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Clade stability and the addition of data: A case study from erigonine spiders (Araneae: Linyphiidae, Erigoninae)

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Abstract

This study presents a new phylogeny of erigonine spiders with emphasis on genera from the Neotropics. Thirty-nine exemplar taxa representing mostly Neotropical genera were added to a global sample of 31 erigonine and 12 outgroup exemplar taxa analyzed in a previous study. These 82 taxa were coded for 176 (172 informative) mostly morphological characters. Eighty-one characters were identical to or modified from the 73 (67 informative) characters included in a previous study; the remaining 95 characters are new. The complete data set includes 70 erigonine exemplars representing 65 genera, seven nonerigonine linyphiid exemplars, and five exemplars representing four araneoid families in the outgroup. Cladistic analysis resulted in a single most parsimonious tree (L = 904, CI = 0.23, RI = 0.58; uninformative characters excluded: L = 900, CI = 0.23). This paper explores the implications of the new topology for the evolution of several characters of interest in erigonine evolution. The phylogeny implies that the desmitracheate condition is a synapomorphy of erigonines, with a reversal to the haplotracheate condition in one large clade within Erigoninae. We infer that the loss of the paracymbium in Neotropical erigonines occurred twice and may have progressed by different evolutionary pathways. Our phylogeny differs markedly from the previous cladistic hypothesis of erigonine relationships. We investigate how the addition of characters and taxa (alone and together) have altered the earlier hypothesis of erigonine phylogeny. We conclude that topological changes from the previous study to the current one are largely the result of adding and modifying characters, not adding taxa. Continuous Jackknife Function (CJF) analysis predicts that the inclusion of additional character data will continue to imply changes in the relationships among taxa in our analysis.

With over 4200 described species, linyphiids are the most speciose family of web-building spiders (Platnick, 2004). Linyphiids are descendents of orb-weaving ancestors (Coddington, 1986a, 1990a,b; Wunderlich, 1986; Coddington and Levi, 1991; Hormiga et al., 1995; Griswold et al., 1998), although their webs are typically sheets of mesh with little geometric regularity. They attain their highest diversity in north temperate regions where they may account for about one to two thirds of the local spider species richness, especially at higher latitudes and colder places [e.g., Iceland: 61/84 = 72.6% (Agnarsson, 1996); Washington State: 265/760 = 34.9% (Crawford, 1988); Connecticut: 161/597 = 27.0% (Kaston, 1981); Finland: 91/154 = 59.1% (Koponen, 1976); Quebec: 246/623 = 39.5% (Paquin et al., 2001); Great Britain and Ireland: 261/642 = 40.7% (Roberts, 1993); Denmark: 82/149 = 55% (Toft, 1976)]. Erigoninae is the largest linyphiid subfamily. The taxonomic limits of Erigoninae are somewhat controversial and no contemporary circumscription dividing the world's 562 linyphiid genera (Platnick, 2004) among subfamilies is available. Erigonines are typically tiny spiders (1–3 mm in total length), although a few species attain lengths of up to 10 mm (Millidge, 1991). Erigonines are also found at tropical and south temperate latitudes, although this fauna has been relatively neglected compared to the Holarctic fauna. New Zealand lacks native erigonine species, but populations of several introduced species have been established (Millidge,

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1988a). Australia has been reported as having a small number of native erigonines (Wunderlich, 1976, 1995), but at least some of these accounts are erroneous (Platnick, 1997; Miller, in press a).

Brignoli (1983) was the last author to provide a comprehensive classification of linyphiid genera into subfamilies. Since that time, much has changed in linyphiid subfamily circumscription with several new subfamilies proposed, rejected, and ignored (van Helsdingen, 1986; Millidge, 1984a, 1993a). Although the subfamilial placement of many linyphiid genera is not controversial, there are enough ambiguously allied genera to make the task of generating a complete list of erigonine genera difficult. The evolution of a desmitracheate (median trunks highly branched) tracheal system and the loss of the distal macroseta on tibia IV have both been cited as diagnostic, if not synapomorphic, for erigonines (Locket and Millidge, 1953; Merrett, 1963; Blest, 1976; Millidge, 1980, 1984a, 1986, 1993a; Wunderlich, 1986; Hormiga, 1993, 1994a,b). Hormiga (2000) defined Erigoninae in cladistic terms citing the presence of a palpal tibial apophysis in the male and the loss of the palpal claw in the female as synapomorphies. Hormiga's (2000) analysis concluded that the desmitracheate condition is synapomorphic only for a large clade of erigonines, whereas loss of the second tibia IV macroseta supports an even less inclusive clade of erigonines.

Recent authors who attempted to create taxonomic groupings within Erigoninae largely failed to find agreement (Wiehle, 1960; Merrett, 1963, 1965; Blest, 1976; Millidge, 1977, 1984a, 1993a; Hormiga, 2000). The lack of stability among previous attempts to understand erigonine systematics suggested that erigonine relationships might prove to be a difficult question. Hormiga (2000) recovered six most parsimonious trees that could be summarized as a strict consensus tree with two trichotomies, one within Erigoninae (Fig. 1). Although his study was by far the most rigorous attempt to understand both erigonine relationships and relationships among linyphiid subfamilies, Hormiga (2000) stated that the addition of taxa and characters might lead to revisions of his hypothesis, especially given the relatively low Bremer support values at most nodes.

We built upon Hormiga's (2000) previous phylogenetic analysis of erigonine genera by adding mostly Neotropical exemplar taxa and mostly morphological characters to identify a new phylogeny. Although historically neglected, Neotropical linyphiid taxonomy has seen more activity in recent years (e.g., Millidge, 1985; 1991). Millidge advanced many new generic concepts covering a broad sample of erigonine diversity of South America. Millidge relied exclusively on the condition of the tracheal system to assign genera to subfamily, even when other characters indicated otherwise. For example, of the genus *Lygarina* Simon, 1894, Millidge (1991, p. 107) wrote, "The members of this genus have a simple tracheal system, and despite the very erigonine appearance, they cannot be regarded as members of the Erigoninae." Our goal was to add representatives of a broad sample of Neotropical erigonine genera. Because our concept of the limits of Erigoninae followed Hormiga (2000), not Millidge, many of the taxa we included were haplotracheate erigonines.

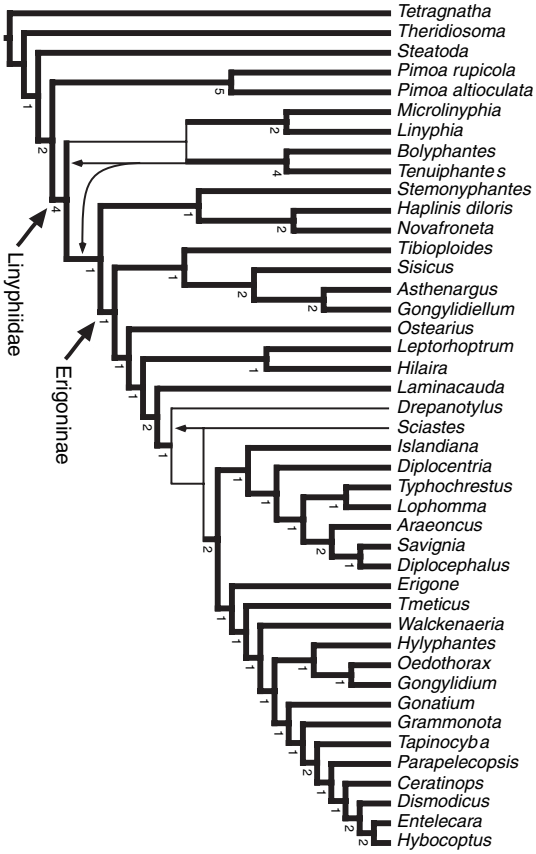

Fig. 1. Summary of six most parsimonious trees found by Hormiga (2000). The preferred tree is shown in rectangular form; alternative topologies are indicated by arrows. Thin lines indicate nodes that are collapsed in the strict consensus tree. Numbers next to nodes indicate Bremer support values.

There has been substantial discussion recently as to whether it is better to add taxa or characters to difficult phylogenetic problems. Studies in this field are diverse in their methodology and tend to reach one of two contradictory conclusions. Some find that increasing the number of characters and limiting the number of taxa is the best strategy for achieving a robust phylogeny (e.g., Kim, 1996, 1998; Poe, 1998; Rannala et al., 1998; Bremer et al., 1999; Poe and Swofford, 1999; Yoder and Irwin, 1999; Mitchell et al., 2000; Rosenberg and Kumar, 2001, 2002). Others conclude that increasing the density of taxon sampling improves results, often with the rationale that adding taxa may break up long branches (*sensu* Felsenstein, 1978, e.g., Hendy and Penny, 1989; Hillis,

1996, 1998; Graybeal, 1998; Pollock et al., 2002; Ryden and Källersjö, 2002; Zwickl and Hillis, 2002; Hillis et al., 2003; see also Poe, 2003 for a more nuanced view). As we have added both taxa and characters to a previous analysis, we were interested in exploring the effect of doing so on erigonine phylogeny. We propose a method based on Poe (1998) for assessing how the addition of taxa on the one hand and characters on the other have changed the topological results using two nested datasets.

Materials and methods

Abbreviations, conventions, and nomenclature

References to figures published elsewhere are listed in lowercase type (fig. or pl.); references to figures in this paper are listed with an initial capital (Fig.). Abbreviations related to anatomical structures and phylogenetic analysis are listed in Appendix A. Institutional abbreviations appear in the Acknowledgments.

New taxon names and nomenclatural changes referred to in this article follow Miller (in press a); they are disclaimed and unavailable for nomenclatural purposes (ICZN Art. 8.3). Miller (in press a) will provide diagnoses, descriptions, type designation, and formal synonymy for all new taxon names and nomenclatural acts referenced in this article.

Study design

Hormiga's (2000) analysis comprised 41 taxa including 31 erigonine exemplars scored for 73 morphological and behavioral characters, 67 of which were phylogenetically informative. This was the first attempt to use phylogenetic methods to resolve higher-level relationships within Erigoninae. We built on Hormiga's data matrix by adding new characters, modifying old characters, and adding new exemplar taxa. The current analysis features 82 taxa coded for 176 morphological characters, 172 of which are phylogenetically informative (Appendix B). Of the six uninformative characters in Hormiga's study, two have been modified and recoded to produce informative characters; the others remain uninformative. As in Hormiga's analysis, the majority of characters concern male genitalia, somatic morphology, and female genitalia; a few characters concern behavior and web architecture. Some taxonomic nomenclature has been updated from that found in Hormiga (2000) following Platnick (2004).

Taxon sampling

Hormiga (2000) suggested that future efforts in linyphiid phylogeny should focus on the relatively understudied faunas of the tropics and Southern Hemisphere. Our study was conducted in concert with a revision of Neotropical erigonine genera (Miller, in press a). The Neotropics are considered herein to include tropical Central and South America, temperate South America, and nearby South Atlantic and Pacific islands (Wallace, 1876). At least one exemplar species was included from every previously known endemic Neotropical erigonine genus for which at least a few specimens of each sex could be found; some new genera were also included (Appendix C). Miller (in press a) found that reports of some widespread genera previously thought to have representatives in the Neotropics were erroneous or dubious (e.g., *Macrargus* Dahl, 1886, *Minyriolus* Simon, 1884, *Phanetta* Keyserling, 1886); representatives of these genera were excluded. Genera represented in the Neotropics by cosmopolitan species (e.g., *Microctenonyx* Dahl, 1886) were also excluded.

A primary objective of this study was to identify major clades of erigonine genera. As testing generic monophyly was not a major goal of this research, few genera were represented by more than one exemplar species.

Multiple specimens were required to enable examination using destructive techniques, e.g., scanning electron microscopy and determination of the tracheal system. Where possible, the type species was used as the exemplar; where this was prevented by limited available material, another species was substituted. Sometimes, this species was previously undescribed. Taxa known from only one sex were excluded from the analysis to avoid compounding an already difficult phylogenetic problem with missing data (Platnick et al., 1991a; Wilkinson, 1995a,b; Strong and Lipscomb, 1999; but see Kearney, 2002). A complete list of taxa included in the analysis and detailed notes on taxon sampling and nomenclatural issues are given in Appendix C.

Taxa chosen to explore character evolution. Evolution of the tracheal system is an important issue in linyphiid systematics (Blest, 1976; Millidge, 1984a, 1986, 1988b, 1993a; Hormiga, 1994a, 2000). Hormiga (2000) included four haplotracheate erigonine exemplars in his analysis, plus two exemplars with a tracheal system coded as "intermediate" between haplotracheate and desmitracheate. For the current study, we increased the number of haplotracheate erigonines to evaluate Hormiga's conclusions about tracheal evolution in erigonines. Sixteen of the new exemplar taxa added for this study are haplotracheate erigonines; in one of these, we found that the median trunks pass through the pedicel into the prosoma, a characteristic usually associated with desmitracheate erigonines.

The loss of the paracymbium is a feature of interest in the evolution of Neotropical erigonines. Among erigonines, the loss of the paracymbium is known only from species in the Neotropics and the southern United States. All of these species were circumscribed by

Millidge (1985, 1991, 1993b) into six genera: *Sphecozone* O. Pickard-Cambridge, 1870, *Brattia* Simon, 1894, *Gymnocymbium* Millidge, 1991, *Psilocymbium* Millidge, 1991, *Gonatoraphis* Millidge, 1991, and *Dolabritor* Millidge, 1991. Species of "*Brattia*" from outside the Neotropics are misplaced and either have a paracymbium or are not linyphiids (Holm, 1962; Miller, in press b). Hormiga noted that at least in *Gonatoraphis* and *Dolabritor* the paracymbium appears to be "fused to the cymbial margin (not intersegmental), rather than absent" (Hormiga, 1994a, p. 22). Seven exemplars without paracymbia were included to explore the loss of the paracymbium. The exemplars represented all six genera recognized by Millidge (1985, 1991) plus the type species of *Hypselistoides* Tullgren, 1901, a subjective junior synonym of *Sphecozone* (Millidge, 1985). *Intecymbium antarcticum* (Simon, 1895) was also included because of its unusual paracymbium, which is well-developed and fused to the cymbium. Millidge (1985, p. 68) may have had this species in mind when he talked about the fusion of the paracymbium to the cymbium as a possible intermediate step toward paracymbium loss. The type species of *Gymnocymbium*, *G. grave* Millidge, 1991 is known only from the type specimen, so *G. crassum* (Millidge, 1991) [now *Sphecozone*] was used to represent the genus. Unfortunately, examination of *G. grave* raised doubts that these species are particularly closely related (Miller, in press a).

Characters

The data matrix (Appendix B) includes 176 characters (172 phylogenetically informative). Characters concern the male genitalia (78), female epigynum (22), prosoma and legs (55 including three uninformative characters), abdomen and spinnerets (19 including one uninformative character), and behavior (6). Fifteen characters are multistate; all were treated unordered.

Successive character weighting (Farris, 1969; Carpenter, 1988) of the unordered data set was conducted in PAUP* (Swofford, 2001). We investigated the stability of our analysis under successive weighting for comparison with Hormiga (2000).

A list of characters and character states appears in Appendix D. Some characteristics show variation that may have phylogenetic information content, but could not be satisfactorily divided into character states. These include the path of the female copulatory ducts, relative size of eyes, thickness of legs, truncation of the sternum, abdominal pattern, and number of aciniform gland spigots on the PLS.

Specimen examination. Exemplar taxa included in Hormiga (2000) were coded for new characters by re-examining the material in appendix 4 of Hormiga (2000), mostly using light microscopy. Some specimens prepared by Hormiga for SEM analysis were re-examined; additional material of a few species was prepared and examined (Appendix C).

Exemplar taxa newly added to this analysis were examined using a Leica DMRM compound microscope, an Olympus BH-2 compound microscope, and a Leica MZ APO dissecting microscope. Palpi and epigyna were examined using methyl salicylate as a temporary clearing agent (Holm, 1979), then examined on a temporary slide mount using the method described by Coddington (1983).

SEM images were taken using the AMRAY 1800 at the National Museum of Natural History Scanning Electron Microscope Facility. Specimens were prepared for SEM examination by brief ultrasonication (15 s to 1 min) and either air-dried or critical point dried. Specimens were attached to round-headed rivets using polyvinyl resin dissolved in acetone (polyvinyl acetate) and sputter coated with gold-palladium. In most cases, the cephalothorax of the male, the abdomen of both the male and female, and the male palpus were examined by scanning electron microscopy. Homology assessment of spinneret spigots followed Coddington (1989).

For examination of tracheal structures, abdomens of adult females were digested in potassium hydroxide or sodium hypochlorite solution over low heat. Digested abdomens were then stained with chlorazol black and mounted on slides for examination with a compound microscope (Hormiga, 1994a). Species of the following exemplars were limited and tracheal characters were scored based on published accounts: *Deichomma pretiosum* Millidge, 1991, *Dolabritor spineus* Millidge, 1991, *Hypselocara altissimum* Millidge, 1991, *Lygarina silvicola* Millidge, 1991, *Pseudotyphistes cristatus* (Ott and Lise 1997), and *Onychembolus subalpinus* Millidge, 1985.

Scoring of tracheal characters and characters evaluated using the SEM was based on only one or two specimens, so intraspecific variation could not be evaluated.

Adding characters and taxa

We have more than doubled the number of characters and ingroup taxa that were included in Hormiga (2000). But are we any closer to solving the problem of erigonine phylogeny? Just by adding a substantial number of new observations, we have satisfied one criterion of phylogenetic progress (i.e., total evidence; e.g., Kluge, 1997a,b; Wenzel, 1997; but see Rieppel and Kearney, 2002). Our study is an improvement over its predecessor because having more observations in a taxon-by-character matrix allows more opportunities for those observations to conflict with (i.e., falsify) each other. A cladogram is the least falsified hypothesis for a given data matrix, therefore the number of observations

in a matrix is directly related to the empirical content of the resulting hypothesis (Farris, 1983; Kluge and Wolf, 1993; Kluge, 1997a,b). As the most severely tested hypothesis of erigonine relationships available, we use our phylogenetic hypothesis to discuss the evolution of some characters of interest in erigonine systematics. It is worth noting that even our expanded taxon sample represents only a small proportion of known erigonine genera.

We assessed relationships among Hormiga's original set of 43 taxa in the expanded data set. We determined which clades in the original study survived in the current analysis. The number of surviving clades is an indicator of the stability of the original study. If a substantial number of clades survived from the previous study to the current one, then Hormiga's phylogeny could be seen as stable to the addition of new data. Such a result would also predict that those same relationships are robust and likely to persist in the future as even more data are added. Conversely, if there is a great deal of change in relationships among Hormiga's original set of taxa from the previous study to the current one, then the addition of new taxa and characters may or may not have led to a more stable phylogeny. We have used a variety of approaches to evaluate the stability of our analysis.

Since we have added both taxa and characters to Hormiga's (2000) study, we were able to parse their respective contributions to differences between the original and current studies (Fig. 2). We used Poe's (1998) method for assessing sensitivity to taxon sampling to account for the effect of adding taxa as follows. We created a matrix with Hormiga's set of 43 taxa, but all characters from the complete data set. This is the reduced-taxa matrix (RTM). We generated most parsimonious trees from the RTM. We then compared these results with the tree derived from the complete data set with the new taxa pruned after analysis. Thus, we are left with two sets of 43-taxon trees generated from the same characters, but in one case, additional taxa were included during analysis. Thus, any difference in length or topology must be due to the addition of taxa.

To account for the effect of adding characters, we created a 43-taxon matrix composed of characters included in or modified from Hormiga's (2000) data set, including any revised coding found in the complete data set and excluding any characters that could not be maintained in the complete data set (i.e., due to reinterpretation of the homology postulates or observational data). This revised-characters matrix (RCM) is a subset of the complete matrix and includes the following characters: 1–3, 5, 11–13, 16, 17, 19, 24, 25, 29, 34–38, 40, 43, 50–53, 55, 64–67, 73–75, 79, 81, 82, 91, 92, 94, 95, 97–110, 116, 117, 121, 123, 126, 133, 136–143, 152, 155, 157, 158, 161–168, 171, 172; of these 81 characters, 11 characters (2, 100, 104–106, 136, 138, 142, 155, 167, and

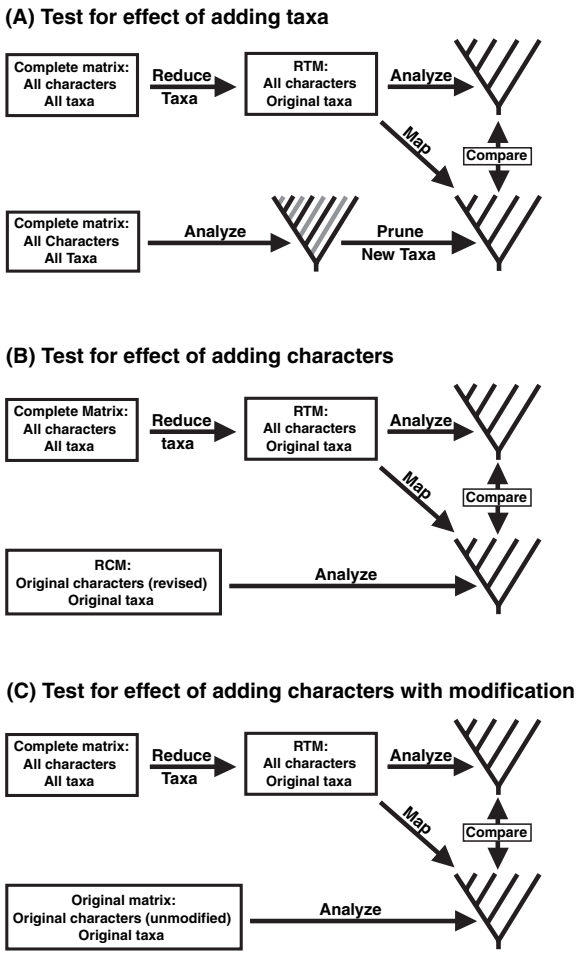

Fig. 2. Method for determining effects of (A) adding taxa (B) adding characters, or (C) adding and modifying characters to changes in phylogeny, modified from Poe (1998). (A) To determine the contribution of adding taxa, a pruned tree is compared to the results of a reduced-taxon matrix (RTM). The RTM is formed by eliminating all newly added taxa, leaving the 43 taxa in Hormiga's (2000) original study. Analysis of this matrix produces three trees. The pruned tree is formed by analyzing the complete data set, then removing the new taxa, leaving Hormiga's 43 taxa. Characters from the RTM are then mapped onto the pruned tree. Length difference is calculated based on phylogenetically informative characters. The Templeton test is used to evaluate the significance of differences between the RTM trees and the pruned tree. The pruned topology is compared to the trees from the RTM to determine the number of shared clades and the symmetric difference. (B) To determine the contribution of adding characters, trees from a revised-characters matrix (RCM) are compared to the results of a RTM. The RCM is formed by eliminating all newly added taxa, leaving the 43 taxa in Hormiga's (2000) original study, and eliminating all characters not derived from characters in Hormiga's (2000) original study. The RCM is a subset of the complete matrix. Characters from the RTM are then mapped onto trees from the RCM. Length differences, Templeton test, shared clades, and symmetric difference calculated as above. (C) To determine the effect of adding and modifying characters, the RTM was mapped onto trees from Hormiga' s (2000) study. Interpretation of these results is complicated by the fact that Hormiga's (2000) matrix is not a subset of the complete data set because several characters have been recoded, modified or eliminated. Length differences, Templeton test, shared clades, and symmetric difference calculated as above.

168) are phylogenetically uninformative. Results from the RCM were compared to the results from the RTM described above, with 43 taxa and all characters from the current analysis. Again, differences between these nested data sets must be due to the addition of novel characters. We also evaluated the combined effect of adding and modifying characters by comparing the results from Hormiga's original study to the results from the RTM. In all three cases, we assessed the number of shared clades, the symmetric difference between topologies (Penny et al., 1982; Penny and Hendy, 1985), differences in length (based on the RTM), and used a Templeton test (Larson, 1994; Templeton, 1983) to evaluate the significance of the differences between trees. The symmetric difference is the number of steps required to convert between two trees using the partition method (Robinson and Foulds, 1981). The partition method involves collapsing branches in one tree one at a time until all conflicting taxa are contained in a polytomy, then moving taxa one at a time to build the second tree. Each operation (collapse or move) is counted as a step. The Templeton test is based on characters that differ in length on two trees for the same data matrix. Length differences are evaluated according to a two-tailed Wilcoxon rank sum test, a non-parametric statistic (see Larson, 1994).

We have employed Continuous Jackknife Function (CJF) analysis (Miller, 2003) to explore the stability of estimates of erigonine phylogeny. CJF analysis graphically displays progress toward a stable phylogeny. This is accomplished by removing increasing quantities of characters from a matrix and deriving most parsimonious trees from these rarefied data sets. Trees from rarefied matrices are then compared to a reference tree (usually a most parsimonious tree). Congruence between the reference tree and rarefied trees is plotted on a graph as a function of the severity of character removal. As the rate of character removal increases, the number of clades shared between trees from a rarefied matrix and the reference tree should decrease. The shape of the curve indicates the completeness of a phylogenetic investigation toward a stable result. The shape of the CJF curve predicts the degree to which additional characters drawn from the same statistical universe as characters in the matrix can be expected to change the phylogeny. Asymptotic curves with a high degree of congruence indicate stability; curves that show rapid loss of congruent nodes indicate instability. The CJF curve for the current study is based on the single most parsimonious tree as the reference tree (Fig. 3); the CJF curve for Hormiga's (2000) study is based on his preferred of six trees as the reference tree (Fig. 1). CJF analysis focuses on the adequacy of a set of characters to produce a stable phylogeny for a given set of taxa.

Analysis

The data matrix was produced using NDE (Page, 2001). Analyses were conducted using WinClada (Nixon, 2002) to explore character evolution and as a shell for launching NONA (Goloboff, 1993a). Further analyses were conducted using PAUP* (Swofford, 2001) and NONA. In WinClada, two alternate tree searching strategies were used: the Ratchet (Nixon, 1999), as implemented in WinClada using default settings, and heuristic searching using 1000 replications of random taxon addition (**mult*1000**) with up to 10 starting trees per replicate (**h/10**) and branch swapping (**max***). We also ran a heuristic search in PAUP* with 1000 replicates of random taxon addition (**hsearch/addseq=random nrep=1000**). We also ran heuristic searches in NONA (without WinClada) with 1000 replications of random taxon addition (**mult*1000**) with up to 10 starting trees per replicate (**h/10**) and branch swapping (**max***) under two criteria of support: ambiguous optimizations considered support (**amb=**) or not considered support (**amb-**) (see Coddington and Scharff, 1996). Successive character weighting was conducted in PAUP* using the maximum value of the rescaled consistency index (Farris, 1989) and a base weight of 1000 (**Reweight/index=rc basewt=1000**).

CJF analysis of both the current analysis and the data set from Hormiga (2000) was conducted as described in Miller (2003) using NONA (Goloboff, 1993a) and PEST (Zujko-Miller and Miller, 2002). Further exploration of nodes shared between topologies was also conducted in PEST. The symmetric difference metric was calculated in PAUP* using the **treedist** command; Templeton tests were run in PAUP* using the **pscores/non-param-test=yes** command.

Bremer support values (Bremer, 1988, 1994) were conducted in two stages. Values up to 5 were calculated in NONA **(amb=mult*25; max* h 5000; sub 1; find*; h 10000; sub 2; find*; h 15000; sub 3; find*; h 25000; sub 4; find*; h 32759; sub 5; find*; bs;)**. Higher levels of Bremer support were subsequently determined node-by-node by enforcing converse constraint trees in PAUP*, then running a heuristic tree search with 100 replicates of random taxon addition (**hsearch/addseq=random nrep=100**).

Average Bremer support per node was calculated by dividing the sum of Bremer support scores by the number of applicable nodes (number of taxa minus three for the entire tree). Nodes collapsed in the strict consensus tree received a Bremer support score of zero. This score was calculated for the entire tree and for nodes concerning relationships among erigonine genera.

Characters with multiple possible optimizations (Maddison and Maddison, 1992) were usually resolved to favor parallel losses or simplification where possible (e.g., see Chars. 55, 67, Appendix D; see Char. 52 for

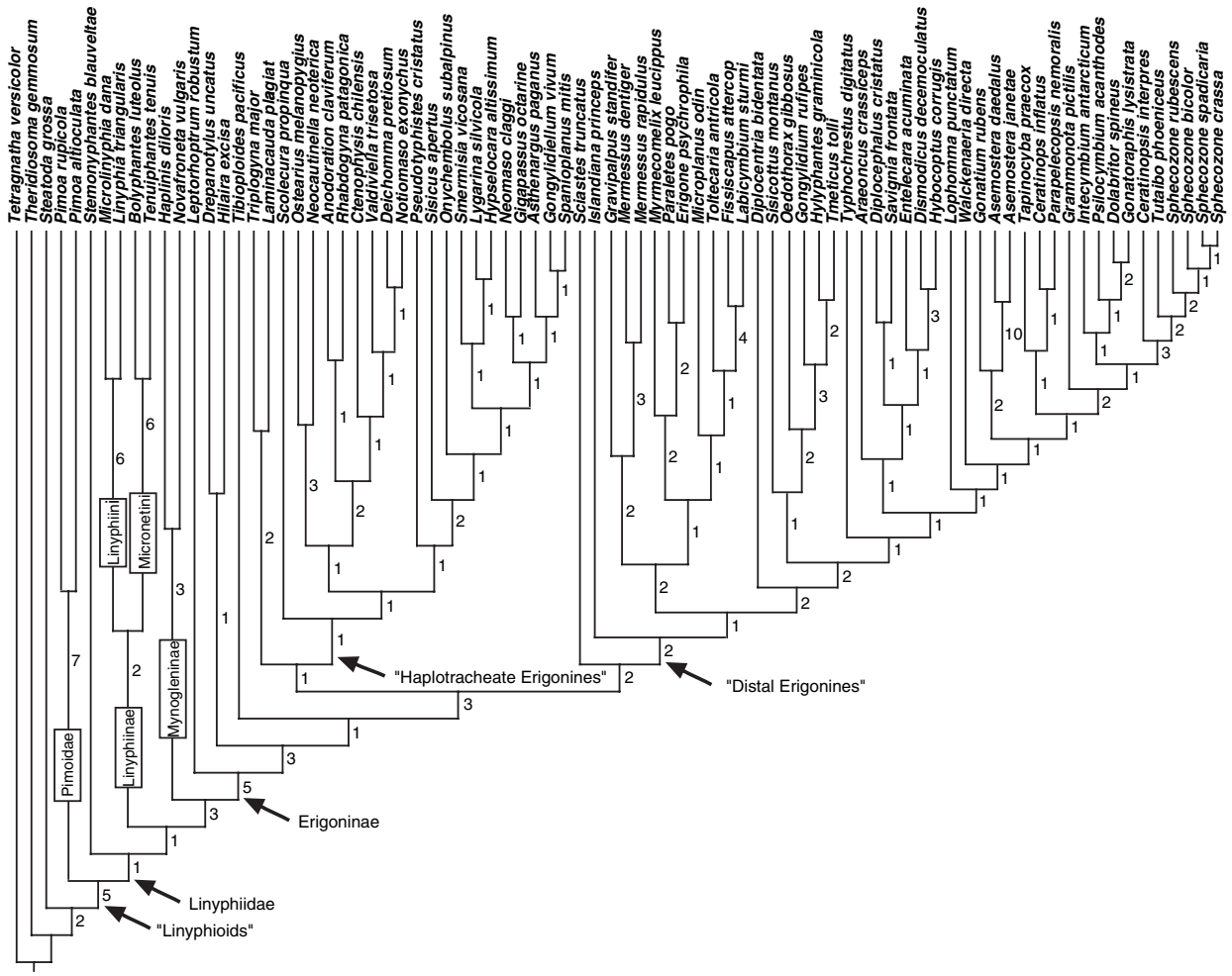

Fig. 3. Single most parsimonious tree resulting from phylogenetic analysis of the matrix in Appendix B (L = 904, CI = 0.23, RI = 0.58; uninformative characters excluded: L = 900, CI = 0.23). Numbers next to nodes indicate Bremer support.

exception). This is not equivalent to either the accelerated (ACCTRAN) or delayed (DELTRAN) transformation convention because it depends on an evaluation of the meaning of the character states, not just on the pattern of homoplasy. For example, given the choice between two parallel losses of a structure, or one loss and one gain of that structure, the first option preserves the homology of the structure better. This is equivalent to DELTRAN optimization. Alternatively, given the choice between two parallel gains of a structure, or one gain and one loss of that structure, the second option preserves the homology of the structure better. This is equivalent to ACCTRAN optimization. Where alternative character states did not clearly distinguish between the presence or absence of something, increase or decrease of something, etc., we often drew upon information from previous studies to resolve ambiguous optimizations.

In addition to the matrix in Appendix B, several alternative coding schemes were tried. Rationale and results of these experiments are detailed in Appendix D (Chars. 12, 23, 24, 52, 53, 110, 168; see also Appendix E).

Results

Analysis of the matrix in Appendix B yielded a single most parsimonious tree (L = 904, CI = 0.23, RI = 0.58; uninformative characters excluded: L = 900, CI = 0.23; Table 1). Figure 3 shows this topology with Bremer support values. Figures 4–7 show sections of this tree with character optimizations. Support values for the tree in Fig. 3 are quite low for most clades with 1.92 steps of Bremer support per node on average (Table 1). This is an improvement over Hormiga's (2000) analysis, which had 1.48 steps of Bremer support per node. Considering only relationships among erigonine genera, average Bremer support per node falls to 1.63 for this study and 1.24 for Hormiga's analysis.

Table 1
Matrix dimensions and results for Hormiga's original study, the revised-character matrix (RCM; Hormiga's taxa, characters from Hormiga's study modified to reflect coding changes in the current study), the reduced-taxon matrix (RTM; Hormiga's taxa, all characters), and the complete matrix (all taxa, all characters). Density is ratio of characters to taxa, CI is ensemble consistency index. RI is ensemble retention index. Tree length, density, and CI calculated with autapomorphic characters excluded

Matrix	Characters	Informative characters	Taxa	Density	Trees	Length	CI	RI	Average bremer support/ node	
									All taxa	Erigonines
Hormiga (2000)	73	67	43	1.56	6	220	0.38	0.68	1.48	1.24
RCM	81	70	43	1.63	154	238	0.36	0.65	1.30	0.79
RTM	176	141	43	3.28	3	525	0.32	0.58	2.18	1.55
Complete matrix	176	172	82	2.10	1	900	0.23	0.58	1.92	1.63

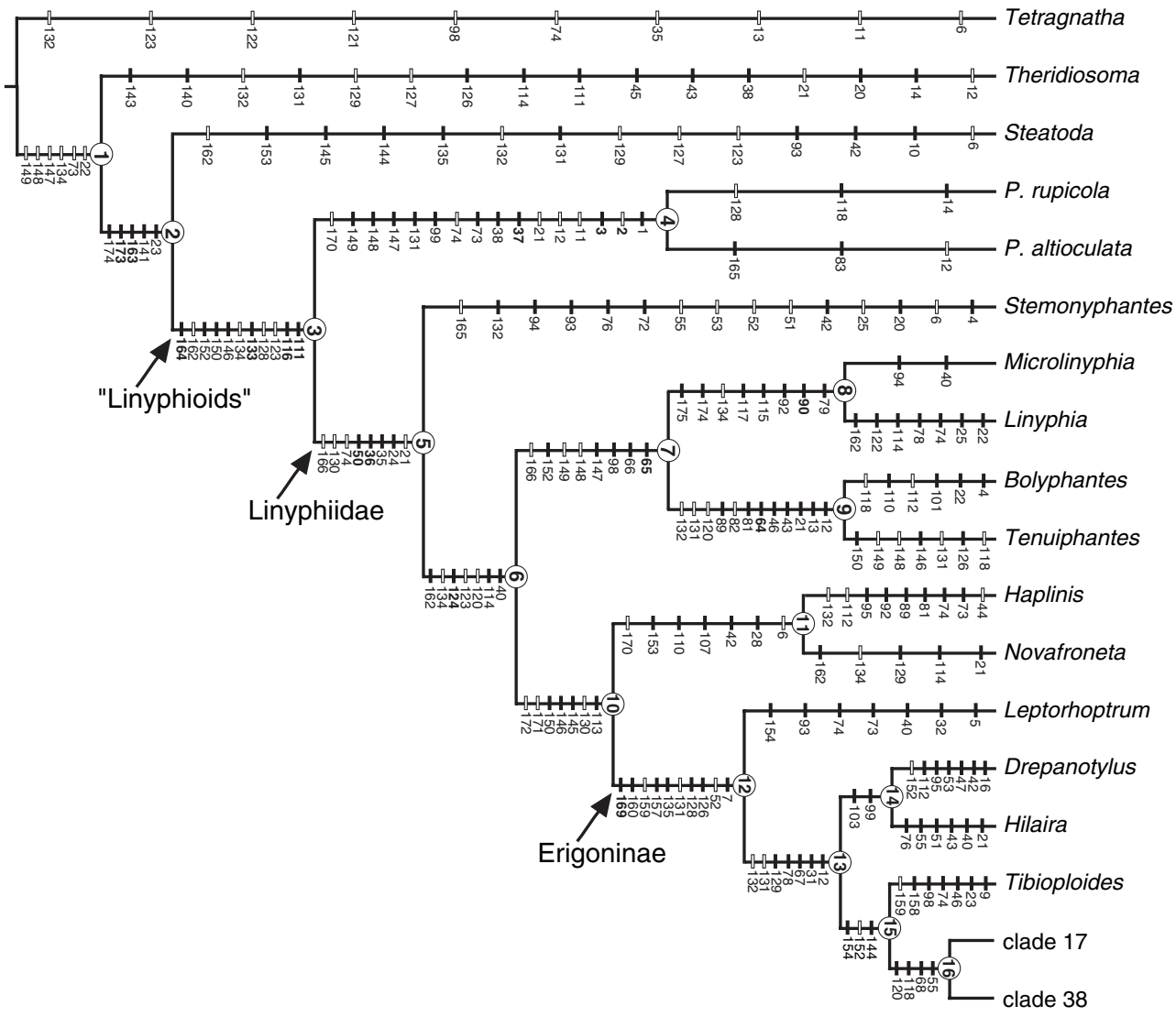

Fig. 4. Cladogram detail including outgroups, nonerigonine linyphiids, and basal erigonines. Optimizations for each character shown at internodes; black bars indicate unambiguous changes, white bars indicate ambiguous changes. Optimizations in bold indicate synapomorphic character state changes without homoplasy on the cladogram. *P.* = *Pimoa*. Numbers at nodes are referred to in the text. Tree continues in Figs 5 and 6.

