

AMERICAN MUSEUM *Novitates*

PUBLISHED BY THE AMERICAN MUSEUM OF NATURAL HISTORY
CENTRAL PARK WEST AT 79TH STREET, NEW YORK, N.Y. 10024
Number 3056, 32 pp., 27 figures, 4 tables March 23, 1993

A Reanalysis of Mygalomorph Spider Families (Araneae)

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ABSTRACT

The higher classification of the mygalomorph spiders is reviewed. A data set of 42 taxa and 71 characters is analyzed, applying a new method for character weighting. Most families were represented by two or more genera, so that their monophyly could be tested. The trees that best conform to the data have Atypidae plus Antrodiaetidae, Mecicobothriidae, Hexathelidae, non-diplurine "diplurids," and diplurines as successive sister groups of Rastelloidina plus Crassitarsae. Neither Fornicephalae nor Tuberculotae appear as monophyletic groups. The groups Atypoidea (restricted to Atypidae plus Antrodietidae) and Avicularioidea (the rest of the Mygalomorphae) are resurrected. The groups Orthopalpae and Quadrithel-

ina should be relimited to include the Microstigmatidae and Rastelloidina. The group Crassitarsae should include also the Microstigmatidae. The group formed by the Diplurinae and Rastelloidina plus Crassitarsae is called Bipectina. Three of the currently recognized families appear as paraphyletic: Cyrtaucheniidae (in terms of Domiothelina), Nemesiidae (in terms of Microstigmatidae and Theraphosidae plus Paratropididae plus Barychelidae), and Dipluridae (in terms of Crassitarsae plus Rastelloidina). Support for the monophyly of Hexathelidae is weak; the data are explained almost as well by trees in which the family is paraphyletic.

INTRODUCTION

The higher classification of the spider infraorder Mygalomorphae was recently analyzed by Raven (1985). Prior to Raven's work, the relationships among the families were ter-

ra incognita. The mygalomorphs had been traditionally divided into atypoids (atypids, antrodiaetids, and mecicobothriids, families with a complex male palpal bulb, traces of

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abdominal segmentation, and six spinnerets) vs. non-atypoids (the remaining families, with male bulb sclerites fused, completely unsegmented abdomen, and only four spinnerets). Platnick (1977) showed that the atypoids shared only plesiomorphies, and were thus likely to be a paraphyletic group. Raven (1978, 1979, 1980, 1981, 1982), Raven and Platnick (1981), Gertsch and Platnick (1979, 1980), and Platnick and Shadab (1976) tried to resolve some groups, notably the "Dipluroidea" (mecicobothriids, microstigmatids, diplurids, and possibly all or some "pycnothelids"). Finally, Raven (1985) divided the mygalomorphs into two groups, Fornicephalae and Tuberculotae, both including some atypoids and some non-atypoids. The interested reader is referred to Raven (1985), and references therein, for a more historical perspective.

Raven's (1985) paper was the first to attempt an understanding of the relationships within the Mygalomorphae as a whole. Consequently, it became a starting point for the higher systematics in Mygalomorphae. Coddington and Levi (1991) rightly referred to Raven's results as "impressive."

At the time of Raven's study, however, computerized parsimony programs were not readily available, and analysis could be done only by hand. Raven explicitly attempted to minimize homoplasy for his data, which had nothing less than 240 terminals (genera). For that many taxa, finding the optimal tree(s) is, because of the extremely large number of cladograms to be considered, a very difficult task. Raven (1985) divided the mygalomorphs into 15 families, proposed a familial cladogram, and provided separate generic cladograms for most of the families. The number of terminals in the cladograms varied from 7 to 26. It appears very likely, then, that some of the trees that Raven presented were not actually most parsimonious trees; in fact, some cladogram nodes are said to be supported by characters which are ambiguously, or even incorrectly, optimized.

Not that Raven was unaware of this problem, of course. In recent years, powerful microcomputer parsimony programs have been developed (see Platnick, 1989; Fitzhugh, 1989), the use of which has also increased general awareness of the complexities of par-

simony analysis. Using these new tools, Raven (personal commun.), Coddington (personal commun.), and I have now reanalyzed the relationships among the families of Mygalomorphae using the characters mentioned in Raven (1985). Given Raven's data, if every one of the 15 families he considered is treated as a terminal and scored as having the character states he considered plesiomorphic for each family, Raven's familial tree (1985: fig. 1) is one among several most parsimonious trees. This, however, does not guarantee optimal results: even if each of the 8 cladograms presented by Raven is in itself maximally parsimonious, putting all those cladograms together may result in a less than optimal solution. In fact, some lines of evidence suggest that some of the families considered by Raven (1985) might not be monophyletic. The best example is the Nemesiidae; Raven (1985: 28) discussed the possibility that some of the proposed synapomorphies of Nemesiidae might actually be synapomorphies of the more inclusive group Crassitarsae (secondarily modified in most non-nemesiid Crassitarsae). This would leave the monophyly of Nemesiidae unsupported, and it would be unwarranted to use "Nemesiidae" as a terminal in the analysis. Other cases are discussed below (see under Taxa).

The aim of this paper is to present a reanalysis of the relationships of the Mygalomorphae. I intend to show that some of the hypotheses of monophyly proposed by Raven (1985) are indeed weakly supported or counterindicated by the data, and that a different tree is a better hypothesis of mygalomorph relationships. This paper also constitutes the first application of a new method for character weighting. The method is being described in detail elsewhere (Goloboff, in prep.), but a short discussion can be found in the section on "Methods."

This paper uses data that have been collected over several years, in the course of studies focused on aspects other than the relationships of mygalomorph families. I wish to express my gratitude to a number of arachnologists who have helped me in the course of such studies: María E. Galiano, Norman I. Platnick, Robert J. Raven, Frederick A. Coyle, Martín J. Ramírez, Emilio A. Maury, Charles Griswold, and Jonathan A.

Coddington. Specimens kindly lent by Robert J. Raven (Queensland Museum, Brisbane), Norman I. Platnick (American Museum of Natural History, New York), Emilio A. Maury (Museo Argentino de Ciencias Naturales, Buenos Aires), Herbert W. Levi (Museum of Comparative Zoology, Harvard), Ana T. Da Costa (Museu Nacional de Rio de Janeiro), and Jonathan A. Coddington (Smithsonian Institution, Washington) were relevant for the present study. María E. Galiano kindly shared her unpublished observations of postembryonic development of several mygalomorphs. I also wish to express my gratitude to a number of nonarachnologists (nobody is perfect!) who have also helped me: James M. Carpenter, James S. Farris, James K. Liebherr, Kevin C. Nixon, and Quentin D. Wheeler. My wife Claudia A. Szumik used the computer program developed for this paper to analyze her own data on embiids, and helped eliminate many errors. Norman I. Platnick, Robert J. Raven, Frederick A. Coyle, and María E. Galiano provided helpful criticisms of different versions of the manuscript. Financial support from the American Museum of Natural History and the Department of Entomology of Cornell University are greatly appreciated.

METHODS

Abbreviations. Abbreviations used in this study are standard for the group: PLS, posterior lateral spinnerets; PMS, posterior median spinnerets; ALS, anterior lateral spinnerets; STC, superior tarsal claws; ITC, inferior tarsal claw.

Parsimony analysis. A data set in which 42 taxa were scored for 71 characters was analyzed. As pointed out by Coddington and Levi (1991), cladistic analysis is essentially a problem of how to allocate homoplasy. If there is conflict between two characters, postulating extra steps for one or the other character may not be equally reasonable. It is better to postulate homoplasy for those characters which are more discordant with the tree. This forms the basis for some methods of character weighting, such as "successive weighting" (Farris, 1969; Carpenter, 1988; Platnick et al., 1991).

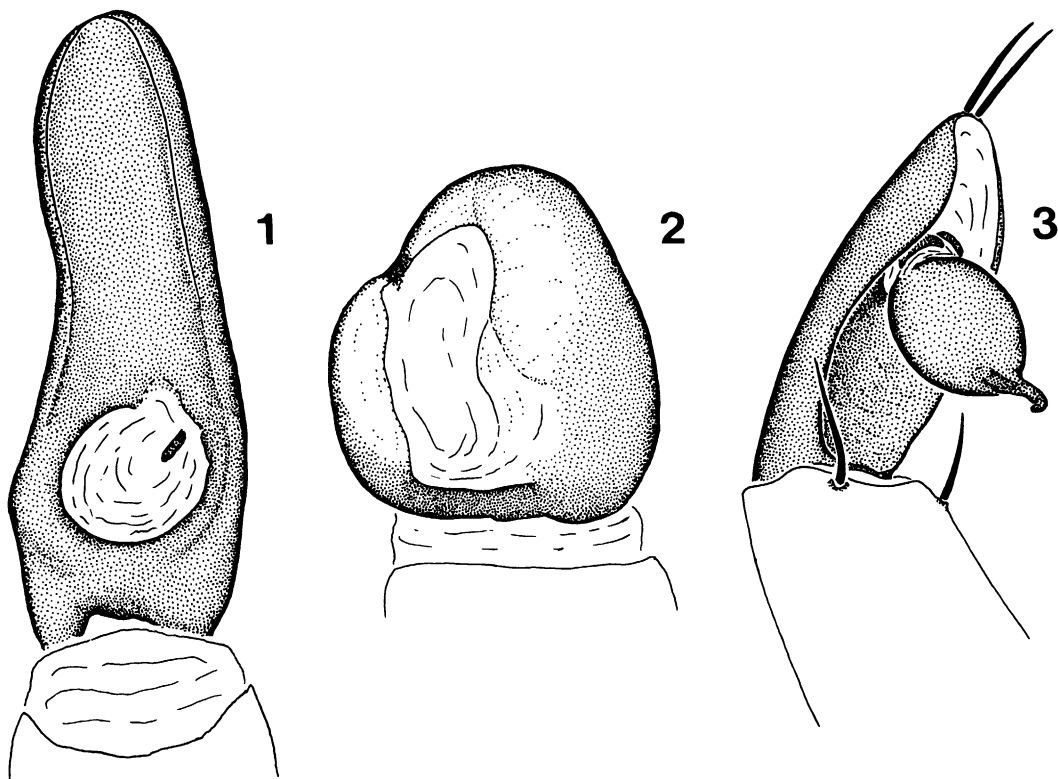
The weighting method used here is derived from successive approximations weighting

(Goloboff, in prep.). Given two trees A and B, choosing B instead of A may save a step for one character and require an additional extra step in another. Even when the two trees require the same number of steps, if the character in which we could save some steps shows more homoplasy on the trees being compared, tree A should be kept. If by choosing B instead we would save a step in a character which shows less homoplasy, B would be a better choice than A. It is possible to take into account automatically the relative amounts of homoplasy of the characters when counting steps to compare trees. This can be done by searching for trees in which the "total fit" (i.e., the sum of the fits for all the characters) is maximum, where fit for each character is measured with a nonlinear, concave function of the homoplasy (see Goloboff, in prep., for a full discussion). A well-known concave function of the homoplasy is the (character) consistency index, c , of Kluge and Farris (1969). The effect of using that function to measure fit is that the difference in fit between two trees will be smaller for characters with more extra steps.

An MS-DOS computer program, Pee-Wee 1.45 (available from the author), was used to calculate the fit for each character using the consistency index (multiplied by 10, with one significant digit), and to search for trees with higher total fits. Pee-Wee's branch-swapping algorithms are less effective than those of other parsimony programs (such as Hennig86); to increase the chance of finding all or most of the optimal trees, several runs were made, using different initial trees.

For some of the characters, the terminals may have more than one state. Those steps "within" terminals were counted to calculate the fit for the corresponding characters. For simple step-counting analyses, those steps are uninformative (they are the same in all the trees), but in the present context they are indeed relevant, because they lower the weight of characters which are known to be variable for some terminals.

Hennig86 version 1.5 (Farris, 1988) was used to find shortest trees in the preliminary analyses, to handle the trees produced by Pee-Wee, and to calculate consensus trees. Clados version 1.2 (Nixon, 1992) was used to find most parsimonious optimizations.



Figs. 1-3. Male palps. 1. *Megahexura fulva* (Mecicobothriidae), right palp. 2. *Stenoterommata plattense*, left palp. 3. *Pseudonemesia* sp. (Colombia), right palp.

TAXA

Atypidae. Four atypid synapomorphies have been proposed (Gertsch and Platnick, 1980; Raven, 1985): maxillae rotated, very elongated and curved maxillary lobes, tarsal claw teeth on a common process, and truncated PMS. The truncation of the PMS results because the spinning field of those spinnerets forms a continuous surface with the spinning field of the second article of the PLS (and covers the basal article of the PLS, which does not have spigots) (see Gertsch and Platnick, 1980: figs. 23, 49). The labium and sternum of atypids are also unique among mygalomorphs; the sternum is abruptly narrowed in front, and the labium is much narrower than the sternum (Gertsch and Platnick, 1980). One additional, sixth character is that the anterior legs of atypids are outwardly "rotated" in such a way that the prolateral spines have become dorsal (although no spines are

present on the highly modified leg I of *Calommata*, the spines on leg II conform to the above description); to a lesser extent, the metatarsal trichobothria are displaced posteriorly. No other mygalomorph has similarly modified spinnerets or legs. Given that there are no serious reasons to doubt the monophyly of the group as currently constituted, it is included as one terminal.

Antrodiaetidae. Coyle (1971) and Raven (1985) considered that *Antrodiaetus* plus *Atypoides* form a monophyletic group, based on the shared anterodorsal male cheliceral process and reduction of ALS, and possibly the strongly developed inner conductor. No characters which would be apomorphic for any placement are shared by this group and *Aliatypus*, the only other antrodiaetid genus (provisionally included in Antrodiaetidae by Coyle, 1971: 393). Given that the monophyly of the family seems arguable, the two groups were included separately in the analysis.

Cyrtaucheniidae. Raven (1985: 61, 65) considered this family to be of doubtful monophyly. Some cyrtaucheniids are the only rastelloids to have two rows of teeth on broad paired tarsal claws (jointly with female palpal claw teeth located prolaterally; figs. 8, 9, 13). Some aporoptychine cyrtaucheniids also share with some Tuberculotae the presence of a serrula, scopula, and corrugiform bothria. Five cyrtaucheniid taxa were included in the analysis: *Bolostromus* and *Fufius* (two typical Aporoptychinae), *Myrmekiaphila* (Euctenizinae, a more typical "rastelloid"), *Rhytidicolus* (which Raven included with doubts in the Aporoptychinae), and *Cyrtauchenius* (Cyrtaucheniinae).

