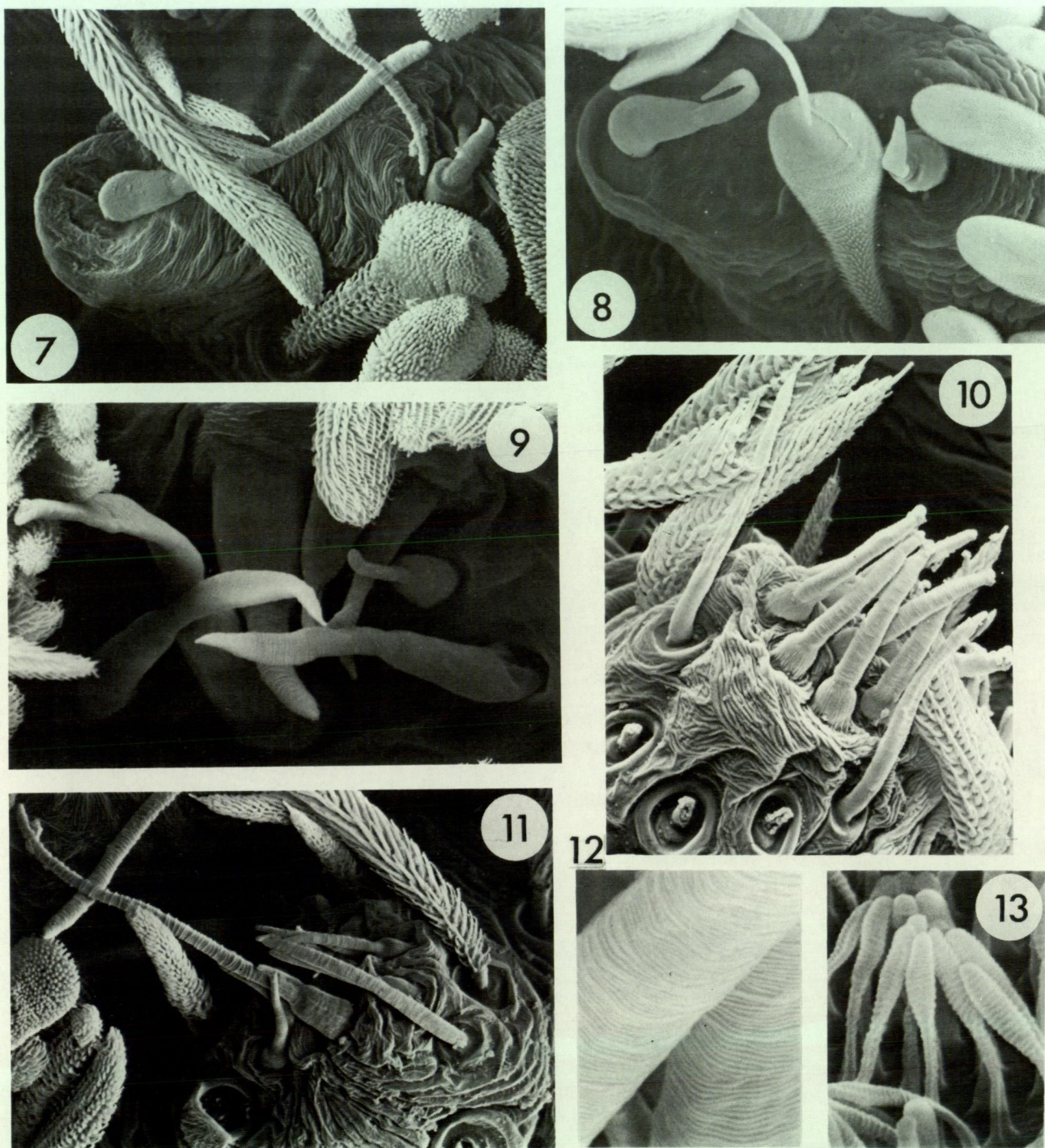
Of the filistatine genera other than *Sahastata*, Brignoli (1982) figured a peculiar biseriata calamistrum for *Zaituna* (but gave no other details), while *Filistata* and *Kukulcania* are always reported as having uniseriate calamistra. In fact, the