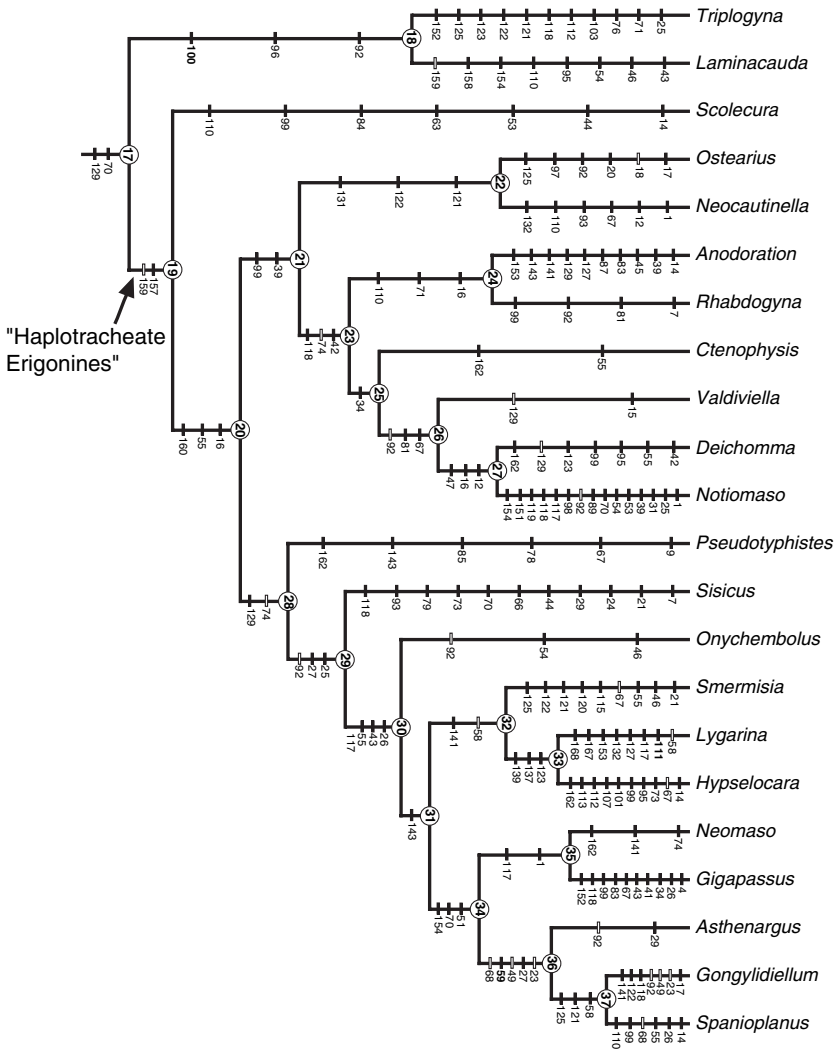

Fig. 5. Cladogram detail showing clade 17 including the "haplotracheate erigonines". Optimizations and node numbers as in Fig. 4.

Successive weighting by the maximum value of the rescaled consistency index stabilized on a single tree after four iterations (Fig. 8). This tree differs substantially from the equal weights analysis. With weights reset to 1 and uninformative characters excluded, this topology is 913 steps (CI = 0.23, RI = 0.57), 13 steps longer than under the equal weights analysis. One interesting feature of this tree is that basal erigonines are haplotracheate, which is consistent with Hormiga's (2000) hypothesis and inconsistent with the equal weights analysis (Fig. 9; see also Char. 161, Appendix D). The relationship between tracheal morphology and the limits of Erigoninae is a perennial issue in linyphiid systematics (e.g., Blest, 1976; Millidge, 1984a, 1986).

Contrast with Hormiga 2000

The current analysis implies substantially different relationships among Hormiga's original 43 taxa than those implied by Hormiga's (2000) study, especially within Erigoninae. Relationships among Hormiga's original 43 taxa implied by the current study are shown in Fig. 10. This pruned version of the current analysis shares 13–15 nodes (33–38%) with Hormiga's six most parsimonious trees; only 5–6 of these represent relationships among erigonine genera. Symmetric difference analysis indicates that 50–53 branch moves would be required to convert between Hormiga's topologies and the pruned tree. CJF curves for Hormiga's (2000) study and the current study are virtually indistinguishable (Fig. 11); both predict that additional characters will produce substantial changes in the hypothesis of relationships among taxa in these analyses.

Effect of adding taxa

To study the effect of adding taxa, we compared the results from the pruned analysis (all taxa and characters

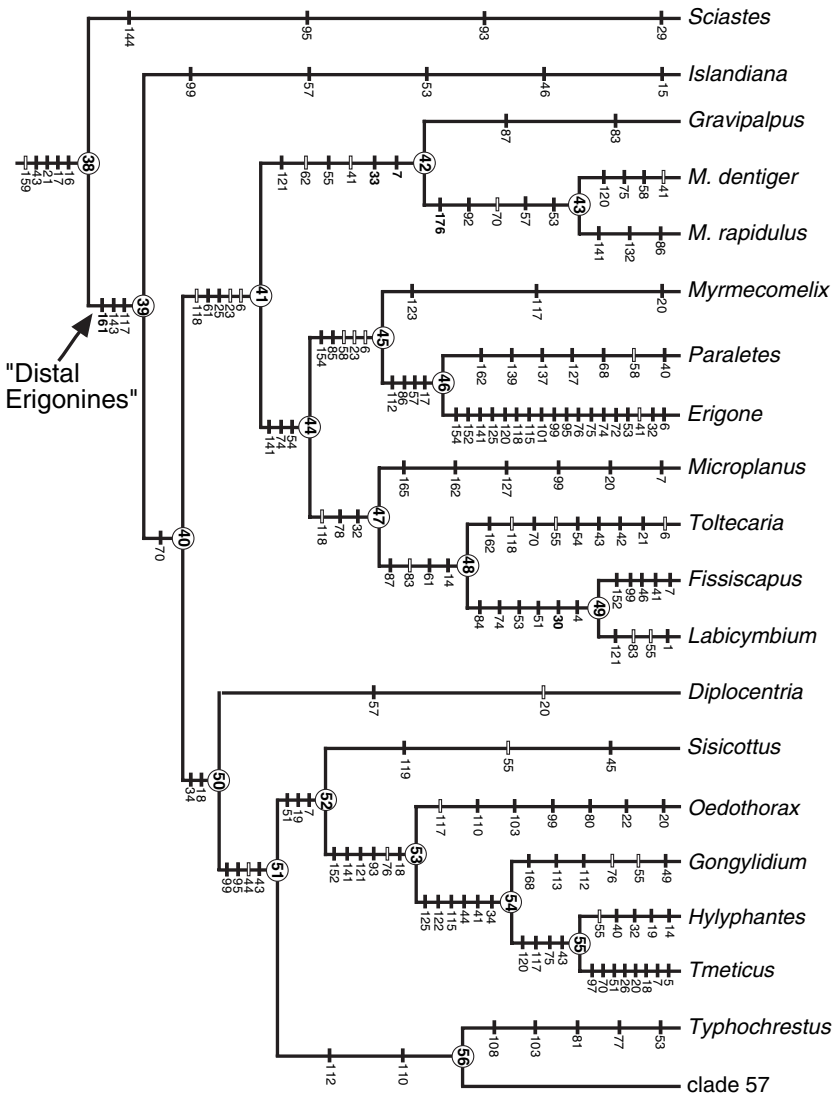

Fig. 6. Cladogram detail showing basal part of clade 38 including some "distal erigonines". Optimizations and node numbers as in Fig. 4. *M.* = *Mermessus*. Tree continues in Fig. 7.

included in analysis, then new taxa removed subsequently) with the RTM (Hormiga's original taxa and all informative characters included in analysis; Fig. 2A). The RTM excluded all but the original 43 taxa from Hormiga's (2000) study. This left 141 phylogenetically informative characters. Analysis of the RTM yielded three most parsimonious trees differing only in the position of one taxon, *Diplocentria* Hull, 1911 (Fig. 12). The RTM has a relatively high ratio of characters to taxa (density) and the average Bremer support per node is 2.18, higher than either Hormiga's original study or the complete data set (Table 1). However, considering only relationships among erigonine genera, the average Bremer support is 1.55, lower than that for the complete matrix. The RTM was used to investigate the relative contributions of taxa and characters to the question of erigonine relationships.

The pruned topology shares 32 nodes (80%) in common with the three trees from the RTM. Symmetric difference analysis indicates that 16 branch moves would be required to convert between the pruned tree and the trees from the RTM. The pruned topology (with only informative characters considered) is 532 steps, 7 steps longer than the trees from the RTM. A Templeton test indicates that differences between these trees are insignificant (Table 2). These lengths are comparable because they are calculated on the same matrix. The only difference is that in one case, 39 taxa were included for the analysis and then pruned; in the other, the 39 taxa were never included. In both cases, the same 141 characters are informative and used to calculate length for the 43-taxon trees.

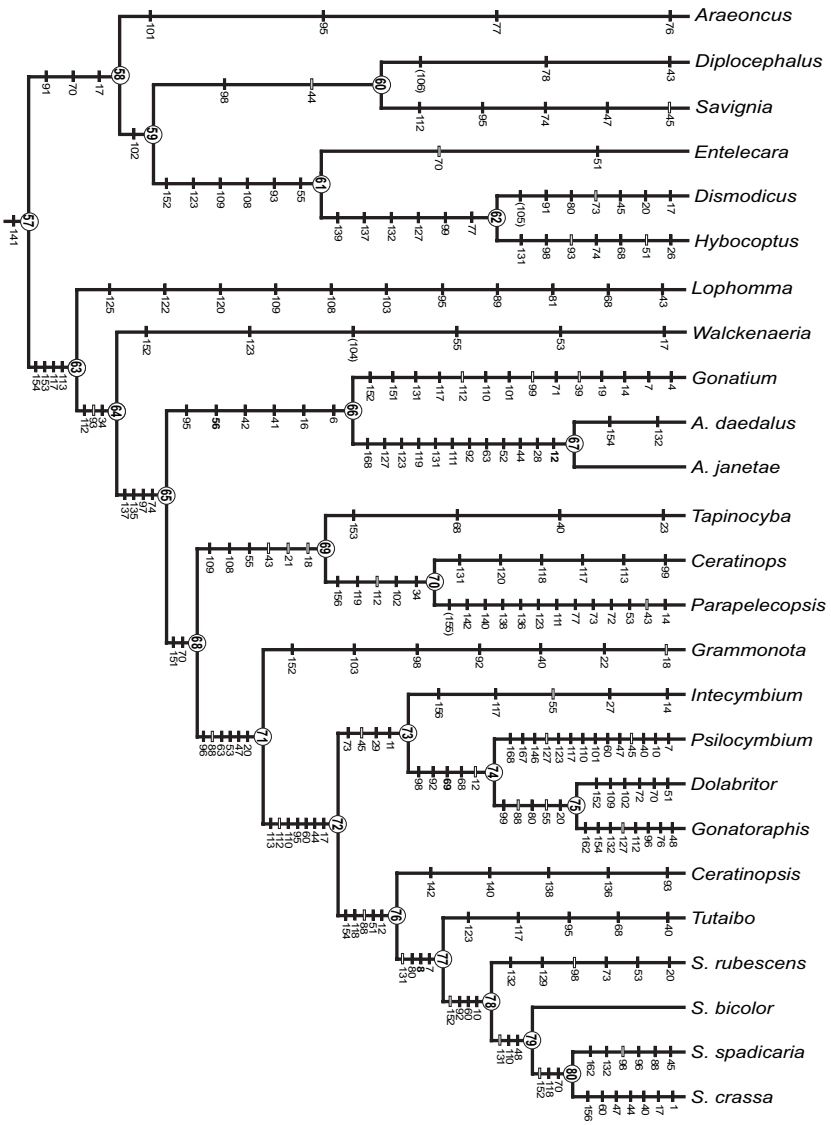

Fig. 7. Cladogram detail showing clade 57 including some "distal erigonines" and *Sphecozone*. Optimizations and node numbers as in Fig. 4; optimizations in parentheses indicate phylogenetically uninformative characters. *A.* = *Asemostera*; *S.* = *Sphecozone*.

Effect of adding characters

To study the addition of characters, we compared the results from the RCM [characters included in or modified from Hormiga's (2000) analysis] with the RTM (Fig. 2B). Analysis of the RCM produced up to 154 trees (154 found in PAUP*, 153 found in NONA, 55 found in WinClada; probably due to contrasting criteria for branch support available in different phylogenetic software packages, see Coddington and Scharff, 1996). In all cases, 13 nodes collapsed in the strict consensus to produce the topology in Fig. 13. With so many most parsimonious trees, the low average Bremer support overall (1.30) and for erigonine relationships (0.79) is not surprising. Trees from the RCM share 17–23 (43–58%) nodes in common with the trees from the RTM. Symmetric difference analysis indicates that 34–46 branch moves would be required to convert between trees from the RCM and the trees from the RTM. Trees from the RCM imposed on the RTM cost an additional 9–23 steps. Fifty-eight per cent of the comparisons between the 154 RCM trees found in PAUP* and the RTM trees are significantly different according to the Templeton test (Table 2).

Effect of adding characters with modification

We compared Hormiga's (2000) results to those from the RTM (Fig. 2C). In contrast to the matrix derived from adding characters, Hormiga's matrix is

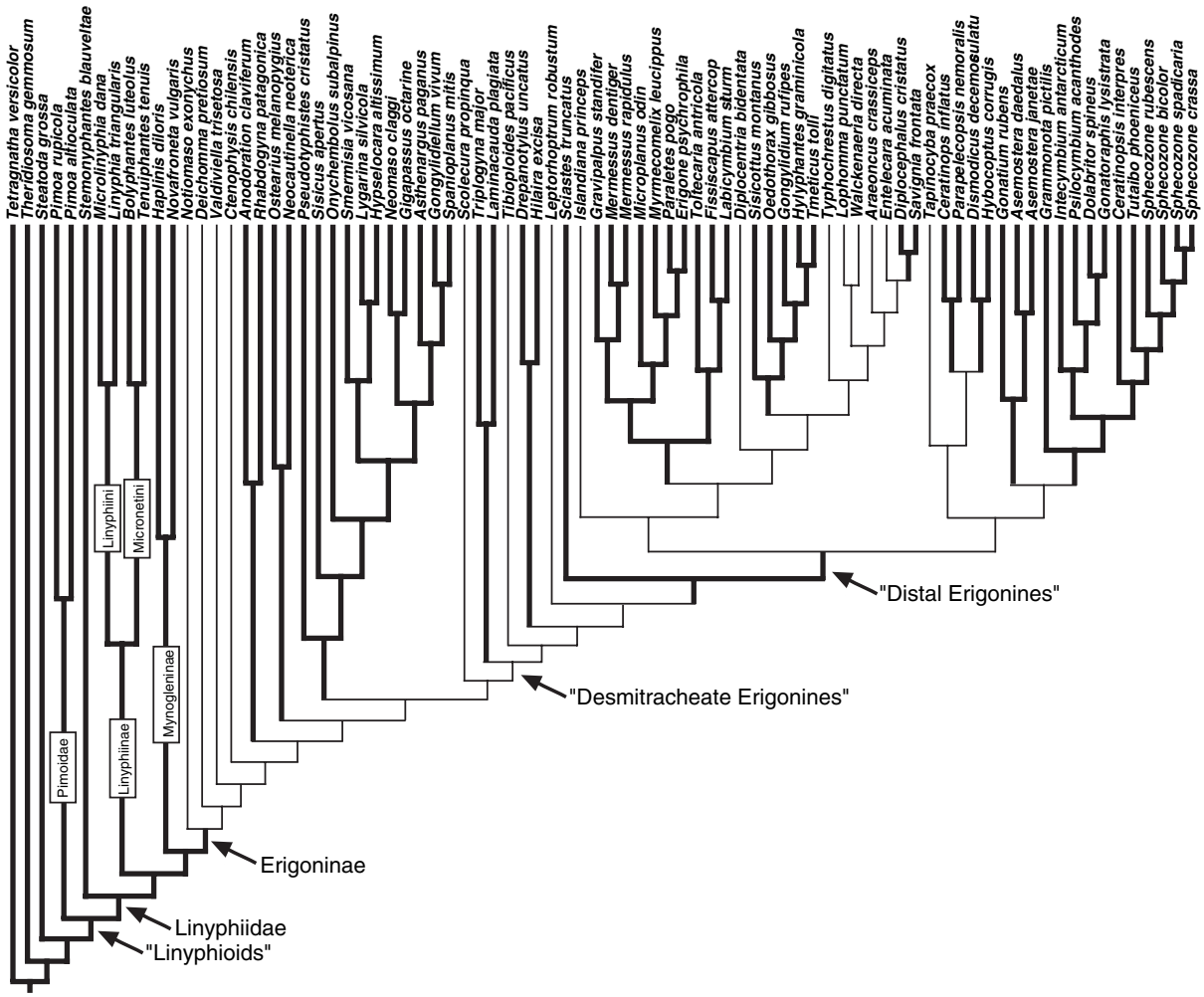

Fig. 8. Single tree resulting from successive character weighting by the rescaled consistency index (uninformative characters excluded: L = 913, CI = 0.23, RI = 0.57). Thick lines represent clades that are shared with the equal weights analysis.

not a subset of the complete matrix because some characters have been modified whereas others have been eliminated. The six trees found in Hormiga's analysis shared 13–15 nodes (33–38%) in common with the three trees from the RTM. Symmetric difference analysis indicates that 50–53 branch moves would be required to convert between Hormiga's topologies and the RTM trees. Hormiga's topologies imposed on the RTM cost an additional 32–36 steps, which is highly significant according to the Templeton test (Table 2).

Discussion

Adding characters versus taxa

Adding characters and adding taxa are not symmetrical, independent alternatives. Adding taxa can have profound effects on existing characters. New taxa may blur the distinction between morphological character states that were previously discrete, imply new character states, or lead to re-evaluation of previous homology statements in other taxa (e.g., due to conjunction, Patterson, 1982).

To investigate the effect of adding characters, we created a matrix of characters that were included in or modified from Hormiga's (2000) data set, coded for the 43 taxa in Hormiga's study. The RCM is a subset of the RTM, so any changes in results between the RCM and the RTM can be attributed to the addition of characters. However, the large number of trees resulting from our RCM made interpretation of these results problematic. Clearly, adding characters to the RCM resulted in fewer trees and most (but not all) of the RCM trees were significantly longer than the RTM trees, indicating that the addition of characters tended to account for significant changes in topology. An alternative approach

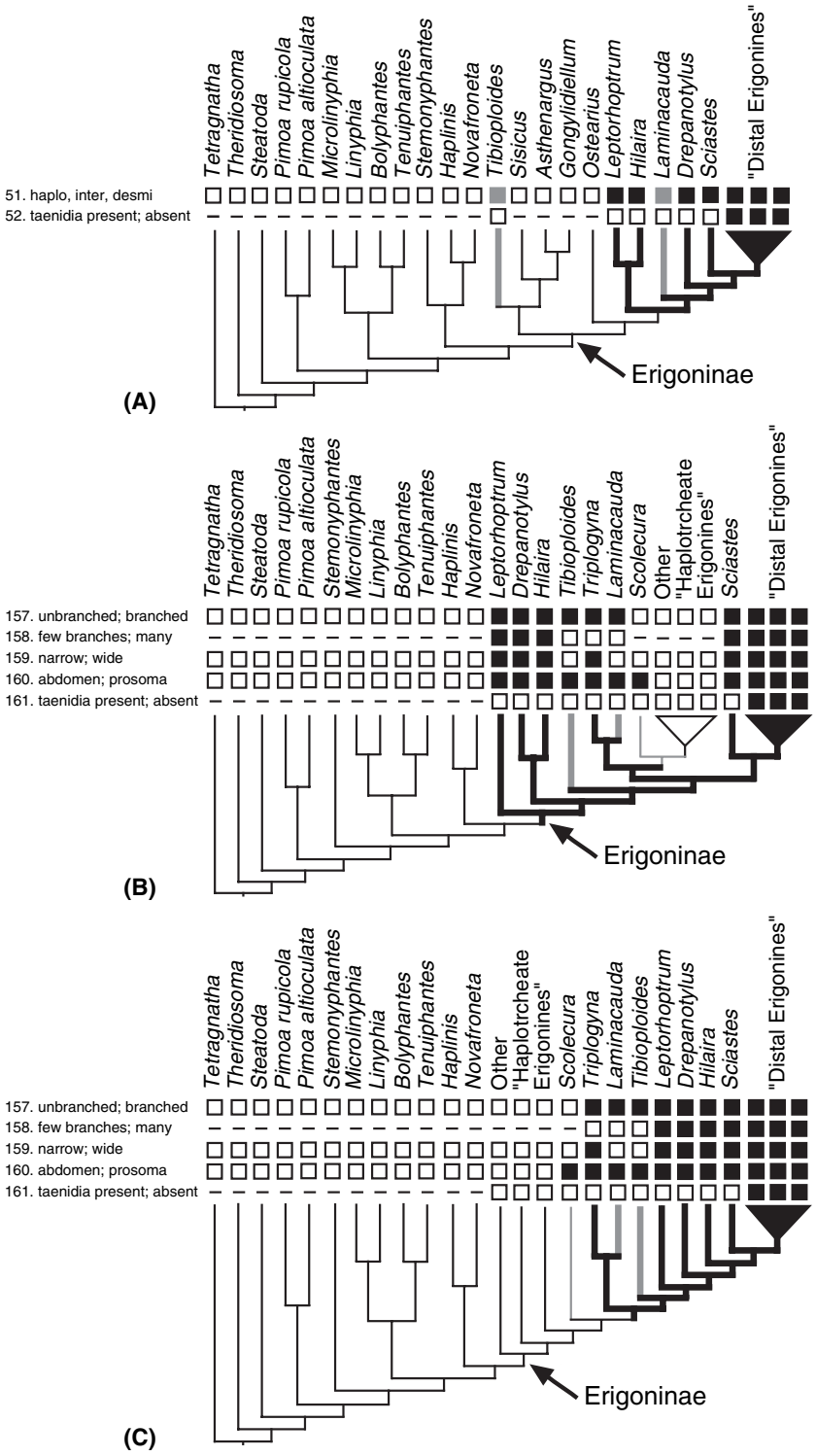

Fig. 9. Schematic trees showing hypotheses of tracheal evolution in (A) Hormiga (2000), (B) the current study equal weights analysis, and (C) the current study successive character weighting analysis. Text to the left of the trees are character states for tracheal characters. Boxes represent character states; the first state is a white box, the last state is a black box. For three-state characters, the middle state is a gray box, a dash indicates inapplicable. Thin black lines indicate typical haplotracheate condition; thick black lines indicate typical desmitracheate condition; thick gray lines indicate moderate branching of the median tracheal trunks; thin gray lines indicate unbranched median tracheal trunks that enter the prosoma.

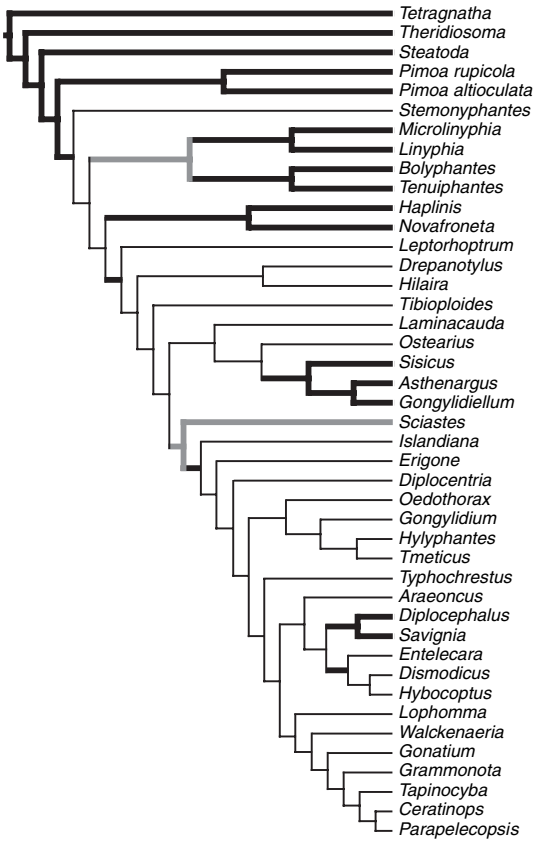

Fig. 10. Pruned cladogram showing relationships among taxa included in Hormiga's (2000) analysis as implied by the complete data set. Thick black lines represent nodes that are congruent with all six most parsimonious trees from Hormiga's study; thick gray lines represent nodes that are congruent with some of Hormiga's most parsimonious trees; thin lines represent nodes that are incongruent with Hormiga's results.

was to compare the results reported by Hormiga (2000) to the RTM. Since some characters in Hormiga's study were modified, recoded, or eliminated in the RTM, Hormiga's data set is not a direct subset of the RTM. Thus, any differences in the results from Hormiga's analysis and the RTM analysis must be attributed to the addition, elimination, and modification of characters. The results of such a comparison can point with limited precision to the cause of topological changes. However, when cladistic studies are revisited and expanded, we expect characters to be added, deleted, and modified. So, the comparison between Hormiga's study and the RTM can be thought of as an exploration of that process.

Bremer et al. (1999) concluded that increasing the ratio of characters to taxa should result in a better supported tree. If true for our data, we should expect the RTM to yield better supported results than both the RCM and the complete data set. In the case of the indecisive RCM, support was indeed lower than the RTM, with the average support per node 60% of that found for the RTM (Table 1). The comparison between the RTM and complete matrix is more complex. While we did find higher overall Bremer support per node for the RTM than for the complete matrix, the pattern did not hold for the erigonine part of the tree, where Bremer support per node was higher for the complete data set. Evidence for the pattern predicted by Bremer et al. (1999) seems to be ambiguous for our data. Note that while Bremer et al. (1999) based their conclusions on bootstrap support, we based ours on Bremer support.

We found little indication that adding taxa to Hormiga's original set of 43 exemplars led to major changes in inferred relationships among those taxa.

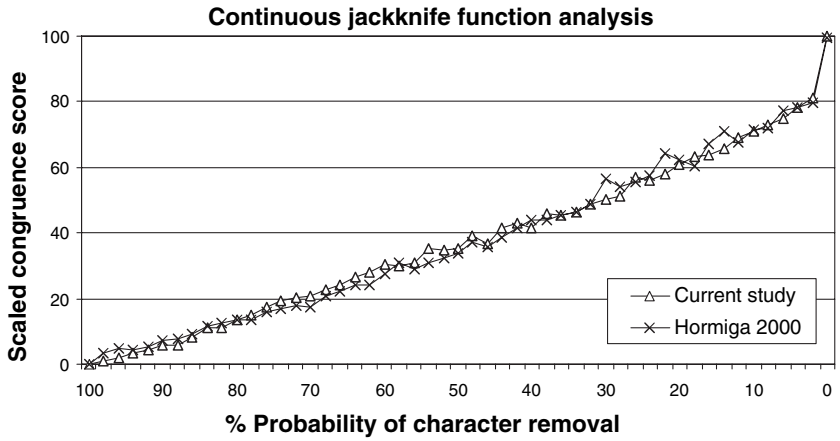

Fig. 11. Continuous jackknife function analysis curves for the current study and Hormiga (2000). Curves plot congruence with a reference tree, expressed as the average scaled congruence score (see Miller, 2003), as a function of the percent probability of character removal. The reference tree for the current study is the single most parsimonious tree; the reference tree for Hormiga (2000) is his preferred of six most parsimonious trees. See text for details.

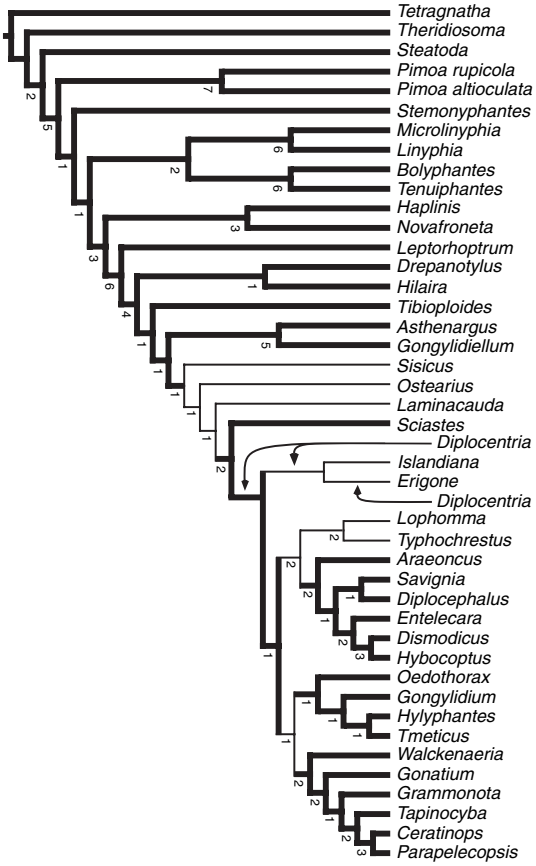

Fig. 12. Summary of results from the reduced-taxon matrix (RTM). The RTM was formed by removing all taxa except those included in Hormiga (2000), but retaining all phylogenetically informative characters from the complete data set. Three trees result (uninformative characters excluded: L = 525, CI = 0.32, RI = 0.58); alternative placements of *Diplocentria* shown with arrows. Thick lines represent nodes that are congruent with the results from the complete data set. Numbers next to nodes indicate Bremer support.

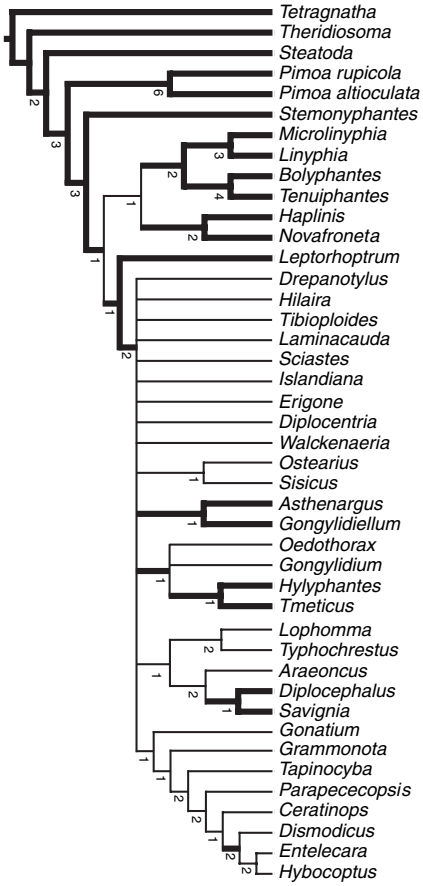

Fig. 13. Strict consensus of 154 trees from revised-character matrix (RCM; uninformative characters excluded: L = 238, CI = 0.36, RI = 0.65). The RCM was formed by removing all taxa except those included in Hormiga (2000), but retaining phylogenetically informative characters derived from Hormiga's original analysis. Eighty-one characters in the complete analysis were identical to or derived from characters in the original analysis; 70 of these are informative for the 43-taxon set. Thick lines represent nodes that are congruent with the results from the complete data set. Numbers next to nodes indicate Bremer support.

Topological differences between the pruned topology and trees from the RTM are insignificant according to the Templeton test. We added 2.7-fold more characters than taxa to the Hormiga (2000) analysis, so our results suggesting a larger effect from the addition of characters than taxa must be interpreted with this in mind. Certainly we do not generalize that it is better to add characters than taxa to difficult phylogenetic problems. Key taxa with critical combinations of character states can radically alter our understanding of relationships among groups (e.g., Gauthier et al.,

Table 2
Effect of adding taxa maps the pruned tree from complete analysis onto reduced-taxon matrix (RTM). Effect of adding characters maps trees from the revised-character matrix (RCM; the subset of characters from the complete data set that were found in Hormiga's (2000) matrix, incorporating any coding changes) onto the RTM. Effect of adding characters with modification maps six trees from Hormiga (2000) onto the RTM. Length calculated using informative characters only. Shared clades calculated for unrooted tree with 40 nodes

	Shared clades	Symmetric difference	Length	Templeton test
Effect of adding taxa	32 (80%)	16	532 (+7)	ns
Effect of adding characters	17–23 (43–58%)	34–46	552–566 (+9–23)	$P < 0.05$*[a]
Effect of adding characters with modification	13–15 (33–38%)	50–53	557–561 (+32–36)	$P < 0.01$**

[a]In 58% of the trees.

1988; Donoghue et al., 1989; Eernisse and Kluge, 1993). However, our CJF analysis indicates that the future addition of morphological characters to the question of erigonine phylogeny will likely imply revisions to the topology in Fig. 3. Since our addition of taxa had a relatively small effect on changes in the topology, it may be that the future addition of a moderate number of taxa will imply only minor revisions to the topology in Fig. 3.

In defense of data exploration

The methods used here to evaluate the relative impacts of adding taxa versus characters were derived from Poe (1998). Poe (1998) was criticized by Grant and Kluge (2003) along with a broad spectrum of data exploration methods, most of which were labeled as neither scientific nor heuristic. The chief criticism of Poe (1998) was the use of regression statistics because, "…application of frequentist statistics in estimating optimal taxonomic sampling cannot be rationally justified because the history of species is necessarily unique" (Grant and Kluge, 2003, p. 402; see also Wenzel and Carpenter, 1994). The unique history of species is not in dispute. However, evidence for relationships (synapomorphies) can occur with variable frequencies at nodes, and can be congruent or in conflict with each other. Evaluation of the evidence supporting a tree need not be unscientific, especially when, "…support is secondary to the scientific optimality criterion of maximizing explanatory power" (Grant and Kluge, 2003, p. 380). In other words, when data exploration is used to evaluate an optimal phylogenetic hypothesis but not to justify an alternative suboptimal hypothesis, we see this as a perfectly appropriate scientific exercise. As Grant and Kluge point out, "…a hypothesis is…supported if the critical evidence confers a greater degree of corroboration on it than on any competing hypothesis, even if the absolute degree of corroboration of the optimal hypothesis is disturbingly low" (Grant and Kluge, 2003, p. 383, citing Lakatos, 1978). We believe that many data exploration methods are simply evaluating the absolute degree of corroboration. The effectiveness with which various methods accomplish this is of course debatable. In any case, our adaptation of Poe's method does not include regression statistics. Poe's main objective was to explore the uncontroversial observation that variation in taxon sampling can impact phylogenetic results. Poe recognized that there are many reasons why particular taxa may or may not be available for a particular study, some of which will be beyond the control of the investigator. Poe (1998) never advocated favoring hypotheses based on less data over more and only removed taxa as a tool for exploring sensitivity to taxon sampling. We agree with Grant and Kluge (2003, p. 411) that highlighting weakly supported nodes as in particular need of further attention and testing is a valid scientific use of data exploration methods.

Weighted characters

Hormiga (2000) used successive character weighting (Farris, 1969; Carpenter, 1988) to assess internal consistency of the data and cladistic reliability of the results (Carpenter et al., 1993). Hormiga found the same six cladograms as in the equal weights analysis after a single round of successive weighting and his results were stable in successive iterations. The results of the current analysis are quite different, stabilizing on a novel tree topology (Fig. 8) after four rounds of weighting. It is unclear what exactly this result says about the internal consistency and cladistic reliability of our data, as the relationship, if any, between the internal consistency and cladistic reliability of the results (*sensu* Carpenter et al., 1993) and the topological stability of these results to the addition of data is far from simple. Our analyses show that matrices with almost identical CJF curves (Fig. 11) can have very different levels of "internal consistency" as measured by successive character weighting. While Hormiga's solution set was stable under successive weighting, we have shown that his results were sensitive to the addition of new data. This calls into question the proper interpretation of successive weighting analysis.

Kluge (1997a,b) strongly criticized successive character weighting on the grounds that it weakens corroboration (the degree of support for a hypothesis given by the evidence in light of the background knowledge) and severity of the test (the potential for the evidence to falsify a hypothesis) by adding untested background knowledge (the set of differential weights). Implied weighting (Goloboff, 1993b, 1995) suffers from similar problems (Kluge, 1997a,b). In spite of these concerns, we allow that weighting methods can have a place in phylogenetic investigation. Carpenter (1988) discussed successive weighting as a method for selecting among most parsimonious trees, although he later (1994) defended conclusions from successive weighting that selected unique (i.e., longer under equal weights) trees (e.g., Platnick et al., 1991b; Brothers and Carpenter, 1993). When the successive weighting solution is longer (under equal weights) than the equal weights solution, Kluge's concerns clearly apply. The first criterion for cladistic support must be parsimony, i.e., minimization of *ad hoc* hypotheses of character state change (Farris, 1983; Kluge, 1997a,b; Grant and Kluge, 2003). When multiple most parsimonious solutions are recovered, secondary criteria of support (e.g., successive weighting) can be invoked to select among them (Coddington and Scharff, 1996; Scharff and Coddington, 1997). This is justified because it can result in a bolder hypothesis of relationships. Bolder hypotheses are preferred because they are more falsifiable and therefore more scientific

(Kluge and Wolf, 1993; Kluge, 1997a,b). Further testing of a bold hypothesis will be severe because the more a hypothesis claims, the greater the potential for evidence to conflict with some aspect of it. By contrast, a weak hypothesis (e.g., a consensus tree with many branches collapsed) says comparatively little about relationships and is more difficult to falsify. Weak hypotheses have relatively little scientific value. Selecting a working hypothesis from among a set of most parsimonious trees does not violate the first criterion of support, parsimony. Character weighting can also play an important role in data exploration. Disagreement between our equal weights and successive weights trees contributes to concern that our phylogeny is unreliable (i.e., the absolute degree of corroboration of the best corroborated hypothesis is low).