Idiopidae. Although there are several characters which support the monophyly of this family, some genera share possible synapomorphies with taxa outside Idiopidae. *Neocteniza* shares several apomorphies with both Migidae and Actinopodidae; some arbanitines share the presence of a scopula with cyrtaucheniids; and the Idiopinae share with the Ctenizidae and Migidae the presence of strong digging spines on the anterior legs. For this reason, and also because for some placements of the family the main idiopid autapomorphy (bulb with second haematodocha extending below embolus) might be better considered as a plesiomorphic retention, three taxa (*Neocteniza*, *Idiops*, and *Misgolas*) were included to test the monophyly of Idiopidae.

Ctenizidae. The monophyly of Ctenizidae was also considered doubtful by Raven (1985: 57, 66). The only characters thought to support the monophyly of the group (female superior tarsal claws with only one strong tooth and anterior legs with strong digging spines) might be synapomorphies at a level higher than Ctenizidae. However, no characters were found which would resolve the relationships of the ctenizid groups; no important apomorphies seem to be shared by only some ctenizid and other non-ctenizid taxa. In the absence of characters, the addition of several ctenizid taxa would only decrease resolution; therefore, only one genus is included (*Ummidia*). The results of the present analysis therefore cannot test the monophyly of Ctenizidae.

Actinopodidae. *Actinopus* and *Plesiolenia* are included. Raven (1985) and Goloboff and

Platnick (1987) gave two synapomorphies for the family, comprising only three genera.

Migidae. The monophyly of Migidae appears well supported (see Raven, 1985; Goloboff and Platnick, 1987; Goloboff, 1991), and no important apomorphies are shared by only some migids and any non-migid taxon. However, some characters (such as the male tibial apophysis, or the presence of an intercheliceral tumescence) show variation within Migidae, and two genera, *Calathotarsus* and *Heteromigas*, are included in the analysis, with the purpose of more accurately estimating the homoplasy of those characters.

Mecicobothriidae. The family is included as only one terminal; Gertsch and Platnick (1979) and Raven (1985) proposed synapomorphies for the group. Eskov and Zonstein (1990: 352) stated that "the spermathecae of all the mecicobothriids are apomorphously modified," and that this supports the monophyly of the family. However, they actually refer to autapomorphies in the spermathecae of each mecicobothriid genus, which might, at best, support the monophyly of each genus (and not the family).

Microstigmatidae. There are currently two subfamilies included in this family, Microstigmatinae (Raven and Platnick, 1981) and Micromygalinae (Platnick and Forster, 1982). The Microstigmatinae differ from the Micromygalinae by having the superior tarsal claws broad and bipectinate (and the female palpal claw has teeth located prolaterally) and by lacking the ALS. These characters are also found in some non-microstigmatid taxa. Raven (1985) and Griswold (1985) have suggested that microstigmatids, and especially *Micromygale* (the world's smallest mygalomorph), may be neotenic in many characters.

Raven (1985) proposed that, plesiomorphically, the Microstigmatidae have the male palpal bulb parallel to the cymbium; that condition is approached only in *Micromygale*. *Microstigmata* has a palpal bulb inserted orthogonally to the cymbium. Although the bulb in *Pseudonemesia* is inserted apically, the bulb itself is not directed apically (as in mecicobothriids, atypids, and antrodiaetids), but toward the base; the tarsus is very long, basally excavated, and the bulb (smaller than in most mygalomorphs, see Raven and Platnick, 1981) rests in that cymbial cavity (fig. 3). In

most mygalomorphs the bulb rests instead in a tibial cavity. The cymbial shape and type of bulb insertion found in *Pseudonemesia* are thus different from those in any other mygalomorph, except perhaps *Micromygal* and *Ministigmata* (and possibly some Anamini; see Raven, 1984: figs. 38, 39). In the latter two genera, the cymbium is very short but, as in *Pseudonemesia*, the apex of the cymbium lacks the evident notch present in most mygalomorphs. Some uncertainty exists also regarding the homology between the mecicobothriid conductor and that of *Micromygal* (considered as doubtful by Raven, 1985). Some species of *Pseudonemesia* (or a closely related genus) have a form of paraembolic apophysis which is almost certainly not homologous with the mecicobothriid conductor, and the structure which has been considered a "conductor" in *Micromygal* may well represent a modification of that apophysis.

A detailed examination of the palps of *Micromygal* and *Ministigmata* was not possible, because of the paucity of available specimens and their tiny size, and scoring *Micromygal* for palpal characters proved difficult. The bulb and cymbium in *Micromygal* and *Ministigmata* may represent an additional modification of the state found in *Pseudonemesia*, or they may represent an independent modification arising from a more plesiomorphic type of palp. Given the uncertainties regarding palpal characters in *Micromygal*, at the present time it seemed wiser to code that genus as having a palp representing additional modifications from those found in *Pseudonemesia*. Such scoring was admittedly based not only on actual observations, but also to some degree on existing hypotheses of relationships, and is therefore arguable. Representatives of Microstigmatidae included are the genera *Pseudonemesia*, *Micromygal*, and *Microstigmata*, together with some currently undescribed genera (see below).

Hexathelidae. Only one character, the presence of numerous labial cuspules, has been proposed to support the monophyly of this family (Raven, 1978, 1980, 1985). Because some apomorphies (loss of ALS, for example) are shared by some non-hexathelids and some but not all Hexathelidae, there may be good reason to doubt the monophyly

of the group. Therefore, four genera are included in the analysis: *Scotinoecus*, *Atrax*, *Hexathele*, and *Porrhothele*.

Dipluridae. The only characters supporting the monophyly of this family are the PLS widely separated, with a long apical article, and the low, hirsute thorax (Raven, 1985: fig. 6; the cladogram shows only the latter two characters). The second character is too vaguely defined and, because of difficulties in scoring, is not considered here (see below). Some diplurids (Diplurinae) share with taxa outside the family several characters; Raven (1985: 51) discussed the possibility of a closer relationship between diplurines and nemesiids. Because the monophyly of the family seems debatable, four genera currently assigned are included in the analysis: *Diplura* (which shares several apomorphies with some Crassitarsae), *Ischnothele*, *Chilehexops*, and *Euagrus*.

Nemesiidae. As mentioned above, it is plausible that the characters used by Raven (1985) to support the monophyly of the family might actually be plesiomorphies. Several nemesiid genera, representing most of the subfamilies proposed by Raven (1985), are included in the present analysis: *Stenotermomata*, *Ixamatus*, *Acanthogonatus*, *Nemesia*, *Xenonemesia* (which could not be placed in any of Raven's subfamilies; Goloboff, 1988), and *Neodiplothele*. The genus *Neodiplothele* was tentatively included by Raven (1985) in Pycnothelinae; it shares several possible apomorphies with some theraphosoid taxa (the presence of clavate tarsal trichobothria, two rows of tarsal trichobothria, and the characters mentioned by Raven, 1985: 103). I examined the types of *Neodiplothele irregularis* Mello-Leitão and *N. fluminensis* Mello-Leitão only at an early stage of this study and therefore some of the characters could not be scored for that genus.

Barychelidae. No unequivocal synapomorphies for this family were proposed by Raven (1985); the characters that he proposed would be, under some placements of the family, simply plesiomorphies. However, there seems to be a character which unambiguously supports the monophyly of the group: the anterior rim of the booklung opening has a series of teeth (forming a kind of comb) (figs. 4, 5). This character (absent in

all the non-barychelid genera I have examined) is present in trichopelmattines (considered by Raven, 1985, as the sister group of all the other barychelids), sasonines, and barychelins. Raven (in litt.) also has found that the tarsal organ of barychelids is placed apically on the tarsus (whereas other mygalomorphs have the tarsal organ at a distance from the tip), which appears to be an additional synapomorphy for the group. Barychelidae is therefore included as one terminal in the analysis. The ancestral states for the family were inferred under the assumption that trichopelmattines are the sister group of the other barychelids (as proposed by Raven, 1985), with the exception (for the reasons indicated below under Characters) of character 13. Probably our understanding of the Barychelidae will change substantially with ongoing revisionary studies by Raven.

Theraphosidae. One of the aims of the present analysis is to test whether the presence of two rows of teeth is actually a synapomorphy for nemesiids. Some male theraphosids have two rows of teeth on the superior tarsal claws. The family is therefore represented in the present analysis by two taxa, *Ischnocolus* (for which the males have two rows of teeth), part of a basal unresolved tetrachotomy in Theraphosidae, and Theraphosinae (in which both sexes have unarmed claws). Theraphosinae is a group of uncertain limits, due to the large number of genera, but the inclusion of many genera in this group is clear (see Raven, 1985: 118).

Paratropididae. The family Paratropididae was enlarged by Raven (1985) to include the genus *Melloina* (= *Glabropelma*). *Melloina* and Paratropidinae are included as two terminals.

Currently unplaced taxa. Two new genera (from South America) are included in the analysis. Both have two rows of teeth on broad superior tarsal claws, and a female palpal claw with teeth located prolaterally, which would in principle indicate affinities with Nemesiidae. However, placing those genera in the Nemesiidae seemed as parsimonious as placing them in the Microstigmatinae, which also have two rows of teeth. The booklung spiracles of these genera, although not as modified as in *Microstigmata*, are smaller and more rounded than in most nemesiids (the same is

true of *Xenonemesia*). These new genera will be described shortly (in collaboration with N. Platnick); they are included in the data matrix as "New genus from Ecuador" and "New genus from Mexico."

Rooting. The tree was rooted using Mesothelae. Although the sister group of mygalomorphs is the Araneomorphae, they are so highly modified that in only a few characters (detailed below under Characters) could they be used for comparison. For the characters which are comparable in araneomorphs but variable within that group, Platnick et al.'s (1991) and Coddington and Levi's (1991) cladograms were used to determine the plesiomorphic states for araneomorphs.

CHARACTERS

The characters in the following listing are tabulated in the data matrix of table 1. All the multistate characters were considered nonadditive; in most cases, there is no evidence for ordering the states, but when some evidence for ordering might exist, the reasons why the character is considered as nonadditive are discussed (i.e., characters 13, 21).

Character 0: Thorax flat = 0; thorax sloping = 1.

Character 1: Eyes sessile = 0; eyes on a common tubercle = 1. Although the eyes in Mesothelae are set on a tubercle, the outgroup is coded as missing (i.e., having either state), because araneomorphs have sessile eyes.

Character 2: Serrula absent = 0; present = 1. Raven (1985) considered that the structure found on the maxillary lobe of liphistiids was not homologous to that in mygalomorphs. However, in both mygalomorphs and liphistiids the structure is—although not identical—relatively similar and located in the same position. The structure in mygalomorphs and Mesothelae may or may not be homologous, and the state in Mesothelae is therefore coded as missing. Because the ixamatines include both serrulate and aserrulate species (Raven, 1982), the fit for this character was calculated counting one additional step.

Character 3: Tarsal spines present = 0; absent = 1. Araneomorphs have state 1, but the Mesothelae and Amblypygi have state 0; the outgroup is therefore coded as 0.

Character 4: Labium short = 0; subquadrate = 1; long = 2. One step within terminals

TABLE 1
Data Matrix
(Steps within terminals: 1 step for characters 2, 4, 6, 9, 22, 29, 36, 34, and 46, and 2 steps for character 41)

Taxa	1	2	3	4	5	6	7
Characters:	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789
Root	0--010000	00--01000-0	0000--00020	0000--02002	100--00000	1000000000	0
Atypidae	000-10-000	0000101011	0000000000	0000300100	110--10000	0000000000	0
<i>Atrod + Atypoides</i>	0001100-31	0000001101	0000000011	0000300000	0100-00000	0000000000	0
<i>Aliatypus</i>	0000100031	0000100010	0000000000	0000300-00	0100-0000-	-0000000000	0
Mecicobothriidae	11110000-0	0000100000	0000000011	0000400010	0101-0001-	-0000000000	0
<i>Scotinocetus</i>	1110111011	0000100000	0000010-1	000040001-	--01-0001-	-100000100	0
<i>Hexathele</i>	111011101-	0000100000	00000-011	0000010--	-101-0001	-100000100	0
<i>Porrhothele</i>	11111111-0	0000010000	00001000-1	0000401010	0-01-0001-	-10000-00	0
<i>Atrax</i>	1110111111	0010101000	000000011	000000101-	--1-0001-	-100000200	0
<i>Ischnothele</i>	1110111110	0010100000	-000101011	0000400012	0101-00010	1100000300	0
<i>Chilehexops</i>	1110110110	0000010000	1000101011	0000400010	0101-0001-	-100000000	0
<i>Euagrus</i>	1110110110	0000000000	1000101011	0000400010	0101-0001-	-100000200	0
<i>Diplura</i>	1111111111	0102000000	1000101011	0000010101	1-01100010	1100000300	0
<i>Neodiplothele</i>	1101011111	1114000000	-000000011	111020100-	--0110001-	-100000000	0
<i>Barychelidae</i>	1101-11111	11120-0000	1000000011	0011201101	010100001-	-100000400	0
<i>Ischnocolus</i>	1111111111	1111110000	1000010001	001120100-	--01-00011	0100000400	0
<i>Theraphosinae</i>	1101111111	1114110000	1000010011	0011201001	0101-00011	0100000400	0
<i>Melloina</i>	1100111111	1114110000	0000000021	001120100-	--0110001-	-110001400	0
<i>Paratropidinae</i>	1100111111	1003110000	0000000021	0000201002	2101-0001-	-110001000	0
<i>Ixamatus</i>	11-1011111	1002000000	1000010000	000000100-	--0110001-	-100000300	0
<i>Xenonemesia</i>	1101011111	1002000000	1000010000	1000000221	1-01100011	0100000000	0
<i>Micromygalae</i>	11110-00-0	0000000000	1101020000	100000021-	0000-0100-	-200000300	0
<i>Microstigmata</i>	1111011111	0002000000	0000000222	0000001001	2101-0001-	-100000300	0
<i>Pseudonemesia</i>	11110-1111	0002000000	1000000212	000000100-	--01-0001-	-200000300	0
N. gen., Ecuador	1111011111	1002000000	1-00-00222	000000200-	--01-0-01-	-100000300	0
N. gen., Mexico	1101011111	1002000000	1010000212	000000100-	--01-0001-	-100000300	0
<i>Nemesia</i>	1110101111	1020000100	1000000000	1000000001	0101000011	0100010300	0
<i>Stenoterommata</i>	1111011111	1102000000	1000000001	0100000011	0101100011	0100010-00	0
<i>Acanthogoratus</i>	11001-1121	01020-0101	1---000011	--00111102	0-1110001-	--00000-00	0
<i>Rhytidicolus</i>	0001211121	0102001100	1000100011	000011101	1-1110001-	-100000300	0
<i>Bolostromus</i>	0011211121	0102001100	1000100011	000011101	1-1110011-	-100000300	0
<i>Fufus</i>	0001111121	0102001111	-000-000-1	0000001102	110000001-	-100000000	0
<i>Cyrtachenius</i>	0001111121	0103001111	-0000000-1	0000101102	110000001-	-100000000	0
<i>Myrmekiaphila</i>	0001111121	0003000011	1000000010	0000101002	1110-1011-	-100000011	1
<i>Heteromigas</i>	0000111121	0003000011	11110101100	0000101002	1110-1011-	-100000011	1

TABLE 1--(Continued)

Taxa	1	2	3	4	5	6	7
Characters:	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789
<i>Calathotarsus</i>	0000111121	0003000011	1111011100	0000000010	0100101002	1110-1011-	-100000311
<i>Actinopus</i>	0000211121	0003001111	1111011100	00000000-1	0000111102	1110-10011	0101100000
<i>Plesiotena</i>	0000211120	0003001111	1111010100	00000000-1	0000411110-	--10-1001-	-1011000000
<i>Idiops</i>	0000111121	0003001111	1011011000	0111000011	0000101102	-00-00101-	-100000501
<i>Neocteniza</i>	0000110121	0003001111	1011011100	1111000011	0000101102	0100-1111-	-101000000
<i>Misgolas</i>	0001111121	0103001111	1011010000	1111000011	0000001102	--0000111-	-100000500
<i>Ummidia</i>	0000111121	0003001111	1111011000	1000000011	0010101102	1100-00010	-100000000

counted, because barychelids include species with state 0 and species with state 1.