Figures 1-6 1, *Wandella orana*, female. 2-6, calamistra: 2, 3, *Wandella orana*: 2, triseriate calamistrum; 3, toothed setae; 4, *Sahastata nigra*, triseriate calamistrum; 5, 6, *Filistata insidiatrix*: 5, compressed calamistrum on ridge; 6, ribbed calamistrum setae.

calamistrum setae of these two genera are crowded onto a distinct cuticular ridge (absent in the Prithinae) near the base of metatarsus IV, producing a compressed 'zig-zag linear' structure (Fig. 5), readily derivable from the more plesiomorphic triseriate calamistrum type. A somewhat broader calamistrum ridge is present in *Sahastata* (Fig. 4).

The highly modified calamistrum setae provide further support for the separation of these two filistatid groups. All calamistrum setae of Prithine genera are provided with silk combing teeth (Fig. 3), presumably homologous with the toothed setae of the calamistra of hypochilids (Foelix and Jung 1978), austrochiloids and many higher neocribellates (including examined representatives



Figures 7–13 Spinnerets and spigots (females). 7–9, posterior median spinnerets: 7, *Pikelinia* sp., Argentina; 8, *Wandella orana*; 9, *Sahastata nigra*; 10, 11, *Pikelinia* sp., Argentina: 10, anterior lateral spinneret; 11, posterior lateral spinneret; 12, 13, *Felistata insidiatrix*: 12, ALS spigot shaft annular structure; 13, *Sahastata nigra*, cribellum spigots.

of the families Hickmaniidae, Gradungulidae, Desidae, Amaurobiidae, Stiphidiidae, Zoropsidae, Eresidae and Deinopidae). However, filistatine genera (excluding *Zaituna*, no data) lack combing teeth. They apparently rely instead upon numerous longitudinal ribs developed upon the large, sinuous calamistrum setae (Fig. 6) for drawing cribellate silk.

The absence of combing teeth has also been noted

for the dictynid genus *Mallos* and the uloborid genera *Uloborus* (Foelix and Jung 1978) and *Philoponella*. Outgroup comparison suggests that the toothed state is plesiomorphic with independent, apomorphic reduction in several lineages.

Cribellum

The strongly bipartite cribellum of filistatid

spiders has counterparts in the Amaurobioidea and Lycosoidea. By contrast most dictynoid and orbicularian cribellates have an undivided cribellum field (Coddington 1990). The presence of an undivided cribellum field in primitive cribellates (hypochilids and austrochiloids) suggests that this state is primitive in the araneomorph spiders. This hypothesis requires that the evolutionary history of the cribellum has involved transformation from paired anterior median spinnerets via fusion to an unpaired cribellum, subsequent division into paired cribellar fields and at least one reversal to the unpaired state. Given the origin of the cribellum from paired spinnerets, it is curious that the most primitive form of the cribellum was not bipartite (with subsequent, independent fusion occurring in some palaeocribellate and neocribellate lines). In this context, it would be useful to know more about the ontogenetic history of the cribellum in the primitive cribellates.

Cribellum spigots have a characteristic strobilate structure in all cribellate spiders except the Filistatidae (Forster *et al.* 1987) in which the spigot shafts are circumferentially ribbed (annulate) and the spigots are clavate distally (Fig. 13; Gray 1994). The claviform spigot shape is particularly well-developed in the filistatine genera and this state is assumed to be the more derived condition of what is a highly specialised spigot structure.