Regardless of the weight given to each character, our successive weighting tree requires 13 additional *ad hoc* hypotheses of character state change (Fig. 8). This topology is dependent on a complex model of character weights. Although the weighting scheme is derived from the consistency of characters with each other, it represents a suite of strong assumptions that underlie the results. This seems to depart from the core idea of parsimony. When a weighting scheme is introduced, the ability of some characters to falsify others is decreased. The weighting regime itself is not under test, and it is unclear whether the weight of a character has any transitive value (Kluge, 1997a; *contra* Goloboff, 1993b). Conversely, equally weighted characters have clear empirical value as independent lines of evidence[1] that can be counted as either in conflict with or consistent with every possible clade (Kluge, 1997a). This is not to say that all characters are equally good at resolving relationships for a given phylogenetic question; this is demonstrated empirically in every real phylogenetic data set (Farris, 1983; Carpenter, 1988; Goloboff, 1993b; Kluge, 1997b). However, complex models of character weights introduce assumptions into a method whose fundamental justification is the minimization of assumptions.

The shortest tree under equal weights is not guaranteed historically accurate, only the least falsified by the evidence. Since the minimization of *ad hoc* hypotheses is critical to the relationship between evidence and science (Farris, 1983), defense of a hypothesis requiring more than the minimum number of character state changes to explain observation must be accompanied by a compelling argument for why the parsimony criterion should be relaxed (Wiens et al., 2003), or justified by something other than parsimony.

[1]The potential problem of inadvertently non-independent characters is set aside here, except to say that successive character weighting can only exacerbate it by reinforcing the amplified signal of non-independent characters at the expense of independent conflicting characters (Kluge, 1997b).

Homoplasy is a valid indicator that some characters should be revisited with an eye toward recoding or reinterpretation (i.e., reciprocal illumination). However, we cannot do either unless observational evidence warrants it (Farris, 1983; Kluge, 1997b).

Apart from theoretical philosophical concerns, there are empirical reasons to question successive weighting. Several studies from molecular systematics have shown that the quickly evolving characters (e.g., third nucleotide positions versus first and second positions, nucleotides versus amino acids) can be more phylogenetically informative than slowly evolving characters (e.g., Källersjö et al., 1999; Simmons et al., 2002). Under successive weighting, much of this information could be lost.

Despite stability issues with our equal weights analysis, we consider this our preferred working hypothesis of erigonine relationships. Discussion below of clade support and character evolution refers to the equal weights cladogram (Fig. 3) unless otherwise specified.

Have we made progress?

For this study, we have more than doubled the number of characters and ingroup taxa over the previous effort. This has led to a new hypothesis of erigonine relationships that provides a more severe test of congruence among the characters. If progress in systematics is made by adding new observations to a phylogenetic data matrix (*sensu* Farris, 1983; Kluge, 1997a,b; Wenzel, 1997), then we have been successful. However, multiple lines of evidence indicate that our hypothesis is weakly supported and is likely to change with the addition of yet more character data.

Although Bremer support values are generally low, we have improved the average Bremer support per node over the previous study, especially for relationships among erigonine genera. CJF analysis of Hormiga's (2000) data predicted that the addition of more characters would produce substantial changes in the topology. This prediction was born out in incongruence between Hormiga's topology and the results from the current study. However, the CJF analysis results for the current study are indistinguishable from the Hormiga (2000) curve, indicating that we can expect continued change in hypotheses of erigonine relationships as more data are brought to bear on the problem, at least until much more data have accumulated. Despite problems with the stability of our phylogeny, it remains the best available context for a discussion of erigonine evolution.

Previous groupings revisited

Linyphiid subfamilies. Our study is only the second attempt to investigate relationships among erigonine genera using cladistic methods. However, several

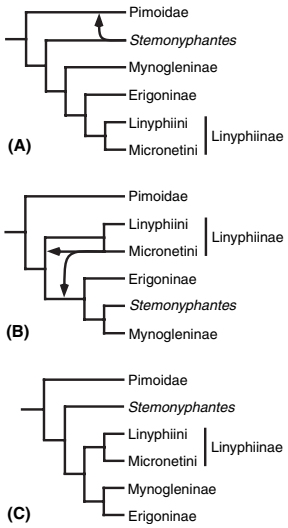

Fig. 14. Hypotheses of linyphiid subfamily relationships in (A) Hormiga (1993, 1994a,b), (B) Hormiga (2000), and (C) the current study and Wunderlich (1987). The preferred tree is shown in rectangular form; alternative topologies are indicated by arrows.

studies have addressed relationships among linyphiid subfamilies using cladistic or tree-based methods (Wunderlich, 1987; Hormiga, 1993, 1994a,b, 2000). Compared to Hormiga's (2000) analysis, we have added new characters relevant to the question of linyphiid subfamily relationships. However, we have added only erigonine taxa. It seems clear that progress in the question of linyphiid subfamily phylogeny would be well served by the addition of nonerigonine linyphiid taxa. Hormiga (2000) found a clade composed of *Stemonyphantes* Menge, 1866 and mynoglenines sister to erigonines (Fig. 1). His preferred tree placed linyphiines sister to this complex, but equally parsimonious alternatives placed Linyphiini and Micronetini in a trichotomy with the other linyphiids or linyphiines in a grade with the Micronetini alone sister to the other linyphiids exclusive of Linyphiini (Fig. 14B). In his previous studies, Hormiga (1993, 1994a,b) suggested that Linyphiinae and Erigoninae are sister taxa, forming a clade exclusive of Mynogleninae (Fig. 14A). Equally parsimonious solutions placed *Stemonyphantes* sister to the remaining linyphiids, or sister to the Pimoidae (the uncontroversial sister group to linyphiids). This later solution implied a paraphyletic Linyphiidae. Hormiga (1993, 1994a,b) argued for the former. Wunderlich (1986) published the first tree-based hypothesis of linyphiid subfamilies. Although it was not matrix based, it provided synapomorphies for all clades proposed in his tree. Wunderlich's (1987) topology is identical to that recovered in the current study (Fig. 14C).

Erigonine genera. Hormiga (2000) based his taxon sample on the groups of erigonine genera delimited by Millidge (1977), which was the most detailed classification available at the time. Millidge established 16 groups of erigonine genera. When specimens were available and groups were not monotypic, Hormiga selected exemplars from at least two genera representing each group. In this way, Hormiga was able to test the monophyly of 11 of Millidge's groups. Hormiga was also able to use his taxon sample to test the coarser classification scheme of Merrett (1963, 1965). Hormiga's phylogeny recovered none of Merrett's three groups as monophyletic. Three of Millidge's groups were supported by Hormiga's analysis: the *Gongylidium* group (*Gongylidium*, *Oedothorax*), the *Savignia* group (*Araeoncus*, *Diplocephalus*, *Savignia*), and the *Entelecara* group (*Entelecara* Simon, 1884, *Hybocoptus*). We have repeated Hormiga's investigation into the predictive quality of Merrett's and Millidge's classification systems using our pruned topology as a reference (Fig. 8). As in Hormiga (2000), none of Merrett's groups are monophyletic. None of Millidge's groups are monophyletic either. In our study, the *Gongylidium* group is paraphyletic with respect to *Hylyphantes* and *Tmeticus*; the *Entelecara* group is disrupted by the *Hybocoptus–Dismodicus* clade, and the *Savignia* group is disrupted by the *Entelecara–Hybocoptus–Dismodicus* clade sister to the *Diplocephalus–Savignia* clade (see Appendix F).

As noted above, Wunderlich's (1987) synonymy of *Ceratinopsis* and several other genera under *Sphecozone* has been generally rejected (Millidge, 1991). The common ancestor of the type species of *Ceratinopsis* and *Sphecozone* is represented by node 76. Wunderlich's synonymy would be incomplete without *Tutaibo*. In the current study, *Sphecozone* is both monophyletic and diagnosable. The monophyly of *Tutaibo* and the relimited *Ceratinopsis* (without *Intecymbium antarcticum*) have not been tested in the current study. *Tutaibo* is diagnosable by a unique sclerite on the tegulum, by the ectal origin of the copulatory ducts from the spermathecae, and by the combination of a hook-like paracymbium and a basal cymbial excavation; the monophyly of *Tutaibo* is therefore not in doubt. The monophyly of *Ceratinopsis* is less clear and a study of the relationships among genera such as *Ceratinella* Emerton, 1882, *Syloctetor* Simon, 1884, and others may be necessary to resolve this issue.

Wunderlich (1978) synonymized *Drepanotylus* Holm, 1945 under *Notiomaso* Banks, 1914. This was rejected by Merrett et al. (1985) and has not been adopted by others, although Merrett et al. provided no explicit justification for their rejection. The inclusion of *Notiomaso* as an exemplar in this study allows us to evaluate these positions. We found that *Drepanotylus* and *Notiomaso* are quite distantly related. *Drepanotylus* belongs to one of the most basal clades of Erigoninae, retaining the desmitracheate system with tracheoles in the taenidia, the primitive condition for the subfamily. *Notiomaso* is part of a clade of haplotracheate erigonines endemic to southern South America and some South Atlantic islands. *Notiomaso* and *Drepanotylus* do share some

unusual characteristics including a distally projecting distal suprategular apophysis, a posterior origin of the embolus, and the presence of an anteriorly directed radical tailpiece. Note that we did not use the type species of *Notiomaso* to represent the genus. However, *Notiomaso* (including several synonyms; Miller, in press a) is a rather unusual erigonine genus that is likely to be monophyletic.

Conclusions

We built upon Hormiga's original analysis of erigonine relationships, adding 95 new characters and 39 new taxa. Significant differences between Hormiga's hypothesis and our revised phylogeny are explained mostly by the addition and modification of characters, not taxa. Although we have not made significant progress toward a stable phylogeny of erigonine relationships, the addition of so much new data has certainly provided a more severe test of character congruence than was previously available.

It may be that the ratio of characters to taxa must be much higher before relationships begin to stabilize. To this end, new sources of data including molecular sequences may be required. This study presents the largest data matrix yet for the study of erigonine relationships. The resulting hypothesis is therefore the best available for investigating the evolution of characters of interest to erigonine evolution. However, investigations of character evolution are only as robust as the phylogeny they are built on, and interpretations should be made with caution. We expect that the addition of future data to the question of erigonine phylogeny, especially the addition of new characters, will change the hypothesis of relationships presented here.

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Appendix A

Abbreviations used in the text and figures

Male palp

ARP anterior radical process
AT anterior tooth of radix
BL basal lobe of embolus
DL distal lobe of radix
DSA distal suprategular apophysis
DTA distal tibial apophysis
E embolus
EB embolic basal lobe
EBP embolic basal process
EM embolic membrane
F fundus
FO foramen
MT mesal tooth of radix
PC paracymbium
PEP pimoid embolic process
PT protegulum
PTA prolateral tibial apophysis
R radix
RBP retrobasal process of cymbium
RF radical fold
RMP retromedian cymbial process
RR radical ridge
RTA retrolateral tibial apophysis
SPT suprategulum
ST subtegulum
T tegulum
TP tailpiece of radix

Epigynum

A atrium
AL anterior lobe of dorsal epigynal plate
AP anterior process of ventral epigynal plate
CO copulatory opening
DP dorsal plate of epigynum
FD fertilization duct
IM internal membrane of epigynum
S spermatheca
SC scape
SD sperm duct
VP ventral plate of epigynum

Somatic morphology

P pedicel

Appendix B
(Caption on page 411)

MALE PALPAL MORPHOLOGY	1. Cymbial retromedian process: abs; pres	2. Cymbial retromedian process denation: abs; pres	3. Pimoid cymbial sclerite: abs; pres	4. Cymbial retrobasal process: abs; pres	5. Cymbium size: unmodified; reduced	6. Alveolus: long; short	7. Cymbium retrolateral groove: abs; pres	8. Cymbium basal excavation: abs; pres	9. Cymbium height: unmodifed; tall	10. Paracymbium: pres; abs	11. Paracymbium morph: interseg; integral	12. Paracymbium morphology: 0; 1; 2; 3; 4; 5; 6; 7	13. Paracymbium apophyses: abs; pres	14. Paracymbium basal setae: absent; present	15. Paracymbium basal setae form: unmodified; large	16. Protegulum: abs; pres	17. Protegular papillae: abs; pres	18. Protegular papillae form: scale-like; rod-like	19. Tegular sac: abs; pres	20. Papillae on tegulum: abs; pres	21. Tegulum-subtegulum orientation: distal; mesal; ventral	22. Sperm duct first loop switchback: abs; pres	23. Sperm duct path distal tegulum: continuous; loop	24. Suprategulum: abs; pres	25. Suprategulum-tegulum: continuous; artic	26. Suprategulum orientation: continuous; angle	27. Suprategulum texture: smooth; striated	28. Foramen: in suprategulum; in tegulum	29. Distal suprategular apophysis: abs; pres	30. DSA: continuous; membranous division	31. DSA orient: distal; ventral	32. DSA texture: smooth; grooves or papillae	33. DSA basal papillae: abs; pres	34. Marginal suprategular apophysis: abs; pres	35. Median apophysis: abs; pres	36. Conductor: abs; pres	37. Pimoid embolic process: abs; pres	38. Column: abs; pres	39. Column position: dorsal; ventral	40. Embolic membrane: abs; pres	41. Embolic membrane texture: unmodified; papillae	42. Embolus origin: distal; proximal	43. Embolus length: long; short	44. Embolus shape: straight to curved; spiral	45. Embolic tip: unmodified; projection beyond opening	46. Embolic papillae: abs; pres	47. Embolic axis at origin: continuous; distinct angle	48. Embolic basal process: abs; pres	49. Embolic basal lobe: abs; pres	50. Radix: abs; pres	51. Radix-embolus connection: continuous; membranous	52. Radical tailpiece: abs; pres	53. Radical tailpiece: straight; spiral; recurved; mesal; ant	54. Radix texture: smooth; striations or tubercles	55. Anterior radical process: abs; pres	56. Anterior radical process type: robust; flagelliform	57. Anterior tooth of radix: abs; pres	58. Mesal tooth of radix: abs; pres	59. Distal lobe of radix: abs; pres	60. Radical ridge: abs; pres
Tetragnatha	0	-	0	0	0	1	0	0	0	0	0	0	1	1	0	0	-	-	0	0	0	0	1	0	-	-	-	-	-	-	-	-	0	-	0	1	0	1	-	0	-	0	0	1	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	0
Theridiosoma	0	-	0	0	0	0	0	0	0	0	1	1	0	0	-	0	-	-	0	1	1	1	1	0	-	-	-	-	-	-	-	-	-	-	1	1	0	0	-	-	-	0	1	-	1	0	0	0	0	0	-	-	-	-	-	-	-	-	-	0
Steatoda	0	-	0	0	0	1	0	0	0	1	-	-	-	-	-	0	-	-	0	0	0	1	0	0	-	-	-	-	-	-	-	-	0	-	1	1	0	1	-	0	-	1	0	1	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	0
P. rupicola	1	1	1	0	0	0	0	0	0	0	1	2	0	0	-	0	-	-	0	-	2	1	0	0	-	-	-	-	-	-	-	-	-	-	1	1	1	0	-	-	-	0	0	1	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	0
P. altioculata	1	1	1	0	0	0	0	0	0	0	1	3	0	1	0	0	-	-	0	0	2	1	0	0	-	-	-	-	-	-	-	-	-	-	1	1	1	0	-	-	-	0	0	1	0	0	0	0	0	0	-	-	-	-	-	-	-	-	-	0
Stemonyphantes	0	-	0	1	0	1	0	0	0	0	0	4	0	1	0	0	-	-	0	1	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	-	1	0	1	0	0	0	0	0	1	1	1	4	0	1	0	0	0	0	0
Microlinyphia	0	-	0	0	0	0	0	0	0	0	0	4	0	1	0	0	-	-	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	-	0	0	1	0	0	0	0	0	1	0	0	-	0	0	-	0	0	0	0
Linyphia	0	-	0	0	0	0	0	0	0	0	0	4	0	1	0	0	-	-	0	0	1	1	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	0	-	0	0	-	0	0	0	0
Bolyphantes	0	-	0	1	0	0	0	0	0	0	0	5	1	1	0	0	-	-	0	0	0	1	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	-	0	1	0	0	0	1	0	0	-	0	0	-	0	0	0	0
Tenuiphantes	0	-	0	0	0	0	0	0	0	0	0	5	1	1	0	0	-	-	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	-	0	1	0	0	0	1	0	0	-	0	0	-	0	0	0	0
Haplinis	0	-	0	0	0	1	0	0	0	0	0	4	0	1	0	0	-	-	0	0	1	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	-	1	0	1	0	1	0	0	0	0	0	1	0	0	-	0	0	-	0	0	0	0
Novafroneta	0	-	0	0	0	1	0	0	0	0	0	4	0	1	0	0	-	-	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	1	-	1	0	1	0	0	0	0	0	0	0	1	0	0	-	0	0	-	0	0	0	0
Leptorhoptrum	0	-	0	0	1	0	1	0	0	0	0	4	0	1	0	0	-	-	0	0	1	0	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	1	0	0	-	0	0	0	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Drepanotylus	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	1	4	0	0	-	0	0	0	0
Hilaira	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	0	-	-	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	-	0	1	-	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0
Tibioploides	0	-	0	0	0	0	1	0	1	0	0	5	0	1	0	0	-	-	0	0	1	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Triplogyna	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	0	-	-	0	0	1	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0
Laminacauda	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	0	-	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0
Scolecura	0	-	0	0	0	0	1	0	0	0	0	5	0	0	-	0	-	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	3	0	1	0	0	0	0	0
Ostearius	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	0	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Neocautinella	1	0	0	0	0	0	1	0	0	0	0	4	0	1	0	1	0	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Anodoration	0	-	0	0	0	0	1	0	0	0	0	5	0	0	-	0	-	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Rhabdogyna	0	-	0	0	0	0	0	0	0	0	0	5	0	1	0	0	-	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Ctenophysis	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0
Valdiviella	0	-	0	0	0	0	1	0	0	0	0	5	0	1	1	1	0	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Deichomma	0	-	0	0	0	0	1	0	0	0	0	4	0	1	0	0	-	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	1	1	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
Notiomaso	1	0	0	0	0	0	1	0	0	0	0	4	0	1	0	0	-	-	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	0	1	0	1	4	1	0	-	0	0	0	0
Pseudotyphistes	0	-	0	0	0	0	1	0	1	0	0	5	0	1	0	1	0	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Sisicus	0	-	0	0	0	0	0	0	0	0	0	5	0	1	0	1	0	-	0	0	0	0	0	0	1	0	1	0	0	-	-	-	-	0	0	0	0	1	-	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Onychembolus	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	1	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0
Smermisia	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	0	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	1	0	0	0	1	0	1	0	0	0	-	0	1	0	0
Lygarina	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	1	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0
Hypselocara	0	-	0	0	0	0	1	0	0	0	0	5	0	0	-	1	0	-	0	0	1	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	0	0	1	0	0	1	0	0
Neomaso	1	0	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	1	0	0	1	1	1	1	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	1	1	0	0	1	-	0	0	0	0
Gigapassus	1	0	0	1	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	1	0	0	1	1	0	1	0	1	0	1	0	0	1	0	0	0	1	0	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	-	0	0	0	0
Asthenargus	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	?	1	0	1	1	1	1	0	0	0	-	-	-	-	0	0	0	0	1	0	1	?	0	1	-	0	0	0	0	1	1	1	1	0	0	1	0	0	0	1	0
Gongylidiellum	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	1	0	0	1	0	0	1	1	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	1	1	0	0	1	0	0	1	1	0
Spanioplanus	0	-	0	0	0	0	1	0	0	0	0	5	0	0	-	1	0	-	0	0	1	0	1	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	1	1	1	1	0	0	0	-	0	1	1	0
Sciastes	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	0	-	-	-	-	0	0	0	0	1	-	1	0	0	1	-	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0
Islandiana	0	-	0	0	0	0	1	0	0	0	0	5	0	1	1	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	1	0	0	0	1	0	1	2	0	1	0	1	0	0	0
Gravipalpus	0	-	0	0	0	1	0	0	0	0	0	5	0	1	0	1	1	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	0	1	-	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
M. dentiger	0	-	0	0	0	1	0	0	0	0	0	5	0	1	0	1	1	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	2	0	0	-	1	1	0	0
M. rapidulus	0	-	0	0	0	1	0	0	0	0	0	5	0	1	0	1	1	1	0	0	0	0	1	1	1	0	0	0	1	0	1	0	1	0	0	0	0	1	0	1	1	0	1	-	0	0	0	0	0	1	0	1	2	0	0	-	1	0	0	0
Paraletes	0	-	0	0	0	0	0	0	0	0	0	5	0	1	0	1	0	-	0	0	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	-	0	1	-	0	0	0	0	0	1	0	1	0	1	1	0	1	0	0	0
Erigone	0	-	0	0	0	1	1	0	0	0	0	5	0	1	0	1	0	-	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0	1	1	0	1	-	0	0	0	0	0	1	0	1	2	1	1	0	1	1	0	0
Myrmecomelix	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	1	0	1	0	0	0	1	1	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	0	1	1	0	0	1	0	0
Microplanus	0	-	0	0	0	1	1	0	0	0	0	5	0	1	0	1	1	1	0	1	0	0	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	0	1	1	0	0	0	0	0
Toltecaria	0	-	0	0	0	0	0	0	0	0	0	5	0	0	-	1	1	1	0	0	1	0	1	1	1	0	0	0	1	0	1	1	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Fissiscapus	0	-	0	1	0	1	1	0	0	0	0	5	0	0	-	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	1	0	1	-	0	1	0	0	0	1	1	1	1	1	1	0	0	0	0	0
Labicymbium	1	0	0	1	0	1	0	0	0	0	0	5	0	0	-	1	1	1	0	0	0	0	1	1	1	0	0	0	1	1	1	1	0	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	1	1	1	1	0	-	0	0	0	0
Diplocentria	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0
Sisicottus	0	-	0	0	0	0	0	0	0	0	0	5	0	1	0	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	1	1	1	0	0	0	-	0	0	0	0
Oedothorax	0	-	0	0	0	0	0	0	0	0	0	5	0	1	0	1	1	1	1	1	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0
Gongylidium	0	-	0	0	0	0	0	0	0	0	0	5	0	1	0	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	-	0	0	0	0
Hylyphantes	0	-	0	0	0	0	0	0	0	0	0	5	0	0	-	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	1	0	0	0	0	0	1	0	0	-	0	1	-	0	0	0	0	0	1	1	1	0	0	0	-	0	0	0	0
Tmeticus	0	-	0	0	1	0	1	0	0	0	0	5	0	1	0	1	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0
Typhochrestus	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0
Araeoncus	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0
Diplocephalus	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0
Savignia	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0	0	0	0
Entelecara	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	0	0	0	1	0	0	0	0	1	0	1	0	?	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	-	0	0	0	0
Dismodicus	0	-	0	0	0	0	?	0	0	0	0	5	0	1	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Hybocoptus	0	-	0	0	0	0	1	0	0	0	0	5	0	?	?	1	0	-	0	0	0	0	0	1	0	1	?	0	1	0	1	0	?	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	1	0	0	0	-	0	0	0	0
Lophomma	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	0	0	1	0	0	0	0	0
Walckenaeria	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	0	-	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	-	0	0	0	0
Gonatium	0	-	0	1	0	1	0	0	0	0	0	5	0	0	-	0	-	-	1	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	1	0	0	0	0	0	1	0	1	0	0	1	1	0	0	0	0
A. daedalus	0	-	0	0	0	1	1	0	0	0	0	6	0	1	0	0	-	-	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	-	1	1	1	0	0	0	0	0	0	0	1	0	0	-	0	1	1	0	0	0	0
A. janetae	0	-	0	0	0	1	1	0	0	0	0	6	0	1	0	0	-	-	0	0	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	0	0	1	-	1	1	1	0	0	0	0	0	0	0	1	0	0	-	0	1	1	0	0	0	0
Tapinocyba	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	1	0	0	0	0	1	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	-	0	1	-	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Ceratinops	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	1	-	0	0	0	0	0	1	0	1	0	0	0	-	0	0	0	0
Parapelecopsis	0	-	0	0	0	0	1	0	0	0	0	5	0	0	-	1	1	-	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	1	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	1	0	1	1	0	0	-	0	0	0	0
Grammonota	0	-	0	0	0	0	1	0	0	0	0	5	0	1	0	1	1	1	0	1	1	1	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	-	0	0	1	0	0	1	0	0	1	0	1	1	0	1	0	0	0	0	0
Intecymbium	0	-	0	0	0	0	1	0	0	0	1	5	0	0	-	1	0	-	0	1	1	0	0	1	0	0	1	0	0	-	-	-	-	0	0	0	0	1	-	1	0	0	0	0	1	0	1	0	0	1	0	1	1	0	0	-	0	0	0	1
Psilocymbium	0	-	0	0	0	0	0	0	0	1	-	-	-	-	-	1	0	-	0	1	1	0	0	1	0	0	0	0	0	-	-	-	-	0	0	0	0	1	-	0	-	0	0	0	0	0	0	0	0	1	0	1	1	0	1	0	0	0	0	0
Dolabritor	0	-	0	0	0	0	1	0	0	0	1	7	0	1	0	1	0	-	0	0	1	0	0	1	0	0	0	0	0	-	-	-	-	0	0	0	0	1	-	1	0	0	0	0	1	0	1	0	0	1	1	1	1	0	0	-	0	0	0	1
Gonatoraphis	0	-	0	0	0	0	1	0	0	0	1	7	0	1	0	1	0	-	0	0	1	0	0	1	0	0	0	0	0	-	-	-	-	0	0	0	0	1	-	1	0	0	0	0	1	0	1	1	0	1	0	1	1	0	0	-	0	0	0	1
Ceratinopsis	0	-	0	0	0	0	1	0	0	0	0	4	0	1	0	1	0	-	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	1	0	0	0	0	1
Tutaibo	0	-	0	0	0	0	0	1	0	0	0	4	0	1	0	1	0	-	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	-	0	0	0	0	0	1	0	0	1	1	1	1	0	1	0	0	0	0	1
S. rubescens	0	-	0	0	0	0	0	1	0	1	-	-	-	-	-	1	0	-	0	0	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	1	1	1	0	0	1	0	0	0	0	0
S. bicolor	0	-	0	0	0	0	0	1	0	1	-	-	-	-	-	1	0	-	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0
S. spadicaria	0	-	0	0	0	0	0	1	0	1	-	-	-	-	-	1	0	-	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	1	0	0	0	0	1	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0
S. crassa	1	0	0	0	0	0	0	1	0	1	-	-	-	-	-	1	1	0	0	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	0	0	1	0	0	-	0	0	1	0	0	0	1	0	1	1	1	1	0	1	0	0	0	0	1
steps	6	1	1	5	2	9	12	1	2	3	3	11	2	11	2	6	9	6	3	12	12	6	7	2	6	5	3	2	4	1	2	4	1	6	2	1	1	2	4	11	7	8	14	10	8	7	6	2	3	1	10	3	13	5	20	1	4	6	1	4
ci	.16	1	1	.20	.50	.11	.08	1	.50	.33	.33	.63	.50	.09	.50	.16	.11	.16	.33	.08	.16	.16	.14	.50	.16	.20	.33	.50	.25	1	.50	.25	1	.16	.50	1	1	.50	.25	.09	.14	.12	.07	.10	.12	.14	.16	.50	.33	1	.10	.33	.30	.20	.05	1	.25	.16	1	.25
ri	.28	1	1	.20	.00	.42	.63	1	0	.60	.60	.66	.50	.16	0	.79	.68	.28	.50	.31	.72	.37	.50	.80	.78	.50	.71	.66	.50	1	.87	.50	1	.70	.66	1	1	.50	.50	.16	.33	.46	.56	.57	.12	.14	.58	.66	.00	1	.57	.71	.52	.50	.47	1	.40	.16	1	.40

Appendix B
Continued

MALE PALPAL MORPHOLOGY

Taxon	61. Radix median excavation: abs; pres	62. Radix median excavation orient: ventral; prolateral	63. Sperm duct in radix: short; long	64. Fickert's gland: abs; pres	65. Terminal apophysis: abs; pres	66. Lamella characteristica: abs; pres	67. Male prolateral palpal tibial apo: abs; pres	68. Male PTA apo orient: distal; dorsal	69. Male PTA distal tooth: abs; pres	70. Male retrolateral palpal tibial apo: abs; pres	71. Male distal palpal tibial apo: abs; pres	72. Male ventral palpal tibial apo: abs; pres	73. Male palpal tibia prolat tricho: 2; 1; 0	74. Male palpal tibia retrolat tricho: 4; 3; 2; 1	75. Male ventral palpal patella apo: abs; pres	76. Male palpal patella: short; long	77. Male palpal patella dorsal macroseta: abs; pres	78. Male palpal patella dorsal macroseta: weak; strong
Tetragnatha	-	-	-	0	-	-	0	-	-	0	0	0	0	0	0	1	1	1
Theridiosoma	-	-	-	0	-	-	0	-	-	0	0	0	1	3	0	0	1	1
Steatoda	-	-	-	0	-	-	0	-	-	0	0	0	1	3	0	0	1	1
P. rupicola	-	-	-	0	-	-	0	-	-	0	0	0	0	1	0	0	1	1
P. altioculata	-	-	-	0	-	-	0	-	-	0	0	0	0	1	0	0	1	1
Stemonyphantes	0	-	0	0	0	0	0	-	-	0	0	1	1	2	0	1	1	1
Microlinyphia	0	-	0	0	1	1	0	-	-	0	0	0	1	2	0	0	1	1
Linyphia	0	-	0	0	1	1	0	-	-	0	0	0	1	1	0	0	1	0
Bolyphantes	0	-	0	1	1	1	0	-	-	0	0	0	1	2	0	0	1	1
Tenuiphantes	0	-	0	1	1	1	0	-	-	0	0	0	1	2	0	0	1	1
Haplinis	0	-	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	1
Novafroneta	0	-	0	0	0	0	0	-	-	0	0	0	1	2	0	0	1	1
Leptorhoptrum	0	-	0	0	0	0	0	-	-	0	0	0	0	1	0	0	1	1
Drepanotylus	0	-	0	0	0	0	1	1	0	0	0	0	1	2	0	0	1	0
Hilaira	0	-	0	0	0	0	1	1	0	0	0	0	1	2	0	1	1	0
Tibioploides	0	-	0	0	0	0	1	1	0	0	0	0	1	3	0	0	1	0
Triplogyna	0	-	0	0	0	0	1	0	0	1	1	0	1	2	0	1	1	0
Laminacauda	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0
Scolecura	0	-	1	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0
Ostearius	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0
Neocautinella	0	-	0	0	0	0	0	-	-	1	0	0	1	2	0	0	1	0
Anodoration	0	-	0	0	0	0	1	0	0	1	1	0	1	3	0	0	1	0
Rhabdogyna	0	-	0	0	0	0	1	0	0	1	1	0	1	3	0	0	1	0
Ctenophysis	0	-	0	0	0	0	1	0	0	1	0	0	1	3	0	0	1	0
Valdiviella	0	-	0	0	0	0	0	-	-	1	0	0	1	3	0	0	1	0
Deichomma	0	-	0	0	0	0	0	-	-	1	0	0	1	3	0	0	1	0
Notiomaso	0	-	0	0	0	0	0	-	-	0	0	0	1	3	0	0	1	0
Pseudotyphistes	0	-	0	0	0	0	0	-	-	1	0	0	1	3	0	0	1	1
Sisicus	0	-	0	0	0	1	1	0	0	0	0	0	2	3	0	0	1	0
Onychembolus	0	-	0	0	0	0	1	0	0	1	0	0	1	3	0	0	1	0
Smermisia	0	-	0	0	0	0	0	-	-	1	0	0	1	3	0	0	1	0
Lygarina	0	-	0	0	0	0	1	0	0	1	0	0	1	3	0	0	1	0
Hypselocara	0	-	0	0	0	0	0	-	-	1	0	0	2	3	0	0	1	0
Neomaso	0	-	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	0
Gigapassus	0	-	0	0	0	0	0	-	-	0	0	0	1	3	0	0	1	0
Asthenargus	0	-	0	0	0	0	1	1	0	0	0	0	1	3	0	0	1	0
Gongylidiellum	0	-	0	0	0	0	1	1	0	0	0	0	1	3	0	0	1	0
Spanioplanus	0	-	0	0	0	0	1	0	0	0	0	0	1	3	0	0	1	0
Sciastes	0	-	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	0
Islandiana	0	-	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	0
Gravipalpus	1	1	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0
M. dentiger	1	1	0	0	0	0	1	0	0	0	0	0	1	2	1	0	1	0
M. rapidulus	1	1	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	0
Paraletes	1	0	0	0	0	0	1	1	0	1	0	0	1	3	0	0	1	0
Erigone	1	0	0	0	0	0	1	0	0	1	0	1	1	2	1	1	1	0
Myrmecomelix	1	0	0	0	0	0	1	0	0	1	0	0	1	3	0	0	1	0
Microplanus	1	0	0	0	0	0	1	0	0	1	0	0	1	3	0	0	1	1
Toltecaria	0	-	0	0	0	0	1	0	0	0	0	0	1	3	0	0	1	1
Fissiscapus	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	1
Labicymbium	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	1
Diplocentria	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0
Sisicottus	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0
Oedothorax	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	1	1	0
Gongylidium	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0
Hylyphantes	0	-	0	0	0	0	1	0	0	1	0	0	1	2	1	1	1	0
Tmeticus	0	-	0	0	0	0	1	0	0	0	0	0	1	2	1	1	1	0
Typhochrestus	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	0	-
Araeoncus	0	-	0	0	0	0	1	0	0	0	0	0	1	2	0	1	0	-
Diplocephalus	0	-	0	0	0	0	1	0	0	0	0	0	1	2	0	0	1	1
Savignia	0	-	0	0	0	0	1	0	0	0	0	0	1	3	0	0	1	0
Entelecara	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0
Dismodicus	0	-	0	0	0	0	1	0	0	0	0	0	0	2	0	0	0	-
Hybocoptus	0	-	0	0	0	0	1	1	0	0	0	0	?	3	0	0	0	-
Lophomma	0	-	0	0	0	0	1	1	0	1	0	0	1	2	0	0	1	0
Walckenaeria	0	-	0	0	0	0	1	0	0	1	0	0	1	2	0	0	1	0
Gonatium	0	-	0	0	0	0	1	0	0	1	1	0	1	3	0	0	1	0
A. daedalus	0	-	1	0	0	0	1	0	0	1	0	0	1	3	0	0	1	0
A. janetae	0	-	1	0	0	0	1	0	0	1	0	0	1	3	0	0	1	0
Tapinocyba	0	-	0	0	0	0	1	1	0	0	0	0	1	3	0	0	1	0
Ceratinops	0	-	0	0	0	0	1	0	0	0	0	0	1	3	0	0	1	0
Parapelecopsis	0	-	0	0	0	0	1	0	0	0	0	1	2	3	0	0	0	-
Grammonota	0	-	1	0	0	0	1	0	0	0	0	0	1	3	0	0	1	0
Intecymbium	0	-	1	0	0	0	1	0	0	0	0	0	2	3	0	0	1	0
Psilocymbium	0	-	1	0	0	0	1	1	1	0	0	0	2	3	0	0	1	0
Dolabritor	0	-	1	0	0	0	1	1	1	1	0	1	2	3	0	0	1	0
Gonatoraphis	0	-	1	0	0	0	1	1	1	0	0	0	2	3	0	1	1	0
Ceratinopsis	0	-	1	0	0	0	1	0	0	0	0	0	1	3	0	0	1	0
Tutaibo	0	-	1	0	0	0	1	1	0	0	0	0	1	3	0	0	1	0
S. rubescens	0	-	1	0	0	0	1	0	0	0	0	0	2	3	0	0	1	0
S. bicolor	0	-	1	0	0	0	1	0	0	0	0	0	1	3	0	0	1	0
S. spadicaria	0	-	1	0	0	0	1	0	0	1	0	0	1	3	0	0	1	0
S. crassa	0	-	1	0	0	0	1	0	0	1	0	0	1	3	0	0	1	0
steps	2	1	3	1	1	2	7	9	1	13	3	4	10	16	3	9	4	5
ci	.50	1	.33	1	1	.50	.14	.11	1	.07	.33	.25	.20	.18	.33	.11	.25	.20
ri	.83	1	.84	1	1	.75	.70	.33	1	.64	.33	0	.33	.64	.33	.11	.25	.76