Character 5: Axis of bulb parallel to cymbial axis = 0; orthogonal or directed toward the base = 1.

Character 6: Maxillary cuspules absent = 0; present = 1. The character is variable in atypids, and thus one step within terminals was added to this character.

Character 7: ALS present = 0; absent = 1.

Character 8: Thoracic fovea an open pit (sometimes longitudinal) = 0; transverse = 1; very wide = 2; closed and longitudinal = 3. Most mygalomorphs have states 1 or 2. The problems in scoring this character are mainly in the plesiomorphic groups of mygalomorphs. Antrodiaetids have state 3; I consider mecicobothriids as having state 0 and diplurids and hexathelids as having state 1.

Character 9: ITC dentate = 0; edentate = 1.

Character 10: ITC normal = 0; reduced in size (or absent) = 1.

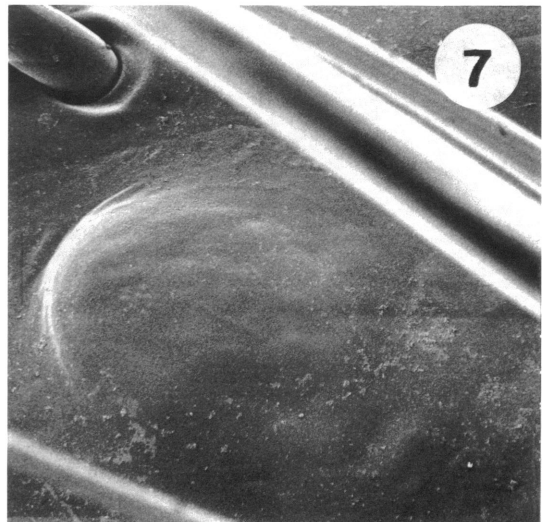
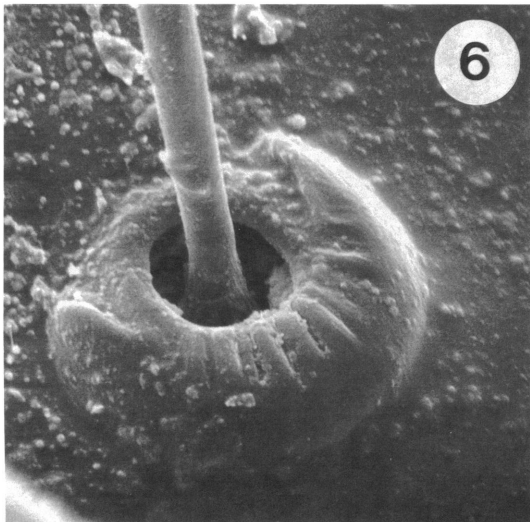
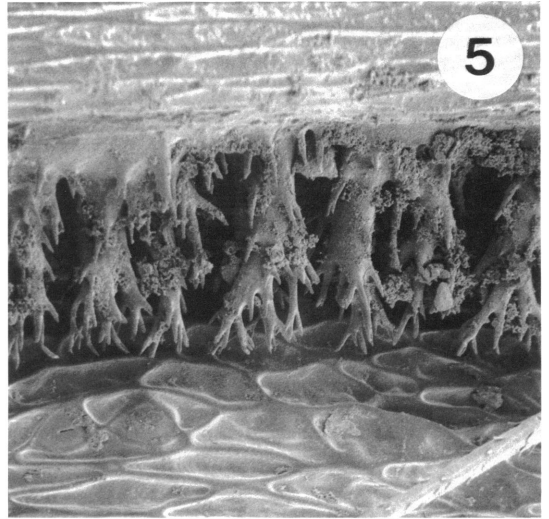
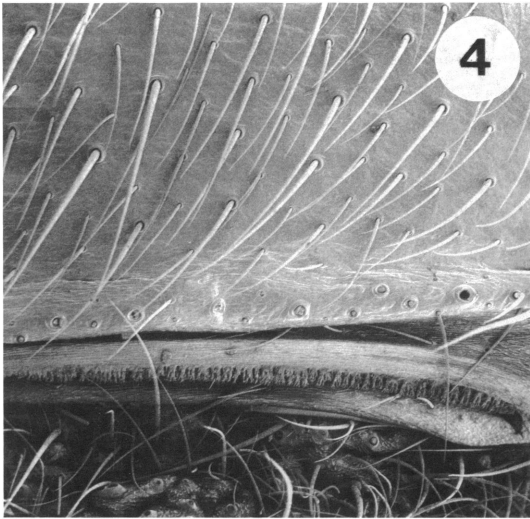
Character 11: Female tarsi I–II without scopula = 0; scopulate = 1.

Character 12: Claw tufts absent = 0; present = 1.

Character 13: Superior tarsal claws. Raven (1985) used the dentition of STC to support his cladogram. I consider the broadening of the STC as a necessary correlate of the presence of two rows of teeth, and therefore do not consider it a separate character. Raven (1985) included as an additional character for nemesiids the teeth of the palpal claw located prolaterally. The female palpal claw teeth tend, in fact, to be located toward the prolateral side of the claw, even in taxa where the leg claws have only one row of teeth (figs. 10, 11). That displacement is even more evident in those taxa in which the leg claws are bipectinate (figs. 8, 9, 12, 13). Thus, I consider the displacement of the teeth in the female palpal claw and the double row of teeth as the same character.

The alternative states for the taxa included in the analysis are:

State 0: in Mesothelae (and, plesiomorphically, in araneomorphs), antrodiaetids, atypids, non-diplurine diplurids, hexathelids, mecicobothriids, and micromygalines, there is a single row of several teeth;



Figs. 4–7. 4, 5. *Strophaeus* sp. (Peru), left booklung and booklung comb. 6. *Ummidia* sp. (Mexico), bothrium from tarsus II. 7. *Rhytidicolus* sp. (Venezuela), tarsal organ from tarsus I.

State 1: in *Ischnocolus* (Theraphosidae) and many barychelids, males have two rows, and females have only one row, of few, minute teeth;

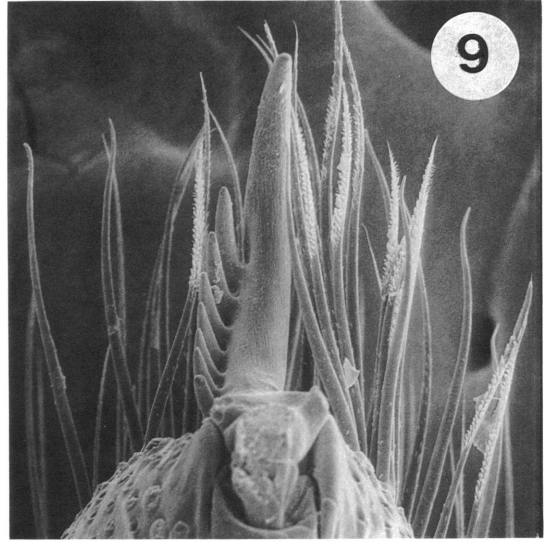
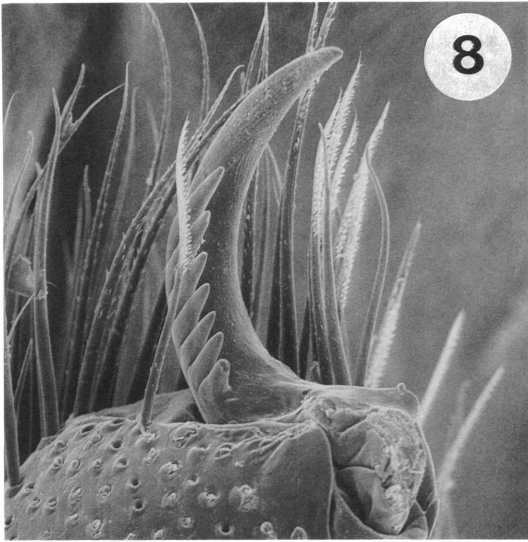
State 2: in nemesiids, microstigmatines, dipurines, and aporoptychines, both sexes have two rows of teeth; Raven (in prep.) describes a new barychelid genus in which both sexes have two rows of teeth, and suggests that this could be the plesiomorphic state for barychelids (that suggestion is followed here);

State 3: in paratropidines, ctenizids, some idiopids (*Neocteniza*), and actinopodids there

is only one strong tooth on the STC (the other idiopids included in the data set, the migids, and *Myrmekiaphila*, also seem to have this state, or a homolog of it);

State 4: in most Theraphosidae (including Theraphosinae), some barychelids, and *Melloina* there is only one row of a few, minute teeth in both sexes.

Males of *Rhytidicolus* are unknown; the genus is coded as a missing entry (presumably males have two rows of teeth on the STC). In Bemmerinae (currently included in Nemesiidae) males have one row of teeth and



Figs. 8, 9. *Bolostromus* sp. (Peru), left female palpal claw.

females have two; no bemmerines are included in the present data set, and so the state is not considered further.

Given the differences between sexes, an obvious possibility seems to be coding this character separately for males and females. Doing so, however, would imply more instances of homoplasy for Raven's (1985) familial cladogram. For example, given that nemesiids, diplurines, and microstigmatids have bipectinate STC in both sexes, such coding would imply that claws provide twice the number of extra steps against Raven's cladogram (i.e., that the double rows of teeth was acquired independently in males and females). Each one of the five possible dentitions for the STC was considered as an alternative state of the same, nonadditive (unordered) character, so that each state can transform into any other state with equal cost. This coding is not too constraining of the possible outcomes; for example, if *Ischnocolus* and barychelids were to be placed within a group having only one strong tooth in the STC (as in ctenizids and some idiopids), only one step and no homoplasy would be counted, even when the similarities between male tarsal claws among *Ischnocolus* + barychelids and nemesiids, microstigmatines, etc. are being ignored by such a cladogram. Although less informative, the nonadditive coding was preferred, so that

the present analysis is a stronger test of Raven's cladogram (i.e., an additive coding would imply more steps against Raven's tree).

Character 14: Maxillary lobe unmodified = 0; anteriorly produced = 1.

Character 15: Few or no labial cuspules = 0; numerous labial cuspules = 1.

Character 16: Caput low = 0; elevated = 1.

Character 17: Rastellum absent = 0; present = 1.

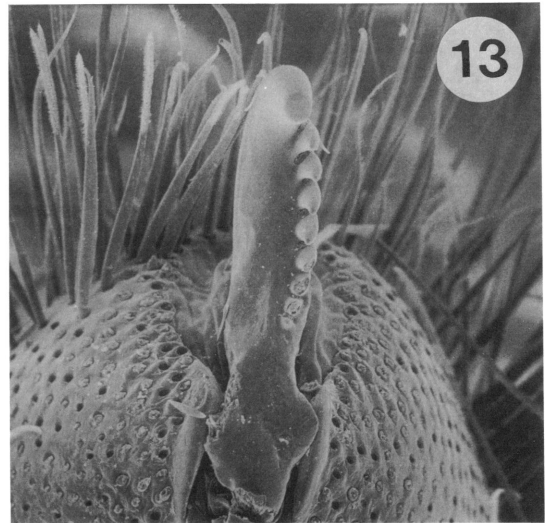
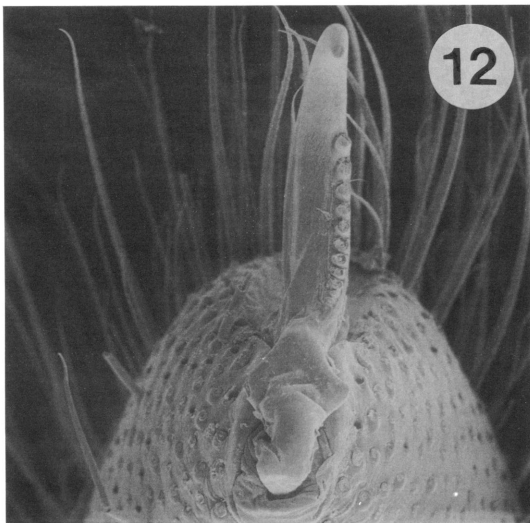
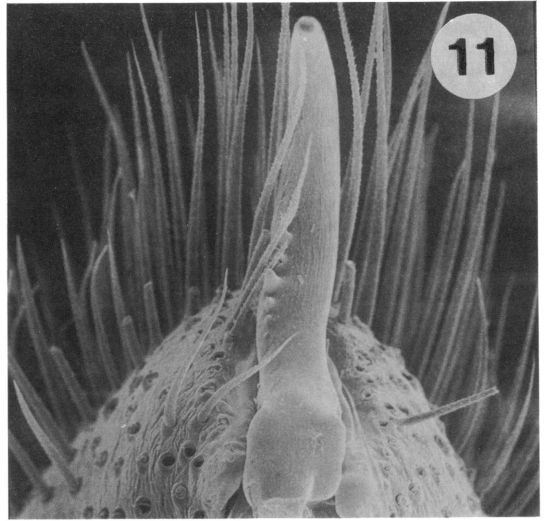
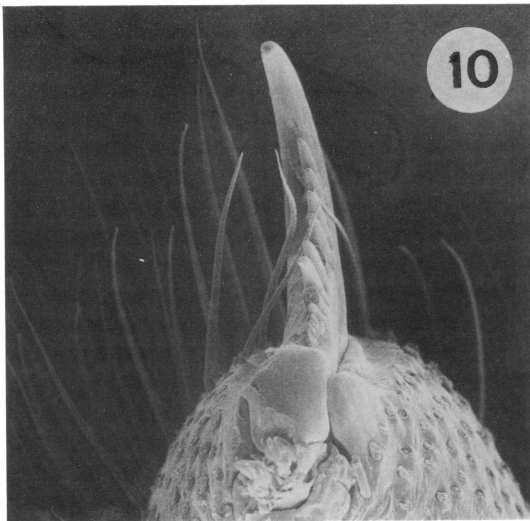
Character 18: Anterior and posterior legs of approximately the same size = 0; anterior legs shorter and more slender than posterior legs = 1.