Spinnerets

Spinneret morphology is discussed and figured for *Kukulcania* and *Filistata* by Platnick *et al.* (1991), and for *Wandella* by Gray (1994). The spigots are set on raised or recessed bases, their spinning tubes (Fig. 12) sharing the annulate, ribbed structure of the cribellum spigots. The densities of the spinneret spigot fields differ markedly. Filistatine spiders typically have numerous spigots, 45–100 (including three major ampullate gland spigots) on the ALS, 25–70 on the PLS, 7–11 on the PMS (Fig. 9). Spigot density is much lower in the prithine genera, the ALS having 15–30, including one or two major ampullate gland spigots (Fig. 10), the PLS with 2–12 spigots (Fig. 11), and the PMS with 2–5 spigots, the larger posterior spigot separated from the rest (Figs 7, 8). Ensiform PMS spigots (flared behind the tip) in *Filistata* and *Kukulcania* are given a tentative paracribellar function by Coddington (1990) and Platnick *et al.* (1991). A similar set of PMS spigots occurs in *Sahastata* (Fig. 9). Ensiform spigots are also present in genera such as *Wandella* and *Pikelinia*. In *Wandella* both PMS spigots show this shape (Fig. 8). In *Pikelinia*, of the two larger PMS spigots only the shorter anterior spigot (with three small aciniform spigots at its base) has a more or less ensiform appearance (Fig. 7).

A unique row of specialised setae along the anteromedian surface of the ALS (Platnick *et al.* 1991) is best developed in filistatine spiders. In the Prithinae the spinneret fields are characterised by the presence of large, claviform setae (Figs 7, 8; and Gray 1994).

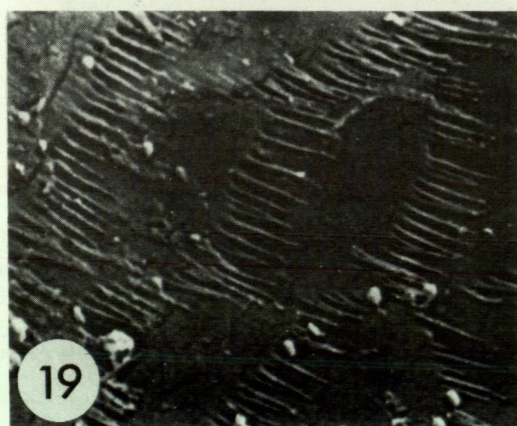
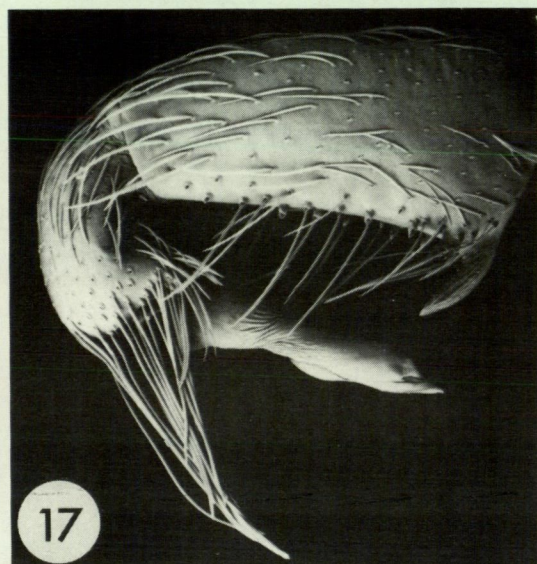
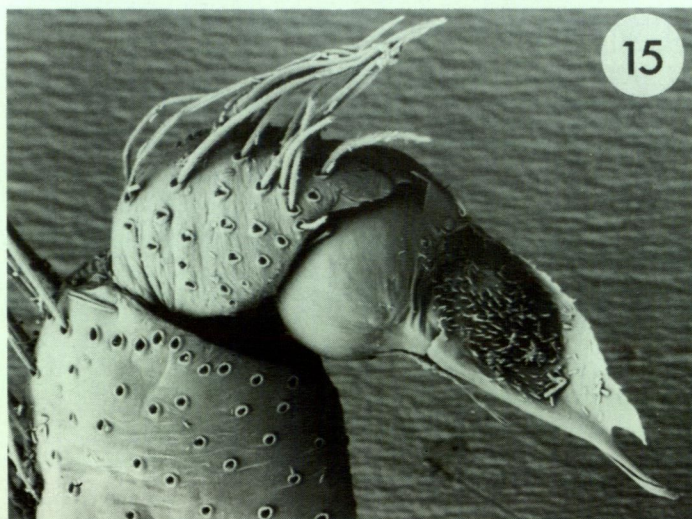
Mating structures