EPIGYNUM

Taxon	79. Epigynum dorsal plate scape: abs; pres	80. Epigynum dorsal plate anterior lobe: abs; pres	81. Epigynum ventral plate scape: abs; pres	82. Epigynum ventral plate scape form: straight; sigmoid	83. Epigynum length: short; long	84. Epigynum shape: entire; bifid	85. Epigynum ventral plate texture: smooth; striated	86. Epigynum margin: unmodified; rebordered	87. Copulatory opening: DP-VP junction; VP envelope	88. Epigynum ventral plate anterior process: abs; pres	89. Epigynum ventral plate socket: abs; pres	90. Epigynum dorsal plate socket: abs; pres	91. Epigynal bisection: abs; pres	92. Atrium: abs; pres	93. Epigynum dorsal plate orient: dorsal; flush with VP	94. Copulatory duct: separate from FD; spirals FD	95. Copulatory duct encapsulation: absent; present	96. Internal membrane: absent; present	97. Spermathecae: two; four	98. Spermathecae shape: round; oblong	99. Fertilization duct orientation: post; mesal; ant; dor	100. CD and FD: arise independently; share common duct
Tetragnatha	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-
Theridiosoma	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Steatoda	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
P. rupicola	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
P. altioculata	0	0	0	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
Stemonyphantes	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0
Microlinyphia	1	0	0	-	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0	0
Linyphia	1	0	0	-	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0	1	0	0
Bolyphantes	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Tenuiphantes	0	0	1	1	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0
Haplinis	0	0	1	0	0	0	0	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0
Novafroneta	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Leptorhoptrum	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
Drepanotylus	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Hilaira	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tibioploides	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
Triplogyna	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	-	1
Laminacauda	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	1	-	1
Scolecura	0	0	0	-	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0
Ostearius	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0
Neocautinella	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
Anodoration	0	0	0	-	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Rhabdogyna	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	3	0
Ctenophysis	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Valdiviella	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Deichomma	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Notiomaso	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0
Pseudotyphistes	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sisicus	1	0	0	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Onychembolus	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Smermisia	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Lygarina	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hypselocara	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0
Neomaso	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Gigapassus	0	0	0	-	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Asthenargus	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Gongylidiellum	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Spanioplanus	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Sciastes	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Islandiana	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Gravipalpus	0	0	0	-	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
M. dentiger	0	0	0	-	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
M. rapidulus	0	0	0	-	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Paraletes	0	0	0	-	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Erigone	0	0	0	-	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Myrmecomelix	0	0	0	-	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Microplanus	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Toltecaria	0	0	0	-	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Fissiscapus	0	0	0	-	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Labicymbium	0	0	0	-	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Diplocentria	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Sisicottus	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Oedothorax	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Gongylidium	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0
Hylyphantes	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0
Tmeticus	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	0	1	0
Typhochrestus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Araeoncus	0	0	0	-	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0
Diplocephalus	0	0	0	-	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	0
Savignia	0	0	0	-	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0
Entelecara	0	0	0	-	0	0	0	0	0	0	0	0	1	0	1	0	1	0	0	0	1	0
Dismodicus	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Hybocoptus	0	0	0	-	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0	0
Lophomma	0	0	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0
Walckenaeria	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0
Gonatium	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0
A. daedalus	0	0	0	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
A. janetae	0	0	0	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
Tapinocyba	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Ceratinops	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	1	0
Parapelecopsis	0	0	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
Grammonota	0	0	0	-	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	1	0	0
Intecymbium	0	0	0	-	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Psilocymbium	0	0	0	-	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1	0	0
Dolabritor	0	1	0	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	1	0
Gonatoraphis	0	1	0	-	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	0
Ceratinopsis	0	0	0	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tutaibo	0	1	0	-	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	0
S. rubescens	0	1	0	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0
S. bicolor	0	1	0	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
S. spadicaria	0	1	0	-	0	0	0	0	0	1	0	0	0	1	1	0	0	1	0	1	0	0
S. crassa	0	1	0	-	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0
steps	2	4	6	1	6	2	2	2	3	4	4	1	2	16	11	2	14	2	3	11	20	1
ci	.50	.25	.16	1	.16	.50	.50	.50	.33	.25	.25	1	.50	.06	.09	.50	.07	.50	.33	.09	.15	1
ri	.50	.62	.37	1	0	.50	.66	.50	.50	0	.25	1	.75	.44	.64	0	.40	0	0	.41	.45	1

PROSOMA AND LEGS

Taxon	101. Male cephalic region: not raised; raised	102. Male PME cephalic lobe: abs; pres	103. Male post-PME lobe: abs; pres	104. Male inter AME-PME lobe: abs; pres	105. Male clypeal lobe: abs; pres	106. Male AME lobe: abs; pres	107. Subocular clypeal sulci: abs; pres	108. Male lateral sulci: abs; pres	109. Male prosomal pits: abs; pres	110. Male cephalic cuticular pores: rare; common	111. Thoracic setae: glabrous; rare; radii; *Lygar*; *Asemos*	112. Clypeus texture in male: smooth; squamate	113. Clypeal seate in female: hirsute; one	114. Thoracic furrow: smooth; invagination	115. Chelicerae size: unmodified; larger in males	116. Cheliceral lateral face in male: smooth; striated	117. Cheliceral stridulatory striae: ridged; scaly; imbricated	118. Striae: wide even; com prox; com dist; com even; *Bylo*
Tetragnatha	0	0	0	0	0	0	0	0	0	?	0	?	0	1	1	0	-	-
Theridiosoma	0	0	0	0	0	0	0	0	0	?	1	?	0	0	0	0	-	-
Steatoda	0	0	0	0	0	0	0	0	0	?	0	?	0	1	0	0	-	-
P. rupicola	0	0	0	0	0	0	0	0	0	0	2	?	0	1	0	1	-	0
P. altioculata	0	0	0	0	0	0	0	0	0	0	2	?	0	1	0	1	0	3
Stemonyphantes	0	0	0	0	0	0	0	0	0	0	2	1	0	1	0	1	0	?
Microlinyphia	0	0	0	0	0	0	0	0	0	0	2	1	0	0	1	1	1	3
Linyphia	0	0	0	0	0	0	0	0	0	0	2	1	0	1	1	1	1	3
Bolyphantes	1	0	0	0	0	0	0	0	0	1	2	0	0	0	0	1	0	4
Tenuiphantes	0	0	0	0	0	0	0	0	0	0	2	?	0	0	0	1	0	0
Haplinis	0	0	0	0	0	0	1	0	0	1	2	0	1	0	0	1	0	3
Novafroneta	0	0	0	0	0	0	1	0	0	1	2	?	1	1	0	1	0	3
Leptorhoptrum	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	3
Drepanotylus	0	0	1	0	0	0	0	0	0	0	2	0	1	0	0	1	0	3
Hilaira	0	0	1	0	0	0	0	0	0	0	2	1	1	0	0	1	0	3
Tibioploides	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	3
Triplogyna	0	0	1	0	0	0	0	0	0	0	2	0	1	0	0	1	0	1
Laminacauda	0	0	0	0	0	0	0	0	0	1	2	1	1	0	0	1	0	0
Scolecura	0	0	0	0	0	0	0	0	0	1	2	1	1	0	0	1	0	0
Ostearius	0	0	0	0	0	0	0	0	0	0	2	?	1	0	0	1	0	0
Neocautinella	0	0	0	0	0	0	0	0	0	1	2	1	1	0	0	1	0	0
Anodoration	0	0	0	0	0	0	0	0	0	1	2	1	1	0	0	1	0	1
Rhabdogyna	0	0	0	0	0	0	0	0	0	1	2	1	1	0	0	1	0	1
Ctenophysis	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	1
Valdiviella	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	1
Deichomma	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	1
Notiomaso	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	0
Pseudotyphistes	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	0
Sisicus	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	2
Onychembolus	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	0
Smermisia	0	0	0	0	0	0	0	0	0	0	2	1	1	0	1	1	2	0
Lygarina	0	0	0	0	0	0	0	0	0	0	3	1	1	0	0	1	0	0
Hypselocara	1	0	0	0	0	0	1	0	0	0	2	0	0	0	0	1	2	0
Neomaso	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	0
Gigapassus	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	1
Asthenargus	0	0	0	0	0	0	0	0	0	?	2	1	1	0	0	?	?	?
Gongylidiellum	0	0	0	0	0	0	0	0	0	0	?	1	1	0	0	1	2	1
Spanioplanus	0	0	0	0	0	0	0	0	0	1	2	1	1	0	0	1	2	0
Sciastes	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	0
Islandiana	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	0
Gravipalpus	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	1
M. dentiger	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	1
M. rapidulus	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	1
Paraletes	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	2	1
Erigone	1	0	0	0	0	0	0	0	0	0	2	0	1	0	1	1	2	3
Myrmecomelix	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	1
Microplanus	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	0
Toltecaria	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	1
Fissiscapus	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	0
Labicymbium	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	0
Diplocentria	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	0
Sisicottus	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	2	0
Oedothorax	0	0	1	0	0	0	0	0	0	1	2	1	1	0	0	1	1	0
Gongylidium	0	0	0	0	0	0	0	0	0	0	2	0	0	0	1	1	2	0
Hylyphantes	0	0	0	0	0	0	0	0	0	0	2	1	1	0	1	1	1	0
Tmeticus	0	0	0	0	0	0	0	0	0	0	2	1	1	0	1	1	1	0
Typhochrestus	0	0	1	0	0	0	0	1	0	1	2	0	1	0	0	1	2	0
Araeoncus	1	0	0	0	0	0	0	0	0	1	2	0	1	0	0	1	2	0
Diplocephalus	0	1	0	0	0	1	0	0	0	1	2	0	1	0	0	1	2	0
Savignia	0	1	0	0	0	0	0	0	0	1	2	1	1	0	0	1	2	0
Entelecara	0	1	0	0	0	0	0	1	1	1	2	0	1	0	0	1	2	0
Dismodicus	0	1	0	0	1	0	0	1	1	?	2	0	1	0	0	1	-	0
Hybocoptus	0	1	0	0	0	0	0	1	1	?	?	?	?	0	0	1	-	?
Lophomma	0	0	1	0	0	0	0	1	1	1	2	0	0	0	0	1	0	0
Walckenaeria	0	0	0	1	0	0	0	0	0	1	2	1	0	0	0	1	0	0
Gonatium	1	0	0	0	0	0	0	0	0	0	2	0	0	0	0	1	1	0
A. daedalus	0	0	0	0	0	0	0	0	0	1	4	1	1	0	0	1	0	0
A. janetae	0	0	0	0	0	0	0	0	0	1	4	1	1	0	0	1	0	0
Tapinocyba	0	0	0	0	0	0	0	1	1	1	2	1	0	0	0	1	0	0
Ceratinops	0	1	0	0	0	0	0	1	1	1	2	0	1	0	0	1	2	2
Parapelecopsis	0	1	0	0	0	0	0	1	1	1	4	0	0	0	0	1	0	0
Grammonota	0	0	1	0	0	0	0	0	0	1	2	1	0	0	0	1	0	0
Intecymbium	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	2	0
Psilocymbium	1	0	0	0	0	0	0	0	0	1	2	0	1	0	0	1	1	0
Dolabritor	0	1	0	0	0	0	0	0	1	0	2	0	1	0	0	1	0	0
Gonatoraphis	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	1	0	0
Ceratinopsis	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	0	3
Tutaibo	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	2	3
S. rubescens	0	0	0	0	0	0	0	0	0	0	2	0	1	0	0	1	0	3
S. bicolor	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	1	0	3
S. spadicaria	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	1	0	0
S. crassa	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	1	0	0
steps	6	3	6	1	1	1	2	4	4	13	5	14	7	4	5	1	15	17
ci	.16	.33	.16	1	1	1	.50	.25	.25	.07	.80	.07	.14	.25	.20	1	.13	.23
ri	0	.71	.16	0	0	0	.50	.57	.57	.53	.66	.48	.64	.50	.42	1	.59	.51

Appendix B
Continued

PROSOMA AND LEGS

Taxon	119.Cheliceral stridulatory striae ridges: abs; pres	120.Cheliceral setal bases: small; distinct; tooth-like	121.Cheliceral frontal spur in male: abs; pres	122.Cheliceral fang furrow in male: tapered; wide and flat	123.Retrolateral teeth female chelicerae: 0; 1; 2; 3; 4+	124.Sternum-labium attachment: separate; fused	125.Endites of male: smooth; tuberculate	126.Palpal tarsus claw in female: abs; pres	127.Female palpal tarsus prox dorsomesal m-seta; abs; pres	128.Female palpal tarsus dist dorsomesal m-seta; abs; pres	129.Female palpal tarsus prox dorsoectal m-seta; abs; pres	130.Female palpal tarsus dist dorsoectal m-seta; abs; pres	131.Fem pdp tar ventromesal m-setae: 0; 2; 3; 4; 5-6; 11-12	132.Female palpal tarsus ventroectal m-setae: 0; 1; 2; 3; 4	133.Autospasy: coxa-trochanter; patella-tibia	134.Femur I dorsal macroseta(ae): abs; pres	135.Femur I prolateral macroseta(ae): abs; pres	136.Tibia I proximal dorsal macroseta: abs; pres	137.Tibia I distal dorsal macroseta: abs; pres	138.Tibia II proximal dorsal macroseta: abs; pres	139.Tibia II distal dorsal macroseta: abs; pres	140.Tibia III proximal dorsal macroseta: abs; pres	141.Tibia III distal dorsal macroseta: abs; pres	142.Tibia IV proximal dorsal macroseta: abs; pres	143.Tibia IV distal dorsal macroseta: abs; pres	144.Tibia I prolateral macroseta(ae): abs; pres	145.Tibia I retrolateral macroseta(ae): abs; pres	146.Tibia I ventral macroseta(ae): abs; pres	147.Metatarsus I dorsal macroseta(ae): abs; pres	148.Metatarsus I prolateral macroseta(ae): abs; pres	149.Metatarsus I retrolateral macroseta(ae): abs; pres	150.Metatarsus I ventral macroseta(ae): abs; pres	151.Leg I ventral setae in male: unmodified; stronger	152.Metatarus IV trichobothrium: abs; pres
Tetragnatha	-	0	1	1	4	0	0	0	1	0	1	0	4	4	0	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	0	0	0
Theridiosoma	-	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0
Steatoda	-	0	0	0	0	0	0	0	0	0	0	0	1	2	0	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
P. rupicola	?	0	0	0	2	0	0	0	1	0	1	0	5	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
P. altioculata	0	0	0	0	2	0	0	0	1	1	1	0	5	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1
Stemonyphantes	0	0	0	0	2	0	0	0	1	1	1	1	4	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	0	1
Microlinyphia	0	1	0	0	4	1	0	0	1	1	1	1	4	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Linyphia	0	1	0	1	4	1	0	0	1	1	1	1	4	3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Bolyphantes	0	0	0	0	4	1	0	0	1	1	1	1	3	2	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0
Tenuiphantes	0	0	0	0	4	1	0	1	1	1	1	1	2	2	1	0	1	1	1	1	1	1	1	1	1	1	1	0	1	0	0	0	0	0
Haplinis	0	1	0	0	4	1	0	0	1	1	1	0	4	2	1	0	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
Novafroneta	0	1	0	0	4	1	0	0	1	1	0	0	4	3	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
Leptorhoptrum	0	1	0	0	4	1	0	1	1	0	1	0	3	3	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
Drepanotylus	0	1	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Hilaira	0	1	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1
Tibioploides	0	1	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Triplogyna	0	0	1	1	3	1	1	1	1	0	1	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	1
Laminacauda	0	0	0	0	4	1	0	1	1	0	1	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Scolecura	0	0	0	0	4	1	0	1	1	0	1	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Ostearius	0	0	1	1	4	1	1	1	1	0	1	0	3	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Neocautinella	0	0	1	1	4	1	0	1	1	0	1	0	3	3	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Anodoration	0	0	0	0	4	1	0	1	0	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Rhabdogyna	0	0	0	0	4	1	0	1	1	0	1	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Ctenophysis	0	0	0	0	4	1	0	1	1	0	1	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Valdiviella	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Deichomma	0	0	0	0	3	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Notiomaso	1	0	0	0	4	1	0	1	1	0	1	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0
Pseudotyphistes	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Sisicus	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Onychembolus	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
Smermisia	0	2	1	1	4	1	1	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Lygarina	0	0	0	0	3	1	0	1	0	0	0	0	2	1	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Hypselocara	0	0	0	0	3	1	0	1	1	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Neomaso	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Gigapassus	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1
Asthenargus	?	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Gongylidiellum	0	0	1	1	4	1	1	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Spanioplanus	0	0	1	0	4	1	1	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Sciastes	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0
Islandiana	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Gravipalpus	0	0	1	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
M. dentiger	0	2	1	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
M. rapidulus	0	0	1	0	4	1	0	1	1	0	0	0	2	3	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Paraletes	0	0	0	0	4	1	0	1	0	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Erigone	0	2	0	0	4	1	1	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	1
Myrmecomelix	0	0	0	0	3	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Microplanus	0	0	0	0	4	1	0	1	0	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Toltecaria	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Fissiscapus	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1
Labicymbium	0	0	1	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Diplocentria	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Sisicottus	1	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Oedothorax	0	0	1	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1
Gongylidium	0	0	1	1	4	1	1	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1
Hylyphantes	0	1	1	1	4	1	1	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1
Tmeticus	0	1	1	1	4	1	1	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1
Typhochrestus	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Araeoncus	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Diplocephalus	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Savignia	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Entelecara	0	0	0	0	3	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1
Dismodicus	0	0	0	0	3	1	0	1	0	0	0	0	2	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Hybocoptus	?	0	0	0	3	1	0	1	0	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Lophomma	0	1	0	1	4	1	1	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0
Walckenaeria	0	0	0	0	3	1	0	1	1	0	0	0	2	2	1	0	0	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	1
Gonatium	0	0	0	0	4	1	0	1	1	0	0	0	3	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	1	1
A. daedalus	1	0	0	0	3	1	0	1	0	0	0	0	2	1	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
A. janetae	1	0	0	0	3	1	0	1	0	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Tapinocyba	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Ceratinops	1	1	0	0	4	1	0	1	1	0	0	0	3	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Parapelecopsis	1	0	0	0	2	1	0	1	1	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Grammonota	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Intecymbium	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Psilocymbium	0	0	0	0	3	1	0	1	0	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	1	0	0	0	0	0	0
Dolabritor	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
Gonatoraphis	0	0	0	0	4	1	0	1	0	0	0	0	2	1	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
Ceratinopsis	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Tutaibo	0	0	0	0	3	1	0	1	1	0	0	0	3	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
S. rubescens	0	0	0	0	4	1	0	1	1	0	1	0	3	3	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
S. bicolor	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	1
S. spadicaria	0	0	0	0	4	1	0	1	1	0	0	0	2	3	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
S. crassa	0	0	0	0	4	1	0	1	1	0	0	0	2	2	1	0	0	1	0	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0
steps	4	9	8	8	14	1	7	3	10	3	10	2	13	15	1	5	2	2	4	2	4	3	10	2	5	3	2	4	3	4	4	3	2	16
ci	.25	.22	.12	.12	.28	1	.14	.33	.10	.33	.10	.50	.38	.26	1	.20	.50	.50	.25	.50	.25	.33	.10	.50	.20	.33	.50	.25	.33	.25	.25	.33	.50	.06
ri	.40	.46	.50	.30	.33	1	.33	.77	.18	.71	.50	.75	.42	.21	1	.33	.90	0	.85	0	.85	0	.75	0	.85	.85	.87	.50	.66	.40	.40	.60	0	.34

ABDOMEN AND SPINNERETS

Taxon	153.Male pedicel sternite and pleurites: separated; juxtaposed	154.Male booklungs: reticulate; grooved; squamate; smooth	155.Male dorsal scutum: abs; pres	156.Ventral sclerite anterior to spinnerets: abs; pres	157.Median tracheal trunks: unbranched; branched	158.Median tracheal trunks branching: few; many	159.Median tracheal trunks width: equal to laterals; wider	160.Median tracheal trunk length: short; long	161.Tracheole taenidia: abs; pres	162.Aciniform spigots in female PMS: 0; 1; 2; 3; 4	163.Minor ampullate nubbin in female PMS: abs; pres	164.Mesal cylindrical spigot in fem PLS: unmod; enlarged	165.Aciniform spigots in female PLS: abs; one or more	166.Aggregate-flagelliform triplet in male: abs; pres	167.Aggregate spiggots in female: 2; 1	168.Flagelliform spiggot in female: pres; nubbin; abs	169.Epiandrous gland spigots: abs; pres	170.Epiandrous gland spigot arrangement: grouped; sep
Tetragnatha	0	?	0	0	0	-	?	?	-	3	1	0	1	0	0	0	1	1
Theridiosoma	0	?	0	0	0	-	?	?	-	3	1	0	1	0	0	0	?	?
Steatoda	1	?	0	0	0	-	?	?	-	4	0	0	1	0	0	0	1	1
P. rupicola	0	?	0	0	?	?	?	?	?	0	0	1	1	?	0	0	?	?
P. altioculata	0	?	0	0	0	-	0	0	-	0	0	1	0	0	0	0	1	0
Stemonyphantes	0	?	0	0	0	-	0	0	-	0	0	1	0	1	0	0	1	1
Microlinyphia	0	?	0	0	0	-	0	0	-	2	0	1	1	0	0	0	1	1
Linyphia	0	?	0	0	0	-	0	0	-	3	0	1	1	0	0	0	1	1
Bolyphantes	0	?	0	0	0	-	0	0	-	2	0	1	1	0	0	0	1	1
Tenuiphantes	0	?	0	0	0	-	0	0	-	2	0	1	1	0	0	0	1	1
Haplinis	1	?	0	0	0	-	0	0	-	2	0	1	1	1	0	0	1	0
Novafroneta	1	?	0	0	0	-	0	0	-	3	0	1	1	1	0	0	1	0
Leptorhoptrum	0	0	0	0	1	1	1	1	1	2	0	1	1	1	0	0	0	-
Drepanotylus	0	1	0	0	1	1	1	1	1	2	0	1	1	1	0	0	0	-
Hilaira	0	1	0	0	1	1	1	1	1	2	0	1	1	1	0	0	0	-
Tibioploides	0	2	0	0	1	0	0	1	1	2	0	?	1	1	0	0	0	-
Triplogyna	0	2	0	0	1	1	1	1	1	2	0	1	1	1	0	0	0	-
Laminacauda	0	1	0	0	1	0	0	1	1	2	0	1	1	1	0	0	0	-
Scolecura	0	2	0	0	0	-	0	1	-	2	0	1	1	1	0	0	0	-
Ostearius	0	2	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Neocautinella	0	2	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Anodoration	1	2	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Rhabdogyna	0	2	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Ctenophysis	0	2	0	0	0	-	0	0	-	1	0	1	1	1	0	0	0	-
Valdiviella	0	2	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Deichomma	0	2	0	0	0	-	?	0	-	1	0	1	1	1	0	0	0	-
Notiomaso	0	1	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Pseudotyphistes	0	2	0	0	0	-	?	0	-	1	0	1	1	1	0	0	0	-
Sisicus	0	2	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Onychembolus	0	2	0	0	0	-	?	?	-	2	0	1	1	1	?	?	0	-
Smermisia	0	2	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Lygarina	1	2	0	0	0	-	?	0	-	2	0	1	1	1	1	2	0	-
Hypselocara	0	2	0	0	0	-	?	0	-	1	0	1	1	1	0	0	0	-
Neomaso	0	1	0	0	0	-	0	0	-	1	0	1	1	1	0	0	0	-
Gigapassus	0	1	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Asthenargus	0	?	0	0	0	-	0	0	-	?	?	1	1	1	?	?	?	?
Gongylidiellum	0	1	0	0	0	-	0	0	-	2	0	1	1	1	0	0	0	-
Spanioplanus	0	1	0	0	0	-	0	0	-	?	?	?	?	1	?	?	0	-
Sciastes	0	2	0	0	1	1	1	1	1	2	0	1	1	1	0	0	0	-
Islandiana	0	?	0	0	1	1	1	1	0	2	0	1	1	1	0	0	?	?
Gravipalpus	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
M. dentiger	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
M. rapidulus	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Paraletes	0	3	0	0	1	1	1	1	0	0	0	1	1	1	0	0	0	-
Erigone	0	0	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Myrmecomelix	0	3	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Microplanus	0	2	0	0	1	1	1	1	0	0	0	1	0	1	0	0	0	-
Toltecaria	0	2	0	0	1	1	1	1	0	1	0	1	1	1	0	0	0	-
Fissiscapus	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Labicymbium	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Diplocentria	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Sisicottus	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	?	?
Oedothorax	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Gongylidium	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	1	0	-
Hylyphantes	0	?	0	0	1	1	1	1	0	2	0	1	1	1	0	0	?	?
Tmeticus	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Typhochrestus	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Araeoncus	0	?	0	0	1	1	1	1	0	2	0	1	1	1	0	0	?	?
Diplocephalus	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Savignia	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Entelecara	0	?	0	0	1	1	1	1	0	?	0	?	?	1	0	0	0	-
Dismodicus	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Hybocoptus	0	?	0	0	1	1	1	1	0	?	?	?	?	?	?	?	?	?
Lophomma	1	3	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Walckenaeria	1	3	0	0	1	1	1	1	0	2	0	1	1	1	0	0	?	?
Gonatium	1	3	0	0	1	1	1	1	0	2	0	1	1	1	0	0	?	?
A. daedalus	1	2	0	0	1	1	1	1	0	2	0	1	1	1	0	1	0	-
A. janetae	1	3	0	0	1	1	1	1	0	2	0	1	1	1	0	1	0	-
Tapinocyba	0	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Ceratinops	1	2	0	1	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Parapelecopsis	1	2	1	1	1	1	1	1	0	2	0	1	1	1	0	0	?	?
Grammonota	1	2	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Intecymbium	1	2	0	1	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Psilocymbium	1	2	0	0	1	1	1	1	0	2	0	1	1	1	1	2	0	-
Dolabritor	1	2	0	0	?	?	?	?	?	2	0	1	1	1	0	0	0	-
Gonatoraphis	1	3	0	0	1	1	1	1	0	1	0	1	1	1	0	0	0	-
Ceratinopsis	1	3	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
Tutaibo	1	3	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
S. rubescens	1	3	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
S. bicolor	1	3	0	0	1	1	1	1	0	2	0	1	1	1	0	0	0	-
S. spadicaria	1	3	0	0	1	1	1	1	0	1	0	1	1	1	0	0	0	-
S. crassa	1	3	0	1	1	1	1	1	0	2	0	1	1	1	0	0	0	-
steps	6	12	1	3	2	2	4	2	1	15	1	1	3	2	2	4	1	2
ci	.16	.25	1	.33	.50	.50	.25	.50	1	.26	1	1	.33	.50	.50	.50	1	.50
ri	.77	.55	0	.33	.96	0	.87	.96	1	.21	1	1	0	.85	0	.33	1	.50

BEHAVIOR

Taxon	171.Male during spermweb construction: above; below	172.Male during ejaculation: above; below	173.Web type: orb; irregular mesh	174.Web placement: aerial; close to substrate	175.Web knock-down lines: few or absent; numerous	176.Resinous copulatory plug: abs; pres
Tetragnatha	?	?	0	0	0	0
Theridiosoma	?	?	0	0	0	0
Steatoda	?	?	1	1	0	0
P. rupicola	?	?	?	?	?	0
P. altioculata	?	?	1	1	1	0
Stemonyphantes	?	?	1	1	0	0
Microlinyphia	0	0	1	0	1	0
Linyphia	0	0	1	0	1	0
Bolyphantes	?	?	?	?	?	0
Tenuiphantes	0	0	1	1	0	0
Haplinis	1	1	?	?	?	0
Novafroneta	?	?	?	?	?	0
Leptorhoptrum	?	?	?	?	?	0
Drepanotylus	?	?	?	?	?	0
Hilaira	?	?	?	?	?	0
Tibioploides	?	?	?	?	?	0
Triplogyna	?	?	?	?	?	0
Laminacauda	?	?	?	?	?	0
Scolecura	?	?	?	?	?	0
Ostearius	1	1	?	?	?	0
Neocautinella	?	?	?	?	?	0
Anodoration	?	?	?	?	?	0
Rhabdogyna	?	?	?	?	?	0
Ctenophysis	?	?	?	?	?	0
Valdiviella	?	?	?	?	?	0
Deichomma	?	?	?	?	?	0
Notiomaso	?	?	?	?	?	0
Pseudotyphistes	?	?	?	?	?	0
Sisicus	?	?	?	?	?	0
Onychembolus	?	?	?	?	?	0
Smermisia	?	?	?	?	?	0
Lygarina	?	?	?	?	?	0
Hypselocara	?	?	?	?	?	0
Neomaso	?	?	?	?	?	0
Gigapassus	?	?	?	?	?	0
Asthenargus	?	?	?	?	?	0
Gongylidiellum	?	?	?	?	?	0
Spanioplanus	?	?	?	?	?	0
Sciastes	?	?	?	?	?	0
Islandiana	?	?	?	?	?	0
Gravipalpus	?	?	?	?	?	0
M. dentiger	?	?	?	?	?	1
M. rapidulus	?	?	?	?	?	1
Paraletes	?	?	?	?	?	0
Erigone	1	1	1	1	0	0
Myrmecomelix	?	?	?	?	?	0
Microplanus	?	?	?	?	?	0
Toltecaria	?	?	?	?	?	0
Fissiscapus	?	?	?	?	?	0
Labicymbium	?	?	?	?	?	0
Diplocentria	?	?	?	?	?	0
Sisicottus	?	?	?	?	?	0
Oedothorax	?	?	?	?	?	0
Gongylidium	?	?	1	1	0	0
Hylyphantes	?	?	?	?	?	0
Tmeticus	?	?	?	?	?	0
Typhochrestus	?	?	?	?	?	0
Araeoncus	?	?	?	?	?	0
Diplocephalus	?	?	?	?	?	0
Savignia	?	?	?	?	?	0
Entelecara	?	?	?	?	?	0
Dismodicus	?	?	?	?	?	0
Hybocoptus	?	?	?	?	?	0
Lophomma	?	?	?	?	?	0
Walckenaeria	?	?	?	?	?	0
Gonatium	?	?	?	?	?	0
A. daedalus	?	?	?	?	?	0
A. janetae	?	?	?	?	?	0
Tapinocyba	?	?	?	?	?	0
Ceratinops	?	?	?	?	?	0
Parapelecopsis	?	?	?	?	?	0
Grammonota	?	?	?	?	?	0
Intecymbium	?	?	?	?	?	0
Psilocymbium	?	?	?	?	?	0
Dolabritor	?	?	?	?	?	0
Gonatoraphis	?	?	?	?	?	0
Ceratinopsis	?	?	?	?	?	0
Tutaibo	?	?	?	?	?	0
S. rubescens	?	?	?	?	?	0
S. bicolor	?	?	1	1	0	0
S. spadicaria	?	?	1	1	0	0
S. crassa	?	?	?	?	?	0
steps	1	1	1	2	2	1
ci	1	1	1	.50	.50	1
ri	1	1	1	.66	.50	1

Phylogenetic analysis

ci consistency index (for a character)
CI ensemble consistency index
L tree length
RCM revised-character matrix
ri retention index (for a character)
RI ensemble retention index
RTM reduced-taxon matrix

Appendix B

Phylogenetic data matrix (see following pages). Top row shows character numbers and abbreviated character names followed by abbreviated character states. The first state is "0", followed by "1", etc., "?" is missing data, "–" is inapplicable. See Appendix D for details. Bottom rows indicate step cost of each character on most parsimonious tree, ci is consistency index, ri is retention index. Genera abbreviated *A.* = *Asemostera*, *M.* = *Mermessus*, *P.* = *Pimoa*, *S.* = *Sphecozone*.

Appendix C

Taxon sample and material examined with notes on taxon sampling and nomenclature

Taxa newly added to the study are indicated by bold type, followed by collection data for specimens examined. Material examined for taxa included in Hormiga's (2000) study appears in his appendix 4. In some cases, additional specimens of these taxa were examined and are listed below. One taxon (*Sisicottus montanus*) was first added to Hormiga's (2000) matrix by Miller (1999).

Previously unknown sexes for several genera were discovered in the course of this research and these genera were represented by exemplar taxa. These include *Dolabritor* Millidge, 1991, *Fissiscapus* Millidge, 1991, *Gravipalpus* Millidge, 1991, *Microplanus* Millidge, 1991, *Myrmecomelix* Millidge, 1993, *Smermisia* Simon, 1894, and *Spanioplanus* Millidge, 1991. *Asemostera* Simon, 1898 and *Mermessus* O. Pickard-Cambridge, 1899 were previously known only from the male, but females have been described in some junior synonyms (Miller, in press a). The male of *Barycara comatum* Millidge, 1991 and female of *Triplogyna major* Millidge, 1991 were found to be conspecific (Miller, in press a) and are included as a single taxon. The female described as *Onychembolus subalpinus* (in Millidge, 1991, p. 127) is actually the female of *Microsphalma exonychus* Miller, in press a; the correct female of *Onychembolus subalpinus* was apparently described as both *Neomaso bidentatus* Millidge, 1991 and *Neomaso tridentatus* Millidge, 1991 (Miller, in press a).

Three new monotypic genera (to be described in Miller, in press a) are included in this study: *Intecymbium*, *Toltecaria* and *Gigapassus*. Monotypic genera are undesirable because they convey no grouping hypothesis (Platnick, 1976). In the absence of a tree, a monotypic genus implies only ignorance of relationships (Zujko-Miller, 1999). However, even with a phylogeny, uncertainty can persist due to conflicting trees, lack of resolution, missing data, or weak support. Since these monotypic genera are included in a phylogenetic analysis and contribute to an explicit hypothesis of their relationships, an implicit hypothesis of their relationships using generic placement is arguably of minor importance. Our phylogeny found that "*Ceratinopsis" antarctica* Simon, 1895 is not the sister taxon to *Ceratinopsis interpres* (O. Pickard-Cambridge, 1874), the type species for the genus, but is instead sister to a group of several well-defined genera. For this reason, the new genus *Intecymbium* will be created to accommodate this species (Miller, in press a). The male of *Toltecaria antricola* (Millidge, 1984b) was discovered in the course of this research, establishing that this species does not belong to *Tunagyna* Chamberlin and Ivie, 1933 or *Phanetta* Keyserling, 1886, the two genera that have contained this species. Like *Intecymbium*, *Toltecaria* is sister to a group of well defined genera. In our judgment, erigonine systematics would not be well served by synonymizing these genera just to avoid the creation of two monotypic genera. *Gigapassus octarine* (Miller, in press a) is a distinctive new erigonine from Argentina. Our phylogeny found that *Gigapassus* is sister to *Neomaso*. *Gigapassus octarine* could have been described within *Neomaso*, but this would have complicated the diagnosis of *Neomaso*.

The exemplar for *Smermisia* was described in the genus *Sciastes* Bishop and Crosby, 1938, but was explicitly excluded from *Sciastes* by Millidge (1984b). Exemplars for the genera *Asemostera* (two species), *Fissiscapus*, *Gigapassus*, *Gonatoraphis*, *Gravipalpus*, *Microplanus*, *Myrmecomelix*, *Notiomaso*, *Paraletes*, and *Psilocymbium*, are new species described in Miller in press a. Nomenclature in this study reflects the following generic synonymies (Miller, in press a): *Eperigone* Crosby and Bishop, 1928 and *Sinoria* Bishop and Crosby, 1938 with *Mermessus*; *Antronetes* Millidge, 1991 with *Pseudotyphistes* Brignoli, 1972; *Brattia* and *Gymnocymbium* with *Sphecozone*; and the following species synonymies: *Neocautinella ochoai* Baert, 1990 with *Erigone* [now *Neocautinella*] *neoterica* (Keyserling, 1886); *Sphecozone affinis* (Tullgren, 1901) and *Sphecozone ardens* Millidge, 1985 with *Linyphia* [now *Sphecozone*] *bicolor* Nicolet, 1849. Some non-Neotropical genera were included in this study, such as *Sisicottus* Bishop and Crosby, 1938, which was added to Hormiga's (2000) matrix in a previous study (Miller, 1999), and *Ceratinopsis* Emerton, 1882, which has been suggested

to be a close relative or synonym of the Neotropical genus *Sphecozone* (Millidge, 1985; Wunderlich, 1987); inclusion of *Ceratinopsis* also served to test the phylogenetic position of *Intecymbium* [formerly *Ceratinopsis*] *antarcticum*. The inclusion of *Notiomaso* allows us to evaluate Wunderlich's (1978) rejected synonymy of *Drepanotylus* under *Notiomaso*; *Drepanotylus* was part of Hormiga's (2000) original taxon sample.

Linyphiidae: Erigoninae

Anodoration claviferum Millidge, 1991: ARGENTINA. *Salta*: El Rey Nat. Pk., Rio La Sala, 5 Dec 1987, humid chaco forest, night beating, 900 m (S. and J. Peck, AMNH), 5♂, 3♀. BRAZIL. *Rio Grande do Sul*: Três Coroas, 15 Dec 1976 (E.H. Buckup, MCN, 5833), 3♂, 3♀, 3juv.

Araeoncus crassiceps (Westring, 1861)

Asemostera daedalus Miller, in press a: PANAMA. *Canal Zone*: Barro Colorado Island, May 1964 (A.M. Chickering, MCZ), 2♂, 6♀.

Asemostera janetae Miller, in press a: BOLIVIA. *La Paz*: Sorata, 11–14 Nov 1984, 2800 m (L.E. Peña, AMNH), 2♂, 3♀.

Asthenargus paganus (Simon, 1884)

Ceratinops inflatus (Emerton, 1923)

Ceratinopsis interpres (O. Pickard-Cambridge, 1874): UNITED STATES. *New Hampshire*: Hillsborough Co., Hollis, "Beaver Brook Assc." 26 May 1977 (J. Coddington, USNM, 658), 2♂, 2♀.

Ctenophysis chilensis Millidge, 1985: CHILE. *Región del Bíobío (VIII)*: Concepcíon Prov., Lagunillas, 5 Oct 1991 (T. Cekalovic, AMNH, TC-293), 6♀. Región de la Araucanía (IX): Cautín Prov, Volcán Villarrica, 15–29 Dec 1982, *Nothofagus dombeyi-pumilio* forest with *Chusquea*, window trap, 1250 m (A. Newton, M. Thayer, AMNH, paratypes), 4♂; Cautín Prov., Volcán Villarrica, 15–29 Dec 1982, 1120 m (A. Newton, M. Thayer, AMNH, paratypes), 15♂, 2♀. *Región de Los Lagos (X)*: Osorno Prov., P.N. Puyehue, Antillanca road, 18–24 Dec 1982, *Nothofagus* spp. forest, Berlese leaf and log litter, 720 m (A. Newton, M. Thayer, AMNH, paratypes), 1♂, 1♀, 1juv.

Diechomma pretiosum Millidge, 1991: COLOMBIA. *Cundinamarca*: Paramo de Chisaca, ca. 40 km SSW of Bogotá, near Laguna Negra, 7 Sep 1985, 3720 m (H. Sturm, MCZ, paratypes), 10♀, 24♂.

Diplocentria bidentata (Emerton, 1882)

Diplocephalus cristatus (Blackwall, 1833)

Dismodicus decemoculatus (Emerton, 1882)

Dolabritor spineus Millidge, 1991: COLOMBIA. *Cundinamarca*: La Calera, Cerro del Chocolatero, ca. 5 km NE of Bogotá, 31 Jan 1996 (G. Hormiga, J. Miller, J. Barriga, J.C. Bello, A. Sabogal, USNM), 2♂, 4♀.