Character 19: Spines on posterior legs distributed ventrally as well as dorsally = 0; located on dorsal surfaces = 1.

Character 20: Female tarsi slender = 0; stout = 1.

Character 21: Second haematodocha extending below embolus = 0; not = 1. The males of the new microstigmatid genus from Ecuador have a strongly modified bulb, with a very inflated second haematodocha; because this condition may or may not be homologous with that in idiopids (although apparently the membranes do not extend below the embolus as much as in that group), the state is coded as missing.

Character 22: Apical article of PLS short, domed = 1; digitiform = 0. The character is



Figs. 10–13. Female palpal claws. 10. *Porrhothele antipodiana*, right palp. 11. *Atypoides gertschi*, left palp. 12. *Diplura* sp. (Bolivia), right palp. 13. *Fufius* sp. (Bolivia), right palp.

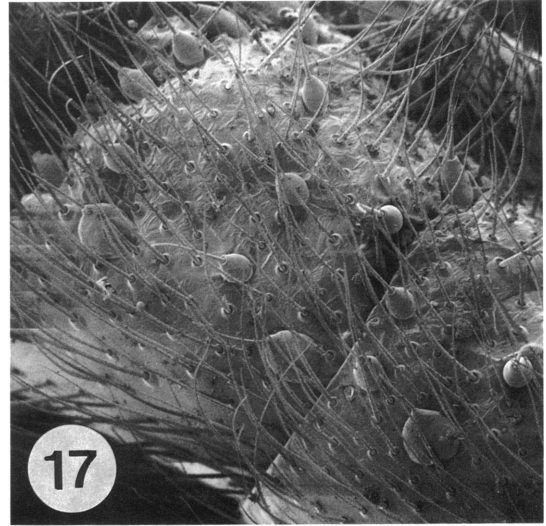
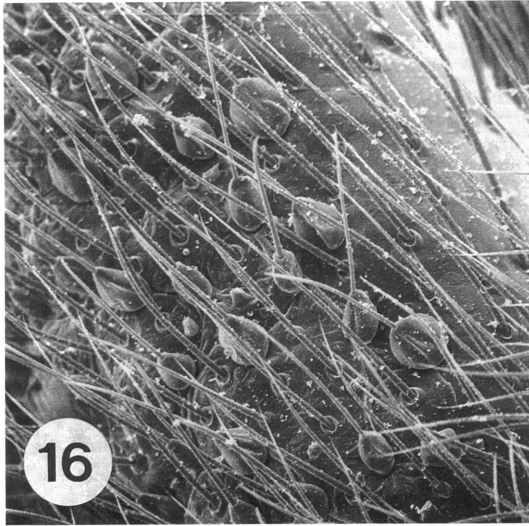
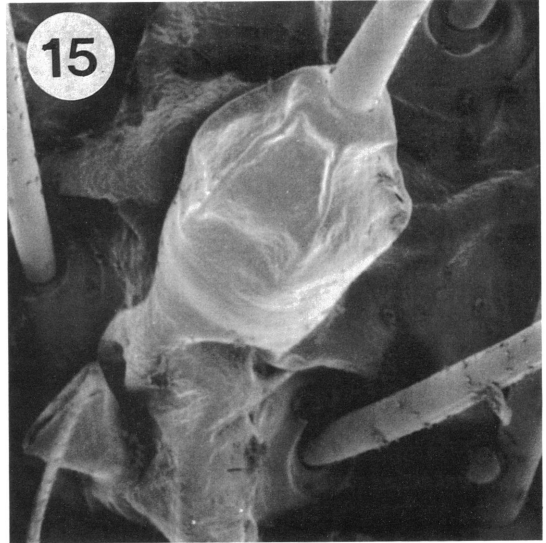
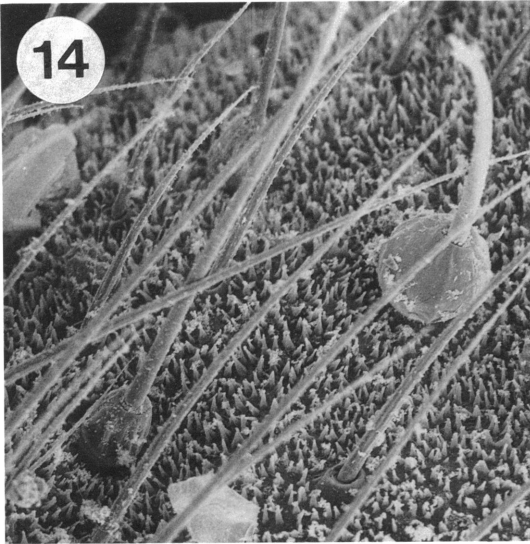
variable within *Acanthogonatus*, and so one additional step was counted when calculating the fit for this character.

Character 23: Cheliceral furrow with two rows of teeth = 1; teeth only on promargin = 0.

Character 24: Leg cuticle scaly = 1; smooth = 0. Although Raven and Platnick (1981), and Platnick and Forster (1982) considered that the cuticular modifications in ixamatines were different from those in microstigmatids

(because microstigmatids have scales and pustules and ixamatines only have the latter), they are coded here as having the same state.

Character 25: Dorsal abdominal tergite present = 0; absent = 1; abdomen with dorsal scutum = 2. Raven (1985) considered the scutum in some microstigmatids as “questionably homologous” with the abdominal tergites. By the present coding and non-additive interpretation for this character, the homology between tergites or scuta, or the



Figs. 14–17. Spigots of PLS. 14. *Ixamatus broomi*. 15. *Fufius* sp. (Bolivia). 16. *Acanthogonatus* sp. (Chile). 17. *Stenoterommata* sp. (Argentina).

lack of it, can be decided by congruence with other characters.

Character 26: Female anterior tibiae and metatarsi with digging spines = 1; with normal, elongated spines = 0.

Character 27: Ocular quadrangle wide = 1; narrow = 0.

Character 28: Male palpal bulb with conductor = 1; without conductor = 0.

Character 29: Male tarsi pseudosegmented = 1; integral = 0. One step within terminals

counted for *Acanthogonatus*, variable for this character.

Character 30: Bothria corrugiform = 1; smooth = 0. Corrugiform bothria appear to be much more widely distributed than previously thought; in the present study, they were observed in *Fufius*, *Bolostromus*, *Rhytidicolus*, *Neocteniza*, and *Ummidia* (fig. 6); *Idiops* has smooth bothria.

Character 31: Second haematodocha extending below embolus = 1; small = 0.

Character 32: Male palpal tibia with thorn-like spines = 1; with normal spines or unarmed = 0.

Character 33: One cymbial lobe pointed = 1; palpal tarsus normal = 0.

Character 34: Multilobular spermathecae. Raven (1985) considered this character to be one of the synapomorphies for Cyrtoucheniidae. By multilobular Raven apparently referred to the presence of multiple divisions of each spermathecal receptaculum; this eliminates taxa having paired undivided receptacula (what has been called "2 + 2 spermathecae"; Platnick and Gertsch, 1976). Several taxa outside Cyrtoucheniidae were scored as having multilobular spermathecae (state 1): *Diplura* (see Goloboff, 1982b), *Ischnothele*, *Porrhothele*, and *Ischnocolus*. The plesiomorphic state of this character for *Stenoterommata* is presumed to be multilobular (as in *S. platense* Holmberg, see Goloboff, 1982a); because some species in the genus have undivided receptacula, one step within terminals is counted for this character.

Character 35: Anterior tarsi very densely scopulate = 1; less densely scopulate = 0.

Character 36: PLS widely separated = 1; close = 0. Some species of *Hexathele* have the spinnerets more separated (see Forster and Wilton, 1968), and therefore one additional step was counted when calculating the fit for this character.

Character 37: Booklung openings normal = 0; small and rounded = 1 (Raven and Platnick, 1981: figs. 1, 2). The booklung openings of the new genera from Mexico and Ecuador, and those of *Xenonemesia*, were coded as for *Microstigmata*, *Pseudonemesia*, and *Micromyale* despite some apparent differences. In the three former genera the booklung openings are not as small, and the posterior margin is not as sclerotized as the anterior one, as is the case for the other three genera. All of them, however, seem to share a common type of modification (which progresses further in *Microstigmata* and *Pseudonemesia*, and possibly *Micromyale*), and are therefore coded as having state 1.

Character 38: Tarsal organ low and smooth = 0; low with concentric ridges = 1; domed and smooth = 2. The distinction between states 0 and 1 is sometimes difficult; *Neocenteniza*, *Idiops*, *Ummidia*, *Fufius*, *Rhytidico-*

lus, and *Bolostromus* have a low tarsal organ with concentric ridges; those ridges are almost inconspicuous in *Ummidia*, *Rhytidicolus*, and *Idiops*. As with character 30, the state previously thought to define some restricted groups (i.e., state 1; see Raven, 1985: 22) is actually quite widely distributed.

Character 39: PLS with spigots on medial and basal articles only = 0; spigots on the three articles of the PLS = 1; spigots only on the apical article (if present on the medial article, only on the apical edge) = 2. Palmer (1990) reported paratropidids as lacking spigots on both the basal and medial article of the PLS. However, she examined only one species of *Anisaspis*; in *Paratropis* (and also *Melloina*) there are numerous spigots on the basal and medial article (as well as the apical, which is not known to lack spigots in any mygalomorph); the plesiomorphic state for paratropidines is therefore considered to be basal and medial article with spigots.

Character 40: Low parallel ridges on the male palpal bulb = 1; no ridges = 0.

Character 41: Interchelicerar tumescence present = 1; absent = 0. The character is variable in *Nemesia* and the barychelids; two additional steps were counted to calculate the fit.

Character 42: Tarsi with clavate trichobothria = 1; without = 0. *Liphistius* (Mesothelae) has clavate trichobothria, but *Hepthathela*, the other genus in the Mesothelae, has only filiform trichobothria; this would suggest scoring Mesothelae as a missing entry (i.e., having either state). In *Liphistius*, however, there are alternating, distinct rows of clavate and filiform trichobothria (Murphy and Platnick, 1981; Platnick and Sedgwick, 1984). In the theraphosoids and some ctenizids and idiopids, in contrast, the clavate trichobothria are interspersed among the filiform ones. The state in *Liphistius* is thus considered nonhomologous with that in theraphosoids and some rastelloids, and because clavate trichobothria are also absent in araneomorphs and *Hepthathela*, the outgroup is coded as zero.

Character 43: A strongly curved row of trichobothria on the anterior metatarsi, extending retrolaterally (sometimes the basal trichobothria separated from the others) = 1; a straight or gently curved dorsal row = 0.

Character 44: Tarsal trichobothria in a zig-zag row = 0; forming a wide (usually diagonal) band = 1; in two longitudinal lines separated by setae = 2; reduced = 3; in a straight row = 4. In theraphosids, non-paratropidine paratropidids, barychelids, and *Neodiplothele* the tarsal trichobothria form two zig-zag rows, separated by a band of setae. The trichobothria of both the theraphosoids and several rastelloid taxa have been previously described as a "broad band of trichobothria" (see Raven 1985: 116); in rastelloids, however, there is no medial row of setae, and those taxa (*Actinopus*, migids, ctenizids, *Idiops*, *Neocteniza*, and *Myrmekiaphila*) are here considered as having a different state. The tarsal trichobothria of paratropidines do not fit exactly in either states 1 or 2. Although there is no medial row of setae, the trichobothria form a longitudinal band. The state in paratropidines is here considered as a further modification of the state in the other theraphosoids (i.e., state 2); because that unique state would be uninformative within theraphosoidina, paratropidines are scored as having state 2.

Raven (1985: 143) erroneously described the family Actinopodidae as having "a more or less straight row" of trichobothria on the tarsi. That statement is true only of *Plesiolena* and *Missulena*; *Actinopus* has a wide band of trichobothria (Goloboff and Platnick, 1987).

Character 45: Palpal coxae subquadrate = 1; elongate = 0.

Character 46: Spermathecae paired (2 + 2) = 0; unpaired = 1; nonreceptaculate = 2. Although some species of *Stenoterommata* have 2 + 2 spermathecae (see Goloboff, 1982a), other species in that genus have unpaired spermathecae, and I consider the latter to be the plesiomorphic state for the genus. One step within terminals is counted.

Character 47: More than three spines on patella III = 1; 3 or fewer = 0. Ctenizids, actinopodids, idiopids, and cyrtaucheniids have numerous prolaterodorsal spines on patella III. Those taxa also have the spines on the posterior legs situated dorsally, a possibly associated character. In some species, however, one of the characters is present and the other is absent, and the presence of dorsal spines and the number of patellar spines are therefore considered independent characters.

Character 48: Posterior lateral spinnerets long = 1; short = 0. Raven (1985) suggested that the spinneret elongation in diplurids was of a different nature than that in hexathelids and mecicobothriids, which would suggest scoring them differently. According to Raven, in diplurids the three articles of the PLS are elongated, whereas in the other two groups only the apical article is elongated. The distinction between the two types, however, is not clear for some of the species included in the present data set (e.g., the relative lengths of the PLS segments in *Scotinoecus* and *Eugrurus* are essentially the same), and the mecicobothriids and long-spinnereted hexathelids are therefore scored as having the same state as the diplurids.

Character 49: Spigot types (Palmer, 1990): articulated = 0; pumpkiniform = 1; fused = 2. Among the taxa included in the data set, those studied by Palmer (1990), except *Stenoterommata* and *Acanthogonatus*, were scored on the basis of her study. For the present study, the spinnerets of the following taxa were examined (figs. 14–19): six species of *Acanthogonatus* [*A. fuegiana* (Simon), the species identified as *A. frankii* Karsch by Palmer, 1990, plus four undescribed species], three undescribed species of *Stenoterommata*, *Ixamatus broomi* Hogg, *Nemesia dubia* O. P.-Cambridge, *Xenonemesia platensis* Goloboff, and unidentified species of *Diplura*, *Rhytidicolus*, *Fufius*, and *Bolostromus*, plus a variety of "nemesiids" not included in the data set [*Pycnothele singularis* (Mello-Leitão), *Lycinus epiptusa* (Zapfe), *Diplotheopsis bonariensis* Mello-Leitão, an undescribed genus of Diplothelopsini, *Chaco obscura* Tullgren, and two undescribed species of *Chaco*]. As discussed by Palmer (1990), classifying a particular spigot as being "pumpkiniform" or "articulate" is sometimes equivocal. According to Palmer (1990), *Acanthogonatus* lacks pumpkiniforms, but all the species of *Acanthogonatus* examined for this study (including specimens collected in the same locality as Palmer's, and probably conspecific) have what I consider to be clear examples of pumpkiniform spigots. Those pumpkiniforms are larger than the articulated spigots, and are all located on the inner edge of the spinning field (figs. 16, 18) (see character 65).