Male palp

A long, more or less cylindrical cymbium characterises the filistatine genera (Fig. 18). This character (along with the possession of a strongly coiled ejaculatory duct and tarsal spines) allies *Zaituna* with this group. Shorter cymbium length is characteristic of prithine genera. These short cymbia vary considerably, ranging from the 'horseshoe-shaped' *Pritha/Wandella* form (Fig. 15) to the vestigial cymbium of *Pikelinia* which is fused with the tegulum (Fig. 16). *Wandella*, *Yardiella* and an undescribed Pacific genus (near *Wandella*) share a paraembolic, lamina-like process on the male palp (Fig. 15; Gray 1994). They share also the presence of minute teeth, often in comb-like rows, on the post-tegular palpal area (Fig. 19). Some of these teeth are greatly enlarged on the retrolateral palpal surface in the Pacific genus referred to above (Fig. 15). Microteeth also occur on the palpi of the South American genus *Pikelinia*. Such palpal teeth are not recorded outside the Filistatidae. *Pritha*, the dominant Oriental genus, lacks both palpal teeth and processes (Fig. 14). The flanged post-tegular structure of several *Pikelinia* species (Fig. 16) could represent a fused state of the paraembolic process and embolus but the variation in palpal form within this genus requires more investigation. *Filistatinella*, with its thick, folded lamellate palpal structure (Fig. 17), and *Filistatoides* with its very elongate palp represent divergent types not easily related to other palpal types. Palpal tibial modifications, apart from the simple incrassate form (Fig. 14), are unusual in filistatid spiders. However, both *Filistatinella* (Fig. 17) and *Pikelinia* (Fig. 16) possess both incrassate tibiae and basoventral and apicodorsal processes respectively. *Pikelinia* also possesses modified first legs, often with coupling spines on the metatarsi (Gray and Platnick, in prep.).