Drepanotylus uncatus (O. Pickard-Cambridge, 1873)

Entelecara acuminata (Wider, 1834)

Erigone psychrophila Thorell, 1871

Fissiscapus attercop Miller, in press a: ECUADOR. *Pichincha*: 42.5 km E Quito, Quito-Baeza road, 27 May 1993, litter near stream, 10 600 ft (L. Herman, AMNH, 2745), 2♂, 6♀, 2juv.

Gigapassus octarine Miller, in press a: ARGENTINA. *Jujuy Prov*. Calilegua N. P., área de entrada al parque, 23–24 Sep 1995 (M. Ramírez, P. Goloboff, C. Szumik, MACN), 2♂, 1♀; Calilegua, Calilegua N. P., 20 Oct 1994, transitional forest with lianas, partially deciduous, leaf litter around decaying tree trunk, Winkler sample, 850 m (J.M. Carpenter, D. Agosti, AMNH), 5♀.

Gonatium rubens (Blackwall, 1833)

Gonatoraphis barada Millidge, 1991: COLOMBIA. *Boyacá*: S.F.F. Iguaque, near margin of Laguna Iguaque, 5–8 February 1998, sifting moss, 3450–3650 m (G. Hormiga, J. Coddington, J. Miller, V. Rodríguez, USNM), 1♂, 1♀.

Gongylidiellum vivum (O. Pickard-Cambridge, 1875)

Gongylidium rufipes (Linnaeus, 1758)

Grammonota pictilis (O. Pickard-Cambridge, 1875)

Gravipalpus standifer Miller, in press a: ARGENTINA. *Salta*: Aguas Blancas-Yaculica (Arg/Bol Frontier), 25 Oct 1994, yungas forest (young secondary forest), leaf litter, Winkler sample, 460 m (J.M. Carpenter, D. Agosti, AMNH), 2♂, 3♀, 1juv.

Hilaira excisa (O. Pickard-Cambridge, 1871)

Hybocoptus corrugis (O. Pickard-Cambridge, 1875)

Hylyphantes graminicola (Sundevall, 1830)

Hypselocara altissimum Millidge, 1991: VENEZUELA. (MNHN; no other label data), 8♂, 21♀ syntypes.

Intecymbium antarcticum (Simon, 1895): CHILE. *Región de Los Lagos (X)*: Llanquihue, 7 km N of Ensenada, 26 Nov 1981, moss in disturbed forest, 1300 ft (R.T. Schuh and N. Platnick, AMNH), 1♀; Llanquihue, Lago Chapo, 34 km E Puerto Montt, 24 Dec 1984–2 Feb 1985, 2nd growth *Nothofagus*, FIT, 300 m (S. and J. Peck, AMNH), 1♂. *Región de Magallanes (XII)*: Esperanza Prov., Torres del Paine, near Refugio Pudeto, 7 Dec 2000, scrub, pitfall, 100 m (Miller, Agnarsson, USNM), 1♀.

Islandiana princeps Braendegaard, 1932

Labicymbium sturmi Millidge, 1991: COLOMBIA. *Boyacá*: S.F.F. Iguaque, 5–8 Feb 1998, forest patch nr. margin of L. Iquaque, 3450–3650 m (G. Hormiga, J. Coddington, J. Miller, V. Rodríguez, USNM), 9♂, 15♀.

Laminacauda plagiata (Tullgren, 1901): CHILE. *Magallanes*: Canal Fitz Roy, Punta Turn, 31 Jan 1976 (T. Cekalovic, AMNH), 1♂, 2♀.

Leptorhoptrum robustum (Westring, 1851): RUSSIA. *Siberia*: Sakhalin Island, NE part, East Sakhalin Range, Chamginski Pass, 8 Aug 2001, 770 m (Y.M. Marusik, CAS), 5♀, 6♂.

Lophomma punctatum (Blackwall, 1841)

Lygarina silvicola Millidge, 1991: BRAZIL. *Rio Grande do Sul*: Cachoeira do Sul, Fazenda dal Pedras, 18 May 1993 (R.G. Buss, MCP, 4576), 1♀; Cachoeira do Sul, Purterra sete, 24 May 1993 (R.G. Buss, MCP, 4002), 1♂; Viamáo, 2 Dec 1994 (A.A. Lise et al. MCP, 7891), 1♀. *São Paulo*: São Paulo, forest reservation, 16 Jan 1959 (A.M. Nadler, AMNH, paratype), 1♀.

Mermessus dentiger O. Pickard-Cambridge, 1899: PUERTO RICO. Mayagüez, university campus, Jan 1964 (Chickering, MCZ), 8♂, 27♀.

Mermessus rapidulus (Bishop and Crosby, 1938): COSTA RICA. *Heredia*: La Selva, Feb 1997, 20 m (W. Eberhard, MCZ), 1♂, 2♀; La Selva, near Puerto Viejo de Sarapiqui [no date], 20 m (W. Eberhard, MCZ), 2♀.

Microplanus odin Miller, in press a: PANAMA. *Bocas del Toro*: 25 km NNE San Felix, 6 Jun 1980, Qda. Alicia cloud forest, Berlese conc. upper floor litter near ridge top, 1500 m (J. Wagner, FMNH), 7♂, 6♀.

Myrmecomelix leucippus Miller, in press a: PERU. *Cuzco*: Pillahuata, Manu road, km 128, 26 Sep 1982, ex moss and litter on xeric slope (L.E. Watrous, G. Mazurek, FMNH, FMHD 82-305), 2♀, 2♂.

Neocautinella neoterica (Keyserling, 1886): ECUADOR. *Galápagos Islands*: Isla Santa Cruz, Los Gemelos, 1–28 Feb 1989, Scalesia forest, flight intercept trap, 610 m (Peck and Sinclair, AMNH), 41♂; San Cristobal, Baquerizo, 11–23 Feb 1989, arid zone, flight intercept trap, 10 m (S. Peck, AMNH), 15♀. *Tungurahua*: Baños, Jul–Aug 1938, 2000 m (W.C. Macintyre, MCZ), 2♂, 3♀.

Neomaso claggi Forster, 1970: CHILE. *Región de Magallanes (XII)*: Reserva Nacional Laguna Parrillar, 1–10 Dec 2000, in shrubs, grass near Chorio Hermoso, pitfall, 350 m (Miller, Agnarsson, USNM), 3♂, 2♀; Reserva Nacional Laguna Parrillar, 1–10 Dec 2000, forest, Berlese, 350 m (Miller, Agnarsson, USNM), 2♂, 2♀.

Notiomaso exonchus Miller, in press a: CHILE. *Región del Bíobío (VIII)*: Concepcíon Prov., Escuadron, 2 Apr 1988 (T. Cekalovic, AMNH, TC-204), 1♂. *Región de Magallanes (XII)*: Esperanza Prov., P.N. Torres del Paine, Laguna Azul, 6 Dec 2000, *Nothofagus pumilio* forest, Berlese, 300 m (J. Miller, I. Agnarsson, USNM), 1♂, 9♀; Magallanes Prov, Río Chabunco, 17 Feb 1990 (T. Cekalovic, AMNH, TC-265), 1♂.

Oedothorax gibbosus (Blackwall, 1841)

Onychembolus subalpinus Millidge, 1985: ARGENTINA. *Neuquén*: 16 km from Rahué, on Route 46, 1 Feb 1972 (L. Herman, AMNH, 909), 1♂. CHILE. *Región de Los Lagos (X)*: Osorno Prov., P.N. Puyehue, Antillanca road, 12 Dec 2000–2 Jan 2001, alpine meadow, pitfall, 1050–1350 m (J. Miller, I. Agnarsson, F. Alvarez, J. Coddington, G. Hormiga, USNM), 3♂, 1♀; Osorno Prov., P.N. Puyehue, Antillanca, 12 Dec 2000–2 Jan 2001, alpine meadow, 1050–1350 m (J. Miller, I. Agnarsson, F. Alvarez, J. Coddington, G. Hormiga, USNM), 1♀.

Ostearius melanopygius (O. Pickard-Cambridge, 1879): CHILE. *Santiago*: Pirque, 30 Feb 1982 (L.E. Peña, AMNH), 1 ♂; Vina: Dec 1978 (A. Tobar, AMNH), 2♀.

Paraletes pogo Miller, in press a: PERU. *Cuzco*: Consuelo, Manu road, km 165, 7 Oct 1982, ex leaf litter (L.E. Watrous, G. Mazurek, FMNH, FMHD 82-353), 2♂, 3♀.

Parapelecopsis nemoralis (Blackwall, 1841)

Pseudotyphistes cristatus (Ott and Lise, 1997): BRAZIL. *Rio Grande do Sul*: Faz Souza, Caxias do Sul, 19 Nov 1995 (A.A. Lise et al. MCP, 9135), 1♂, 2♀; Viamão, 8 Dec 1992 (L.F. Schmidt, MCP, 2812), 1♂, 1♀.

Psilocymbium acanthodes Miller, in press a: ARGENTINA. *Buenos Aires*: Río Luján, FCGM, 5 Oct 1993 (M. Ramírez, A. Pérez, MACN), 4♂, 3♀.

Rhabdogyna patagonicus (Tullgren, 1901): CHILE. *Región de Coquimbo (IV)*: Limari, P.N. Talinay, Rt. 5, km 355, 12 Jan 1995, 600 m (Platnick, Catley, Silva, AMNH), 6♂, 9♀.

Savignia frontata Blackwall, 1833

Sciastes truncatus (Emerton, 1882)

Scolecura propinqua Millidge, 1991: ARGENTINA. *Jujuy*: Calilegua, Calilegua N. P., 20 Oct 1994, transitional forest with lianas, partially deciduous, leaf litter around decaying tree trunk, Winkler sample, 850 m (J.M. Carpenter, D. Agosti, AMNH), 1♂, 3♀. *Salta*: El Rey Nat. Pk., Rio La Sala, 5–15 Dec 1987, humid mossy chaco forest, malaise FIT, 900 m (S. and J. Peck, AMNH), 8♂.

Sisicottus montanus (Emerton, 1882): UNITED STATES. *Massachusetts*: Berkshire Co., Mr Greylock, 3400 ft, decid. litter, 15 Oct 1990 (R.L. Edwards, USNM), 2♂, 1♀.

Sisicus apertus (Holm, 1939)

Smermisia vicosana (Bishop and Crosby, 1938): BRAZIL. *Minas Gerais*: Viçosa, 6 Jul 1933 (E.J. Hambleton, AMNH, syntypes), 2♂, 7♀. *Rio Grande do Sul*: Guaíba, 28 Apr 1995 (A.A. Lise et al. MCP, 9161), 2♂, 2♀; Guaíba, 14 Jul 1995 (A.A. Lise et al. MCP, 8743), 1♂, 1♀.

Spanioplanus mitis Millidge, 1991: PERU. *Cuzco*: Pillahuata, Manu road, km 128, 17 Sep 1982, wood chips (L.E. Watrous, G. Mazurek, FMNH, FMHD 82–250), 2♂, 2♀; Pillahuata, Manu road, km 128, 26 Sep 1982, litter along stream (L.E. Watrous, G. Mazurek, FMNH, FMHD 82-299), 1♂; Pillahuata, Manu road, km 128, 26 Sep 1982, rotten logs (L.E. Watrous, G. Mazurek, FMNH, FMHD 82-302), 1♀.

Sphecozone bicolor (Nicolet, 1849): CHILE. *Región de Magallanes (XII)*: Magallanes Prov., Reserva Nacional Laguna Parrillar, 1–10 Dec 2000, 350 m (J. Miller, A. Agnarsson, USNM), 11♂, 35♀.

Sphecozone crassum (Millidge, 1991): COLOMBIA. *Caquetá*: Parque Nacional Cordillera de los Picachos, Guayabal-Andalvcía, 20 Nov 1997, 2000 m (V. Rodrí-

guaz, ICN, 1AvH-Ar-13), 5♂, 1♀; Parque Nacional Cordillera de los Picachos, L. Upd, 22 Nov 1997, 2000 m (V. Rodríguaz, ICN, 1AvH-Ar-43), 5♂, 2♀.

Sphecozone rubescens O. Pickard-Cambridge, 1870: BRAZIL. *Rio De Janeiro*: Serra dos Orgãos, 20 Apr 1965, logs and stones, 1500 m (H. Levi, MCZ), 1♂, 2♀; Guanabara, Barra da Tijuca, 16 Apr 1965, sand dunes, shore vegetation (H. Levi, MCZ), 1♂. *Rio Grande do Sul*: Canela, 27 Mar 1966 (A.A. Lise, MCZ), 1♂.

Sphecozone spadicaria (Simon, 1894): COLOMBIA. *Cundinamarca*: Finca Bella Vista, nr. Sasaima, 26 Mar 1965 (P.R. & D.L. Craig, CAS), 1♂, 1♀; Finca Bella Vista, nr. Sasaima, 27 May 1965, under leaf litter and duff (P.R. & D.L. Craig, CAS), 1♀. VENEZUELA. *Mérida*: El Vigia, road La Victoria, 22 Feb 1968 (P. and B. Wygodzinsky, AMNH), 1♂, 2♀.

Tapinocyba praecox (O. Pickard-Cambridge, 1873)

Tibioploides pacificus Eskov and Marusik, 1991

Tmeticus tolli Kulczynski, 1908

Toltecaria antricola (Millidge, 1984b): MEXICO. *Hidalgo*: 4 mi. SW of Chapulhuacan, 5 Jul 1976, cloud forest litter, Berlese, 3500 m (A. Newton, MCZ), 9♂, 3♀.

Triplogyna major Millidge, 1991: COLOMBIA. *Boyacá*: S.F.F. Iguaque, 5–8 Feb 1998, near margin of Laguna Iguaque, sifting moss, 3450–3650 m (G. Hormiga, J. Coddington, J. Miller, V. Rodríguez, USNM), 4♂, 32♀.

Tutaibo phoeniceus O. Pickard-Cambridge, 1894: MEXICO. *Chiapas*: near Bochil, 2 Aug 1964, on plants by road (J. Shetterly, MCZ), 2♂, 4♀.

Typhochrestus digitatus (O. Pickard-Cambridge, 1872)

Valdiviella trisetosa Millidge, 1985: CHILE. *Región de Los Lagos (X)*: Osorno Prov., P.N. Puyehue, 21 Nov 1993, 480 m (Platnick, Catley, Ramírez, Allen, AMNH), 2♂, 4♀; Osorno Prov., P.N. Puyehue, Aguas Calientes, 16 Jan 1995, 500 m (Platnick, Catley, Silva, AMNH), 2♂, 10♀.

Walckenaeria directa (O. Pickard-Cambridge, 1874)

Other Linyphiidae

Bolyphantes luteolus (Blackwall, 1833)

Linyphia triangularis (Clerk, 1757): DENMARK. *Hestehaven*: Rønde, 22 km NE of Århus, 31 Aug 1994 (Bjørn, Christiansen, Coddington, Griswold, Hormiga, Krat, Langenmark, Scharff and Sørensen, USNM), ♂♂, ♀♀.

Microlinyphia dana (Chamberlin and Ivie, 1943)

Stemonyphantes blauveltae Gertsch, 1951: UNITED STATES. *New York*: Sea Cliff (N. Banks, MCZ, 36891), ♂♂, ♀♀.

Tenuiphantes tenuis (Blackwall, 1852): CHILE. *Región de Los Lagos (X)*: Osorno Prov., P.N. Puyehue, Antillanca road, 12 Dec 2000–2 Jan 2001, *Nothofagus pumilio* forest, pitfall, 1000 m (Miller, Agnarsson, Alvarez, Coddington, Hormiga, USNM), 1♂.

Pimoidae

Pimoa altioculata (Keyserling, 1886)

Pimoa rupicola (Simon, 1884)

Theridiidae

Steatoda grossa (C.L. Koch, 1838): UNITED STATES. *California*: San Diego, Jun 1970 (B.J. Kaston, USNM), 1♂; San Diego 1972 (USNM), 2♀; Lemon Grove, 10 Jul 1976 (O. Padilla, USNM), 1♂.

Theridiosomatidae

Theridiosoma gemmosum (L. Koch, 1877): UNITED STATES. *Georgia*: Rabun Co., Ellicott Rock Wilderness Area, 1 km SW Ellicott Rock, cove hardwood for., 24 May 1993, ground, night, 750–800 m (Bond, Dellinger, Dobyns, USNM), 1♂, 3♀.

Tetragnathidae

Tetragnatha versicolor Walckenaer, 1842: UNITED STATES. *Virginia*: Floyd Co., B.R. pkwy, at intersection of cty. rd. 785, 1st intersection after turning S. on pkwy from cty rd 799 from Willis (B.R. 42). 8 May 1965. (E.P. McDonnell, B.F. Hall, USNM), 1♂, 3♀, 1juv.

Appendix D

Characters and character state descriptions

The current study adds taxa and characters to the matrix created by Hormiga (2000). However, some characters included in Hormiga's study could not be maintained in the expanded taxon sample and had to be redefined or deleted. Major changes to Hormiga's (2000) characters include paracymbium morphology (Hormiga's char. 5; see Char. 12), the synonymy of the mynoglenine tegular apophysis (Hormiga's char. 7) with the suprategulum (Hormiga's char. 11; see Char. 24), and re-evaluation of the lamella characteristica in erigonines (Hormiga's char. 27; see Char. 52). Recoding of the erigonine lamella characteristica necessitated changes in other characters (e.g., Hormiga's chars. 21, 22, 23). Coxae IV-booklung stridulatory organ (Hormiga's char. 54; see Char. 154) was greatly modified into a character of the booklung cover ultrastructure because of difficulty maintaining character state boundaries as originally defined.

Male palpal morphology

1. Cymbial retromedian process: 0, absent (*Asemostera*, Fig. 15A); 1, present (*Neocautinella*, Fig. 15B; *Labicymbium*, Fig. 15C; *Pimoa*, Hormiga, 1994b, fig. 128).

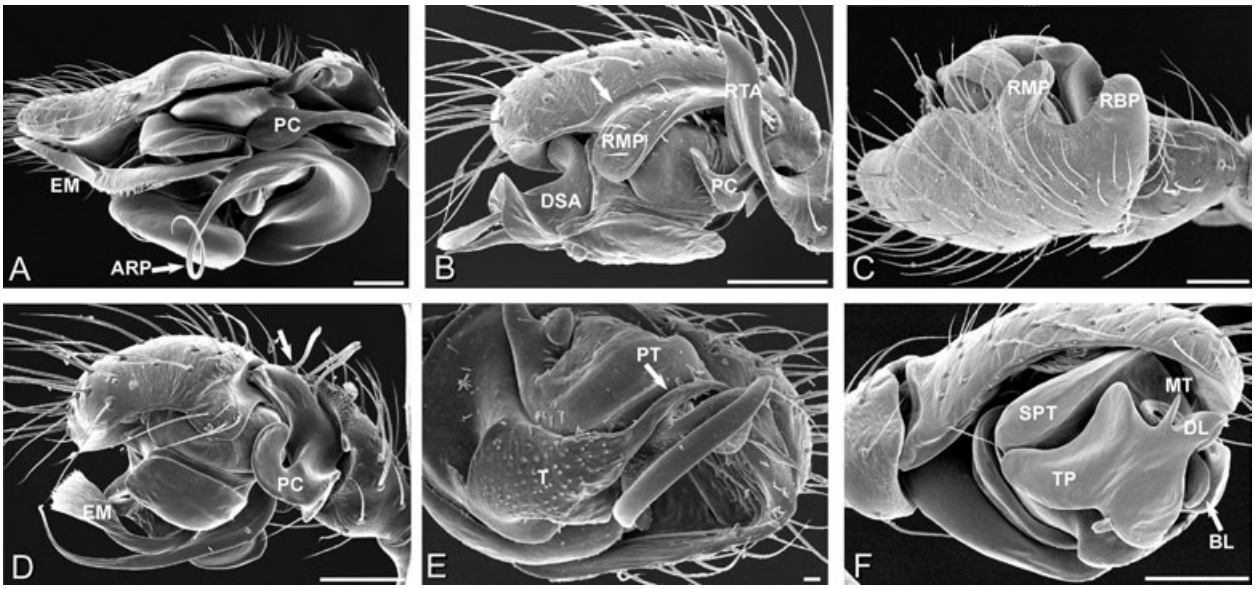

Fig. 15. Male palpi of erigonine spiders. (A) *Asemostera janetae,* retrolateral view showing horizontal U-shaped paracymbium and embolic membrane with papillae. (B) *Neocautinella neoterica*, retrolateral view showing ventro-distally projecting retromedian cymbial process and straight hook paracymbium; arrow indicates retrolateral cymbial groove. (C) *Labicymbium sturmi*, dorsal view of cymbium showing the retromedian and retrobasal cymbial processes. (D) *Valdiviella trisetosa*, retrolateral view showing spiral paracymbium and embolic membrane without papillae; arrow indicates enlarged basal setae of paracymbium. (E) *Psilocymbium acanthodes*, ventral view showing papillae on tegulum, smooth protegulum. (F) *Spanioplanus mitis*, prolateral view showing mesal tooth and radix distal lobe, smooth suprategulum, and embolic basal lobe. Scale bars = 10 μm in (E); 100 μm in other images.

Characters 1 and 2 are modifications of character 1 in Hormiga (1993, 1994a,b, 2000); 10 in Griswold et al. (1998). A retromedian apophysis of the cymbium is synapomorphic for pimoids. An analogous structure is found in some erigonines, and a few other araneoid groups. Hormiga (1993, 1994a,b, 2000) referred to this structure in pimoids as the "cymbial denticulate process". However, whereas *Pimoa* Chamberlin and Ivie, 1943 species exhibit denticles on the process, new data indicate that some newly recognized pimoids have the denticles elsewhere on the cymbium (Hormiga, 2003). Millidge (1988b) considered this apophysis to be an integral paracymbium, additional to the intersegmental one. There is variation in the form of this process, with some projecting ventrodistally out from the margin of the cymbium (e.g., *Neocautinella*, Fig. 15B) and others projecting retrolaterally (e.g., *Labicymbium*, Fig. 15C; *Pimoa*, Hormiga, 1994b, fig. 128). Similar cymbial processes are also found in relatively distantly related araneoids, such as cyatholipids (Griswold, 2001). It would seem that several independently derived apophyses are combined in this character.

2. Cymbial retromedian process dentation: 0, smooth (*Neocautinella*, Fig. 15B); 1. denticulate (*Pimoa*, Hormiga, 1994b, fig. 11). The presence of denticles on the retromedian process provides ambiguous support for *Pimoa* (clade 4; see also character 1).

3. Pimoid cymbial sclerite: 0, absent (*Sphecozone bicolor*, Fig. 16D); 1, present (*Pimoa*, Hormiga, 1994b, fig. 11). Character 3 in Hormiga (1993, 1994a,b, 2000). This sclerite is a synapomorphy of the Pimoidae (clade 4).

4. Cymbial retrobasal process: 0, absent; 1, present (*Labicymbium*, Fig. 15C). This apophysis is located in the proximal region of the cymbium and is directed either retrolaterally or dorsally.

5. Cymbium size: 0, longer and wider than palpal tibia and patella (*Drepanotylus*, Hormiga, 2000, fig. 8B,C); 1, smaller relative to the size of the pedipalpal tibia and patella (*Leptorhoptrum*, Hormiga, 2000, fig. 19A,B; *Tmeticus*, Hormiga, 2000, fig. 29B,C). Character 2 in Hormiga (2000).

6. Alveolus: 0, nearly as long as cymbium (*Neocautinella*, Fig. 15B); 1, much shorter than cymbium (*Asemostera*, Fig. 15A; *Erigone*, Hormiga, 1994, fig. 7B; *Haplinis*, Hormiga, 2000, pl. 3B). Character 12 in Bosselaers (1999); 41 in Bosselaers (2002); 128 in Bosselaers and Jocqué (2002); Schütt (2003). In most linyphiids, the alveolic cavity takes up nearly the entire cymbium. In some taxa, the cymbium is extended distally into an apophysis.

7. Cymbium retrolateral groove: 0, absent (*Sphecozone bicolor*, Fig. 16D); 1, present (*Neocautinella*, Fig. 15B; *Triplogyna*, Miller, in press a, fig. 5B). Character 6 in Griswold et al. (1998); 19 in Wang

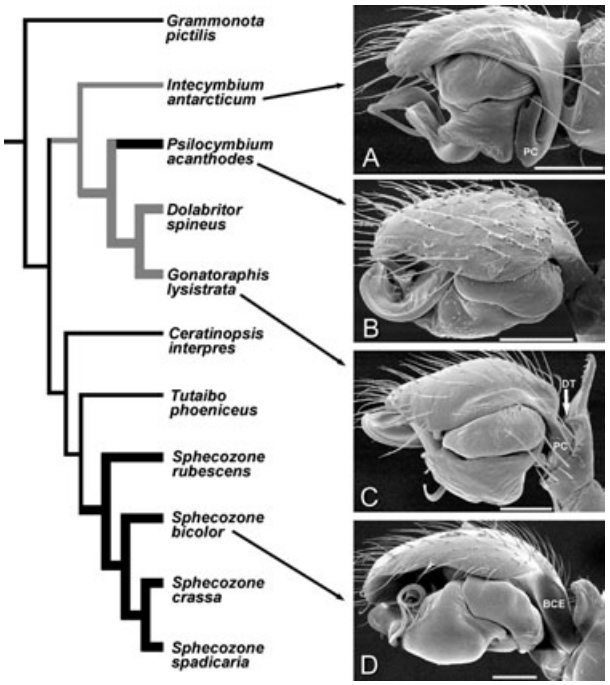

Fig. 16. Illustrated cladogram showing the diphyletic loss of the paracymbium in Neotropical erigonines. Thin lines represent fully formed paracymbium; thin black lines are paracymbium attached to cymbium by a membrane; thin gray lines are paracymbium fused to cymbium. Thick lines represent reduced or lost paracymbium; thick gray lines represent vestigial paracymbium; thick black lines represent paracymbium completely lost. Scanning electron micrographs are retrolateral views of male palps. (A) *Intecymbium antarcticum*. (B) *Psilocymbium acanthodes*. (C) *Gonatoraphis lysistrata*. (D) *Sphecozone bicolor*. Note non-monophyly of *Ceratinopsis* and *Intecymbium*. Scale bars = 100 μm.

(2002); 23 in Silva Dávila (2003). This groove is located on the retrolateral side of the cymbium and defines a lobe.

8. Cymbium basal excavation: 0, absent (*Intecymbium antarcticum*, Fig. 16A); 1, present (*Sphecozone bicolor*, Fig. 16D). This glabrous, excavated region is located on the proximal retrolateral part of the cymbium. The origin of this excavation supports the *Tutaibo* plus *Sphecozone* clade (77).

9. Cymbium height: 0, much longer than tall (*Neocautinella*, Fig. 15B); 1, nearly as tall as long (*Pseudotyphistes*, Fig. 19E; *Tibioploides*, Hormiga, 2000, pl. 65A). In a few taxa, the height of the cymbium is greatly exaggerated.

10. Paracymbium: 0, present (*Valdiviella*, Fig. 15D; *Intecymbium antarcticum*, Fig. 16A); 1, absent (*Psilocymbium*, Fig. 16B; *Sphecozone*, Fig. 16D). Character 4 (table 1) in Coddington (1990b); 33 in Coddington (1990a); 47 in Platnick et al. (1991b); 6 in Scharff and Coddington (1997); 7 in Griswold et al. (1998); 100 in Griswold et al. (1999); 33 in Davies (1999); 37 in Davies and Lambkin (2000a); 67 in Schütt (2003); 29 in Agnarsson (2004). The loss of the paracymbium provides unambiguous support for *Sphecozone* (clade 78); additional losses of the paracymbium occur in *Psilocymbium* and *Steatoda* Sundevall, 1833.

11. Paracymbium attachment: 0, intersegmental (*Valdiviella*, Fig. 15D; *Tetragnatha*, Hormiga et al., 1995, fig. 7C–E); 1, integral (*Intecymbium antarcticum*, Fig. 16A; *Pimoa*, Hormiga, 1994b, fig. 11). Character 7 in Hormiga (1993, 1994a); 10 in Hormiga (1994b, 2003); 22 in Hormiga et al. (1995); 8 in Griswold et al. (1998); 4 in Hormiga (2000); Schütt (2003). A membranous attachment of the paracymbium to the cymbium can be found in many tetragnathids and almost all linyphiids, as well as a new genus of pimoid (Hormiga, 2003). Millidge (1988b) drew a distinction between the conditions found in linyphiids and tetragnathids, asserting that the linyphiid paracymbium is attached to the tibia-cymbium joint membrane, whereas the tetragnathid paracymbium is attached to a non-homologous membrane arising from the cymbium alone. Hormiga (1993, 1994a,b) initially coded these states as the same, but later (Hormiga, 2000) followed Millidge (1988b). However, there is continuity between the joint membrane and the membrane articulating the paracymbium (Hormiga et al., 1995, fig. 7E). We have therefore coded *Tetragnatha* Latreille 1804 and most linyphiids as having the paracymbium articulated by an intersegmental membrane.

12. Paracymbium morphology: 0, straight and narrow (*Tetragnatha*, Hormiga et al., 1995; fig. 7C,D); 1, *Theridiosoma*-type hook (*Theridiosoma*, Coddington, 1986b, fig. 154); 2, linguiform and fused basally to PCS (*Pimoa rupicola*, Hormiga, 1994b, figs 15–17); 3, triangular (*Pimoa altioculata*, Hormiga, 1994b, figs 303, 304); 4, straight hook (*Neocautinella*, Fig. 15B; *Stemonyphantes*, Hormiga, 2000, pl. 12A); 5, spiral (*Valdiviella*, Fig. 15D; *Ceratinops*, Banks, 1905, Hormiga, 2000, pl. 15A); 6, horizontal U-shaped (*Asemostera*, Fig. 15A); 7, vestigial (*Gonatoraphis*, Fig. 16C). Character 4 (table 1) in Coddington (1990b); 8 in Hormiga (1993, 1994a); 11 in Hormiga (1994b); 24 in Hormiga et al. (1995); 9 in Griswold et al. (1998); 5 in Hormiga (2000). The variety and complexity of paracymbium shape offers potential as an important source of phylogenetic information, but this same diversity makes division into useful character states difficult (e.g., Hormiga, 1994a; Griswold et al., 1998). Our treatment of paracymbium morphology is slightly modified from that of Hormiga (2000). Hormiga divided paracymbium morphology (char. 5) into six character states, five of which were uninformative. Thus, Hormiga's version of this character was phylogenetically uninformative. The most significant change in our version of this character (Char. 12) is the breakup of the "U- or J-shaped" character state. We have coded most erigonine taxa as well as exemplars from the Micronetini and some Mynogleninae as having a spiral

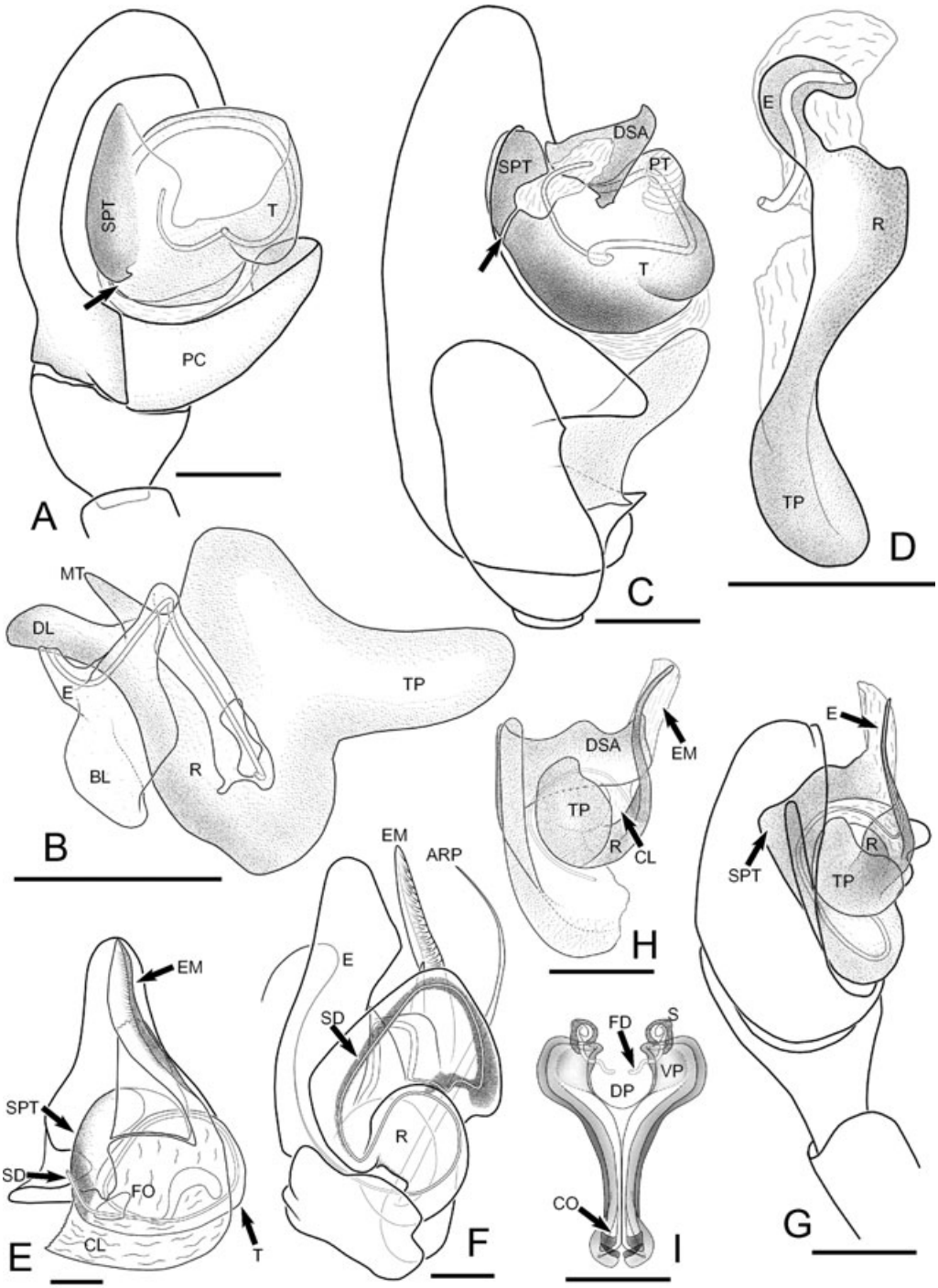

Fig. 17. (A–H) Male palpi of erigonine spiders. (I) Female epigynum. (A) *Spanioplanus mitis*, prolateral view with embolic division removed showing sperm duct loop, arrow indicates membranous connection between tegulum and suprategulum; distal suprategular apophysis broken off. (B) *Spanioplanus mitis*, embolic division, retrolateral view showing membranous connection between radix and embolus, and embolic base. (C) *Labicymbium sturmi*, prolateral view with embolic division removed showing membranous division in distal suprategular apophysis and sperm duct loop, arrow indicates membranous connection between tegulum and suprategulum. (D) *Labicymbium sturmi*, embolic division, retrolateral view showing membranous connection between radix and embolus. (E) *Asemostera janetae*, ventral view with embolic division removed showing foramen in tegulum and embolic membrane with papillae. (F) *Asemostera janetae*, prolateral view showing long path of sperm duct in radix. (G) *Rhabdogyna patagonica*, prolateral view. (H) *Rhabdogyna patagonica*, embolic division prolateral view, showing origin of column from ventral part of distal suprategular apophysis; the proximal apophysis of the suprategulum is unique to *Rhabdogyna*. (I) *Gravipalpus standifer*, dorsal view, showing copulatory openings formed by a ventral plate envelope and posterior elongation of epigynum. Scale bars = 0.1 mm.

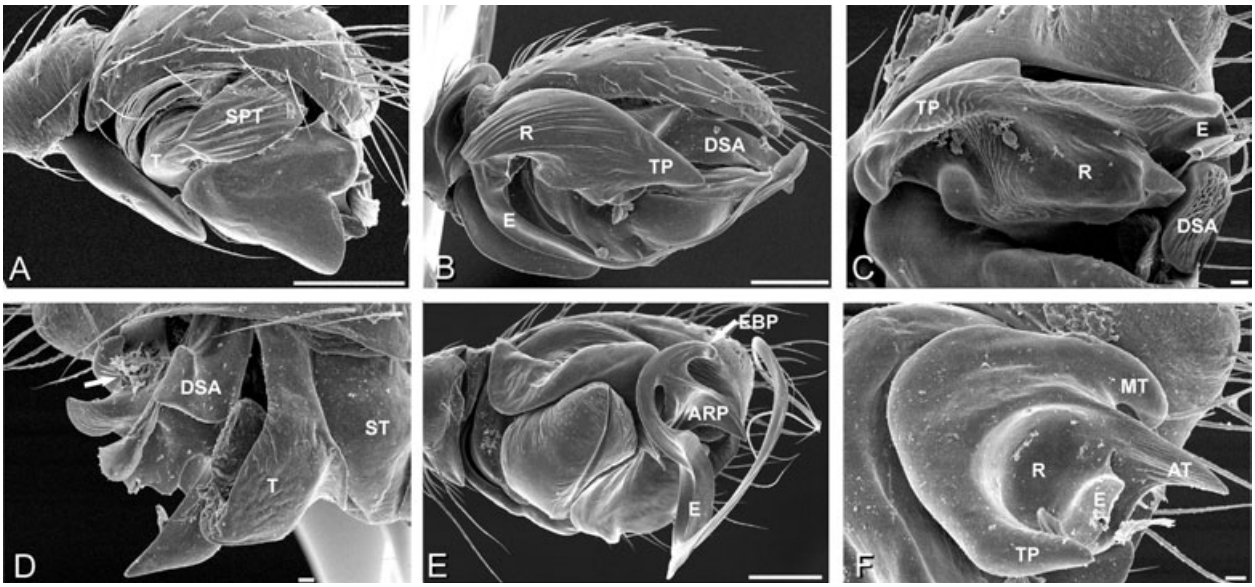

Fig. 18. Male palpi of erigonine spiders. (A) *Neomaso claggi*, prolateral view showing grooved suprategulum arising from tegulum as an angle. (B) *Notiomaso exonychus*, prolateral view showing distal suprategular apophysis extending distally beyond the suprategulum and the proximal origin of the embolus arising at a distinct angle from a striated radix with an anterior tailpiece. (C) *Microplanus odin*, ventral view showing ventrally excavated radix and papillae on distal suprategular apophysis. (D) *Mermessus dentiger*, retrolateral view, arrow indicates papillae at base of distal suprategular apophysis. (E) *Sphecozone spadicaria*, ventral view showing embolic basal process and anterior radical process. (F) *Mermessus dentiger*, detail of embolic division, prolateral view showing ventrally recurved tailpiece, anterior tooth, mesal tooth, and prolaterally excavated radix. Scale bars = 10 μm in (C), (D), and (F); 100 μm in other images.

paracymbium. The spiral paracymbium runs ventrally, then curves ectally so that the mesal surface of the distal part faces out; the ectal surface of the basal part faces out. In other linyphiids, the hook of the paracymbium is in a single plane so that the ectal surfaces of the basal and distal parts faces out; this is the straight hook character state. Previous work has coded *Stemonyphantes* as having a unique paracymbium morphology, based on statements in Millidge (1988b). Although the paracymbium of *Stemonyphantes* is unusual (van Helsdingen, 1968), it is consistent with the straight hook type of paracymbium. The erigonine genus *Asemostera* (including synonyms; Miller, in press a) has a unique paracymbium in the form of a horizontal ''U''. Coding of non-linyphiid outgroup taxa follows Hormiga (2000).