Character 50: Spigot shaft sculpture (Palmer, 1990): overlapping scalelike folds = 0; minimal surface detail = 1; pointed projections = 2. The taxa examined for character 49 were also examined for this character.

Character 51: Slit on spigots present = 0; absent = 1. Palmer (1990) mentioned this character but did not include it in her table. The character was scored based on her photographs.

Character 52: Cheliceral fangs short, thick, and diagonal = 1; long and parallel = 0.

Character 53: Sternum gradually narrowed in front = 0; sternal sides more parallel = 1. In the Ctenizidae, Actinopodidae, Idiopidae, Migidae, and Antrodiaetidae, the sternum narrows gradually from coxae III; the labium is thus approximately as wide as the anterior end of the sternum. In the other mygalomorphs, except Atypidae, the sternum is approximately as wide between coxae II as it is between coxae III; the labium thus appears much narrower than the sternum. The Mesothelae and Atypidae have sternal shapes that are very different from those, and among themselves; because both of those unique states would be uninformative, those taxa are scored as missing entries.

Character 54: Anterior legs with scopula symmetrical = 1; scopula more developed on the prolateral side = 0. In barychelids, scopulate idiopids, and some scopulate cyrtauchiids, the scopula on the anterior tarsi and metatarsi is more developed on the prolateral side. In the Diplurinae, Nemesiidae, Apoptychinae, and Theraphosidae, in contrast, the scopula is equally developed on both sides. The nonscopulate taxa are scored as missing.

Character 55: Postlabial sigillum deeply excavated = 1; a shallow suture = 0.

Character 56: Spermathecal ducts more strongly sclerotized basally = 1; with uniform sclerotization = 0.

Character 57: Fovea sinuous, recurved = 1; straight or procurved = 0.

Character 58: Spinnerets well separated from anal tubercle = 0; spinnerets and anal tubercle close = 1.

Character 59: Second postembryonic instar well developed, with cephalothorax and abdomen in the same plane = 0; less developed, with cephalothorax and abdomen perpendicular = 1. There is currently an ongoing

debate on several aspects of the spider postembryonic development (including the nomenclature of the stages). I will follow Galiano (1969, 1972, 1973a, 1973b) in considering that the first postembryonic instar may occur before hatching (i.e., before the chorionic membranes are broken). Galiano (personal commun.) has kindly provided a summary of the published studies and unpublished observations she has made on the development of *Actinopus insignis* (Holmberg), *Diplura paraguayensis* (Schiapelli and Gerschman), *Oligoxistre argentinensis* (Mello-Leitão), *Xenonemesia platenensis*, and an undescribed *Stenoterommata*. My scoring for this character, as well as that for character 60, was based on Galiano's summary. I have assumed that the two plesiomorphic theraphosids *Oligoxistre* (placed by Raven in the possibly paraphyletic *Ischnocolinae*) and *Ischnocolus* share the same type of postembryonic development. According to Galiano, all mygalomorphs except *Grammostola* have three postembryonic instars [the presence of four instars in *Grammostola* (Galiano, 1969, 1973a) is easily interpretable as an autapomorphy]. There is variation, however, in the degree of development of the stages. *Ischnothele*, *Diplura*, *Atypus*, and *Antrodiaetus* (and *Heptathela*) have a second postembryonic instar more developed, with cephalothorax and abdomen in the same plane, whereas *Actinopus*, theraphosids, and "nemesiids" have the cephalothorax and abdomen at 90° (only later instars have the cephalothorax and abdomen in the same plane).

Character 60: Cheliceral fang with apical tooth in larval stages = 0; with simple, conical claw in all stages = 1. *Diplura* and *Ischnothele* have a simple claw; all the other studied mygalomorphs have a toothed fang (see Galiano, 1973b: 325 for comments on *Antrodiaetus*). The outgroup is coded as 1 because *Heptathela* has a simple claw in the chelicerae (Yoshikura, 1955, quoted in Galiano, 1973b).

Character 61: Cymbium with apical rim sclerotized (bulb cavity apically closed) = 0 (fig. 1); cymbium apically incised and membranous (bulb cavity apically open), enclosing subtegulum = 1 (fig. 2); cymbium with apical edge membranous, but not incised and not enclosing subtegulum = 2 (fig. 3). See

above, Taxa, for discussion of the coding for *Micromygalae* and *Pseudonemesia*.

Character 62: Maxillae normal = 0; maxillae concave in the middle (as in paratropidids) = 1.

Character 63: Patella III without apical comb of spines = 0; with apical comb of spines (Platnick and Shadab, 1976) = 1.

Character 64: Bothria normal = 0; with a sinuous impression around tricheme aperture (Goloboff and Platnick, 1987) = 1.

Character 65: Pumpkiniform spigots dispersed (or absent) = 0; forming a row in the inner edge of spinning field = 1. State 1 is shared by *Acanthogonatus* (figs. 16, 18) and *Stenoterommata* (fig. 17; Palmer, 1990, erroneously stated that the pumpkiniforms in *Stenoterommata* are in a "medial row;" the row is actually lateral, along the inner edge of the spinning field).

Character 66: Labium normal = 0; labium big, squared, and very inclined = 1.

Character 67: Male tibial apophysis: no apophysis = 0; with apical prolateral megaspines (as in *Hexathele* and *Scotinoecus*) = 1; on leg II = 2; a retrolateral apical megaspine = 3; theraphosoid type of tibial spur (Raven, 1985) = 4; idiopid type of tibial spur = 5;

Character 68: Posterior leg spines normal = 0; reduced to spiniform setae = 1.

Character 69: Posterior sternal sigilla normal = 0; reduced = 1.

Character 70: Cheliceral fang normal = 0; keeled = 1.

CHARACTERS NOT CONSIDERED IN THE ANALYSIS

Raven (1985: 51) considered the "lowered caput plus elevated thoracic region" as a synapomorphy for diplurids, shared with some microstigmatids and possibly some barychelids. I have been unable to detect any significant difference between the thorax of diplurids and that of most other mygalomorphs. In *Pseudonemesia*, it is clear that the thorax is more elevated behind the fovea, as noted and illustrated by Raven and Platnick (1981), but for the present choice of taxa *Pseudonemesia* would be autapomorphic for this character.

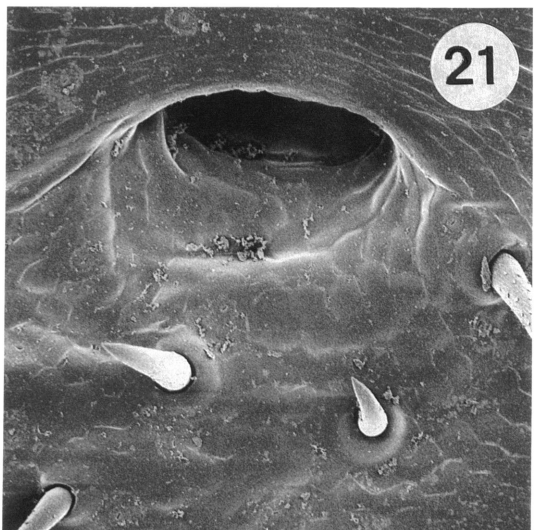
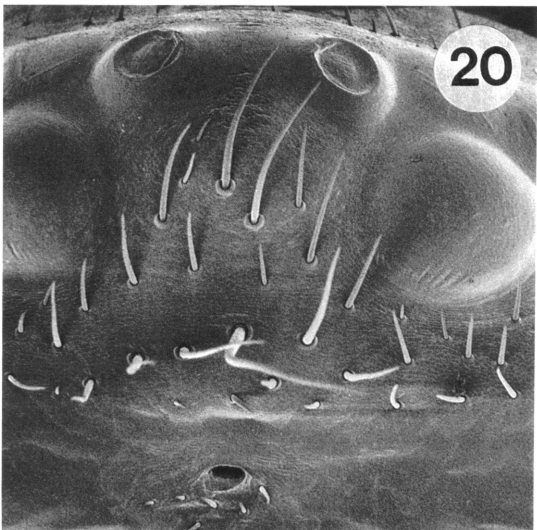
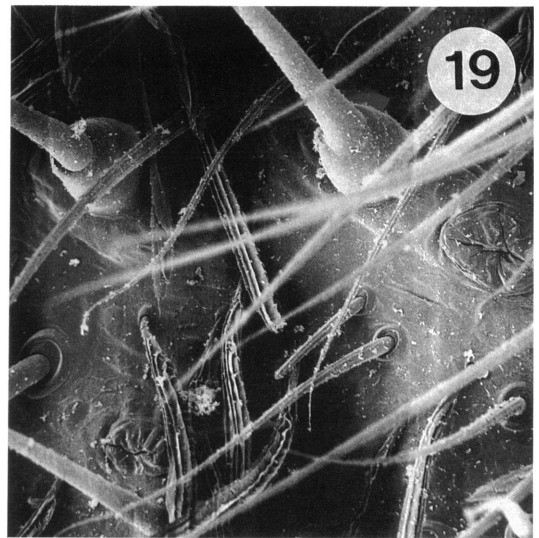
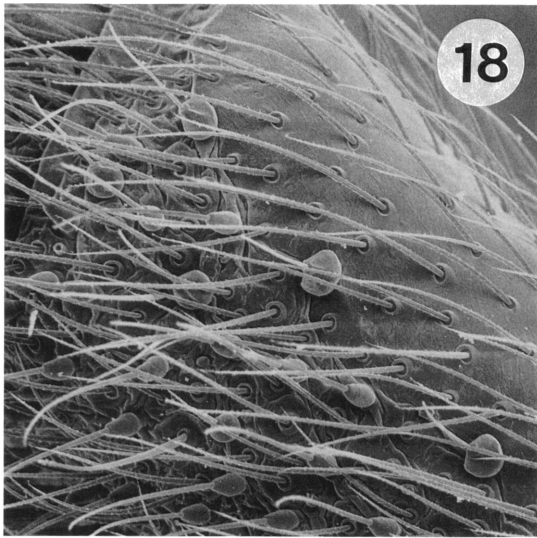
One potentially informative character is the presence of a clypeal opening in some taxa

(figs. 20, 21). This structure is difficult to observe in many cases; it appears to have a scattered distribution (it was observed in barychelids, *Neocteniza*, and *Antrodiaetus*; paratropidines seem to have a modified opening; it appears to be absent in theraphosids, nemesiids, diplurids, and *Idiops*). Given that the distribution of this character in mygalomorphs is still poorly known, it is not included in the analysis.

Another possibly informative character is the presence of a peculiar type of cuticular modification near the maxillary glands of some genera (figs. 22–25). The basal part of the maxillae (the part in contact with the labium) has a less sclerotized, paler, and generally well defined area (in many cases posteriorly delimited by fringes of modified hairs). In that paler area most of the examined genera have conical hairs, with a blunt tip; a glandular secretion apparently would exit from an opening in the base of the hair; the hairs are only visible with scanning electron microscopy. Those hairs have been observed in *Antrodiaetus unicolor* (Hentz), *Mecicobothrium thorelli* Holmberg, *Hexathele hochstetteri* (Ausserer), *Stenoterommata platense*, and unidentified species of *Strophaeus* (Barychelidae, Barychelinae), *Bolostromus*, *Ischnothele* (fig. 25), and *Diplura* (fig. 24). They are absent in *Cyriocosmus* sp. (Theraphosidae, Theraphosinae) and in the two Domiothelina examined, *Idiops clarus* (Mello-Leitão) (figs. 22, 23) and an unidentified *Actinopus*. The loss of the modified hairs may therefore be a synapomorphy of the Domiothelina, or some group within Domiothelina, with parallelisms in the Theraphosidae. Since the distribution of the character in mygalomorphs is poorly known, it is not included in the data set.

The following characters (or scorings of taxa) were mentioned by Eskov and Zonshtein (1990) in support of their scheme. For the reasons discussed in each case, those characters are not included in the data set.

Eyes on a common tubercle in atypids. Eskov and Zonshtein claimed (p. 344) that atypid eyes are set on a tubercle. Unlike the eye tubercle of most of the taxa included by Raven (1985) in his Tuberculotae, however, the atypid eye tubercle comprises only the AME and slopes more gradually; atypids are



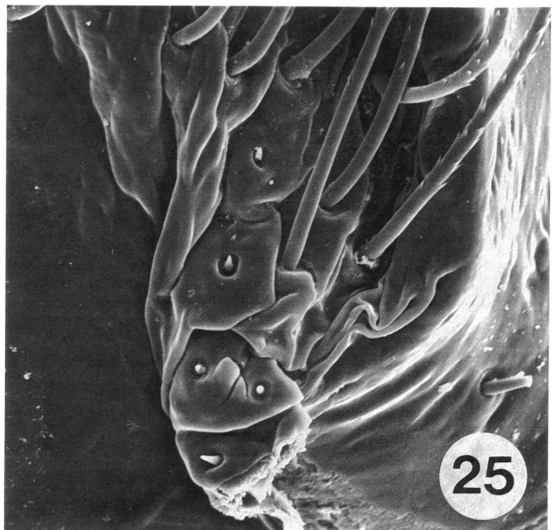
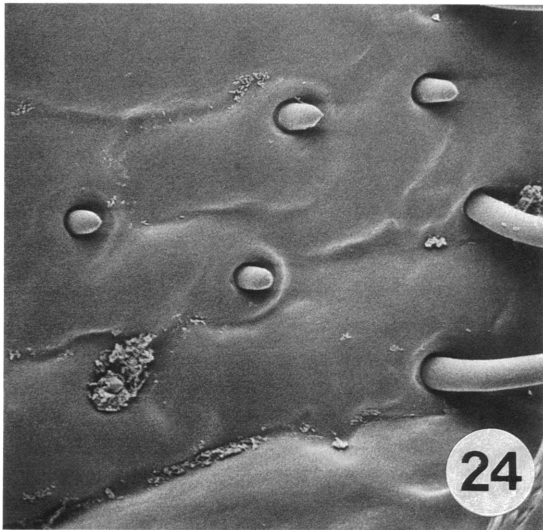
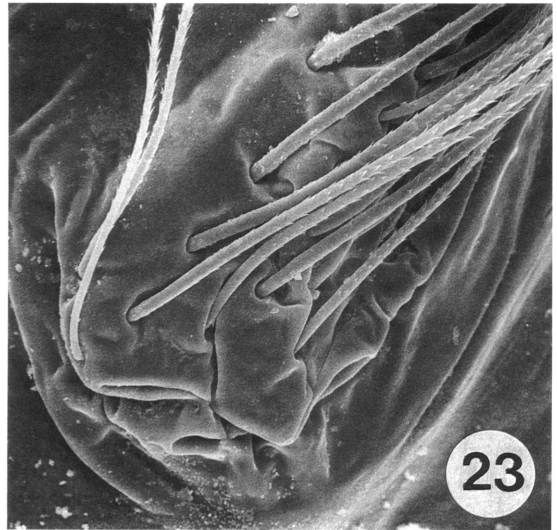
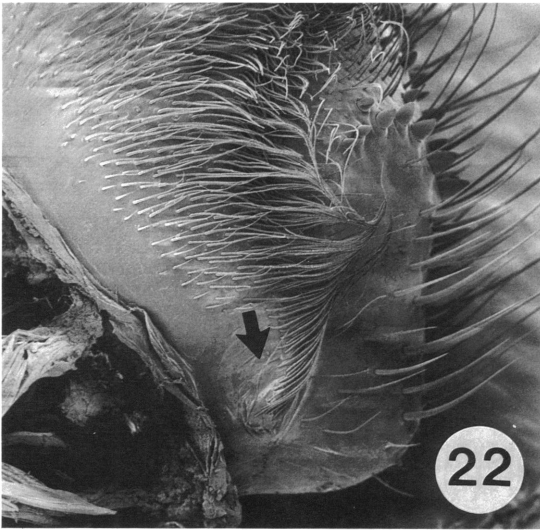
Figs. 18–21. 18. *Acanthogonatus* sp. (Argentina), spigots of PLS. 19. *Diplura* sp. (Bolivia), spigots of PLS. 20, 21. *Antrodiaetus unicolor*, clypeal opening.

therefore scored as not having an eye tubercle (contra Eskov and Zonshtein, 1990).