Female genitalia

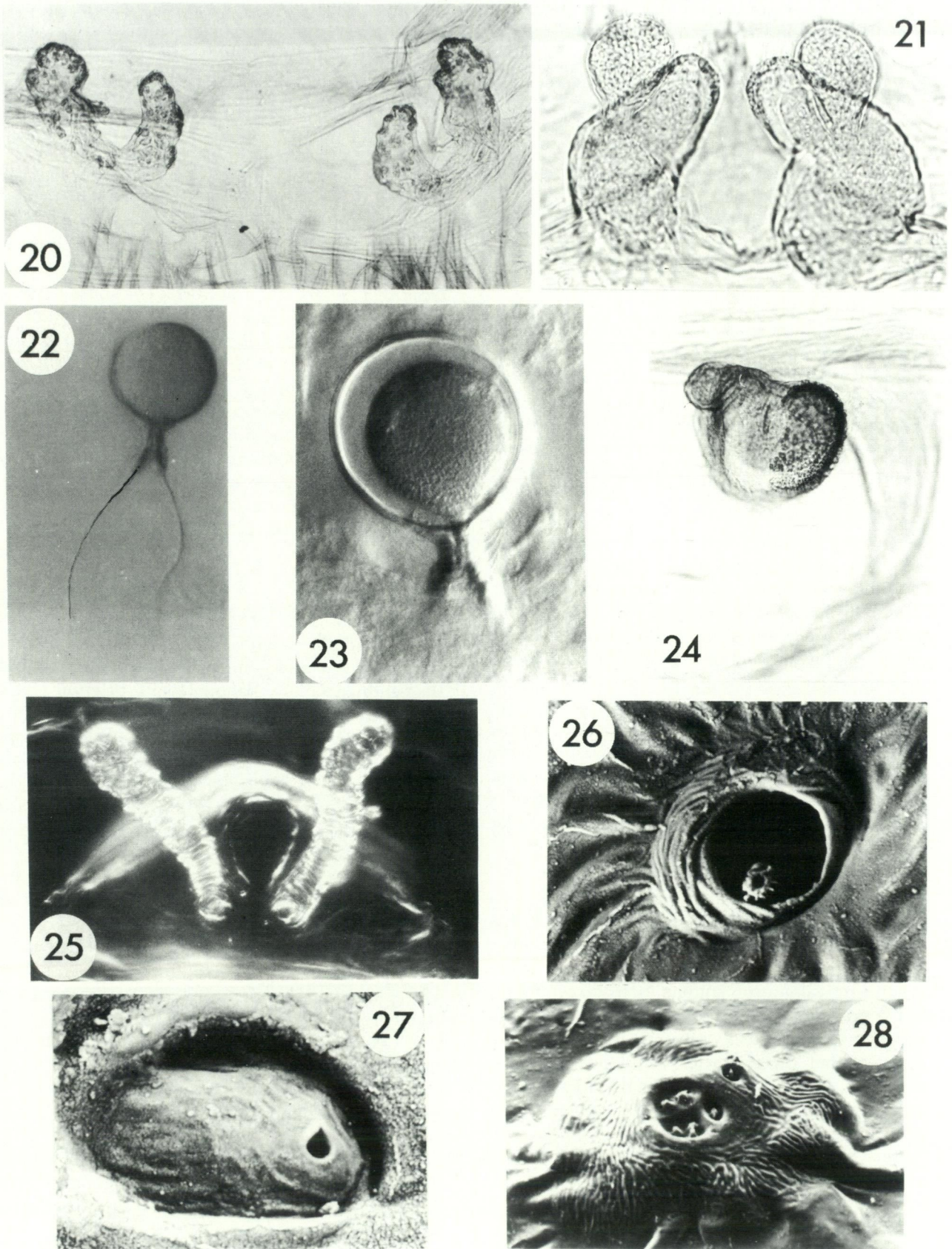
The paired 'bi-lobate' receptacula of *Sahastata* and the *Pritha/Wandella* group of genera (Figs 20, 21) reflect the common pattern seen in the hypochilid spiders. This state, though probably not the most plesiomorphic in spiders (Forster *et al.* 1987), represents the plesiomorphic condition in the filistatids. The receptacula are surrounded by glandular tissue, though this may be reduced around the lateral lobes. An interesting



Figures 14–19 Male palpi. 14–18, tibia, cymbium, bulb: 14, *Pritha nana*; 15, new gen., nr *Wandella* sp., Caroline Islands (cymbium and bulb); 16, *Pikelinia* sp., Argentina; *Filistatinella* sp., Mexico; 18, *Kukulcania hibernalis* (cymbium and bulb); 19, new gen., nr *Wandella* sp., Marshall Islands, microteeth combs on parembolic lamina.

modification of this state is the movement of the lateral lobes from the usual laterad position to an anterior position in *Pikelinia* and *Filistatoides* (Fig. 22). In *Filistatoides* species the posterior lobe seems to be incorporated into the stem and basal region, which still retain the secretory glands of the

formerly discrete lobe (Fig. 23). A further possible reductive product of this 'in line' pattern are the peculiar unilobate tubular receptacula of *Filistatinella* (Fig. 25). A parallel state is seen in the genitalia of the presumptive filistatine genus *Zaituna* (Brignoli 1982). In *Filistata* and *Kukulcania*



Figures 20–28 20–25, female genitalia: 20, *Sahastata* sp., Chad; 21, *Pritha nana*; 22, 23, *Filistatoides* sp. (RHS), Colombia; 24, *Kukulcania hibernalis* (RHS), Texas; 25, *Filistatinella* sp., Mexico; 26–28, sensory structures: 26, *Pikelinia* sp., bothrium; 27, 28, tarsal organs: 27, new gen., nr *Wandella* sp., Caroline Islands; 28, *Kukulcania* sp., variant tarsal organ.

(Fig. 24) the lobes are usually fused to a greater or lesser degree along with reduction of the medial lobes, giving a paired 'unilobate' state, especially evident in *Kukulcania*. This infers a reductive process from the paired bilobed state seen in *Sahastata*. Secretory glands are particularly densely clustered around the filistatine 'unilobate' receptacula. These glands are much less dense in prithine spiders and are even absent from the lateral receptacula lobes of some species.