The loss of the paracymbium in erigonines is unique to a few Neotropical genera. *Sphecozone* (including junior synonyms *Brattia* and *Gymnocymbium*), *Psilocymbium*, *Gonatoraphis*, and *Dolabritor* have all been described as lacking a paracymbium (e.g., Millidge, 1991). Hormiga (1994a) pointed out that *Gonatoraphis* and *Dolabritor* seem to have the paracymbium merely fused to the cymbium and reduced in size. Scanning electron microscopy supports this idea (Fig. 16C). Only *Sphecozone* and *Psilocymbium* seem to have lost all trace of the paracymbium. Our phylogenetic results indicate independent losses of the paracymbium in *Sphecozone* (clade 78) and *Psilocymbium*. The paracymbia of *Ceratinopsis interpres* and *Tutaibo* are both relatively small and hook-like. Loss of the paracymbium in *Sphecozone* may have resulted from a continuation of this size reduction. Loss of the paracymbium in *Psilocymbium* seems to have come about by the fusion and absorption of the paracymbium into the cymbium. The paracymbium in *Intecymbium antarcticum* is relatively large and fused to the cymbium. In *Gonatoraphis* and *Dolabritor*, the paracymbium is fused to the cymbium, but is also greatly reduced in size. In *Psilocymbium*, paracymbium reduction seems to have progressed to the point that the paracymbium has disappeared altogether (Fig. 16B). An alternative coding scheme would represent *Sphecozone*, *Psilocymbium*, *Gonatoraphis*, and *Dolabritor* as having the paracymbium absent (and inapplicable for attribute characters of the paracymbium, Chars. 11–15), reflecting the interpretation of Millidge (1991). This presents a test of the diphyletic loss of the paracymbium. Under this coding scheme, the same topology is recovered.

13. Paracymbium apophyses: 0, absent (*Valdiviella*, Fig. 15D); 1, present (*Tenuiphantes*, Hormiga, 1994a, fig. 13A). Character 9 in Hormiga (1993, 1994a); 12 in Hormiga (1994b); 6 in Hormiga (2000).

14. Paracymbium base: 0, glabrous; 1, with cluster of setae (*Valdiviella*, Fig. 15D; *Tapinocyba*, Hormiga, 2000, pl. 62A). Most linyphiids have one to several setae at the base of paracymbium.

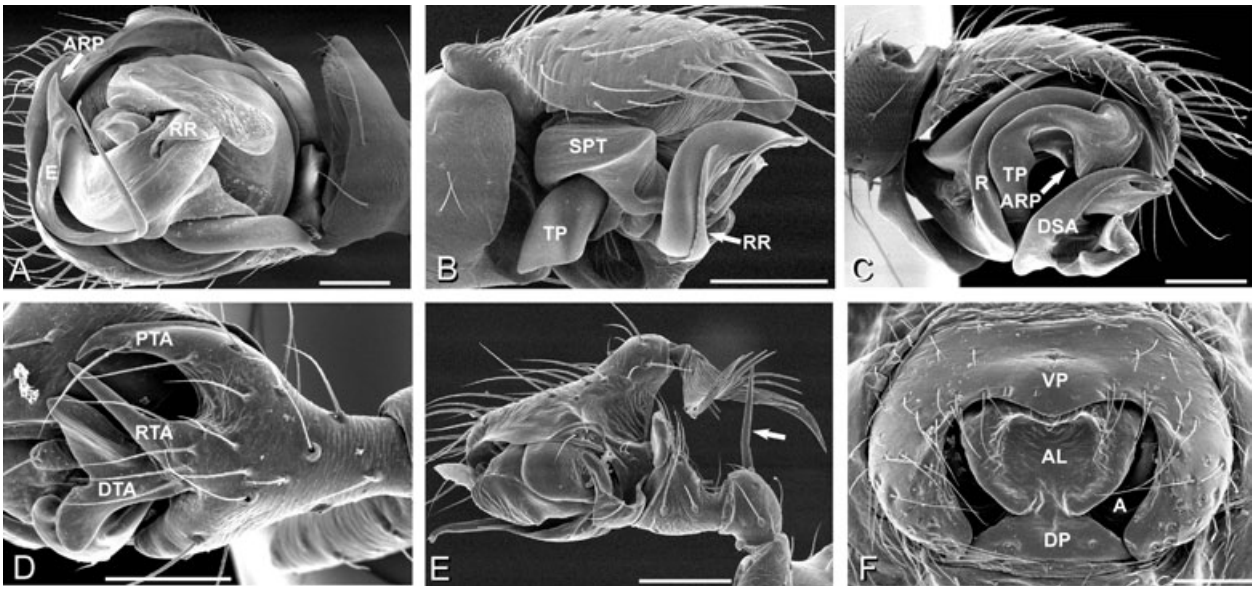

Fig. 19. (A–E) Male palpi of erigonine spiders. (F) Female epigynum. (A) *Ceratinopsis interpres*, ventral view showing embolus arising from radix at a distinct angle, radical ridge, and anterior radical process. (B) *Intecymbium antarcticum*, prolateral view showing radical ridge and striated suprategulum. (C) *Scolecura propinqua*, prolateral view showing mesally projecting radical tailpiece. (D) *Rhabdogyna patagonicus*, dorsal view of palpal tibia showing prolateral, retrolateral, and distal tibial apophyses. (E) *Pseduotyphistes cristatus*, retrolateral view showing strong dorsal macroseta on patella. (F) *Sphecozone crassa*, ventral view showing dorsal plate with anterior lobe and atrium. Scale bars = 100 μm.

15. Paracymbium basal setae form: 0, setae equal or smaller in size and proportions to other setae on cymbium (*Tapinocyba*, Hormiga, 2000, pl. 62A); 1, setae larger than other setae on cymbium (*Valdiviella*, Fig. 15D; *Islandiana*, Hormiga, 2000, pl. 39A). In a few erigonines, the paracymbium basal setae are grossly enlarged and modified.

16. Protegulum: 0, absent (*Hilaira*, Hormiga, 2000; pl. 33D); 1, present (*Ceratinops*, Hormiga, 2000, pl. 15E). Character 8 in Hormiga (2000). *Ostearius melanopygius* has been recoded from Hormiga (2000) as having the protegulum present with scale-like papillae (Hormiga, 2000, pl. 52D).

The problem of the protegulum seems to be one of confusing the modification of a structure with the loss and gain of different structures. As currently defined, the protegulum is a membranous sac, usually located on the distoventral part of the tegulum. However, the limits of this character are somewhat ambiguous. In the current analysis, the protegulum provides ambiguous support for a large clade of erigonines with five reversals, and parallel evolution in *Drepanotylus*. Many linyphiids have a structure, often unnamed, on the same part of the tegulum that might be homologous with the erigonine protegulum (e.g., *Lepthyphantes* Menge, 1866 [Hormiga, 2000, pl. 5D], *Linyphia* Latreille, 1804 [Hormiga, 2000, pl. 7A], *Microlinyphia* Gerhardt, 1928 [Hormiga, 2000, pl. 9C,D], *Stemonyphantes* [Hormiga, 2000, pl. 12C], *Leptorhoptrum* Kulczynski, 1894 [Hormiga, 2000, fig. 19A,C], mynoglenine tegular process of *Haplinis* Simon, 1894 [Hormiga, 2000, pl. 3A]; see also Holm, 1979, p. 256; Hormiga, 2000, p. 6). The protegulum and these other tegular structures are located in roughly the same part of the tegulum as both the median apophysis and conductor of pimoids (Hormiga, 1994b, figs 233, 234), and the conductor of cyatholipids (Griswold et al., 1998, fig. 17B). The sac-like protegulum could be a character state of a much more widespread tegular structure.

17. Protegular papillae: 0, absent (*Psilocymbium*, Fig. 15E; *Erigone*, Hormiga, 2000, pl. 25D); 1, present (*Ceratinops*, Hormiga, 2000, pl. 15E). Character 9 in Hormiga (2000).

18. Protegular papillae form: 0, scale-like (*Diplocentria*, Hormiga, 2000, pl. 18C); 1, rod-like (*Tapinocyba*, Hormiga, 2000, pl. 62C). This character is meant to capture some of the variation in the form of the protegular papillae. They range from being very long and thin (rod-like) to flat and wide (scale-like).

19. Tegular sac: 0, absent (*Diplocentria*, Hormiga, 2000, pl. 18C); 1, present (*Gongylidium*, Hormiga, 2000, pl. 30D). Character 10 in Hormiga (2000).

20. Papillae on tegulum: 0, absent (*Erigone*, Hormiga, 2000, pl. 25A; *Hylyphantes*, Hormiga, 2000, pl. 28A); 1, present (*Psilocymbium*, Fig. 15E; *Dismodicus*, Hormiga, 2000, pl. 22A). In some taxa, the field of papillae on the protegulum extends to cover part of the tegulum as well. In other taxa, papillae may be present on the tegulum but absent from the protegulum (e.g., *Psilocymbium*).

21. Tegulum to subtegulum orientation in unexpanded palp: 0, tegulum distal to subtegulum (*Paraletes*, Miller, in press a, fig. 100D); 1, tegulum mesal to subtegulum

(*Gonatoraphis*, Fig. 16C; *Triplogyna*, Miller, in press a, fig. 5A); 2, tegulum ventral to subtegulum (*Pimoa*, Hormiga, 1994b, fig. 9). The tegular division of the palp, consisting of the subtegulum and tegulum, is roughly spiral in shape, but the orientation of that spiral is variable. In many araneoids, including *Theridiosoma* O. Pickard-Cambridge, 1879 and *Pimoa*, the subtegulum is more or less dorsal to the tegulum so that the axis of the helix defined by the path of the sperm duct is dorsal-to-ventral. In *Tetragnatha*, *Steatoda*, and many linyphiids, the subtegulum is proximal to the tegulum so that the sperm duct axis is proximal-to-distal. In *Theridiosoma* and in many linyphiids, the subtegulum is more or less ectal to the tegulum so that the sperm duct axis is retrolateral-to-prolateral. Millidge (1977, pp. 4–5) discussed the two conditions found in linyphiids, distinguishing between vertical and horizontal tegula.

22. Sperm duct switchback in first loop: 0, absent (*Ceratinops*, Hormiga, 2000, fig. 4A); 1, present (*Pimoa*, Hormiga, 1994b, fig. 9; *Grammonota*, Hormiga, 2000, fig. 13B). Most araneoids have a double switchback in the first loop of the sperm duct trajectory (Coddington, 1986b; Agnarsson, 2004).

23. Sperm duct path in distal part of tegulum: 0, smooth, continuous curve (*Diplocentria*, Hormiga, 2000, fig. 5C); 1, loop or tight kink (*Spanioplanus*, Fig. 17A; *Labicymbium*, Fig. 17C; *Asthenargus*, Hormiga, 2000, fig. 3E). The path of the sperm duct through the tegular division is convoluted in some araneoids. In linyphiids, the path is relatively simple. Two potentially homologous turns of the sperm duct have been identified. In the first loop of the duct on the retrolateral side, the duct may pass through a switchback. Then, in the distal part of the sperm duct path through the tegulum, the duct may pass through a tight kink or loop. In linyphiids, this loop is usually near the junction between the tegulum and the suprategulum (see Zujko-Miller, 1999). Identifying homology between these loops and the loops found in taxa like *Theridiosoma*, with a highly convoluted sperm duct path, is difficult. The most conservative approach is to code *Theridiosoma* as present for both these sperm duct characteristics (see Coddington, 1986b). As the sperm duct features described in Chars 22 and 23 were never observed in conjunction, it is possible that these features are actually positional and shape variation in the same character. When Chars 22 and 23 are merged with the "first loop switchback" and the "distal loop" is considered the same character state, there is no difference to the resulting topology.

24. Suprategulum: 0, absent (*Tetragnatha*, Griswold et al., 1998, fig. 10A) or vestigial (*Sisicus*, Hormiga, 2000, pl. 61B); 1, present (*Spanioplanus*, Fig. 17A; *Asthenargus*, Hormiga, 2000, fig. 3E). Character 13 (in part) in Hormiga (1993, 1994a); 15 (in part) in Hormiga (1994b); 7 and 11 in Hormiga (2000). The origin of a suprategulum supports the monophyly of Linyphiidae (clade 5).

Establishing homologies among the various tegular sclerites of the araneoid palp is a recurring problem in araneoid systematics (e.g., Coddington, 1990b; Griswold et al., 1998). Griswold et al. (1998) was the latest attempt to establish homologies among araneoid palpal sclerites in a phylogenetic context. Homologies among the various sclerites arising from the tegulum, other than the embolus, were of particular concern. By convention, Griswold et al. used the term conductor when only one tegular sclerite was present. Homoplasy in loss was thus allocated to the median apophysis, which was coded as present when a second tegular sclerite was found. Criteria of special similarity were used to determine homology when two sclerites were present (e.g., the conductor is often membranous or lightly sclerotized and covers the distal end on the embolus). The purpose of this rule for homology was to minimize the number of unique sclerites that must be invoked to explain palpal evolution when homologies were difficult to code unambiguously. Almost all linyphiids have a nonembolic sclerite arising from the tegulum, the suprategulum. (A second, less widespread sclerite is the protegulum, see Char. 16.) The suprategulum is considered unique (i.e., not homologous to either the araneoid conductor or median apophysis) because it almost always conducts the sperm duct from the tegulum to the embolic division (Saaristo, 1971). In the most parsimonious cladogram of Griswold et al. (1998), loss of both the conductor and the median apophysis optimized as terminal branch changes for linyphiids (exemplified by a single species, *Linyphia triangularis*). The suprategulum was not coded in their matrix because only one linyphiid exemplar was present and, as an autapomorphy, the change would be uninformative to resolve relationships among araneoid families. In Hormiga (2000, 2003) and in the current study, linyphiids are supported by the loss of the conductor, the loss of the median apophysis, and the gain of the suprategulum. Note also that the basal part of the pimoid embolic process carries the sperm duct and may be homologous to the suprategulum (Hormiga, 2003).

Whether the suprategulum and the mynoglenine tegular apophysis, as defined by Hormiga (1994a), are homologous or not is difficult to establish conclusively. The mynoglenine tegular apophysis (MTA) was called a suprategulum by Blest (1979). The suprategulum and the mynoglenine tegular apophysis are both tegular processes that originate near the distal part of the sperm duct path through the tegulum, although as pointed out by Hormiga (1994a) in several mynoglenine genera the MTA is located far from the column. Hormiga (1994b, p. 24) chose the hypothesis of non-homology between

the MTA and the suprategulum based on the fact that the sperm duct did not run through the MTA and consequently, it did not bear the column. The suprategulum conducts the sperm duct to the column (with rare exceptions, e.g., *Asemostera*). Hormiga's (2000) topology implied that the suprategulum was lost and replaced by the mynoglenine tegular apophysis in the common ancestor of mynoglenines. Although the mynoglenine tegular apophysis clearly has some unique features (see Blest, 1979; Hormiga, 1994a), it is more parsimonious to minimize the number of unique sclerites that must be invoked to explain palpal evolution and encode differences among these nominal sclerites as a series of characters. Also, the functional similarity of the mynoglenine tegular apophysis with the suprategulum (i.e., locking with the female epigynum during copulation; van Helsdingen, 1965, 1969; Blest and Pomeroy, 1978; Hormiga, 1994a) would seem to argue for modification of one structure, rather than the virtually simultaneous loss of the suprategulum and gain of a new structure in roughly the same part of the palp with the same function as the suprategulum. We know of no taxon that demonstrates conjunction by having both the mynoglenine tegular apophysis and the suprategulum, hence sclerites can be conserved by invoking the modification of the suprategulum in mynoglenines. This supposes a shift of the column from the suprategulum to the tegulum (Char. 28). Note that a distally projecting distal suprategular apophysis in mynoglenines (Char. 26) is consistent with other linyphiines and basal erigonines according to our phylogeny. Whether the structure is coded as a mynoglenine tegular apophysis (with Chars. 25–34 coded as inapplicable for *Haplinis* and *Novafroneta*) or a suprategulum, the topological results are the same.

Hormiga (2000) coded *Sisicus* Bishop and Crosby, 1938 as absent for the suprategulum. Clearly, the sclerotization of the typical linyphiid suprategulum is absent in *Sisicus*. However, scanning electron microscopy (Hormiga, 2000, pl. 61B) depicts what looks like a striated suprategulum articulated to the tegulum. The putative suprategulum, its junction with the tegulum, and the striations are in the same location as similar structures in other erigonines (e.g., *Neomaso*, Fig. 18A). Two alternative conclusions can be drawn from this evidence. Either the suprategulum is absent and the junction and striations are not related to those seen in taxa with a suprategulum, or the suprategulum is vestigial and the striations and junction are homologous with those found in other erigonines. When the suprategulum is coded as absent with suprategular characters of *Sisicus* inapplicable (Chars 25–34), 14 trees result. The strict consensus of these trees collapses five nodes, eliminating some resolution among mostly haplotracheate erigonines. Coding *Sisicus* as having a vestigial suprategulum with suprategular characters applicable results in a single most parsimonious tree (Fig. 3). This tree is among the 14 found when suprategulum characters were coded as inapplicable for *Sisicus*. As the "vestigial suprategulum" solution improves character congruence and encodes more potentially homologous observations, it is provisionally accepted here.

25. Suprategulum junction with tegulum: 0, continuous with tegulum (*Islandiana*, Hormiga, 2000, fig. 17C); 1, with partial or complete membranous division (*Spanioplanus*, Fig. 17A; *Labicymbium*, Fig. 17C; *Stemonyphantes*, Hormiga, 1994a, fig. 2C). Character 13 (in part) in Hormiga (1993, 1994a); 15 (in part) in Hormiga (1994b); 12 in Zujko-Miller (1999); 12 in Hormiga (2000). A phylogenetically uninformative version of this character appeared in Hormiga (2000) to document the unusual form of the origin of the suprategulum in *Stemonyphantes*, which is articulated by a membrane (van Helsdingen, 1968; Hormiga, 1994a). Zujko-Miller (1999) modified this character by adding a third state: a partial or complete membranous break at the junction between the tegulum and suprategulum. For this analysis, we consider the membranous division described by Zujko-Miller (1999) and the articulation in *Stemonyphantes* to be indistinguishable.

26. Suprategulum orientation at junction with tegulum: 0, continues in straight line (*Spanioplanus*, Fig. 15F); 1, forms distinct angle (*Neomaso*, Fig. 18A). In some erigonines, the suprategulum arises from the tegulum at a distinctly inclined angle.

27. Suprategulum texture: 0, smooth (*Spanioplanus*, Fig. 15F; *Araeoncus*, Hormiga, 2000, pl. 13C); 1, striated (*Neomaso*, Fig. 18A; *Sisicus*, Hormiga, 2000, pl. 61B). In a few erigonine taxa, the suprategulum has a series of longitudinal striations; the suprategulum is usually smooth.

28. Foramen: 0, in suprategulum (*Islandiana*, Hormiga, 2000, fig. 17C; *Fissiscapus*, Miller, in press a, fig. 115C); 1, in tegulum (*Asemostera*, Fig. 17E). Hormiga (2000) coined the term suprategular foramen for the aperture through which the sperm duct passes to enter the embolic division. In *Asemostera*, this aperture is found proximal to the origin of the suprategulum in the tegulum proper. For taxa without a suprategulum, this character is inapplicable.

29. Distal suprategular apophysis: 0, absent (*Sciastes*, Hormiga, 2000, fig. 25D); 1, present (*Araeoncus*, Hormiga, 2000, fig. 1E; *Fissiscapus*, Miller, in press a, fig. 115C). Character 13 in Hormiga (2000).

30. Distal suprategular apophysis continuity: 0, continuous (*Rhabdogyna*, Fig. 17H; *Lophomma*, Hormiga, 2000, fig. 20C); 1, with membranous division (*Labicymbium*, Fig. 17C). In most erigonines, the degree of sclerotization is more or less constant throughout its length. In *Labicymbium* and *Fissiscapus* (clade 49), the distal suprategular apophysis is membranous basally and heavily sclerotized distally.

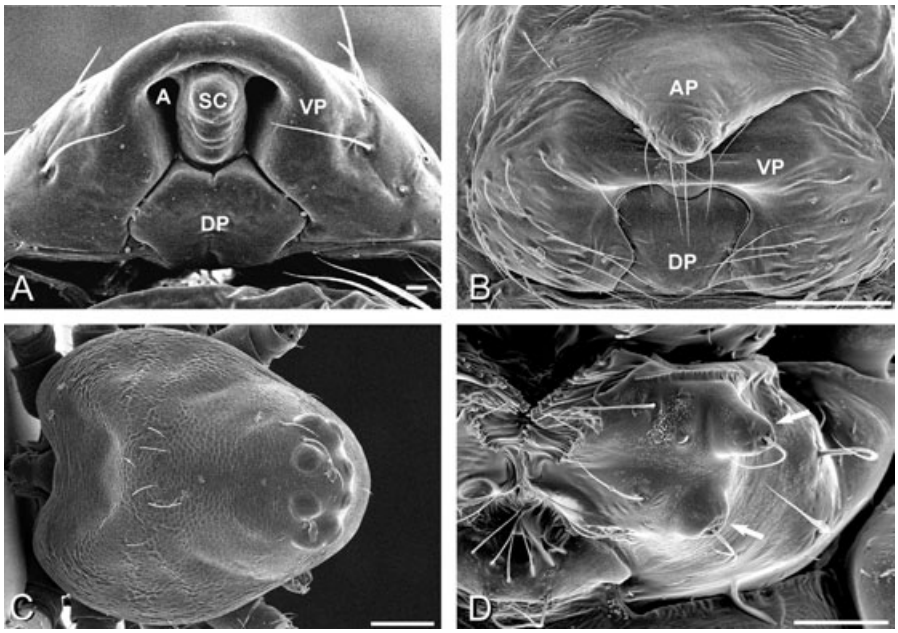

Fig. 20. (A, B) Female epigynum. (C) Female prosoma. (D) Male endites. (A) *Valdiviella trisetosa*, posterior view showing scape. (B) *Intecymbium antarcticum*, ventral view showing anterior process of ventral plate. (C) *Lygarina silvicola*, dorsal view showing sparse patch of thoracic setae. (D) *Triplogyna major*, arrows indicate setal bases modified into tubercles. Scale bar = 10 μm in (A); 100 μm in other images.

31. Distal suprategular apophysis initial orientation: 0, extends distally beyond suprategulum (*Notiomaso*, Fig. 18B; *Leptorhoptrum*, Hormiga, 2000, fig. 19C); 1, extends ventrally from suprategulum (*Rhabdogyna*, Fig. 17H; *Araeoncus*, Hormiga, 2000, fig. 1E). In most erigonines, the distal suprategular apophysis is a ventral projection off of the suprategulum. In some nonerigonine linyphiids and erigonines, the distal suprategular apophysis is a distal projection of the suprategulum.

32. Distal suprategular apophysis texture: 0, smooth (*Neocautinella*, Fig. 15B); 1, with distal grooves or papillae (*Microplanus*, Fig. 18C; *Hylyphantes*, Hormiga, 2000, pl. 38C, 38D).

33. Distal suprategular apophysis basal papillae: 0, absent (*Neocautinella*, Fig. 15B; *Sisicottus*, Miller, 1999, fig. 47); 1, present (*Mermessus dentiger*, Fig. 18D). *Mermessus* and *Gravipalpus* (clade 42) have a unique brush of papillae on the anterior margin of the distal suprategular apophysis near the retrolateral side of the cymbial margin.

34. Marginal suprategular apophysis: 0, absent (*Islandiana*, Hormiga, 2000, fig. 17C; *Triplogyna*, Miller, in press a, fig. 3A); 1, present (*Araeoncus*, Hormiga, 2000, Fig. 1E; *Valdiviella*, Miller, in press a, fig. 35A). Character 6 in Miller (1999); 14 in Hormiga (2000).

35. Median apophysis: 0, present (*Theridiosoma*, Coddington, 1986b, figs 134, 135; *Pimoa*, Hormiga, 1994b, figs 9, 10); 1, absent. Character 22 (Fig. 3) in Coddington (1990b); 12 in Griswold (1993); 14 in Hormiga (1993, 1994a); 16 in Hormiga (1994b); 15 in Ramírez (1995); 30 in Hormiga et al. (1995); 14 in Ramírez (1997); 10 in Scharff and Coddington (1997); 16 in Griswold et al. (1998); 31 in Davies (1999); 109 in Griswold et al. (1999); 45 in Bosselaers and Jocqué (2000); 35 in Davies and Lambkin (2000a); 42 in Davies and Lambkin (2000b); 15 in Hormiga (2000); 14 in Platnick (2000); 39 in Davies and Lambkin (2001); 138 in Bosselaers and Jocqué (2002); 28 in Wang (2002); 21 in Hormiga (2003); 70 in Schütt (2003); 44 in Silva Dávila (2003); 71 in Agnarsson (2004). Loss of the median apophysis supports the monophyly of Linyphiidae (clade 5, but see Chars. 16 and 24).

36. Conductor: 0, present (*Theridiosoma*, Coddington, 1986b, figs 134–137; *Pimoa*, Hormiga, 1994b, figs 9, 10); 1, absent. Character 26 in Coddington (1990a); 5 (fig. 3), 15 (table 1) in Coddington (1990b); 39 in Platnick et al. (1991b); 15 in Hormiga (1993, 1994a); 17 in Hormiga (1994b); 32 in Harvey (1995); 14 in Griswold et al. (1998); 105 in Griswold et al. (1999); 44 in Bosselaers and Jocqué (2000); 16 in Hormiga (2000); 30 in Griswold (2001); 22 in Hormiga (2003); 23 in Bosselaers (2002); 137 in Bosselaers and Jocqué (2002); 62 in Agnarsson (2004). Loss of the conductor supports the monophyly of Linyphiidae (clade 5, but see Chars. 16 and 24).

37. Pimoid embolic process: 0, absent (*Rhabdogyna*, Fig. 17H); 1, present (*Pimoa*, Hormiga, 1994b, figs 9, 10). Character 19 in Hormiga (1993, 1994a); Hormiga (2000); 23 in Hormiga (1994b). In pimoids, the embolus

and the PEP share a common base that is a discrete extension of the mesal margin of the tegulum. This tegular region (Hormiga, 1994b, figs 48, 54; Hormiga, 2003, fig. 1G,H), which may be homologous to the suprategulum, branches off again into the embolus and the so-called PEP. The presence of this process supports the Pimoidae (clade 4).

38. Column: 0, absent (*Pimoa*, Hormiga, 1994b, figs 9, 10); 1, present (*Rhabdogyna*, Fig. 17H; *Diplocentria*, Hormiga, 2000, fig. 6C,D; *Fissiscapus*, Miller, in press a, fig. 115C). Character 35 in Coddington (1990a); 21 (table 1) in Coddington (1990b); 23 in Hormiga (1993, 1994a); 29 in Hormiga (1994b); 38 in Hormiga et al. (1995); 22 in Griswold et al. (1998); 24 in Hormiga (2000); 33 in Hormiga (2003); 97 in Agnarsson (2004). Contrary to previous analyses (e.g., Griswold et al., 1998; Hormiga, 2000, 2003), *Steatoda* has been recoded as having an embolus-tegular membrane (Agnarsson, 2004). The column is lost twice on the cladogram, once supporting the Pimoidae (clade 4), and again in *Theridiosoma*. However, this optimization seems to be an artifact of taxon sampling. Membranous divisions between the embolic and tegular divisions are absent from cyatholipids, synotaxids, nesticids, the symphytognathoid families, and others. Based on the phylogeny of araneoid families in Griswold et al. (1998), this membrane is independently derived in linyphiids, tetragnathids, and theridiids.

39. Column position: 0, dorsal, arises from suprategulum near margin of cymbium (*Entelecara*, Hormiga, 2000, fig. 9C; *Fissiscapus*, Miller, in press a, fig. 115C); 1, ventral, arises from distal part of DSA (*Rhabdogyna*, Fig. 17H). Character 14 in Hormiga (2002); 15 in Hormiga et al. (2003). In most linyphiids, the column arises from the suprategulum near the margin of the cymbium. In a few erigonine taxa, the column seems to have shifted distally so that it arises near the distal limit of the distal suprategular apophysis. In these taxa, the distal suprategular apophysis grades into the embolic membrane. This character is inapplicable for taxa without a distal suprategular apophysis (Char. 29) and for those in which the foramen is in the tegulum (Char. 28).

40. Embolic membrane: 0, absent (*Hylyphantes*, Hormiga, 2000, fig. 16D; *Paraletes*, Miller, in press a, figs 99A, 100C); 1, present (*Valdiviella*, Fig. 15D). Character 18 in Hormiga (1993, 1994a); 22 in Hormiga (1994b); 18 in Hormiga (2000); 13 in Hormiga (2002). Hormiga (2000) argued that pimoids cannot be scored for this character because they lack a column. This applies also to *Theridiosoma*.

41. Embolic membrane papillae: 0, absent (*Valdiviella*, Fig. 15D; *Diplocentria*, Hormiga, 2000, pl. 18B; *Neocautinella*, Miller, in press a, fig. 21A); 1, present (*Asemostera*, Fig. 15A; *Gonatium*, Hormiga, 2000, pl. 27B; *Gigapassus*, Miller, in press a, fig. 83C).

42. Embolus origin: 0, distal (*Microplanus*, fig. 18C; *Laminacauda*, Hormiga, 2000, fig. 18C; *Onychembolus*, Miller, in press a, fig. 58A); 1, proximal (*Notiomaso*, Fig. 18B; *Drepanotylus*, Hormiga, 2000, Fig. 8A). In most linyphiids, the embolus arises from the distal part of the radix. However, in some genera, the embolus arises from the proximal part of the radix.

43. Embolus length: 0, long (*Notiomaso*, Fig. 18B); 1, short (*Microplanus*, Fig. 18C). Character 17 in Hormiga (1993, 1994a); 20 in Hormiga (1994b); 1 in Miller (1999); 17 in Hormiga (2000). The long embolus is defined as being at least a third the length of the cymbium and ranges up to a very long, filiform structure. The short embolus is usually tooth-like or slightly longer. The state boundaries for this character are clearly somewhat arbitrary, and become more difficult to maintain as the taxon sample increases. Nevertheless, this character does capture some phylogenetically useful information. *Leptorhoptrum robustum*, *Ostearius melanopygius*, *Parapelecopsis nemoralis* and *Savignia frontata*, have been recoded from Hormiga (2000) as having long, rather than short, emboli. The point at which the radix becomes the embolus is difficult to define in some taxa (e.g., *Leptorhoptrum*, *Ostearius*, *Neocautinella*) and the coding of these taxa is dependent on that boundary.

44. Embolic shape: 0, straight to curved (*Rhabdogyna*, Fig. 17G); 1, spiral (*Dismodicus*, Hormiga, 2000, fig. 7D; *Sphecozone crassa*, Miller, in press a, fig. 162E). Most linyphiid emboli are spiral; in some taxa, this is more pronounced than in others. Taxa which have the embolus straight or passing through only a gentle curve were assigned the first character state. Taxa with a more strongly developed spiral shape were assigned the second character state. Some taxa with "straight to curved" emboli have rather complex shapes, and are thus difficult to code (e.g., some *Sphecozone* species). This character is considered applicable only to long emboli. However, *Hylyphantes* has a short, corkscrew-shaped embolus that could arguably be coded as spiral (Hormiga, 2000, pl. 38C).

45. Embolic tip: 0, terminating in embolic opening (*Typhochrestus*, Hormiga, 2000, pl. 69D; *Paraletes*, Miller, in press a, fig. 100E); 1, with projection beyond embolic opening (*Sisicottus*, Miller, 1999, fig. 8; *Savignia*, Hormiga, 2000, pl. 56D; *Anodoration*, Miller, in press a, fig. 27F). Character 2 in Miller (1999). In most linyphiids, the embolus terminates at the opening of the sperm duct. However, in a few taxa, a narrow straight or hooked process continues beyond the sperm duct opening.

46. Embolic papillae: 0, absent (*Araeoncus*, Hormiga, 2000, pl. 13A; *Gravipalpus*, Miller, in press a, fig. 89C); 1, present (*Tenuiphantes*, Hormiga, 2000, pl. 6A; *Laminacauda*, Hormiga, 2000, pl. 41D; *Onychembolus*,

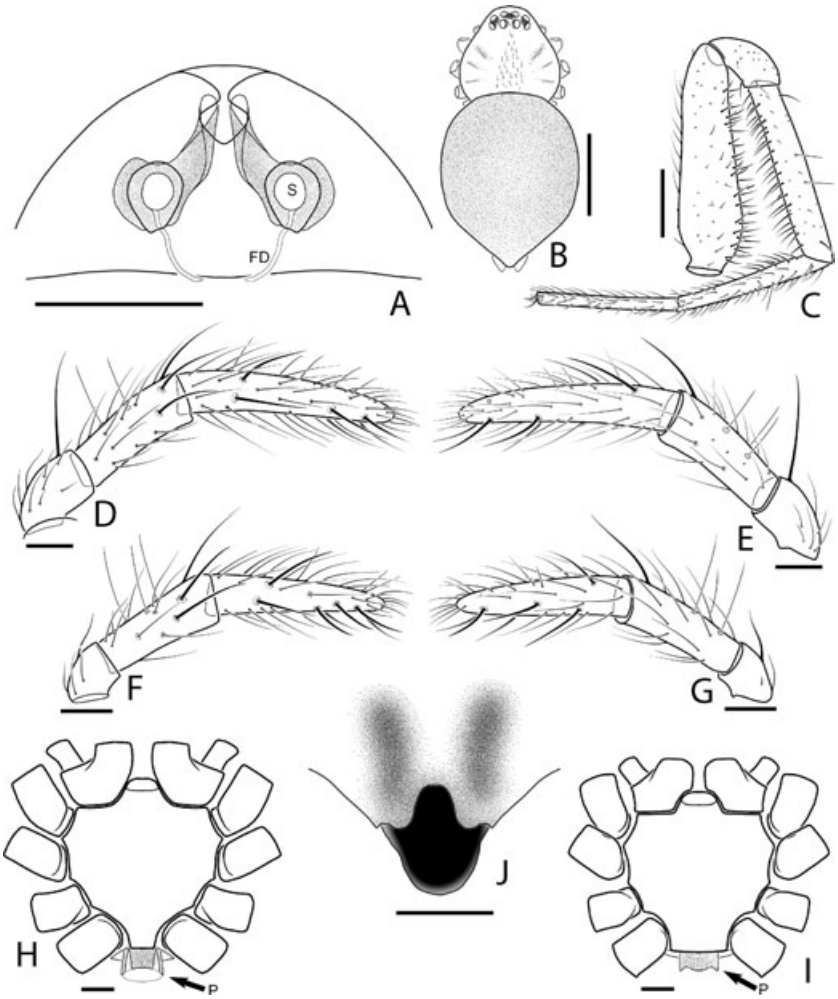

Fig. 21. (A, J) Female epigynum; (B) female habitus; (C) Male leg (I); (D, F) female pedipalp, prolateral view; (E, G) female pedipalp, retrolateral view; (H, I) male sternum with pedicel. (A) *Rhabdogyna patagonica*, posterior view, showing dorsal orientation of fertilization ducts. (B) *Asemostera daedalus*, showing broad field of setae covering head region. (C) *Notiomaso exonychus*, showing strong ventral setae. (D, E) *Triplogyna major*, showing palpal macrosetae. (F, G) *Neocautinella neoterica*, showing palpal macrosetae. (H) *Mermessus dentiger*, showing separation of pleurites and sternite of pedicel. (I) *Gonatoraphis barada*, showing fusion of pleurites and sternite of pedicel. (J) *Mermessus dentiger*, showing copulatory plug. Scale bars = 0.5 mm in (B), 0.1 mm in other images.

Miller, in press a, fig. 58F). In some linyphiid genera, the embolus is clothed in papillae. In this analysis, the presence of embolic papillae does not support any erigonine clade, but it is a synapomorphy for the Micronetini. A brief literature survey revealed that embolic papillae are widespread in micronetines. Scanning electron micrographs indicate the presence of embolic papillae in *Lepthyphantes*, *Mansuphantes* Saaristo and Tanasevitch, 1996, *Improphantes*, Saaristo and Tanasevitch, 1996, and *Metaleptyphantes* Locket, 1968 (Scharff, 1990; Saaristo and Tanasevitch, 1996). In addition, detailed illustrations reveal embolic papillae at least in *Piniphantes* Saaristo and Tanasevitch (1996); *Scotargus* Simon, 1913, and *Troglohyphantes* Joseph, 1881 (van Helsdingen, 1973; Thaler and Polenec, 1974; Saaristo and Tanasevitch, 1996).