Maxillary cuspules of atypids. Eskov and Zonshtein (p. 348) proposed that the maxillary cuspules of atypids are different from those in non-atypoid taxa (all mygalomorphs except Mecicobothriidae, Antrodiaetidae, and Atypidae). They claimed that the cuspules in atypids are “clearly distinguishable by their shape from the [non-atypoid] ones.” They do not mention, however, where the actual dif-

ference lies, and I have been unable to detect any. Therefore, instead of scoring this character as absent in atypids (as they would have it), the character is scored as either absent or present (because *Calommata*, the sister group of cuspulate atypids, lacks cuspules and therefore the ancestral state for this character in atypids is ambiguous).

Shape of the chelicerae. According to Eskov and Zonshtein (p. 348) the chelicerae in Atypidae, Antrodiaetidae, and Mecicoboth-



Figs. 22–25. Maxillary glands. 22, 23. *Idiops clarus*. 24. *Diplura* sp. (Bolivia). 25. *Ischnothele* sp. (Venezuela).

riidae are “strongly gibbose dorsally with a well extended basal constriction.” Although the atypid chelicerae fit this description, the chelicerae of mecobothriids and antrodiatids seem in fact more similar to those of non-atypoid taxa. Because this cheliceral character, unique for atypids, would be uninformative, it is not included.

Pleurital expansions. This character had been found by Gertsch and Platnick (1979). The scoring of this character would be so

ambiguous as to render it completely uninformative; some kind of pleurital expansion exists in most, if not all, mygalomorphs, and intermediate degrees of development make it too difficult to score.

Thoracic fovea. Eskov and Zonshtein claimed (p. 351) that the shape of the thoracic fovea supports the monophyly of both the atypoid and non-atypoid lineages. They, however, contradict themselves when they say that “a few genera (*Microhexura* in ther-

aphosoids, *Atypus*, *Sphodros* and *Aliatypus* in atypoids) independently retain the ancestral modality of this structure."

"*Structure of the male palp.*" According to Eskov and Zonshtein, the structure of the male palp supports the monophyly of both the atypoid and non-atypoid lineages. Those conclusions, however, are based on a highly speculative reconstruction of the evolution of the bulb sclerites. They claim to have identified homologies between the bulbs in Mesothelae and mygalomorphs, despite hypothetical exchanges in position between the sclerites. Since one of the main criteria for homology is relative position, the identification of the sclerites as "the same" must thus be based on the other main criterion: intrinsic similarity (see Coddington, 1989, and Lipscomb, 1992, for a review of the criteria for homology). Eskov and Zonshtein, however, do not mention what structural details led them to recognize the sclerites even after the changes in position they postulated, and in studying the relevant taxa I was unable to find similarities which could support Eskov and Zonshtein's claims.

Strongly enlarged cymbium. Although in both atypids and meciobothriids the cymbium is elongated, the structure in each family is different. In meciobothriids, unlike atypids, the palpal tarsus is long and narrow. The character is considered (contra Eskov and Zonshtein) not to provide evidence of monophyly for meciobothriids plus atypids.

Number of cardiac ostia. The number of cardiac ostia is known for only a couple of the taxa included in the present data set. Until more taxa are examined for this character, it is unlikely to provide useful information.

RESULTS AND DISCUSSION

PRELIMINARY ANALYSES

Initial analyses were conducted using Hennig86 to find shortest trees with all the characters equally weighted. Raven (1985) defended his cladogram on the basis of comparisons of simple step differences; he did not make explicit reference to weighting. The final results presented in this paper include character weighting, so the question might be raised whether the difference in results from

Raven (1985) is due to a different treatment of the data. This section describes results obtained under equal, unitary weights for all characters, which are therefore more comparable with Raven's results.

Hennig86 produced 82 equally parsimonious trees, 227 steps long. Neither Tuberculotae nor Fornicephale, Hexathelidae, Dipluridae, Nemesiidae, or Cyrtoucheniidae appeared as monophyletic. Except for the relationships of hexathelids and non-diplurine diplurids, the trees were quite similar to those produced in the final analyses (shown in fig. 26). The strict consensus showed Atypidae plus Antrodiaidae, *Euagrus* plus *Chilehexops*, *Ischnothele*, *Porrhothele*, *Atrax*, and *Scotinoecus* plus *Hexathele* as successive sister groups of *Diplura* plus the rest of the mygalomorphs. Those trees thus require a regain of ALS for *Scotinoecus* plus *Hexathele*. *Diplura* clustered with clade 66 (of fig. 26), based on the shared absence of tarsal spines, two rows of STC teeth, scopula, and male tibial apophysis (those characters were reversed or modified in some Rastelloidina, clade 65 in fig. 26). The shortest trees in which Dipluridae was monophyletic required three more steps than the shortest trees; the shortest trees in which Hexathelidae was monophyletic required only one. Making Nemesiidae monophyletic required five additional steps. The character considered by Raven (1985) as a synapomorphy of Nemesiidae, the presence of two rows of teeth on the paired tarsal claws, was a synapomorphy at a much higher level even if Nemesiidae was held monophyletic. The microstigmatids appeared as a group within Nemesiidae, as suspected by Raven (1985: 65).

Although the shortest trees in which Dipluridae, Hexathelidae, or Nemesiidae were monophyletic were only slightly inferior to the most parsimonious trees, the case was different for other groups proposed by Raven (1985) that did not appear on the cladograms. Constraining Cyrtoucheniidae to be monophyletic required nine additional steps (many apomorphies shared by *Myrmekiaphila* and the other rastelloids are absent in aporoptychines).

Raven's cladogram required 37 additional steps over the shortest tree found (the taxa not considered by him, *Xenonemesia* and the

new genera from Mexico and Ecuador, were in their most parsimonious placements).

How much did it cost to make monophyletic both Fornicephalae and Tuberculotae, the two main branches in Raven's cladogram? Constraining those two groups to be monophyletic required 11 additional steps. The consensus of the resulting trees would differ from the one in figure 26 in moving the Rastelloidina to the basal part of the cladogram (with *Rhytidicolus* clustering with *Bolostromus* plus *Fufius* instead of being the sister group of the other Rastelloidina), and in having less resolution. The 11 additional steps necessary to make Fornicephalae and Tuberculotae monophyletic indicate that, on a global analysis under the assumption of equal weights, those two groups could be clearly rejected. It is interesting that if the monophyly of all the families were assumed prior to the analysis, the shortest trees would be only six steps longer than those in which Tuberculotae and Fornicephalae were also monophyletic. If one relied on the monophyly of all the families—as Raven (1985) had to—the rejection of Tuberculotae and Fornicephalae would have been much less evident than in a global analysis.

The groups Tuberculotae and Fornicephalae were in conflict with the dichotomy of atypoid vs. non-atypoid mygalomorphs. Platnick (1977) had shown that all the characters shared by the Atypoidea (sensu Simon, 1892, i.e., atypids, antrodiaetids, and meci-cobothriids) were plesiomorphies. Because there were several differences among atypoids and non-atypoids, the implication was that the non-atypoids—which had all the apomorphic states for the characters differing in both groups—were probably monophyletic. Contrary to what might have been expected after Platnick's study, Raven's (1985) analysis considered not only the atypoids, but also the non-atypoids, to be nonmonophyletic groups. Although Raven of course based his rejection of the non-atypoids on several (previously ignored) characters, his familial cladogram (Raven, 1985: fig. 1) shows numerous parallelisms between the Fornicephalae and Tuberculotae—corresponding to the characters potentially defining the non-atypoids.

The results for the complete data set were

essentially paralleled if all the characters not considered by Raven (1985) were deactivated. That resulted in multiple equally parsimonious trees, the consensus of which was consistent with the tree in figure 26, and for which the non-atypoids *did* form a monophyletic group; neither Dipluridae, nor Nemesiidae, nor Hexathelidae appeared as monophyletic. Constraining all the families to be monophyletic, given Raven's characters, required eight steps beyond those required for the unconstrained data; constraining Tuberculotae and Fornicephalae to be monophyletic cost four steps, but if all the families were constrained to be monophyletic, the shortest trees in which Fornicephalae and Tuberculotae were monophyletic were only three steps longer than those in which they were not.

Two things can be concluded at this point. First, the differences between Raven's cladogram and the shortest trees found were caused not so much by the addition of the new characters, but by making the analysis global, without constraining the families to be monophyletic. Second, given his data and the constraints necessary for a hand analysis, Raven (1985) was impressively close to an optimal solution.

FINAL RESULTS

The final analyses included a more careful consideration of the reliability of the characters (as discussed above under Methods), producing a more realistic treatment. At this stage of the analysis, Pee-Wee was used to search for trees.

The data set in table 1 produced 36 trees of maximum fit, 366.9, and 228 steps. Figure 26 shows the strict consensus of those trees. For any of the resolutions of the trichotomies of clades 72 and 52, the characters could be optimized such that there is change along the branch, but alternative optimizations not involving change exist, so that no resolution is actually supported. The polytomy of clade 64 is the consensus of four parsimonious possibilities (shown in fig. 27); each of those possibilities, again, implies the same number of steps for every character in the data set, and is potentially supported only by ambiguous optimizations. The fit and weight (i.e., the

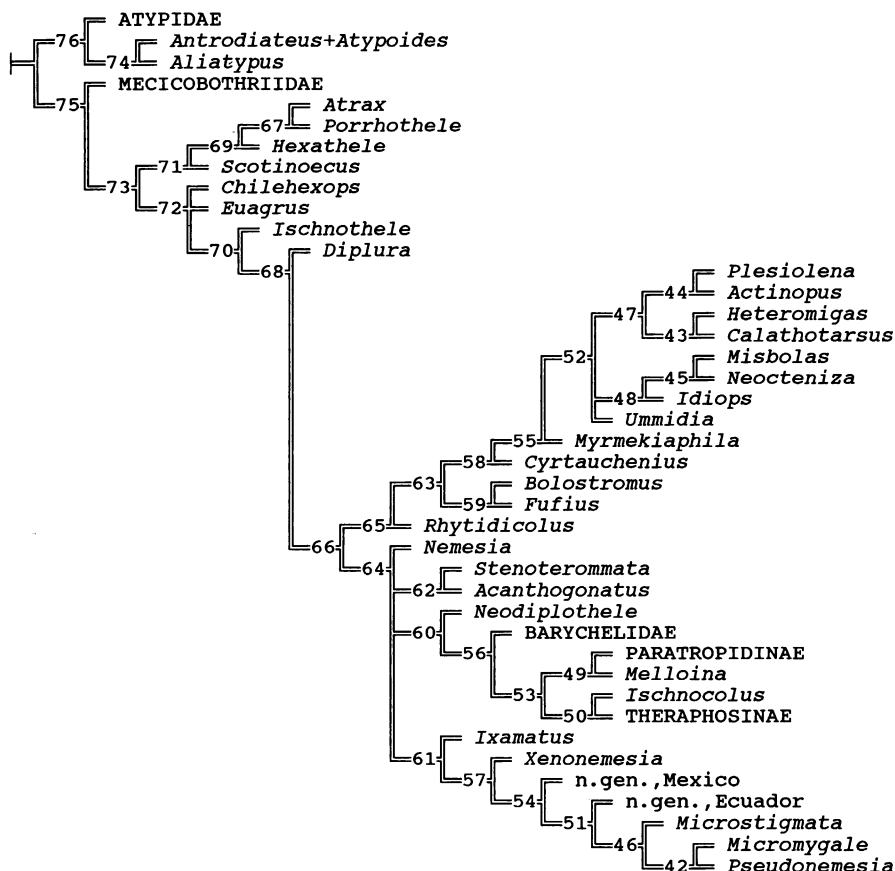


Fig. 26. Cladogram for taxa in table 1. The four possible resolutions of the polytomy of clade 64 are shown in figure 27.

cost of adding a step under the fitting function used) for each character are shown in table 2.

Note that the fittest trees are one step longer than the shortest trees for equally weight-

ed characters (reported in the preceding section); a comparison of those trees may clarify the way in which the weighting method used here works. The fittest trees save one step in

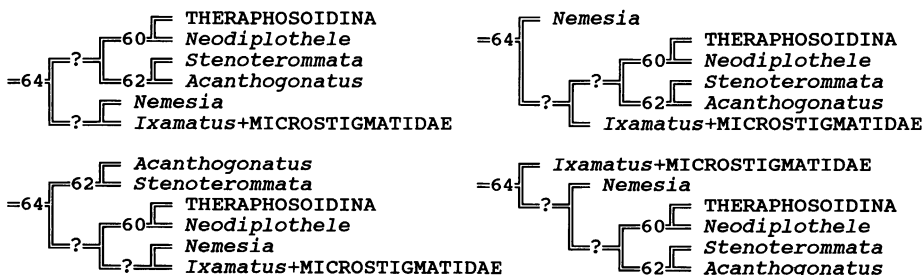


Fig. 27. The four resolutions of clade 64; components not occurring in the four trees are indicated by "?."