Other structures

Setation and sensillae

Primary setation consists of ciliate and plumose hairs. Plumose hairs are not found in the Filistatinae but occur sporadically among the prithine genera, notably the South American *Filistatoides* and *Pikelinia*, the Australian *Yardiella*, and an undescribed African genus. 'Semi-plumose' setae occur in some genera and their presence suggests that the plumose setae of filistatid spiders may be derived. Ventral spines, including tarsal spines, are present on the legs of filistatine spiders. Leg spination is greatly reduced or absent in the Prithinae and tarsal spines are never present. Trichobothria occur in a single row on metatarsi and tibiae, increasing in length distally, in all genera examined; the bothria have circular, raised margins, often ridged (Fig. 26). The tarsal organ is commonly capsulate (or pseudo-capsulate, see Forster *et al.* 1987), an unusual state among haplogyne spiders, with a centro-distally placed pore containing the receptor nodes (Fig. 27). Some variability may be indicated by the observation of multiple (as well as unitary) receptor pores (Fig. 28) in *Kukulcania*.

Tarsal structure

Males of the genera *Filistata* and *Kukulcania* have curved tarsi and tarsal cuticle with 'cracked scaliform' sculpturing. Similar sculpturing occurs in some mygalomorph spiders (both sexes) but not in the araneomorph outgroups. This fact, and the occurrence of 'cracks' only in male filistatids suggests that the character could be derived in filistatids. At present, *Sahastata* males are unknown but the derived character state is predicted in that genus. The presence or absence of this character in *Zaituna* may assist a definitive determination of its placement.

Body size

As in mygalomorph spiders female filistatids continue to moult after maturation. Most filistatine spiders are large animals, females attaining body lengths of 10–15 mm. However, the putative filistatine *Zaituna*, is somewhat smaller, in the range of 3–8 mm body length (Brignoli 1982,

Zonshtein 1990). By contrast, all prithine spiders are small, ranging from 2–5 mm body length. Perhaps concomitant with small body size the sternal sigillae and the fovea are, respectively, weakly developed or absent in the Prithinae.

Respiratory system

In the filistatids the posterior lungbooks are reduced without the development of the tracheal system typical of the higher Araneoclada. *Filistata*, *Kukulcania* and *Sahastata* possess a wide spiracle that opens into a broad atrium. From this four tapering lobes extend anteriorly. The shorter lateral lobes are the booklung remnants; the longer, more centrally placed lobes are their associated apodemes (Forster *et al.* 1987). Only *Wandella* has been dissected in the Prithinae. These spiders possess a pair of spiracles set at each end of a shallow transverse groove. One pair of short tubes was observed extending from the spiracles (Gray 1994), presumably representing booklung vestiges. A cursory examination of several other genera suggests that paired spiracles may be typical in the Prithinae.

RELATIONSHIPS

The cladistic analysis examines relationships among 11 filistatid genera diagnosed or described by Lehtinen (1967), Benoit (1969), Brignoli (1982) and Gray (1994). *Malalistata* and *Tricalamus* are excluded because of their uncertain taxonomic status, and both *Zaituna* and *Microfilistata* are insufficiently characterised for inclusion in the analysis. Outgroup comparisons were made primarily with the Hypochilidae and Austrochiloidea (the primitive cribellates).

The data matrix (Table 1) was analysed using the program 'Hennig86' version 1.5. Multiple states are presented as ordered; the multistate characters used are interpretable in terms of directional variation. Character state codings are given below. Here, and in the data matrix, characters are numbered from 0–17 (46 states).

0. Cribellum spigot morphology: strobilate (0); claviform (1).

1. Spigot shaft surface morphology: variable (non-annulate), typically longitudinally ridged (0); annulate (1).

2. Calamistrum setae teeth: present (0); absent (1). The presence of teeth in hypochilid and austrochiloid spiders (primitive cribellates) supports this polarity.