47. Embolic axis at origin: 0, continuous with radix (*Sciastes*, Hormiga, 2000, fig. 25E; *Valdiviella*, Miller, in press a, fig. 36C); 1, arises from radix at distinct angle (*Notiomao*, Fig. 18B; *Ceratinopsis interpres*, Fig. 19A). In most erigonines, the embolus is more or less continuous with the radix. However, in some erigonine species, especially some species of *Sphecozone* and its relatives, the base of the embolus arises from the radix at a distinct angle.

48. Embolic basal process: 0, absent (*Ceratinopsis interpres*, Fig. 19A); 1, present (*Sphecozone spadicaria*, Fig. 18E). This process arises from the embolus where the sperm duct passes from the radical part of the embolic division. It is usually short and proceeds in the opposite direction from that taken by the sperm duct, but is nearly as long as the embolus in *Sphecozone crassa*.

49. Embolic basal lobe: 0, absent (*Gongylidiellum*, Hormiga, 2000, fig. 11E; *Mermessus*, Miller, in press a, fig. 93E); 1, present (*Spanioplanus*, Figs 15F and 17B; *Asthenargus*, Hormiga, 2000, fig. 3F; *Gongylidium*, Hormiga, 2000, "R" in fig. 12E). See Char. 52.

50. Radix: 0, absent (*Pimoa*, Hormiga, 1994b, figs 9, 10); 1, present (*Labicymbium*, Fig. 17D). Character 36 in Coddington (1990a); 22 (table 1) in Coddington (1990b); 22 in Hormiga (1993, 1994a); 28 in Hormiga (1994b); 20 in Hormiga (2000); see also 34 in Hormiga et al. (1995); 16 in Scharff and Coddington (1997); 20 in Griswold et al. (1998). The presence of a radix supports the monophyly of Linyphiidae (clade 5). Linyphiids and araneids both exhibit a sclerite nominally referred to as a radix. In both cases, the radix is the basal sclerite of the embolic division, attached to the tegular division by a membrane; the embolus may be a continuous extension of the radix, or articulated via a membranous connection. In some araneids, a sclerite called the stipes is inserted between the radix and embolus. The radix is often relatively large with various apophyses or auxiliary sclerites attached. Similar structures appear under different names in several araneoid families. In nephilines (Tetragnathidae), the structure has been called the embolic base (Hormiga et al., 1995); in "metines" (Tetragnathidae), the metine embolic apophysis (Hormiga et al., 1995). Recent analyses have concluded that the radix of araneids and linyphiids are not homologous (Griswold et al., 1998; see also Hormiga, 1994a,b). However, homolog ambiguities in tetragnathids and other taxa (e.g., Hormiga et al., 1995) suggest that this problem needs reassessment within a larger cladistic context.

51. Radix-embolus connection: 0, continuous (*Rhabdogyna*, Fig. 17H); 1, membranous (*Spanioplanus*, Fig. 17B; *Labicymbium*, Fig. 17D). See Char. 52.

52. Radical tailpiece: 0, absent (*Linyphia*, Hormiga, 1994a, fig. 9D); 1, present (*Spanioplanus*, Fig. 15F). Character 21 in Hormiga (2000). Identification of sclerites in the linyphiid embolic division appears to be more difficult than first thought. Merrett (1963) set out a generalized system of linyphiid embolic division sclerites. In this system, the embolus is fused to a radix. The terminal apophysis (Char. 65) may attach to the radix near the base of the embolus. The lamella characteristica (Char. 66) may be attached to the radix via a membrane. The radix often has a conspicuous plate-like tailpiece; the lamella characteristica may also be large and plate-like. Following Merrett's system, Hormiga (2000) coded several erigonines as having a lamella characteristica (*Asthenargus* Simon and Fage, 1922, *Entelecara*, *Gonatium* Menge, 1868, *Gongylidiellum* Simon, 1884, *Gongylidium* Menge, 1868, *Hilaira* Simon, 1884, *Hybocoptus* Simon, 1884, *Hylyphantes* Simon, 1884, *Oedothorax* Bertkau, 1883, and *Sisicus*). In most of these cases, the radical tailpiece was absent or reduced and difficult to define. Furthermore, Hormiga's cladogram demonstrated that the linyphiine lamella characteristica is not homologous with any of the several instances of lamella evolution in erigonines (Hormiga, 2000, fig. 44). Under Hormiga's hypothesis, the radical tailpiece has been reduced or lost multiple times in erigonine evolution, often accompanied by the addition of a lamella characteristica. An alternative interpretation is that the degree of sclerotization on the radix near the origin of the embolus is variable and may become membranous. Thus, the lamella characteristica in erigonines is often simply a radical tailpiece set off by a membranous regions. However, in some erigonine taxa, an enlarged embolic base can be identified beyond the membrane connecting the embolus to the rest of the embolic division (e.g., *Gongylidium*, Hormiga, 2000, "R" in fig. 12E). Whether this represents the entire radix or only part of it will have to be addressed through denser examination of the lineages involved. In those taxa where a distinct lobe can be found distal to the membranous embolus-radix connection, an embolic basal lobe is coded as present. For the current study we have coded all erigonines except *Sisicus* as absent for the lamella characteristica. In *Gonatium*, the lamella characteristica was recoded as a radical anterior process (see Char. 56). Other erigonines formerly coded as having a lamella characteristica have been coded as having a membranous connection between the radix and embolus. Some members of the genus *Sphecozone* also have a membranous connection between the radix and the embolus, but in these cases the sperm duct clearly passes through a radix that is produced posteriorly into a conspicuous tailpiece. One advantage of this coding scheme is that characters such as tailpiece shape (Char. 53) are no longer inapplicable for erigonines that previously were considered to have a lamella characteristica. Also, several distally projecting apophyses arising from the "lamella characteristica" of Hormiga (2000) have been coded as anterior radical processes (Char. 55). The presence of an enlargement at the base of the embolus (the embolic basal lobe, Char. 49) in taxa with a lamella or membranous radix-embolus connection could be argued as an instance of conjunction (Patterson, 1982), i.e., the enlarged embolic base is a radical tailpiece, and therefore the plate beyond the membranous region cannot also be a radical tailpiece. Cladistic analyses are supposed to maximize historical explanations of similarity. The lamella-radical tailpiece problem is a case where competing criteria for recognizing similarity can impact the coding of observations. When taxa are coded according to the standards of Merrett (1963) and Hormiga (2000), one tree results. It differs from the tree in Fig. 3 only in the relationships among some of the taxa in clade 28. Specifically, *Neomaso* and *Gigapassus* form a clade sister to *Sisicus* and *Lygarina* and *Hypselocara* form a clade sister to *Onychembolus*.

The effected characters are shown in their recoded form in Appendix E. Future analyses should continue to critically assess this homology problem.

Stemonyphantes is now recoded for an anteriorly directed tailpiece (see also Char. 53). We have optimized parallel origins of the radical tailpiece in erigonines and *Stemonyphantes*, rather than parallel losses in linyphiines and mynoglenines. This is justified because of the unusual form of the tailpiece in *Stemonyphantes*. *Stemonyphantes* is a highly divergent genus and homology assessment of many characters with other linyphiids is difficult. We have normally tried to err on the side of coding structures as homologous, allowing misidentified homology statements to be revealed from the results of the analysis.

53. Radical tailpiece shape: 0, straight (*Spanioplanus*, Fig. 15F); 1, spiralled (*Intecymbium antarcticum*, Fig. 19B; *Grammonota*, Hormiga, 2000, fig. 13F); 2, recurved ventrally (*Mermessus*, Fig. 18F); 3, projecting mesally (*Scolecura*, Fig. 19C); 4, projecting anteriorly (*Notiomaso*, Fig. 18B). Character 22 in Hormiga (2000). The number of states for this character have been reduced from Hormiga (2000) and several taxa recoded. The states "curved ectally" and "pointing anteriorly" have been fused into a single state: "recurved ventrally." The "recurved ventrally" state recognizes shared similarity in the tailpieces of several genera where the main body of the tailpiece arises from the ventral part of the radix and then doubles back, curving in a more or less anterior direction. Both the "curved ectally" and "pointing anteriorly" states were autapomorphic in Hormiga (2000). The addition of new taxa blurred the distinction between the two states. Also, the "curved mesally" character state, designed to accommodate *Leptorhoptrum robustum*, has been dispensed with; the tailpiece of *Leptorhoptrum* is not out of the range of taxa coded for a straight tailpiece. *Tibioploides* is now recoded with a straight tailpiece to account for the posterior enlargement of the radical part of the embolic division (Hormiga, 2000, figs 28A,D,F,H).

Hormiga (2000) coded *Drepanotylus* as absent for the radical tailpiece, but present for the anterior radical process. Both *Drepanotylus* and *Notiomaso* exhibit a blunt anterior projection of the radix and a posterior origin of the embolus. In this study, we coded both *Drepanotylus* and *Notiomaso* as having an anteriorly projecting radical tailpiece and no anterior radical process. Despite their distant relationship in our phylogeny, there are clear similarities in the embolic divisions of *Drepanotylus* and *Notiomaso*, which may be largely responsible for Wunderlich's (1978) proposal that these genera be synonymized (see also Previous groupings revisited, above). We tried coding both *Drepanotylus* and *Notiomaso* according to Hormiga's (2000) assessment: tailpiece (Char. 52) absent; tailpiece shape (Char. 53) inapplicable; anterior radical process (Char. 55) present; anterior radical process type (Char. 56) robust. Under this coding scheme, two trees result. One is identical to the tree in Fig. 3; the other has *Tibioploides* and the *Drepanotylus-Hilaira* clade trading places. Regardless of whether the anterior projections of *Drepanotylus* and *Notiomaso* are called tailpieces or anterior radical processes, they seem to be convergent. This question of terminology remains open to further investigation.

54. Radix texture: 0, smooth (*Mermessus*, Fig. 18F); 1, with striations and/or tubercles (*Microplanus*, Fig. 18C; *Notiomaso*, Fig. 18B).

55. Anterior radical process: 0, absent (*Ostearius*, Hormiga, 2000, pl. 52D; *Neocautinella*, Miller, in press a, fig. 21A); 1, present (*Laminacauda*, Hormiga, 2000, fig. 18C; *Myrmecomelix*, Miller, in press a, fig. 105C). Character 23 in Hormiga (2000). Assessing homology among the various apophyses on the erigonine radix is challenging. The radical anterior process, as currently conceived, is an apophysis originating near and usually ventral to the origin of the embolus. *Hilaira*, *Asthenargus*, *Gongylidiellum*, and *Oedothorax* were recoded as having a radical anterior process because these processes arise from what Hormiga (2000) regarded as the lamella characteristica, not the radix. In *Gonatium*, the structure considered a lamella characteristica by Hormiga (2000) has been recoded as a radical anterior process. In *Tutaibo*, *Ceratinopsis*, and related genera, the process arises near the boundary between the embolus and the radix. It is sometimes unclear whether the process arises from the radix, the embolus, or bridges the boundary between these structures. It is possible that several similar but non-homologous structures are confused in this character. This is a highly homoplasious character. Several ambiguous optimizations are resolved to preserve the homology of the anterior radical process, with parallel losses favored over secondary origin wherever possible (Figs 6, 7).

56. Anterior radical process type: 0, robust (*Tmeticus*, Hormiga, 2000, fig. 29E; *Myrmecomelix*, Miller, in press a, fig. 105C); 1, flagelliform (*Asemostera*, Fig. 15A; *Gonatium*, Hormiga, 2000, "LC" in fig. 10F). The presence of a flagelliform apophysis of the radix unites *Gonatium* and *Asemostera* (clade 69). The *Gonatium-Asemostera* relationship is well supported regardless of whether or not this character is included, hence homology of the flagelliform apophyses seems credible. However, we have less confidence that the flagelliform apophysis is a modification of the radical anterior process. Hormiga (2000) coded this flagelliform apophysis of *Gonatium* as a lamella characteristica (see Char. 52). The flagelliform apophysis of *Gonatium* is unlike any lamella characteristica known in linyphiids and optimizes as an independent origin of the lamella when coded as one. Further work on this problem will require the examination of putative relatives of *Gonatium* and *Asemostera*.

57. Anterior tooth of radix: 0, absent (*Neomaso*, Fig. 18A); 1, present (*Mermessus*, Fig. 18F). In their discussion of *Erigone* Audouin 1826 and related genera, Crosby and Bishop (1928) identified three "teeth" arising from the radix (scaphium in their terminology): anterior, median, and posterior. The posterior and median teeth are equivalent to the tailpiece and radical anterior process, respectively. The anterior tooth anterior tooth arises near to and above the origin of the embolus. It is often recognized by its striated or squamate texture.

58. Mesal tooth of radix: 0, absent (*Neomaso*, Fig. 18A); 1, present (*Spanioplanus*, Fig. 15F; *Mermessus*, Fig. 18F). In their discussion of *Erigone* and related genera, Crosby and Bishop (1928) described and illustrated the mesal tooth, an anteriorly directed, often curved process arising from the dorsal part of the radix well posterior to the origin of the embolus.

59. Distal lobe of radix: 0, absent (*Laminacauda*, Hormiga, 2000, fig. 18C; *Smermisia*, Miller, in press a, fig. 65A); 1, present (*Spanioplanus*, Figs 15F, 17B). The embolic divisions of *Asthenargus*, *Gongylidiellum*, and *Spanioplanus* (clade 36) are all similar in shape. The distal lobe is a broad, blunt process of the radix dorsal to the origin of the embolus and the anterior radical process.

60. Radical ridge: 0, absent (*Grammonota*, Hormiga, 2000, pl. 31A; *Sphecozone bicolor*, Miller, in press a, fig. 158A); 1, present (*Ceratinopsis interpres*, Fig. 19A, *Intecymbium antarcticum*, Fig. 19B). A ridge runs along the ventrodistal part of the radix in some erigonines. The ridge usually has a short, wide region proximally, but a narrow part may run along the radix for some distance. The ridge sometimes has a more or less serrate edge.

61. Radix median excavation: 0, absent (*Notiomaso*, Miller, in press a, fig. 79A); 1, present (*Microplanus*, Fig. 18C, *Mermessus*, Fig. 18F). The presence of an excavation provides unambiguous support for clade 41; its loss provides unambiguous support for clade 48.

62. Radix median excavation orientation: 0, ventral (*Microplanus*, Fig. 18C); 1, prolateral (*Mermessus*, Fig. 18F). The genera *Erigone*, *Mermessus*, and some of their relatives share a radix that is excavated ventrally or prolaterally.

63. Sperm duct in radix: 0, short (*Valdiviella*, Miller, in press a, fig. 35C); 1, very long (*Asemostera*, Fig. 17F). In most linyphiids, the path of the sperm duct through the radix on the way to the embolus is very short. In some genera, the path is dramatically longer, extending at least half the length of the entire palp.

64. Fickert's gland: 0, absent; 1, present (*Tenuiphantes*, Hormiga, 1994a, fig. 14A,B). Character 24 in Hormiga (1993), (1994a); 30 in Hormiga (1994b); 25 in Hormiga (2000); 15 in Hormiga (2002). The presence of this structure supports Micronetini (clade 9).

65. Terminal apophysis: 0, absent; 1, present (*Bolyphantes*, Hormiga, 1994a, fig. 12B). Character 23 (table 1) in Coddington (1990b); 25 in Hormiga (1993, 1994a); 31 in Hormiga (1994b); 22 in Scharff and Coddington (1997); 26 in Hormiga (2000); 35 in Hormiga (2003). The presence of this apophysis supports Linyphiinae (clade 7).

66. Lamella characteristica: 0, absent (*Spanioplanus*, Fig. 17B); 1, present (*Tenuiphantes*, Hormiga, 2000, pl. 5A–C; *Sisicus*, Hormiga, 2000, fig. 26D). Character 26 in Hormiga (1993, 1994a); 32 in Hormiga (1994b); 27 in Hormiga (2000); 23 in Hormiga (2002). See Char. 52. The presence of this sclerite supports Linyphiinae (clade 7) with an independent origin in *Sisicus*.

67. Palpal tibia of male, prolateral apophysis: 0, absent (*Leptorphorum*, Hormiga, 2000; Fig. 19B; *Neocautinella*, Miller, in press a, fig. 21D); 1, present (*Mermessus rapidulus*, Miller in press a, fig. 96E; *Sphecozone rubescens*, Miller, in press a, fig. 144B). Character 27 in Hormiga (1993, 1994a); 33 in Hormiga (1994b); 28 in Hormiga (2000). The origin of this apophysis provides unambiguous support for Erigoninae exclusive of *Leptorhoptrum* (clade 13). Loss of this apophysis could provide ambiguous support for clade 32 with a secondary origin in *Lygarina*, but we have mapped the character on the cladogram as having undergone independent losses in *Smermisia* and *Hypselocara* Millidge (1991). This preserves the homology of the prolateral apophysis across the entire cladogram, attributing all homoplasy to loss of the apophysis.

Establishing homologies among the various tibial apophyses is a major problem of erigonine systematics. Individual species may present several distinct apophyses. Most erigonines exhibit at least one tibial apophysis with a median or prolateral origin; this is the prolateral tibial apophysis (PTA, Char. 67). In some erigonine taxa, the prolateral apophysis is accompanied by a retrolateral apophysis (RTA, Char. 70). In most cases, the sole tibial apophysis is the prolateral apophysis. However, in some haplotracheate erigonines (e.g., *Neocautinella*; Fig. 15B) the retrolateral apophysis is present, but the prolateral apophysis is reduced or absent. The prolateral tibial apophysis is rotated retrolaterally in other erigonines (e.g., *Dismodicus* Simon, 1884, *Grammonota* Emerton, 1882). In some taxa (e.g., *Anodoration* Millidge, 1985, Rhabdogyna Millidge, 1991, *Triplogyna* Millidge, 1991), a third tibial apophysis arises from the distal part of the tibia on the retrolateral side. Unlike other tibial apophyses, this third apophysis does not seem to be an extension of the outer part of the tibia. Instead, it arises from the smooth, membranous tissue at the anterior part of the tibia close to where it connects to the cymbium and is called the distal tibial apophysis. A small number of linyphiids present a ventral tibial

apophysis (e.g., *Stemonyphantes*, *Erigone*, *Parapelecopsis* Wunderlich 1992; Char. 72); this character was included in some previous analyses of linyphiid relationships (Hormiga, 1993, 1994b). We have hardly begun to capture the variability of form in the palpal tibia. For several taxa in the analysis, alternative codings can be argued. Further exploration of homologies among various tibial apophyses is required. Hormiga (2000) concluded that the origin of a prolateral tibial apophysis supported Erigoninae; we find that it supports Erigoninae exclusive of *Leptorhoptrum* (clade 13).

68. Palpal tibia of male, prolateral apophysis initial orientation: 0, perpendicular (*Drepanotylus*, Hormiga, fig. 8B; *Gonatoraphis*, Miller, in press a, fig. 182B); 1, distal (*Diplocephalus*, Hormiga, 2000, fig. 6C; *Mermessus rapidulus*, Miller in press a, fig. 96E). In most prolateral tibial apophyses, the apophysis is oriented distally, roughly in line with the axis of the palp. In some taxa, the apophysis arises perpendicular to the axis of the palp, although it may curve distally near its tip.

69. Palpal tibia of male, distal tooth on prolateral apophysis: 0, absent (*Drepanotylus*, Hormiga, 2000, fig. 8B; *Tutaibo*, Miller, in press a, fig. 140B); 1, present (*Gonatoraphis*, Fig. 16C). A tooth-like process occurs on the distal surface of the prolateral tibial apophysis in members of clade 74.

70. Palpal tibia of male, retrolateral apophysis: 0, absent (*Hilaira*, Hormiga, 2000, fig. 14A; *Mermessus rapidulus*, Miller in press a, fig. 96E); 1, present (*Neocautinella*, Fig. 15B, *Rhabdogyna*, Fig. 19D, *Ostearius*, Hormiga, 2000, pl. 52A). Character 13 in Griswold (1990); 48 in Platnick et al. (1991b); 62 in Jocqué (1991); 1 in Griswold (1993); 9 in Pérez-Miles et al. (1996); 1 in Bond and Opell (1997); 7 in Davies (1998); 94 in Griswold et al. (1999); 17 in Miller (1999); 31 in Bertani (2001); 125 in Bosselaers and Jocqué (2002); 44 in Davies and Lambkin (2001); 12 in Silva Dávila (2003); 42 in Ramírez (2003). See Char. 67.

71. Palpal tibia of male, distal tibial apophysis: 0, absent (*Lygarina*, Miller, in press a, fig. 69D); 1, present (*Rhabdogyna*, Fig. 19D; *Triplogyna*, Miller, in press a, fig. 5B). See Char. 67.

72. Palpal tibia of male, ventral tibial process: 0, absent (*Mermessus rapidulus*, Miller, in press a, fig. 96B); 1, present (*Parapelecopsis*, Hormiga, 2000, pl. 54A; *Dolabritor*, Miller, in press a, fig. 178B). Character 3 in Griswold (1993); 27 in Hormiga (1993); 33 in Hormiga (1994b); 4 in Silva Dávila (2003). This character revives the ventral apophysis character state assigned to *Stemonyphantes* in some previous analyses. Superficially similar apophyses are found in *Dolabritor*, *Erigone*, and *Parapelecopsis*. None of the three origins support any clade in the context of this analysis.

73. Palpal tibia of male, prolateral trichobothria: 0, two (*Leptorhoptrum*, Hormiga, 2000, fig. 19B); 1, one (*Rhabdogyna*, Fig. 19D; *Triplogyna*, Miller, in press a, fig. 3G); 2, zero (*Sisicus*, Hormiga, 2000, fig. 26E; *Hypselocara*, Miller, in press a, fig. 74C; *Sphecozone rubescens*, Miller in press a, fig. 155F). Character 29 in Hormiga (1993, 1994a, 2002); 35 in Hormiga (1994b); 30 in Hormiga (2000); 19 in Agnarsson (2004). *Steatoda* was incorrectly coded in past analyses as lacking prolateral trichobothria (Hormiga, 2000), and is corrected here.

74. Palpal tibia of male, retrolateral trichobothria: 0, four; 1, three (*Leptorhoptrum*, Hormiga, 2000, fig. 19A); 2, two (*Triplogyna*, Miller, in press a, fig. 3G); 3, one (*Lygarina*, Miller, in press a, fig. 68C). Character 30 in Hormiga (1993, 1994a, 2002); 36 in Hormiga (1994b); 31 in Hormiga (2000).

75. Palpal patella of male, ventral apophysis: 0, absent (*Mermessus rapidulus*, Miller, in press a, fig. 96B); 1, present (*Hylyphantes*, Hormiga, 2000, fig. 16C). Character 18 in Miller (1999); 29 in Hormiga (2000).

76. Palpal patella length in male: 0, short, less than twice as long as wide (*Neocautinella*, Miller, in press a, fig. 20A); 1, long, more than 2.1 times longer than wide (*Gonatoraphis*, Miller, in press a, fig. 181C). Character 1 in Hormiga (2002). In some erigonines and outgroups, the male palpal tibia is relatively long, expressed as a ratio or maximum length to maximum height. Drawing boundaries for continuous characters such as ratios is somewhat arbitrary, but there seems to be a relatively clear break between taxa with a length to height ratio of 2.1 or greater and those with a shorter palpal patella. Only one or two specimens of each species were measured for this character and no attempt was made to take intraspecific variation into account.

77. Palpal patella distal dorsal macroseta in male: 0, present; 1, absent.

78. Palpal patella distal dorsal macroseta strength: 0, weak to moderate (*Gongylidiellum*, Wiehle, 1960, figs 914, 915; *Intecymbium*, Miller, in press a, fig. 166B; *Neomaso*, Miller, in press a, fig. 78A); 1, very strong (*Pseudotyphistes*, Fig. 19E; *Stemonyphantes*, Wiehle, 1956, figs 466, 467; *Bolyphantes* Hormiga, 2000, 1994a, fig. 12A; *Toltecaria*, Miller, in press a, fig. 112B). Character 4 in Scharff and Coddington (1997). The distal dorsal macroseta in the male palpal patella is usually relatively strong. In some cases, it is extremely strong. In a few taxa, this seta is absent.

Epigynum

79. Epigynum dorsal plate scape: 0, absent (*Sphecozone crassa*, Fig. 19F); 1, present (*Linyphia*, Hormiga, 2000, pl. 8D; *Sisicus*, Hormiga, 2000, pl. 77E,F). Character 32 in Hormiga (2000); 33 in Hormiga (2002); 41 in Hormiga (2003); 40 in Hormiga et al. (2003). *Sisicus*

has been recoded from Hormiga (2000) as having a dorsal plate scape, not a ventral plate scape (Hormiga, 2000, pl. 77E,F). *Tetragnatha* is inapplicable for epigynal characters because it is secondarily haplogyne. The presence of a dorsal plate scape supports Linyphiini (clade 8) with an additional origin in *Sisicus*.

80. Epigynum dorsal plate anterior lobe: 0, absent (*Neocautinella*, Miller, in press a, fig. 21F); 1, present (*Sphecozone crassa*, fig. 19F). This is a region of the dorsal plate flanked by the copulatory openings and set of from the posterior part of the dorsal lobe by a constriction or fold.

81. Epigynum ventral plate scape: 0, absent (*Sphecozone crassa*, Fig. 19F); 1, present (*Valdiviella*, Fig. 20A). Character 28 in Scharff and Coddington (1997); 33 in Hormiga (2000); 34 in Hormiga (2002); 42 in Hormiga (2003); 41 in Hormiga et al. (2003). The ventral plate scape projects posteriorly from the epigynum and does not conduct the copulatory ducts. It is equivalent to the pseudoscape of Millidge (1984a, p. 235). In some taxa, the scape arises from near the interface between the dorsal and ventral plates, so its anatomical origin is unclear. Contrary to Millidge, 1984a) classification scheme, *Notiomaso* may carry a socket on the ventral side of the scape (Miller, in press a, fig. 47F). *Ostearius* has been recoded from Hormiga (2000) as lacking a scape (Miller, in press a, fig. 9I); *Typhochrestus* has been recoded as having a scape (*Typhochrestus*, Hormiga, 2000, pl. 70F).

82. Epigynum ventral plate scape form: 0, straight (*Valdiviella*, Fig. 20A); 1, sigmoid (*Tenuiphantes*, pl. 6D). Character 34 in Hormiga (2000); 43 in Hormiga (2003). The sigmoid form scape provides ambiguous support for Micronetini (clade 9).

83. Epigynum length: 0, protruding less than its width (*Sphecozone crassa*, Fig. 19F); 1, protruding much more than its width (*Gravipalpus*, Fig. 17I; *Anodoration*, Miller, in press a, fig. 26E). Character 38 in Hormiga (1994b); 53 in Harvey (1995); 19 (in part) in Miller (1999); 31 in Hormiga (2002). In most erigonines, the epigynum projects only slightly out from the abdomen. In a few erigonines and also most pimoids, the epigynum is greatly elongated. The elongate epigynum is related to the type II "scape" of Millidge (1984a), although Millidge also included epigyna that were hardly elongated at all (e.g., *Asthenargus*). This was continued in Millidge's taxonomic treatment of some Neotropical genera, including *Laminacauda* and *Neomaso*, which usually have short epigyna (Millidge, 1985).

84. Epigynum shape: 0, entire (*Sphecozone crassa*, Fig. 19F); 1, bifid (*Fissiscapus*, Millidge, 1991, figs 592–595). The epigyna of *Scolecura*, *Labicymbium*, and *Fissiscapus* are bifid with the copulatory ducts traveling down distinct projections. The presence of a bifid epigynum supports clade 49. A bifid epigynum is also found in *Scolecura*.

85. Epigynum ventral plate texture: 0, smooth (*Intecymbium antarcticum*, Fig. 20B); 1, striated (*Erigone*, Roberts, 1993, fig. 44D). The ventral plates of *Erigone*, *Paraletes*, and *Myrmecomelix* (clade 45) have a series of transverse striations. The wrinkled base of some *Pseudotyphistes* species is coded here with the striated character state.

86. Epigynum ventral plate posterior margin: 0, unmodified (*Intecymbium antarcticum*, Fig. 20B); 1, rebordered (*Erigone*, Roberts, 1993, fig. 44D). A rebordered posterior margin of the ventral plate supports clade 46, with an additional occurrence coded in *Mermessus rapidula*.

87. Copulatory opening: 0, at junction of dorsal and ventral plate (*Sphecozone crassa*, Fig. 19F; *Valdiviella*, Fig. 20A); 1, formed from ventral plate envelope (*Gravipalpus*, Fig. 17I). In nearly all taxa with a dorsal plate, the copulatory openings are formed from the invagination of the dorsal and ventral plates. However, in a few taxa, the ventral plate carries the copulatory duct beyond the dorsal plate in an envelope formed from the ventral plate alone.

88. Epigynum ventral plate anterior process: 0, absent (*Sphecozone crassa*, Fig. 19F); 1, present (*Intecymbium antarcticum*, Fig. 20B). This is a process of the ventral plate arising from the anterior part of the epigynum.

89. Epigynum ventral plate socket: 0, absent (*Sphecozone crassa*, Fig. 19F); 1, present (*Tenuiphantes*, Hormiga, 2000, pl. 6D). Character 30 in Scharff and Coddington (1997); 43 in Hormiga et al. (2003). The presence of this socket supports Micronetini (clade 9) with three additional origins on the cladogram.

90. Epigynum dorsal plate socket: 0, absent (*Sphecozone crassa*, Fig. 19F); 1, present (*Linyphia*, Wiehle, 1956, fig. 509). Character 35 in Hormiga (2002); 42 in Hormiga et al. (2003). Millidge (1984a) described the occurrence of sockets on both the ventral and dorsal plates. These characters are particularly important for understanding relationships among non-erigonine genera. The dorsal plate socket supports Linyphiini (clade 8).

91. Epigynal bisection: 0, absent (*Sphecozone crassa*, Fig. 19F); 1, present (*Diplocephalus*, Hormiga, 2000, pl. 21D). Character 35 in Hormiga (2000). The presence of an epigynal bisection supports clade 58 with a reversal in *Dismodicus*.

92. Atrium: 0, absent (*Intecymbium antarcticum*, Fig. 20B); 1, present (*Sphecozone crassa*, Fig. 19F). Character 33 in Hormiga (1993, 1994a); 48 in Hormiga (1994b); 36 in Hormiga (2000); 39 in Hormiga (2002); 44 in Hormiga (2003); 48 in Hormiga et al. (2003). *Laminacauda* and *Ostearius* were recoded from Hormiga (2000) as present for an atrium.

93. Epigynum dorsal plate orientation: 0, position of dorsal plate entirely dorsal to ventral plate (*Valdiviella*, Fig. 20A); 1, dorsal plate extends anteriorly, flush with ventral plate (*Intecymbium antarcticum*, Fig. 20B; *Oedothorax*, Hormiga, 2000, pl. 50F). The dorsal plate of the erigonine epigynum (viewed *in situ*) is typically visible only in posterior view. The dorsal plate is sometimes revealed in ventral view by the invagination of the ventral plate but, in most cases, the revealed dorsal plate is deeper in the abdomen than the surface of the ventral plate. In some erigonines, the dorsal plate is more prominent in ventral view with both plates together forming the ventral surface of the epigynum.

94. Copulatory duct: 0, separate from fertilization duct (*Diplocentria*, Hormiga, 2000; Fig. 5H; *Lygarina*, Miller, in press a, fig. 68I); 1, spirals around fertilization duct (*Stemonyphantes*, van Helsdingen, 1968, figs 28, 29). Character 37 in Hormiga (2000); 45 in Hormiga (2003); 51 in Hormiga et al. (2003).

95. Copulatory duct encapsulation: 0, absent (*Gongylidiellum*, Hormiga, 2000, fig. 11F–H); 1, present (*Laminacauda*, Hormiga, 2000, fig. 18D–F). Character 38 in Hormiga (2000).

96. Internal membrane: 0, absent (*Gravipalpus*, Fig. 17I); 1, present (*Sphecozone spadicaria*, Miller, in press a, fig. 150D). This is a membranous, anteriorly directed part of the internal female genitalia.

97. Spermathecae: 0, two (*Gravipalpus*, Fig. 17I); 1, four (*Ostearius*, Hormiga, 2000, figs 22G,H). Character 26 in Griswold et al. (1998); 39 in Hormiga (2000); 47 in Hormiga (2003); 10 in Agnarsson (2004).

98. Spermathecae shape: 0, round to slightly oblong (*Gravipalpus*, Fig. 17I); 1, strongly oblong (*Sphecozone rubescens*, Miller, in press a, fig. 114F). Spermathecae range from being round or slightly oblong to distinctly elongate. The dividing line between these character states is somewhat arbitrary. Probably no spermathecae are perfectly spherical. Oblong spermathecae are defined as having the interior at least two and a half times as long as wide whereas round spermathecae are less than twice as long as wide. Some spermathecae may be more or less curved. In these cases, dimensions are evaluated along the curve, as though the spermathecae had been straightened out. In some cases, coding was hindered by the absence of a clear boundary between the spermathecae and the origin of the copulatory ducts.

99. Fertilization duct orientation: 0, posterior (*Gravipalpus*, Fig. 17I); 1, mesal (*Anodoration*, Miller, in press a, fig. 25F); 2, anterior (*Pimoa*, Hormiga, 1994b, figs 12–14); 3, dorsal (*Rhabdogyna*, Fig. 21A). Character 40 in Griswold (1993), 40 in Hormiga (2000); 41 in Hormiga (2002); 48 in Hormiga (2003); 53 in Hormiga et al. (2003). A new character state, dorsal orientation of the fertilization ducts, has been added to accommodate *Rhabdogyna* and *Scolecura*.

100. Copulatory ducts and fertilization ducts: 0, arise from separate parts of spermathecae (*Gravipalpus*, Fig. 17I); 1, share common duct proximally (*Laminacauda*, Hormiga, 2000, fig. 18F; *Triplogyna*, Miller, in press a, fig. 3C). The copulatory ducts and fertilization ducts nearly always arise independently from the spermathecae. In *Triplogyna* and at least some *Laminacauda* (clade 18), the copulatory ducts and fertilization ducts share a common duct for the first part of their length. This character is inapplicable to the secondarily haplogyne genus *Tetragnatha*.

Prosoma and legs

101. Cephalic region in male: 0, not raised (*Tapinocyba*, Hormiga, 2000, fig. 32A; *Smermisia*, Miller, in press a, fig. 67A); 1, raised (*Araeoncus*, Hormiga, 2000, fig. 32B; *Psilocymbium*, Miller, in press a, fig. 175E). Character 21 in Platnick et al. (1991b); 48 in Scharff and Coddington (1997); 35 in Miller (1999); 41 in Hormiga (2000); 2 in Schütt (2003).

102. Cephalic PME lobe in male: 0, absent (*Smermisia*, Miller, in press a, fig. 67A); 1, present (*Entelecara*, Hormiga, 2000, fig. 32F; *Dolabritor*, Miller, in press a, fig. 179A). Character 42 in Hormiga (2000).

103. Cephalic post-PME lobe in male: 0, absent (*Smermisia*, Miller, in press a, fig. 67A); 1, present (*Oedothorax*, Hormiga, 2000, fig. 32J; *Triplogyna*, Miller, in press a, fig. 7B). Character 36 in Miller (1999); 43 in Hormiga (2000); 49 in Hormiga (2003).

104. Cephalic inter AME-PME lobe in male: 0, absent (*Smermisia*, Miller, in press a, fig. 67A); 1, present (*Walckenaeria*, Hormiga, 2000, pl. 76A). Character 44 in Hormiga (2000). This character is phylogenetically uninformative in the current analysis.

105. Cephalic clypeal lobe in male: 0, absent; 1, present (*Dismodicus*, Crosby and Bishop, 1933, fig. 166). Character 45 in Hormiga (2000). This character is phylogenetically uninformative in the current analysis.

106. Cephalic AME lobe in male: 0, absent; 1, present (*Diplocephalus*, Roberts, 1993, fig. 39G). Character 46 in Hormiga (2000). This character is phylogenetically uninformative in the current analysis.

107. Cephalic sulci of subocular clypeus in male: 0, absent (*Smermisia*, Miller, in press a, fig. 67A); 1, present (*Haplinis*, Hormiga, 2000, pl. 4A–D). Character 34 in Hormiga (1993, 1994a); 49 in Hormiga (1994b); 47 in Hormiga (2000); 50 in Hormiga (2003). The presence of subocular sulci supports Mynogleninae (clade 11) with an additional origin in *Hypselocara* (Miller, in press a, figs 76A,D).

108. Cephalic sulci on sides of male prosoma: 0, absent (*Smermisia*, Miller, in press a, fig. 67A); 1, present (*Ceratinops*, Hormiga, 2000, pl. 17A,E; *Tapinocyba*,

Hormiga, 2000, pl. 70A,C). Character 48 in Hormiga (2000); 51 in Hormiga (2003).

109. Cephalic pits in male: 0, absent (*Smermisia*, Miller, in press a, fig. 67A); 1, present (*Dolabritor*, Miller, in press a, figs 179A,C). Character 49 in Hormiga (2000).

110. Cephalic cuticular pores in male: 0, rare; 1, common (*Laminacauda*, Hormiga, 2000, pl. 43; *Psilocymbium*, Miller, in press a, fig. 175D). Character 50 in Hormiga (2000). Hormiga (2000) noted that the presence of a small number of cuticular pores was common in linyphiids, but that a dense field of pores was more unusual. We have rephrased the states for this character to reflect the dichotomy between rare and common, rather than absent and present. The coding of this character was difficult for some taxa. In some specimens, dirt may have obscured pores from view. For example, in *Gonatoraphis*, the female was found to have a dense field of pores although few pores were observed in the male. Recoding *Gonatoraphis* for the presence of pores makes no difference to the topological results.