TABLE 2

Character Fits and Weights

("Steps" does not include the steps within terminals; "step cost" is the difference in fit produced by adding a step to the character)

Char	Fit	Steps	Step cost
0	5.0	2	1.7
1	5.0	2	1.7
2	1.4	6	0.1
3	1.3	8	0.2
4	3.3	5	0.4
5	10.0	1	5.0
6	2.0	4	0.3
7	3.3	3	0.8
8	10.0	3	2.5
9	1.4	6	0.1
10	5.0	2	1.7
11	2.0	5	0.3
12	5.0	2	1.7
13	5.7	7	0.7
14	3.3	3	0.8
15	5.0	2	1.7
16	3.3	3	0.8
17	2.5	4	0.5
18	5.0	2	1.7
19	3.3	3	0.8
20	5.0	2	1.7
21	5.0	2	1.7
22	1.7	5	0.3
23	2.0	5	0.3
24	3.3	3	0.8
25	10.0	2	3.3
26	3.3	3	0.8
27	5.0	2	1.7
28	10.0	1	5.0
29	1.3	7	0.2
30	1.7	6	0.3
31	10.0	1	5.0
32	5.0	2	1.7
33	10.0	1	5.0
34	1.7	5	0.3
35	10.0	1	5.0
36	2.5	3	0.5
37	10.0	1	5.0
38	3.3	6	0.4
39	6.7	3	1.7
40	3.3	3	0.8
41	1.7	4	0.3
42	3.3	3	0.8
43	5.0	2	1.7
44	4.4	9	0.4
45	3.3	3	0.8
46	4.0	4	0.7
47	2.5	4	0.5

TABLE 2—(Continued)

Char	Fit	Steps	Step cost
48	5.0	2	1.7
49	3.3	6	0.4
50	2.5	8	0.3
51	5.0	2	1.7
52	3.3	3	0.8
53	5.0	2	1.7
54	5.0	2	1.7
55	3.3	3	0.8
56	10.0	1	5.0
57	2.5	4	0.5
58	10.0	1	5.0
59	5.0	2	1.7
60	5.0	2	1.7
61	10.0	2	3.3
62	10.0	1	5.0
63	5.0	2	1.7
64	10.0	1	5.0
65	10.0	1	5.0
66	10.0	1	5.0
67	4.2	12	0.4
68	10.0	1	5.0
69	5.0	2	1.7
70	10.0	1	5.0

characters 15 (numerous labial cuspules), 30 (type of trichobothrial bases), and 36 (separation of PMS and PLS), while requiring two additional extra steps in character 9 (teeth of the ITC), and one in characters 6 (maxillary cuspules) and 44 (tarsal trichobothrial pattern). All of the characters in which steps could be saved (as well as character 30) have three or more extra steps in both the fittest and the shortest trees. In contrast, character 15 has only one extra step on the fittest tree, and character 36 only two. The fittest tree, although slightly longer, saves steps for those characters which have less homoplasy, and is therefore to be preferred.

Most of the groupings that were not supported in the preceding analysis, are not supported, either, when the reliability of the characters is taken into account. These groups are, again, Nemesiidae, Dipluridae, and Cyrtaucheniidae among the families, and Fornicephalae and Tuberculotae among the higher taxa; Microstigmatidae is placed within the paraphyletic Nemesiidae. Hexatheliidae appears as monophyletic, and the pres-

TABLE 3
Comparison with Other Trees

(For all the characters indicated, the trees in which the corresponding group is monophyletic require either one more or one less step than the fittest tree; the difference in fit for those characters is shown in parentheses)

Monophyletic taxon	Total fit diff.	Characters with worse fit	Characters with better fit
Dipluridae	1.6	3 (0.2); 11 (0.3); 13 (0.7); 44 (0.4); 46 (0.7); 67 (0.4)	34 (0.3); 36 (0.8)
Nemesiidae	0.5	12 (1.7); 42 (0.8); 44 (0.4); 50 (0.3)	4 (0.7); 40 (1.7); 41 (0.3)
Cyrtauch.	9.4	0 (1.7); 1 (1.7); 13 (0.7); 16 (0.8); 18 (1.7); 20 (1.7); 23 (0.3); 44 (0.4); 53 (1.7); 54 (1.7); 67 (0.4)	45 (1.7); 52 (1.7)
Forniceph. and Tubercul.	25.6	3 (0.2); 4 (0.4); 5 (5.0); 6 (0.3); 7 (0.8); 11 (0.3); 13 (0.7); 21 (1.7); 25 (3.3); 28 (5.0); 30 (0.3); 34 (0.3); 38 (0.4); 39 (1.7); 44 (0.4); 46 (0.7); 49 (0.4); 58 (5.0); 61 (3.3)	2 (0.3); 17 (0.8); 29 (0.1); 45 (1.7); 52 (1.7)

ence of ALS in *Hexathele* and *Scotinoecus* is a plesiomorphic retention.

Table 3 shows the difference in fit and steps between the best tree and trees in which some groups were constrained to be monophyletic.

For some of the unsupported groups, a relatively small difference in total fit is required to make them monophyletic. If Nemesiidae is made a monophyletic group (but still allowing microstigmatids to be part of the family), the fittest trees account better for the labium length, male bulb ridges, and intercheliceral tumescence, but not as well for the presence of claw tufts, clavate trichobothria, and tarsal trichobothrial pattern, in *Neodiplothele*; the former three characters have more homoplasy than the latter three, and so the total fit favors the tree in which *Neodiplothele* clusters with Theraphosoidina. The trees in which nemesiids form a monophyletic group, and the trees in which they do not, account equally well for the dentition of the paired claws, which is plesiomorphic for nemesiids in both cases. Although microstigmatids are part of Nemesiidae, the presence of scaly cuticle (character 24) in microstigmatids and *Ixamatus* is still more parsimoniously optimized as a parallelism, thereby supporting Raven and Platnick's (1981) hypothesis that the cuticular modifications in both groups are independent.

A greater decrease in fit is required to make

Dipluridae monophyletic. Those trees account more poorly for the absence of tarsal spines, presence of scopula, double row of teeth on the paired claws, zig-zag trichobothrial pattern, unpaired spermathecae, and apical retrolateral male tibial apophysis, shared between *Diplura*, Theraphosoidina + Nemesiidae (clade 64), and (plesiomorphically) the Rastelloidina. It should be pointed out that the advancement of the female palpal claw teeth, and the widening of the paired tarsal claws, which were not included in the data set (on the grounds that they are necessary correlates of the presence of two rows of teeth; see above under Characters), would only strengthen the difference in fit between the best trees and those in which Dipluridae is monophyletic.

The decrease in fit is even greater to make the Cyrtauchenidae monophyletic. *Myrmekeiaphila* shares with the Actinopodidae, Idiopidae, and *Ummidia* the reduction in the tarsal claw teeth, the tarsal trichobothrial pattern, and the presence of two cheliceral tooth rows; and *Cyrtauchenius* shares with that group the shortening of the apical article of the PLS and the strengthening of the posterior legs.

The characters that traditionally had been used in the dichotomy atypoids/non-atypoids fit the best trees very well; those character are disregarded when making mono-

phyletic Fornicephalae and Tuberculotae, resulting in a difference of total fit of 25.6. Then, according to the present results, the traditional division Atypoidea/non-Atypoidea suffered only from the problem of paraphyly of Atypoidea (hardly surprising, since that group was based on plesiomorphies), but not from the problem of polyphyly (since non-Atypoidea was based on real homologies).

Are those comments to be taken as an imprimatur on the views of Eskov and Zonshtein (1990)? Certainly not. Those authors have recently attacked Raven (1985) and his methodology. They propose that Atypidae, Antrodiaetidae, and Mecicobothriidae form a monophyletic group. Although (as shown here) there are good grounds to think that the rest of mygalomorphs form a monophyletic group, no real evidence for the monophyly of Atypidae, Antrodiaetidae and Mecicobothriidae has been produced by Eskov and Zonshtein (some of the characters they proposed are discussed above). In fact, if all the families are scored for the characters they proposed, the shortest trees do not have that group as monophyletic (the consensus of the 51 equally parsimonious trees includes a monophyletic non-Atypoidea, with Micromygalinae, Atypidae plus Mecicobothriidae, and Antrodiaetidae, as their successive sister groups). The few characters that Eskov and Zonshtein themselves propose to use argue against their own conclusions. Many characters proposed by Raven (1985) were disregarded as irrelevant or simply not mentioned by Eskov and Zonshtein. This obscures, more than it enlightens, the nature of the problem. Although Raven (1985) may have failed to find an optimal solution for the problem at hand, he certainly tried to consider all the evidence—and in so doing greatly facilitated subsequent work on the problem.

SYNAPOMORPHIES

The character changes supporting the branches of the tree in figure 26 are shown in table 4.

Some traditional characters fit the tree well. Among those are the characters traditionally used to define the non-atypoids. Platnick and Gerstch (1976) had proposed that the pres-

ence of paired spermathecae (character 46) might be plesiomorphic for mygalomorphs plus araneomorphs. According to the present results, the paired spermathecae are indeed the plesiomorphic state for mygalomorphs (including non-diplurine diplurids and some hexathelids). The change to unpaired spermathecae defines a large group of mygalomorphs, including diplurines, Rastelloidina, and Crassitarsae (theraphosids + paratropidids + barychelids + nemesiids + microstigmatids), with a parallelism in some hexathelids.

Another character which shows little homoplasy, and received a high weight in the analysis, is the presence of spigots on the basal article of the PLS (character 39). Both Mesothelae and Araneomorphae lack such spigots, as do the Atypidae, Antrodiaetidae, and Mecicobothriidae; the presence of spigots on the basal article of the PLS is thus one of the synapomorphies of the non-Atypoidea. Secondary losses of the spigots on the basal article of the PLS characterize a group within Microstigmatidae (where the spigots of the medial article of the PLS are also lost) and the Migidae. This character may shed some light on the placement of the recently described Triassic genus *Rosamygale* Selden and Gall (1992). Those authors placed the genus with doubts in the Hexathelidae; the labial cuspules apparently were not preserved, but the spigots were. Selden and Gall stated that the spigots "occur . . . distally and laterally along the length of the PLS" (Selden and Gall, 1992: 228). If that means that the spigots were absent from the basal article of the PLS, the genus should be excluded from the Hexathelidae (and possibly from the Orthopalpae, as redefined below). All the hexathelids examined for this study (the genera included in the matrix, plus *Mediothele*, *Teranodes*, *Macrothele*, and *Bymainiella*) have spigots on the basal article of the PLS.

The presence of two rows of teeth (character 13), scopula (character 11), a zig-zag row of tarsal trichobothria (character 44), the reduction of tarsal spines (character 3), and the already mentioned paired spermathecae, are the synapomorphies of diplurines plus Crassitarsae and Rastelloidina. Most of those characters are reversed or modified within Rastelloidina.

TABLE 4
Synapomorphies

(Asterisks [*] indicate character changes that occur in only some of the resolutions of clade 64)

Taxon	Changes
Mygalomorphae	24 (0 > 1), 46 (0 > 2), 49 (0 > 2), 51 (1 > 0), 38 (none, 0 > 2, 1 > 2), 50 (none, 0 > 1)
Atypidae	14(0 > 1), 18 (0 > 1), 20 (0 > 1), 47 (0 > 1), 50 (none, 0 > 1), 55 (0 > 1)
<i>Antrod</i> + <i>Atypoides</i>	3 (0 > 1), 29 (0 > 1)
<i>Aliatypus</i>	23 (0 > 1)
Mecicobothriidae	3 (0 > 1), 4 (1 > 0), 14 (0 > 1), 29 (0 > 1)
<i>Scotinoecus</i>	9 (none, 0 > 1), 36 (none, 0 > 1)
<i>Hexathele</i>	44 (none, 4 > 0)
<i>Atrax</i>	9 (none, 0 > 1), 44 (none, 4 > 0), 67 (none, 1 > 2)
<i>Porrhothele</i>	3 (0 > 1), 9 (none, 1 > 0), 34 (0 > 1), 44 (none, 0 > 4)
<i>Chilehexops</i>	—
<i>Euagrus</i>	67 (0 > 2)
<i>Ischnothele</i>	23 (0 > 1), 29* (none, 0 > 1), 49 (none, 0 > 2)
<i>Diplura</i>	29 (none, 0 > 1), 49 (none, 2 > 0), 50* (none, 0 > 1)
<i>Melloina</i>	—
Paratropidinae	11 (1 > 0), 12 (1 > 0), 13 (4 > 3), 23 (0 > 1), 29 (1 > 0), 42 (1 > 0), 43 (1 > 0), 49 (none, 1 > 2), 50 (none, 0 > 2), 67 (4 > 0)
<i>Ischnocolus</i>	2 (0 > 1), 13 (4 > 1), 34 (0 > 1)
Theraphosinae	29 (1 > 0)
Barychelidae	47 (0 > 1), 54 (1 > 0), 13 (none, 4 > 2)
<i>Neodiplohele</i>	13 (none, 2 > 4), 40* (none, 0 > 1),

TABLE 4—(Continued)

Taxon	Changes
	41 (none, 0 > 1), 67 (none, 3 > 0, 4 > 0)
<i>Ixamatus</i>	22 (none*, 1 > 0), 24 (0 > 1)
<i>Xenonemesia</i>	41 (0 > 1), 67 (3 > 0)
<i>Micromygalae</i>	6 (1 > 0), 7 (1 > 0), 9 (1 > 0), 13 (2 > 0)
<i>Microstigmata</i>	30 (1 > 0), 50 (none, 1 > 2)
<i>Pseudonemesia</i>	—
Ecuador	46 (1 > 2)
Mexico	32 (0 > 1), 38 (2 > 1)
<i>Nemesia</i>	17* (none, 0 > 1), 40 (none*, 0 > 1), 57 (0 > 1)
<i>Stenoterommata</i>	40 (none, 0 > 1)
<i>Acanthogonatus</i>	22 (1 > 0), 40* (none, 1 > 0)
<i>Heteromigas</i>	30 (none, 0 > 1)
<i>Calathotarsus</i>	41 (0 > 1), 67 (0 > 3), 30 (none, 1 > 0)
<i>Actinopus</i>	59 (none, 0 > 1)
<i>Plesiolenia</i>	9 (1 > 0), 26 (1 > 0), 44 (1 > 4)
<i>Idiops</i>	30 (1 > 0), 51 (1 > 0), 69 (0 > 1), 67 (none, 0 > 5)
<i>Neocteniza</i>	6 (1 > 0), 27 (0 > 1), 55 (0 > 1), 63 (0 > 1), 50 (none, 1 > 0), 67 (none, 5 > 0)
<i>Misgolas</i>	3 (0 > 1), 11 (0 > 1), 26 (1 > 0), 44 (1 > 0), 67 (none, 0 > 5)
<i>Ummidia</i>	42 (0 > 1), 59 (none, 1 > 0)
<i>Myrmekiaphila</i>	—
<i>Cyrtauchenius</i>	—
<i>Bolostromus</i>	—
<i>Fufus</i>	2 (0 > 1), 57 (0 > 1)
<i>Rhytidicolus</i>	3 (1 > 0), 44 (0 > 1), 19 (none, 0 > 1), 45 (none, 0 > 1), 49 (none, 1 > 2), 50* (none, 1 > 0), 52 (none, 0 > 1)