3. Calamistrum insertion: unmodified sessile (0); on cuticular ridge. The absence of this ridge in prithine genera and non-filistatid groups suggests that its presence is synapomorphic for the Filistatinae.

4. Calamistrum setal rows: three or two rows (0);

Table 1 Data matrix.

Characters	0,	1,	2,	3,	4,	5,	6,	7,	8,	9,	10,	11,	12,	13,	14,	15,	16,	17
<i>Afrofilistata</i>	1	1	0	0	0	1	2	3	0	0	0	2	1	0	1	1	?	1
<i>Andoharano</i>	1	1	0	0	0	1	2	3	0	0	0	1	1	0	1	1	?	1
<i>Filistata</i>	1	1	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Filistatinella</i>	1	1	0	0	0	1	1	1	0	3	3	3	1	0	1	1	0	1
<i>Filistatoides</i>	1	1	0	0	0	1	1	4	0	?	1	0	1	0	1	1	1	1
<i>Kukulcania</i>	1	1	1	1	1	0	0	0	0	0	2	0	0	0	0	0	0	0
<i>Pikelinia</i>	1	1	0	0	0	1	1	4	1	2	1	3	1	0	1	1	1	1
<i>Pritha</i>	1	1	0	0	0	1	2	2	0	0	0	2	1	1	1	1	0	1
<i>Sahastata</i>	1	1	1	1	0	0	0	0	0	0	0	?	0	0	0	0	0	0
<i>Yardiella</i>	1	1	0	0	0	1	2	2	1	1	0	2	1	1	1	1	1	1
<i>Wandella</i>	1	1	0	0	0	1	2	2	1	1	0	2	1	1	1	1	0	1

compressed, staggered 'single' row (1). As argued above, the triseriate calamistrum is a filistatid apomorphy and so is plesiomorphic at the generic level. The biseriate condition is derivative and is commonly associated with triseriate congeners. The most derived compressed 'uniseriate' condition differs clearly from the linear uniseriate (occasionally biseriate) calamistra of other cribellate spiders.

5. Spinneret spigot density: spigots numerous (0); spigot numbers reduced (1). The spinnerets of the primitive cribellates and filistatine genera (Platnick *et al.* 1991) have dense spigot populations by comparison with the Prithinae spiders (Gray 1994).

6. PMS spigot number: more than five (0); three to five (1); two (2). The polarity is justified by the spigot density argumentation.

7. Cymbium shape: long, more or less cylindrical (0); long, anteriorly procurved (1); short, anteriorly deeply procurved - 'horseshoe' shaped (2); short, lozenge-shaped (3); reduced (4). The 'long' cymbial form resembles hypochilid forms (especially *Ectatosticta*) in which the cymbium is as long as, or longer than the palpal bulb. The 'reduced' type of cymbium refers to the free or fused (to the tegulum) cymbial remnants of *Filistatoides* and *Pikelinia* respectively.

8. Palpal bulb teeth: absent (0); present (1). The presence of these micro and macro-teeth seems unique to several genera in the Prithinae and is not recorded outside the Filistatidae.

9. Embolic structure: Simple curved or coiled rod/lamella (0); rod with dorsal paraembolic lamina (1) (Fig. 15); thick, twisted, flanged embolus (2) (Fig. 16); folded, lamellate embolus (3) (Fig. 17). The more complex structures are considered to be apomorphic states that probably are not homologous with the conductor sclerite of the primitive cribellates.

10. Spermathecal structure: two pairs, side-by-side (0); two pairs, anterior-posterior (1); paired 'unilobate', spherical (2); paired unilobate, tubuliform (3).

11. Male palpal tibia: cylindrical (0); distally

tapering (1); moderately incrassate (2); strongly incrassate (3). The strongly incrassate tibiae of *Pikelinia* (Fig. 16) and *Filistatinella* (Fig. 17) differ in shape, but this may relate to the different positions of their tibial processes.

12. Leg spination: ventral spines on tibiae and metatarsus, tarsal spines present (0); tibial/metatarsal spination reduced, tarsal spines absent (1). Their sparse spination differentiates prithine from filistatine genera.

13. Leg spines present or absent: present (0); absent (1). This spination character differentiates between prithine genera. Note that in *Pritha* spination is reduced or absent but is scored as absent here.

14. Body size: large (0); small (1). The primitive cribellates are all large spiders and smaller body size is an apomorphic trend in many spider groups.

15. Fovea: deep pit (0); shallow to absent (1). A pit-like fovea is typically found in the primitive cribellates.

16. Plumose setae: absent (0); present (1). The polarity of this character is equivocal, but polarity reversal does not affect the cladogram.

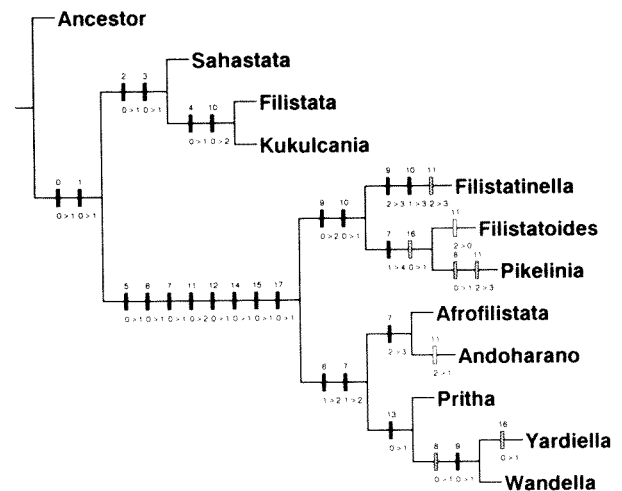


Figure 29 Cladogram of filistatid generic relationships. Black bars = apomorphies; dotted bars = homoplasies; white bars = reversals.

17. Spinneret field with claviform setae: absent (0); present (1).

The cladogram (Fig. 29) represents a single most parsimonious solution using ordered multistate data (tree length 39, consistency index 71, retention index 82). However, it does lack robustness, being supported by single characters at several key nodes. Despite this, the two major clades resolved, corresponding to the subfamilies Filistatinae and the Prithinae respectively, are well supported. Within the former clade the basal placement of *Sahastata* is reflected in its retention of a triseriate calamistrum and two pairs of receptacula, while the more derived *Filistata* and *Kukulcania* are clearly related through their unique calamistrum structure. *Zaituna* has yet to be definitively placed. Relationships within the prithine clade are less certain. The 'horse-shoe' shaped cymbium of *Pritha*, *Wandella* and *Yardiella* is a significant synapomorphy. It unites prithine genera ranging from the southern Palearctic and Oriental regions (*Pritha*) through to India and Australia and across the Pacific to Central America. The less distinctive 'lozenge-shaped' cymbium, perhaps derived from the *Pritha*-type cymbium, places the African (*Afrofilistata*) and Seychelles (*Andoharano*) genera together. The presence of teeth on the palpal bulbs of Australian (*Wandella*, *Yardiella*) and Pacific genera and the South American genus *Pikelinia* may imply a single origin for this character at the basal node of their clade (with secondary loss in some prithine genera), rather than the parallel origins inferred in the cladogram. *Filistatinella*, with its highly derived male palpal and female genitalic morphology, does not seem particularly close to either *Pikelinia* or *Filistatoides*. The latter genera, although united by a common female genitalic structure, are also highly derived, differing markedly in their male mating structures.

Further analysis using additional characters and new genera will clarify these relationships. However, in such a relict group of spiders considerable differentiation is to be expected between filistatid genera, some of whose origins could pre-date the break-up of Pangaea.

ACKNOWLEDGEMENTS

This work was assisted by funding from the Australian Research Council. My thanks to Dr N.I. Platnick (American Museum of Natural History), Mr D. Ubick (Californian Academy of Sciences) and Mr P. Hillyard (Natural History Museum) for the loan of material. Thanks are also due to Norman Platnick for his assistance in providing an important journal reference. Finally, Dr Mark Harvey (Western Australian Museum) deserves congratulations for his efforts in making this testimonial volume possible.

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Manuscript received 28 March 1994; accepted 10 August 1994.