TABLE 4—(Continued)

Taxon	Changes
Clade 42	25 (1 > 2), 38 (2 > 1), 61 (1 > 2)
Clade 43	16 (1 > 0), 17 (1 > 0), 39 (1 > 0), 47 (1 > 0), 57 (0 > 1), 68 (0 > 1), 69 (0 > 1), 70 (0 > 1)
Clade 44	4 (1 > 2), 45 (0 > 1), 63 (0 > 1), 64 (0 > 1), 30 (none, 1 > 0)
Clade 45	57 (0 > 1)
Clade 46	10 (1 > 0)
Clade 47	27 (0 > 1), 52 (0 > 1), 55 (0 > 1), 30 (none, 1 > 0)
Clade 48	21 (1 > 0), 31 (0 > 1), 32 (0 > 1), 33 (0 > 1), 50 (none, 1 > 0), 56 (0 > 1), 67 (none, 0 > 5)
Clade 49	3 (1 > 0), 30 (1 > 0), 38 (1 > 2), 49 (none, 1 > 2), 62 (0 > 1), 50 (none, 0 > 2), 66 (0 > 1)
Clade 50	35 (0 > 1)
Clade 51	2 (0 > 1), 24 (0 > 1)
Clade 52	3 (1 > 0), 11 (1 > 0), 26 (0 > 1)
Clade 53	4 (none, 0 > 1), 13 (none, 2 > 4), 14 (0 > 1), 15 (none, 0 > 1), 22 (1 > 0)
Clade 54	39 (1 > 2), 50 (none, 1 > 2)
Clade 55	13 (2 > 3), 23 (0 > 1), 44 (0 > 1)
Clade 56	4 (none, 0 > 1), 15 (none, 0 > 1), 41 (none, 1 > 0), 43 (0 > 1), 67 (none, 0 > 4, 3 > 4)
Clade 57	37 (0 > 2), 22* (none, 0 > 1)
Clade 58	18 (0 > 1), 19 (none, 0 > 1), 20 (0 > 1), 22 (0 > 1),

TABLE 4—(Continued)

Taxon	Changes
	45 (none, 1 > 0), 49 (none, 1 > 2), 52 (none, 1 > 0), 53 (1 > 0), 54 (1 > 0), 67 (3 > 0)
Clade 59	4 (1 > 2), 19 (none, 1 > 0), 34 (0 > 1), 45 (none, 0 > 1), 49 (none, 2 > 1), 52 (none, 0 > 1)
Clade 60	12 (0 > 1), 13 (none, 2 > 4), 42 (0 > 1), 44 (0 > 2), 67 (none, 3 > 0, 3 > 4)
Clade 61	11 (1 > 0), 38 (none*, 1 > 2)
Clade 62	2 (0 > 1), 40 (none, 0 > 1), 65 (0 > 1)
Clade 63	0 (1 > 0), 1 (1 > 0), 16 (0 > 1), 29* (none, 1 > 0), 50* (none, 0 > 1)
Clade 64	4 (1 > 0), 10 (0 > 1), 22 (none*, 0 > 1), 49 (none, 0 > 1, 2 > 1), 59 (none, 0 > 1)
Clade 65	8 (1 > 2), 17 (none*, 0 > 1), 19 (none, 0 > 1), 47 (0 > 1), 45 (none, 0 > 1), 52 (none, 0 > 1)
Clade 66	2 (1 > 0), 17* (none, 0 > 1), 29* (none, 0 > 1), 34 (1 > 0), 36 (1 > 0), 48 (1 > 0), 60 (1 > 0), 49 (none, 0 > 1, 2 > 1), 59 (none, 0 > 1)
Clade 67	7 (0 > 1), 23 (0 > 1), 36 (none, 1 > 0), 67 (none, 1 > 2)
Clade 68	3 (0 > 1), 9 (0 > 1), 11 (0 > 1), 13 (0 > 2), 44 (4 > 0), 46 (0 > 1), 50 (none*, 0 > 1)
Clade 69	46 (0 > 1), 44 (none, 4 > 0)
Clade 70	6 (0 > 1), 67 (0 > 3), 29 (none, 0 > 1), 49 (none, 0 > 2)

TABLE 4—(Continued)

Taxon	Changes
Clade 71	6 (0 > 1), 9 (none, 0 > 1), 15 (0 > 1), 67 (0 > 1)
Clade 72	7 (0 > 1), 30 (0 > 1), 34 (0 > 1), 36 (none, 0 > 1)
Clade 73	5 (0 > 1), 8 (none, 0 > 1), 21 (0 > 1), 25 (0 > 1), 28 (1 > 0), 36 (none, 0 > 1), 39 (0 > 1), 61 (0 > 1)
Clade 74	8 (0 > 3), 9 (0 > 1), 17 (0 > 1), 50 (none, 1 > 0), 53 (none, 1 > 0)
Clade 75	0 (0 > 1), 1 (none, 0 > 1), 2 (none, 0 > 1), 8 (none, 0 > 1), 38 (none, 0 > 1, 2 > 1), 44 (none, 3 > 4), 48 (0 > 1), 50 (none, 1 > 0), 58 (0 > 1), 53 (none, 0 > 1)
Clade 76	1 (none, 1 > 0), 2 (none, 1 > 0), 16 (0 > 1), 19 (0 > 1), 60 (1 > 0), 38 (none, 1 > 0, 2 > 0), 44 (none, 4 > 3)

The cladograms obtained also reflect quite well the developmental characters (characters 59, 60); although the development of many taxa has not been studied, the optimization of those characters on the trees leads to predictions that second instar larvae of unstudied taxa in the Rastelloidina and Crasitarsae (including Microstigmatidae) should have a bent cephalothorax, and unstudied taxa in the Mecicobothriidae and Hexathelidae should have the cephalothorax and abdomen in the same plane. Because there are many missing entries for these characters there is some ambiguity in their optimization.

Among the characters that fit the tree most poorly are the tarsal spines (character 3, with a fit of 1.3), the reduction of the ITC teeth (character 9, 1.4), the domed apical article of the PLS (character 22, 1.7), the male tarsi

pseudosegmented (character 29, 1.3), and the intercheliceraral tumescence (character 41, 1.7); most of them were already known to be of limited use at higher levels.

The data set did not include any behavioral characters. An interesting implication of the present results is that making webs could be a synapomorphy for all the mygalomorphs excluding Atypidae plus Antrodiaetidae (i.e., clade 76), secondarily lost in most mygalomorphs. *Scotinoecus* (personal obs.) and *Porrhothele*, as well as mecicobothriids and diplurids, build webs used in prey capture. Thus, the Rastelloidina (including the trapdoor spiders), would be burrowers secondarily. In support for that idea, it can be mentioned that the "cyrtoucheniid" *Fufius* (basal to the rastelloid clade) lives in silken tubes in crevices, prolonged with silk (personal obs.), and (as in some nemesiids, such as *Acanthogonatus*) those constructs might represent reduced "webs."

SOME SELF CRITICISM

Besides the ambiguity in the resolution of clade 64, there are several potential problems with the above analysis. First, some alternative topologies have a fit almost as good as that for the tree in figure 26, which is thus only slightly preferable to them. The area with more character conflict seems to be the basal part of the tree, i.e., that part comprising the hexathelids and non-diplurine diplurids. For example, if Hexathelidae is made paraphyletic (by placing *Euagrus* as the sister group of *Chilehexops*, then moving clade 71 as the sister group of *Porrhothele*, and clade 68 as the sister group of clade 67), the difference in total fit is only 0.3. That tree would sacrifice two steps in character 15, and one in characters 30 and 67, and would save one step in characters 7, 9, 34, and 44. Both trees would have the same length; but the former three characters show less homoplasy than the latter four, hence the total fit weakly favors the monophyly of Hexathelidae.

Second, the analysis is based on only some taxa. Including more taxa may greatly change the outcome (examples abound in the cladistic literature!); the only way to have a cladogram guaranteed to be optimal when all the mygalomorph genera are considered is to

conduct a global parsimony analysis of *all* those genera. Pee-Wee, the computer program used here to search for trees, certainly could not handle a data set including the estimated 250 mygalomorph genera, and, especially, no arachnologist has yet been able to gather that huge amount of information in the form of a data matrix. This problem can be overcome by a judicious choice of taxa; if taxa including all the relevant character combinations are included in the analysis, the results are more likely to be stable under the addition of new taxa. There are several taxa, not included in the present analysis, which might introduce important modifications. Among those are some Cyrtacheniiidae (a group which is basal to the Rastelloidina), and several "nemesiid" genera.

Third, for the results based on the weighting method used here to be correct, it is necessary that the present data set adequately represents the relative amounts of homoplasy of the characters. I suspect that the weights assigned would not change much if more genera were included, but that could only be determined by adding them.

Fourth, the characters that support many of the branches in the cladogram appear very weak. Table 4 lists the actual or potential synapomorphies for each clade in figure 26. Many of the characters can be optimized, along some branches, in different ways (in most cases, either as two gains or as a gain and subsequent loss), and they do not constitute actual support for a hypothesis of monophyly. This problem is somewhat related to the previous two, in that the ambiguity could be overcome by adding taxa.

Fifth, there is a regain of ALS in *Micromygale*. Arachnologists have always been reluctant to pose multiple appearances of organs as complex as spinnerets or the cribellum (see Platnick, 1977, for discussion) and have favored secondary losses. Raven (1985) has suggested that many of the apparent plesiomorphies in *Micromygale* may be neotenually correlated with the small size and that the apparently "apomorphic" states in the other microstigmatids would actually be the original (adult) characters, which might place microstigmatids close to nemesiids, or barychelids, or both. Whether or not neoteny is the explanation for that phenomenon, the

cladogram in figure 26 suggests indeed that most of the apparent "apomorphies" for some microstigmatids are the plesiomorphic states for the group, reversed in *Micromygale*. Among these reversals is the "plesiomorphic" presence of ALS. The fittest trees I was able to find in which the presence of ALS in *Micromygale* was a plesiomorphic retention imply the polyphyly of Microstigmatidae and require a decrease of total fit of 10.9. Since not allowing spinnerets to be regained would imply disregarding other lines of evidence solely to fit the preconception (which I myself share!) that gaining an extra pair of spinnerets is much rarer than losing it, the implications of the present data are followed and *Micromygale* is considered as the most apomorphic (instead of the most plesiomorphic) representative of the Microstigmatidae.

NOMENCLATURAL IMPLICATIONS

The results of the present study suggest that the groups Fornicephalae and Tuberculotae will have to be abandoned. As suspected by Platnick (1977), Atypoidea in the traditional sense (i.e., that of Simon, 1892) is a paraphyletic group. However, the group could be made monophyletic just by excluding the Mecicobothriidae (and would then agree with the Atypoidea of Simon, 1903). Names for a few of the other higher taxa in the cladogram have already been proposed by some arachnologists. However, some of those names have been used by other workers to refer to different groups. For example, Aviculariidae designated all mygalomorphs except atypids, antrodiaetids, and mecicobothriids for Simon (1892), but included mecicobothriids for Simon (1903); Ctenizoidea corresponded to the Aviculariidae of Simon (1892) for Chamberlin and Ivie (1945), but to Ctenizidae, Atypidae, Migidae, and Paratropididae for Savory (1926). This makes it difficult to decide which choice would imply greater nomenclatural stability. By using Avicularioidea to refer to mecicobothriids plus the rest of non-atypoids (i.e., Aviculariidae sensu Simon, 1903), the oldest name can be preserved. For the rest of the cladogram, Raven's (1985) classification is the only one that contains roughly corresponding groups. Thus, there are two options: either using Raven's names with some relimitation, or creating

completely new names. I prefer the first option, and propose to relimit both Orthopalpae and Quadrihelina to include also the Microstigmatidae and Rastelloidina (i.e., clades 73 and 72, respectively), and to relimit Crasitarsae to include the Microstigmatidae (i.e., clade 64). No author has so far proposed a group equivalent to clade 68; I propose the name *Bipectina* for that group.

At the family level, and given the problems discussed in the preceding section, the present results are considered too preliminary to warrant nomenclatural changes. If future studies support the hypotheses of relationships proposed here, the family Cyrtachenidae will require substantial changes in composition. Raven (1985: 65) had already suspected that the North American Euctenizinae could be more closely related to the other Rastelloidina than to the other "cyrtachenids." Euctenizinae may well deserve familial status (studies on North America rastelloids by Platnick and Gertsch may clarify this point). Even if euctenizines are excluded, however, Cyrtachenidae will still be a doubtful group; although the "typical" aporoptychines (Aporoptychini) share some synapomorphies, all the similarities between aporoptychines and *Cyrtauchenius* correspond to plesiomorphies in the present scheme of relationships, and *Cyrtauchenius* appears to be more closely related to the other Rastelloidina than to the aporoptychines. That might also be the case for the Australian *Kiama* (considered as Aporoptychinae incertae sedis by Raven, 1985: 63) and the African *Homostola*, not included in the present analysis.

The composition of the family Dipluridae had suffered major changes in recent years; Gertsch and Platnick (1979) separated the Mecicobothriidae (= Hexurinae); Raven (1980) separated the Hexathelidae and later (1985) the short-spinnereted diplurines. It seems likely that more pruning will be necessary in the future; possibly Dipluridae will have to be restricted to the diplurines (*Diplura*, *Trechona*, and *Linothele*). As already discussed, the non-diplurine diplurids form a gray area between the four-spinnereted taxa and the more plesiomorphic, six-spinnereted hexathelids and mecicobothriids.

The family Nemesiidae probably will have to be split in the future. Some genera previously included in the Nemesiidae are more closely related to genera included in the Microstigmatidae. Those are *Xenonemesia*, *Ixamatus*, *Xamiatus*, and possibly the neotropical *Spelocteniza* Gertsch, which has modified booklung openings, an elevated tarsal organ (contra Raven, 1985: 111), basal and medial article of the PLS without spigots, and cuticle apparently scaly (the topotypical specimens studied here were not examined with SEM). Thus, either Nemesiidae must be divided into several families or the Microstigmatidae must become a subfamily of Nemesiidae. More taxa should be included in the analysis to settle that question and allow an adequate rearrangement of the Nemesiidae.

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