111. Prosoma setae in female: 0, hirsute (*Steatoda*, Knoflach, 1996, figs 8–10); 1, setae absent or very rare (*Theridiosoma*, Coddington, 1986b, figs 139), 2, setae sparse, restricted to radii and lateral margins of thorax (*Erigone*, Hormiga, 2000, pl. 26E); 3, only a sparse patch in center of thorax (*Lygarina*, Fig. 20C); 4, head region with broad field of setae (*Asemostera*, Fig. 21B; *Parapelecopsis*, Hormiga, 2000, pl. 55D). In pimoids and most linyphiids, there is a single row of setae between the PMEs and the thoracic apodeme with several rows of sparse setae radiating out from the center of the thorax and around the lateral margin. A few erigonines exhibit a broad field of setae covering the head region. In *Steatoda* and *Tetragnatha*, the entire prosomoa is evenly hirsute, but in *Theridiosoma* there are few thoracic setae forming no clear pattern. *Lygarina* has a unique form with a sparse patch in the middle of the thorax.

112. Clypeus texture in male: 0, nearly smooth (*Diplocephalus*, Hormiga, 2000, pl. 20; *Sphecozone bicolor*, Miller, in press a, fig. 159A); 1, squamate (*Laminacauda*, Hormiga, 2000, pl. 43; *Scolecura*, Miller, in press a, fig. 18D). In most erigonines, the clypeus has a scaly, squamate texture; in some it may approach reticulate (e.g., *Tibioploides*, Hormiga, 2000, pl. 66B; *Gonatoraphis*, Miller, in press a, fig. 183A).Other erigonines have an almost smooth clypeus, although there may be some vestige of texture visible.

113. Clypeal setae in female: 0, hirsute (*Bolyphantes*, Hormiga, 2000, pl. 2A); 1, only one seta below the AMEs (*Laminacauda*, Hormiga, 2000, pl. 44A,B; *Anodoration*, Miller, in press a, fig. 27A). Reduction in the number of setae on the clypeus is synapomorphic for erigonines plus mynoglenines (clade 10) with eight reversals in erigonines.

114. Thoracic furrow: 0, nearly smooth, often recognizable only from pigment, not invagination (*Lygarina*, Fig. 20C; *Tapinocyba*, Hormiga, 2000, pl. 64C); 1, thoracic furrow a distinct invagination (*Pimoa*, Hormiga, 1994b, fig. 356). Character 35 in Jocqué (1991); 15 in Gray (1995); 20 in Bond and Opell (1997); 23 in Ramírez and Grismado (1997); 8 in Ramírez (2003); 7 in Schütt (2003); 68 in Silva Dávila (2003). Many araneoids have a distinct furrow indicating the thoracic apodeme. In erigonines this furrow is greatly reduced or completely absent, often indicated only by pigmentation. The furrow is widespread in nonerigonine linyphioids, especially larger spiders including *Neriene radiata* (Walckenaer, 1842), *Labulla thoracica* (Wider, 1834), *Orsonwelles polites* Hormiga, 2002, *Pityohyphantes costatus* (Hentz, 1850), *Wientrauboa contortipes* (Karsch, 1881), *Stemonyphantes sibiricus* (Grube, 1861), and *Haplinis titan* (Blest, 1979); it is absent from *Frontinella communis* Hentz, 1850. There may be an allometric component to this character, large spiders tending to have well-developed furrows to accommodate larger muscles. However, the largest erigonine, *Laminacauda gigas* Millidge, 1991 (6.5–9.9 mm; Millidge, 1991, pp. 77–78), lacks the furrow.

115. Chelicerae size: 0, subequal in males and females (*Gongylidiellum*, Hormiga, 2000, pl. 28F; *Microplanus*, Miller, in press a; figs 109D,E); 1, larger in males (*Tmeticus*, Hormiga, 2000, pl. 68A,B). Character 15 in Hormiga et al. (1995); 33 in Scharff and Coddington (1997); 33 in Griswold et al. (1998); 36 in Huber (2000); 17 in Ramírez (2003); Schütt (2003); 113 in Agnarsson (2004). Although cheliceral size is usually almost equal in males and females, in a few taxa, the chelicerae are greatly enlarged in the male.

116. Cheliceral lateral face in male: 0, smooth; 1, stridulatory striae (*Gongylidiellum*, Hormiga, 2000, pl. 29A–C). Character 36 in Hormiga (1993, 1994a); 52 in Hormiga (1994b); 2 in Hormiga et al. (1995); 44 in Scharff and Coddington (1997); 37 in Griswold et al. (1998), 55 in Hormiga (2000), 43 in Hormiga (2002); 54 in Hormiga (2003); 55 in Hormiga et al. (2003). The presence of cheliceral striae supports "linyphioids" (clade 3).

117. Cheliceral stridulatory striae in male: 0, ridged (*Laminacauda*, Hormiga, 2000, pl. 42E; *Sphecozone crassa*, Miller, in press a, fig. 163E); 1, scaly (*Oedothorax*, Hormiga, 2000, pl. 49E; *Psilocymbium*, Miller, in press a, fig. 175C); 2, imbricated (*Islandiana*, Hormiga, 2000, pl. 39E; *Mermessus*, Miller, in press a, fig. 94C). Character 56 in Hormiga (2000); 44 in Hormiga (2002); 55 in Hormiga (2003); 56 in Hormiga et al. (2003).

118. Cheliceral stridulatory striae rows in male: 0, widely and evenly spaced (*Diplocephalus*, Hormiga, 2000, pl. 19E; *Smermisia*, Miller, in press a, fig. 67B); 1, compressed proximally (*Gongylidiellum*, Hormiga,

2000, pl. 29A,B; *Valdiviella*, Miller, in press a, fig. 38A); 2, compressed distally (*Ceratinops*, Hormiga, 2000, pl. 16A,B); 3, compressed and evenly spaced (*Erigone*, Hormiga, 2000, pl. 25B,C; *Tibioploides*, Hormiga, 2000, 65D,E; *Tutaibo*, Miller, in press a, fig. 141B); 4, compressed proximally and distally, widely spaced centrally (*Bolyphantes*, Hormiga, 2000, pl. 1E). There is considerable variation in the arrangement of stridulatory striae on the male chelicerae. Mynoglenines and some basal erigonines have many ridges very closely and evenly spaced. Most erigonines seem to have evenly spaced ridges, but these are fewer in number and widely spaced. Some linyphiids have either the proximal or the distal ridges more closely spaced; in *Bolyphantes*, the proximal and distal ridges are closely spaced with the central region widely spaced. Arrangement of the stridulatory striae may vary greatly even within genera (van Helsdingen et al., 1977). Some species demonstrate sexual dimorphism in the stridulatory striae (e.g., *Walckenaeria*, Millidge, 1983, figs 308, 309, *Ceratinops*, Hormiga, 2000, pl. 16A–C. *Laminacauda*, Hormiga, 2000, pl. 42E,F, *Typhochrestus*, Hormiga, 2000, pl. 69E,F).

119. Cheliceral stridulatory striae ridges: 0, absent (*Diplocephalus*, Hormiga, 2000, pl. 19E); 1, present (*Sisicottus*, Miller, 1999, fig. 10; *Ceratinops*, Hormiga, 2000, pl. 16B; *Notiomaso*, Miller, in press a, fig. 48F). In a few erigonines, auxiliary ridges can be found on the plates that make up the stridulatory striae.

120. Cheliceral setal bases on front-lateral face in male: 0, nearly flush with chelicerae to small bumps (*Sisicus*, Hormiga, 2000, pl. 61E; *Scolecura*, Miller, in press a, fig. 18C); 1, formed into distinct bumps (*Novafroneta*, Hormiga, 2000, pl. 10E; *Drepanotylus*, Hormiga, 2000, pl. 23E); 2, greatly enlarged and tooth-like (*Erigone*, Hormiga, 2000, pl. 25B; *Mermessus dentiger*, Miller, in press a, fig. 94B). This character divides the variable strength of setal bases on the male cheliceral into three states. In most chelicerae, the setal bases are not distinctly larger than is typical for setae on other parts of the body. In some taxa, the setae have a much more robust base. In other taxa, the setal bases are greatly enlarged and tooth or horn-like. Blest (1979) noted that mynoglenines have a field of tubercles on the lateral faces of the chelicerae and also that while such tubercles are unusual among linyphiids, they are not restricted to mynoglenines.

121. Cheliceral frontal spur in male: 0, absent (*Scolecura*, Miller, in press a, fig. 18A); 1, present (*Gongylidiellum*, Hormiga, 2000, pl. 28F; *Neocautinella*, Miller, in press a, fig. 22A). Character 39 in Miller (1999); 57 in Hormiga (2000); 56 in Hormiga (2003); 57 in Hormiga et al. (2003). Called a dorsal spur in previous work, this apophysis is a greatly enlarged setal base.

122. Cheliceral fang furrow in male: 0, narrow (*Sciastes*, Hormiga, 2000, pl. 60C; *Scolecura*, Miller, in press a, fig. 18A); 1, wide and flat to concave (*Tmeticus*, Hormiga, 2000, pl. 68A; *Neocautinella*, Miller, in press a, fig. 22A). In most spiders, the cheliceral fang furrow is narrow. In some taxa, the chelicerae are modified with the fang furrow flat and wide.

123. Cheliceral teeth, retrolateral margin of fang furrow in female: 0, zero; 1, one; 2, two; 3, three; 4, four or more. Character 58 in Hormiga (2000); 20 in Bosselaers (2002); 46 in Hormiga (2002); 57 in Hormiga (2003); 61 in Hormiga et al. (2003). The presence of two retromarginal teeth provides ambiguous support for linyphioids (clade 3).

124. Sternum-labium attachment: 0, separate; 1, fused (*Haplinis*, Blest, 1979, fig. 409). Character 38 in Platnick et al. (1991b); 24 in Schütt (2003); 135 in Agnarsson (2004). The fusion of the labium to the sternum is a classic characteristic of linyphiids. The symplesiomorphic retention of sternum-labium separation in *Stemonyphantes* contributes to the hypothesis that *Stemonyphantes* is sister to the rest of the linyphiids.

125. Endites of male: 0, smooth (*Tapinocyba*, Hormiga, 2000, pl. 64A); 1, tuberculate (*Triplogyna*, Fig. 20D). Some setal bases on the endites may be greatly enlarged, forming tubercles.

126. Palpal tarsus claw in female: 0, present; 1, absent. Character 52 (table 1) in Coddington (1990b); 37 in Platnick et al. (1991b); 38 in Hormiga (1993, 1994a); 54 in Hormiga (1994b); 53 in Griswold et al. (1998), 59 in Hormiga (2000); 23 (in part) in Schütt (2003); 176 in Agnarsson (2004). Loss of the palpal claw provides unambiguous support for Erigoninae (clade 12).

127. Palpal tarsus proximal dorsomesal macrosetae in female: 0, absent; 1, present.

128. Palpal tarsus distal dorsomesal macrosetae in female: 0, absent; 1, present.

129. Palpal tarsus proximal dorsoectal macrosetae in female: 0, absent; 1, present.

130. Palpal tarsus distal dorsoectal macrosetae in female: 0, absent; 1, present. In linyphiid spiders, there may be two rows of up to two macrosetae each on the dorsal surface of the palpal tarsus. The distal macroseta is never found without the proximal macroseta being present. Distal macrosetae have not been observed in erigonines.

131. Palpal tarsus ventromesal macrosetae in female: 0, zero; 1, two; 2, three (*Triplogyna*, Fig. 21D); 3, four (*Neocautinella*, Fig. 21F); 4, five or six; 5, 11–12.

132. Palpal tarsus ventroectal macrosetae in female: 0, zero; 1, one; 2, two (*Triplogyna*, Fig. 21E); 3, three (*Neocautinella*, Fig. 21G); 4, four. Establishing homologies among ventral macrosetae is more difficult than for dorsal setae, especially among nonerigonines. Ideally, each seta would be treated as a character. This is possible within erigonines, but becomes more difficult

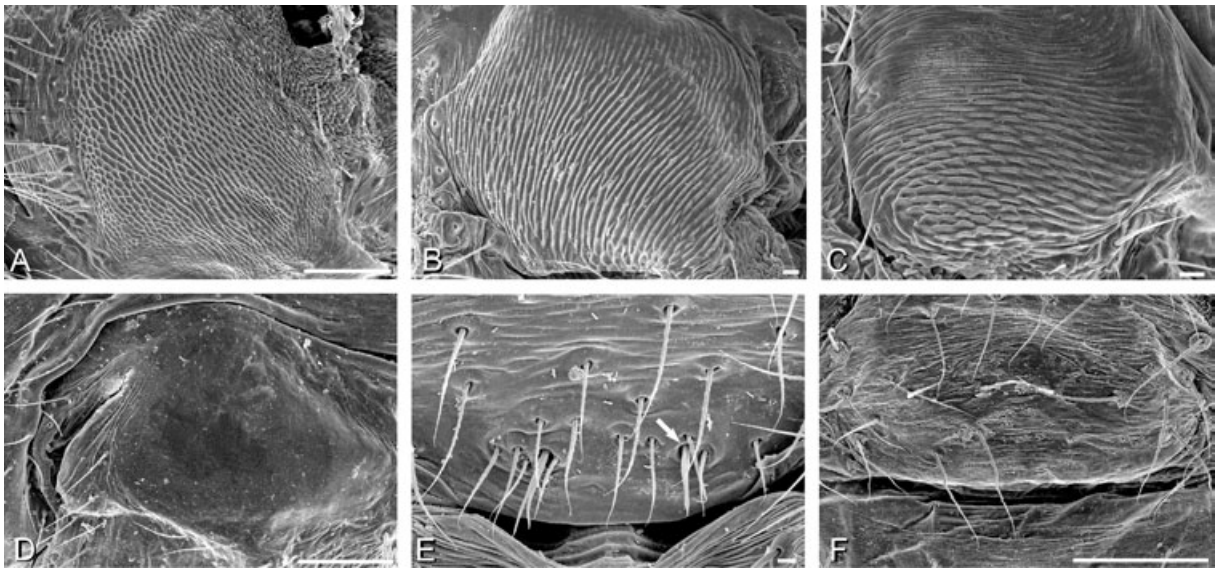

Fig. 22. (A–D) Male booklung cover; (E, F) eipandrous region of male. (A) *Erigone psychrophila*, showing rugose booklung covers. (B) *Gigapassus octarine*, showing grooved booklung covers. (C) *Smermisia vicosana*, showing squamate booklung cover. (D) *Tutaibo phoeniceus*, showing smooth booklung cover. (E) *Stemonyphantes blauveltae*, arrow indicates one of two clusters of epiandrous gland spigots arising from pit. (F) *Leptorhoptrum robustum*, with no eipandrous gland spigots. Scale bars = 10 μm in (B), (C) and (E); 100 μm in other images.

when nonerigonines are considered. Erigonines usually have three ventromesal and two ventroectal macrosetae; when this is not the case, it is usually easy to determine which seta has been lost or which is novel. Erigonines with two ventroectal macrosetae have them positioned quite distally, whereas erigonines with three have the two distal macrosetae plus a proximal seta. When only one is present, the distalmost macroseta is retained. Erigonines have a maximum of four ventroectal macrosetae. Setae 1, 2, and 4 are present in most erigonines, counting distal to proximal; several independent origins of a macroseta in position 3 occur on the cladogram. Most of the nonerigonines in this analysis have far more ventral palpal macrosetae than the erigonines, but we have been unable to determine which macrosetae present in the outgroup are retained in erigonines. Nevertheless, the retention of more macrosetae in *Leptorhoptrum* supports the hypothesis that it is sister to the remaining erigonines.

133. Autospasy: 0, at coxa-trochanter joint; 1, at patella-tibia joint. Character 39 in Hormiga (1993, 1994a); 55 in Hormiga (1994b); 8 in Hormiga et al. (1995); 36 in Scharff and Coddington (1997); 60 in Griswold et al. (1998), 60 in Hormiga (2000); 59 in Hormiga (2003). Patella-tibia autospasy provides unambiguous support for linyphioids (clade 3).

134. Femur I dorsal macroseta(ae): 0, absent; 1, present. Character 59 in Griswold et al. (1998).

135. Femur I prolateral macroseta(ae): 0, absent; 1, present. Character 59 in Griswold et al. (1998). Loss of the prolateral femoral macrosetae provides unambiguous support for Erigoninae (clade 12).

136. Tibia I proximal dorsal macroseta: 0, absent; 1, present.

137. Tibia I distal dorsal macroseta: 0, absent; 1, present.

138. Tibia II proximal dorsal macroseta: 0, absent; 1, present.

139. Tibia II distal dorsal macroseta: 0, absent; 1, present.

140. Tibia III proximal dorsal macroseta: 0, absent; 1, present.

141. Tibia III distal dorsal macroseta: 0, absent; 1, present.

142. Tibia IV proximal dorsal macroseta: 0, absent; 1, present.

143. Tibia IV distal dorsal macroseta: 0, absent; 1, present. Characters 61–64 in Hormiga (2000) have been modified to make more specific homology statements about the individual tibial macrosetae. See also character 62 in Griswold (1993); 2–5 in Bosselaers (2002); 62–65 in Hormiga (2003). The tibial spine formula is a classical character in linyphiid systematics, but it clearly concerns the presence or absence of eight individual macrosetae. There is a potential problem with independence among these characters, because distal macrosetae are never found in the absence of the proximal macrosetae. Also, reductions in macrosetae in one leg may not be independent of reductions in other legs. Absence of the distal dorsal macroseta on tibia IV has been used historically to help circumscribe Erigoninae, although both Hormiga (2000) and the current study found that the loss of this macroseta supports a large

clade of desmitracheate erigonines (39) and a smaller clade of haplotracheate erigonines (31).

144. Tibia I prolateral macroseta(ae): 0, absent; 1, present. Prolateral tibial macrosetae are common among nonerigonine linyphiids and most outgroup families. A prolateral macroseta is found in *Leptorhoptrum*, *Drepanotylus*, *Hilaira*, and *Sciastes*. Loss of these setae supports clade 15.

145. Tibia I retrolateral macroseta(ae): 0, absent; 1, present. Retrolateral tibial macrosetae are found in most linyphiines and outgroup taxa, but the absence thereof is synapomorphic for mynoglenines plus erigonines (clade 10) in this analysis.

146. Tibia I ventral macroseta(ae): 0, absent; 1, present. The presence of these setae supports linyphioids (clade 3); its loss supports clade 10.

147. Metatarsus I dorsal macroseta(ae): 0, absent; 1, present. The presence of these setae provides unambiguous support for Pimoidae (clade 4) and Linyphiinae (clade 7).

148. Metatarsus I prolateral macroseta(ae): 0, absent; 1, present. The presence of these setae provides unambiguous support for Pimoidae (clade 4), and ambiguous support for Linyphiinae (clade 7) with a reversal in *Tenuiphantes*.

149. Metatarsus I retrolateral macroseta(ae): 0, absent; 1, present. As for character 148.

150. Metatarsus I ventral macroseta(ae): 0, absent; 1, present. The presence of these setae support linyphioids (clade 3); their loss supports clade 10.

151. Leg I ventral setae in male: 0, about as strong as other leg setae; 1, distinctly heavier than other leg setae (*Notiomaso*, Fig. 21C). Several erigonine genera have the ventral macrosetae of the tibia, metatarsus, and sometimes other leg segments much stronger than other leg segments. In this analysis, *Notiomaso* and *Gonatium* achieved this state independently.

152. Metatarsus IV trichobothrium: 0, absent; 1, present. Character 40 in Hormiga (1993, 1994a); 57 in Hormiga (1994b); 57 in Harvey (1995); 41 in Miller (1999); 65 in Hormiga (2000); 55 in Hormiga (2002); 66 in Hormiga (2003); 70 in Hormiga et al. (2003); 191 in Agnarsson (2004).

Abdomen and spinnerets

153. Pedicel sternite and pleurites in male: 0, separated (*Mermessus*, Fig. 21H); 1, juxtaposed or fused (*Gonatoraphis*, Fig. 21I). The pedicel is covered by four sclerotized plates: a tergite, a sternite, and two pleurites. In most linyphiids, the pleurites and the sternite are very short and either completely separated by membrane, or fused only at the anterior margin. In some erigonines, the pedicel is longer and more heavily sclerotized, with the sternite and pleurites fused or adjacent to one another for nearly their entire length. There is occasional sexual dimorphism in this character, with the sternite and pleurites juxtaposed in males but separated in females (e.g., *Gonatium*, *Anodoration*).

154. Booklung covers in male: 0, rugose (*Erigone*, Fig. 22A); 1, grooved (*Gigapassus*, Fig. 22B; *Gongylidiellum*, Hormiga, 2000, pl. 29D); 2, squamate (*Smermisia*, Fig. 22C); 3, nearly smooth (*Tutaibo*, Fig. 22D). Character 64 in Scharff and Coddington (1997); 49 in Griswold et al. (1998), 54 in Hormiga (2000). This character replaces character 54 in Hormiga (2000), the coxae IV-booklung stridulatory organ. The original character was difficult to code because many erigonines have some kind of posterior projection of the hind coxae, whether subtle or gross. Inspection of the booklung covers using light microscopy likewise revealed variation, but did not facilitate clear character state definitions. Scanning electron micrographs of the booklung covers revealed four relatively clear character states. Most booklung covers are squamate in texture with many short ridges. In some, these ridges are longer, defining distinct grooves. In others, the ridges are nearly or completely absent, and the booklung cover is smooth. Rarely, there are raised ridges with interconnecting branches forming a rugose network. This character suffers from a relatively large amount of missing data (18 terminals), especially among outgroup taxa.

155. Abdomen of male with dorsal scutum: 0, absent; 1, present. Character 4 in Harvey (1995); 47 in Griswold et al. (1998); 53 in Hormiga (2000); 102 in Bosselaers and Jocqué (2002); 41 in Schütt (2003). This character is phylogenetically uninformative in the current analysis.

156. Abdomen with ventral sclerite anterior to spinnerets: 0, absent; 1, present. The presence of this sclerite supports clade 70 with additional origins in *Sphecozone crassa* and *Intecymbium antarcticum*.

157. Median tracheal trunks: 0, unbranched (Blest, 1976, fig. 1A); 1, branched (*Gonatium*, Hormiga, 1994a, fig. 18A). The presence of branched median trunks provides unambiguous support for Erigoninae (clade 12); the reversal to unbranched trunks provides unambiguous support for clade 19.

158. Median tracheal trunks branching: 0, median tracheae with few branches (*Tibioploides*, Hormiga, 2000, fig. 31A; *Laminacauda*, Hormiga, 2000, fig. 31E; *Triplogyna*, Miller, in press a, fig. 4C); 1, median tracheae highly branched (*Gonatium*, Hormiga, 1994a, fig. 18A). Characters 157 and 158 modified from character 35 in Hormiga (1993, 1994a); 50 in Hormiga (1994b); 51 in Hormiga (2000); 52 in Hormiga (2003); see also 7 (fig. 3), 32 (table 1) in Coddington (1990b); 54 in Griswold et al. (1999); 123 in Silva Dávila (2003). The cladogram implies two independent reductions from highly to sparsely branched median trunks.

159. Median tracheal trunks width: 0, about as wide as laterals (*Triplogyna*, Miller, in press a, fig. 4C); 1, much

wider than laterals (*Gonatium*, Hormiga, 1994a, fig. 18A). The presence of wide median trunks is a component of the desmitracheate system. Although the median trunks are hardly wider than the laterals among the exemplar species of *Laminacauda* in our analysis, some *Laminacauda* species exhibit wide median trunks (Hormiga, 2000, fig. 31G). The presence of wide median trunks provides ambiguous support for Erigoninae (clade 12) with width reductions in *Tibioploides*, *Laminacauda*, and clade 19.

160. Median tracheal trunk length 0, restricted to abdomen (Blest, 1976, fig. 1A); 1, pass through pedicel into prosoma (Blest, 1976, fig. 1C). Character 31 (table 1) in Coddington (1990b). In all erigonines with branched median tracheae, at least one tracheole from each trunk passes through the pedicel into the prosoma. In the haplotracheate genus *Scolecura*, the unbranched median tracheae also enter the prosoma. The extension of the median trunks into the prosoma provides unambiguous support for Erigoninae (clade 12); the secondary restriction of the median trunks to the abdomen supports clade 20.

161. Tracheole taenidia: 0, absent (*Gonatium*, Hormiga, 1994a, fig. 18B); 1, present (*Laminacauda*, Hormiga, 2000, fig. 31G). Character 52 in Hormiga (2000); 53 in Hormiga (2003). The loss of taenidia provides unambiguous support for the "distal erigonines" (clade 39).

Previous analyses (Hormiga, 1993, 1994a,b) coded linyphiid tracheae as haplotracheate (unbranched median trunks) or desmitracheate (many-branched median trunks). Hormiga (2000) added an intermediate condition to accommodate the sparse branching observed in *Tibioploides* and some *Laminacauda*. We divided the tracheal system into several binary characters to explore the variation we observed. First, we scored the presence or absence of branching of the median trunks (Char. 157). We added a new character that describes the amount of branching, either sparse or extensive (Char. 158). We also added a character to contrast the narrow median trunks of most haplotracheate taxa with the enlarged median trunks of most desmitracheate erigonines (Char. 159). Finally, we added a character noting whether the median trunks enter the prosoma, a condition found in most desmitracheate and a few haplotracheate erigonines (Char. 160). Hormiga (2000) found that erigonines were primitively haplotracheate and that the desmitracheate condition characterizes only a large clade of erigonines. He also found that his "intermediate" tracheal condition arose once from a haplotracheate ancestor and once from a desmitracheate ancestor (Fig. 9A). Under equal weights, our analysis implies that the desmitracheate condition is synapomorphic for Erigoninae and that there is secondary reduction and reversal to the haplotracheate condition within the subfamily (Fig. 9B). We found that *Tibioploides* and some *Laminacauda* represent independent reductions from the desmitracheate condition. We also found that *Scolecura*, which has unbranched median tracheae that pass into the prosoma, represents an intermediate condition between desmitracheate erigonines (including *Laminacauda*) and typical haplotracheate erigonines. Under successive character weighting, our results are similar to those of Hormiga (2000) with a basal grade of haplotracheate erigonines (Fig. 9C). As in the equal weights analysis, *Tibioploides* and *Laminacauda* are interpreted to have independent reductions from the desmitracheate condition.

Triplogyna is one of a small number of erigonine genera known to have desmitracheate tracheae with taenidia in the tracheoles. Hormiga (2000) included representatives of six other genera known to exhibit this condition. As our equal weights results indicate that this condition is basal for erigonines, the inclusion of more such taxa in future analyses (e.g., *Donacochara* Simon 1884) is advisable. The discovery of more taxa with this condition would be of value to the study of erigonine evolution.

162. Aciniform gland spigots in female PMS: 0, absent (*Stemonyphantes*, Hormiga, 1994a, fig. 20C); 1, one (*Pseudotyphistes*, Miller, in press a, fig. 54D); 2, two (*Ceratinops*, Hormiga, 2000, pl. 16D; *Triplogyna*, Miller, in press a, fig. 6E); 3, three (*Novafroneta*, Hormiga, 1994a, fig. 21C); 4, four (cf. *Latrodectus* Coddington, 1989, fig. 28). Character 6 in Coddington (1990a); 42 in Hormiga (1993, 1994a); 59 in Hormiga (1994b); 66 in Hormiga (2000); 67 in Hormiga (2003).

163. Minor ampullate nubbin in female PMS: 0, absent (*Tenuiphantes*, Hormiga, 1994a, fig. 28C); 1, present (*Theridiosoma*, Coddington, 1986b, fig. 8). Character 7 in Coddington (1990a); 55 in Hormiga et al. (1995); 72 in Scharff and Coddington (1997); 73 in Griswold et al. (1999); 66 in Hormiga (2000); 220 in Agnarsson (2004). The loss of this nubbin supports clade 2.

164. Mesal cylindrical gland spigot base on female PLS: 0, same size as other CY (*Theridiosoma*, Coddington, 1986b, fig. 9); 1, enlarged (*Novafroneta*, Hormiga, 2000, pl. 11F; *Scolecura*, Miller, in press a, fig. 18E). Character 43 in Hormiga (1993, 1994a); 58 in Hormiga (1994b); 57 in Hormiga et al. (1995), 75 in Griswold et al. (1998), 68 in Hormiga (2000); 69 in Hormiga (2003); 207 in Agnarsson (2004). The enlargement of the mesal cylindrical gland spigot supports linyphioids (clade 3).

165. Aciniform gland spigots in female PLS: 0, absent (*Stemonyphantes*, Hormiga, 1994a, fig. 20D); 1, one or more (*Novafroneta*, Hormiga, 2000, pl. 11F; *Sphecozone spadicaria*, Miller, in press a, fig. 161E). Character 42 in Hormiga (1993, 1994a); 59 in Hormiga (1994b); 69 in Hormiga (2000). The number of aciniform gland spigots in linyphiids is variable. The number of PLS aciniform gland spigots probably has phylogenetic significance. However, we detected no compelling gaps that could be

parleyed into character state boundaries. Also, the small sample size per species examined underestimated the variance within species. The intermediate character state for a single aciniform gland spigot present (Hormiga, 1993, 1994a,b, 2000) has been eliminated. There are three independent losses of these aciniform gland spigots.

166. Aggregate-flagelliform triplet in male PLS: 0, absent; 1, present, at least in part (*Laminacauda*, Hormiga, 2000, pl. 42D; *Psilocymbium*, Miller, in press a, fig. 184F). Character 219 in Agnarsson (2004). The retention of the male triplet provides ambiguous support for Linyphiidae (clade 5) with a reversal in Linyphiinae (clade 7).

167. Aggregate gland spigots in female PLS: 0, two (*Laminacauda*, Hormiga, 2000, pl. 45D; *Anodoration*, Miller, in press a, fig. 27E); 1, one (*Lygarina*, Miller, in press a, fig. 70E). Character 213 in Agnarsson (2004). There are two independent reductions in the number of aggregate gland spigots.

168. Flagelliform gland spigot in female PLS: 0, present (*Laminacauda*, Hormiga, 2000, pl. 45D; *Anodoration*, Miller, in press a, fig. 27E); 1, nubbin (*Gongylidium*, Hormiga, 2000, pl. 30E,F; *Asemostera*, Miller, in press a, figs 131E,F); 2, absent (*Psilocymbium*, Miller, in press a, fig. 184E). The previous three characters are derived from characters 70 and 71 in Hormiga (2000). See also characters 13, 14 in Coddington (1990a); 46, 47 (table 1) in Coddington (1990b); 27 in Platnick et al. (1991b); 77, 78 in Griswold et al. (1998); 86 in Griswold et al. (1999); 71, 72 in Hormiga (2003); 58 in Schütt (2003). Coding variation in the flagelliform gland and aggregate gland spigots of male and female linyphiids was challenging. Hormiga (2000) coded the presence or absence of aggregate gland (character 70) and flagelliform gland (character 71) spigots in the male. Both characters optimize to the same node in Hormiga's analysis and provide the only unambiguous support for the clade Mynogleninae, Erigoninae, and *Stemonyphantes*. The independence of these two characters is dubious, because both are involved in the creation of araneoid sticky silk, although incomplete reductions of the triplet are known for some taxa. Retention of the aggregate-flagelliform triplet in mature males appears to be the phylogenetically interesting phenomenon. In a few erigonine genera, males and females exhibit identical reductions in flagelliform or aggregate spigots. These reductions provide potentially useful phylogenetic information, but cannot be coded as separate characters in males and females without introducing non-independent characters. Our solution is to code the triplet as absent or at least partially present in males as one character (166). Two other characters (167 and 168) independently code variation in the number and form of aggregate and flagelliform spigots. Characters 163 and 164 are specifically tied to observations of female spinnerets, although identical states occur in all erigonine males thus far examined. Reduction of a flagelliform gland spigot to a nubbin supports *Asemostera* (clade 70); there are three additional reductions in this spigot to a nubbin (one) or complete loss (two). An alternative coding scheme following Hormiga (2000), where the male flagelliform gland and aggregate gland spigots are considered as independent characters and the females are not coded, does not alter the topology.

169. Epiandrous gland spigots: 0, absent (*Leptorhoptrum*, Fig. 22F); 1, present (*Stemonyphantes*, Fig. 22E). Character 56 in Griswold et al. (1999); 12 in Huber (2000); 125 in Silva Dávila (2003); 168 in Agnarsson (2004). The loss of epiandrous gland spigots (Fage and Machado, 1951; Machado, 1951; Marples, 1967) is a synapomorphy for Erigoninae (clade 12).

170. Epiandrous gland spigot arrangement: 0, grouped (*Stemonyphantes*, Fig. 22E); 1, separated (*Orsonwelles*, Hormiga, 2002, figs 38C,D). Character 57 in Griswold et al. (1999); 169 in Agnarsson (2004). Among the exemplars in this analysis with epiandrous gland spigots, the spigots may be arranged in groups set in pits, or each may be separated and not set in a pit. The transition from grouped to isolated spigots provides ambiguous support for Mynogleninae (clade 11). However, this character does not adequately capture all variation in epiandrous gland spigot arrangement known within linyphiids and pimoids (see Hormiga, 2002, 2003).

Behavior

171. Mating behavior, male during spermweb construction: 0, above spermweb; 1, below spermweb. Character 46 in Hormiga (1993, 1994a); 61 in Hormiga (1994b); 72 in Hormiga (2000); 73 in Hormiga (2003). Nielsen (1931) reported on the mating of *Erigone atra*. He observed the male biting through threads in the female web, producing a hole while spinning fresh threads. The male then deposited a droplet of sperm at the edge of the hole. Since erigonines do not have epiandrous gland spigots, they must construct a sperm web with a different set of spigots. Schlegelmilch (1974) described and illustrated the sperm webs of several erigonine species. Further observations of erigonine courtship and mating would be helpful. Building the spermweb from above provides ambiguous support for Linyphiinae (clade 7).

172. Mating behavior, male during ejaculation: 0, above spermweb; 1, below spermweb. Character 47 in Hormiga (1993, 1994a); 62 in Hormiga (1994b); 73 in Hormiga (2000); 74 in Hormiga (2003); 242 in Agnarsson (2004). Observations of the mating behavior of *Ostearius melanopygius* were reported in Braun (1961; see also van Helsdingen, 1965). Ejaculating from above the spermweb provides ambiguous support for Linyphiinae (clade 7).

173. Web type: 0, orb web (*Theridiosoma*, Coddington, 1986b, fig. 157); 1, irregular mesh (*Linyphia*, Benjamin et al., 2002, fig. 2; *Pimoa*, Hormiga, 1994b, Fig. 8; *Sphecozone*, Miller, in press a, fig. 2C–E). Character 43 in Hormiga et al. (1995); 74 in Scharff and Coddington (1997); 80 in Griswold et al. (1998); 126 in Griswold et al. (1999); 75 in Hormiga (2003); 80 in Schütt (2003); 225 in Agnarsson (2004). Coddington (1990a,b) did not code the orb web as present or absent, but divided it into its component behavioral units. This is probably the best approach. However, nearly all of the scarce data available on linyphiid webs is from complete structures, not ethology (but see Benjamin et al., 2002), so coding the broadest taxon sample possible required using a character that could be coded from a finished web. Several ethological characters may eventually be shown to support node 3, including the loss of cut-and-reel behavior on structural lines (radii in orb-weavers), and web life, lasting less than a day in orb-weavers, up to at least several weeks in theridiids, linyphiids, and pimoids (Benjamin and Zschokke, 2002, 2003). Although theridiid webs do not obviously resemble orb-webs, *Steatoda* and some other theridiids construct their webs with most structural lines radiating from a single point. Although this point is peripheral rather than central, it may be homologous to the orb-web hub; this character could support node 2 in this analysis (Benjamin and Zschokke, 2003).

174. Web placement: 0, aerial (*Linyphia*, Benjamin et al., 2002, fig. 1); 1, close to substrate (*Pimoa*, Hormiga, 1994b, fig. 7; *Sphecozone bicolor*, Miller, in press a, fig. 2E). The transition from an aerial web to a web built close to the substrate supports clade 2; the secondary origin of aerial webs supports Linyphiini (clade 8).

175. Web knock-down lines: 0, few or absent (*Stemonyphantes*, Jones, 1983, p. 283; *Theridiosoma*, Coddington, 1986b, fig. 157; *Sphecozone*, Miller, in press a, figs 2C–E); 1, numerous (*Linyphia*, Benjamin et al., 2002, fig. 1; *Pimoa*, Hormiga, 1994b, fig. 8). Many members of Linyphiini, and also orb-weavers, construct conspicuous aerial webs away from any substrate. The webs of mynoglenines are described as sheet webs but few details of their architecture are published (Blest, 1979). Other linyphiids and some outgroup taxa construct their webs close to the substrate. Erigonines and *Stemonyphantes* usually construct sheet webs with few knockdown lines. Web architecture is documented for only a few species of erigonines. Web attributes were only coded into the matrix if the actual exemplar species had been photographed in its web. Variation within webs of different *Laminacauda* species indicates that this conservative approach is appropriate to avoid erroneous coding. *Laminacauda newtoni* builds a simple sheet web with no knockdown lines, but an undescribed *Laminacauda* species from Alerce Andino, Chile was found with an extensive system of knockdown lines (see Miller, in press a). The web of *Laminacauda plagiata* has not been photographed so *Laminacauda* was not coded for web architecture characters. The origin of numerous knock-down lines provides ambiguous support for clade 2 with a loss at the linyphiid node (5). A second origin of numerous knock-down lines provides unambiguous support for Linyphiini (clade 8).

176. Copulatory plug of secreted resin: 0, absent; 1, present (*Mermessus*, Fig. 21J; Millidge, 1987, figs 167, 168, see also van Helsdingen, 1982). Character 128 in (Ramírez, 2003). Many forms of copulatory plugs are found in linyphiids and other spiders. The plugs found in some species of *Mermessus* are conspicuous, unusual, and potentially phylogenetically informative; they are brownish, hard, and may obscure a considerable part of the epigynum. In the context of this analysis, the origin of this plug supports *Mermessus* (clade 43).

Appendix E

Alternate coding for some characters of the embolic division following the homology assessment strategy of Hormiga (2000; see following page). Conventions as in Appendix B. See Char. 52, Appendix D for details.

Appendix F

Clades and character support

This section summarizes character support (especially unambiguous support) for clades of interest in this study. Character support for clades found in both Hormiga (2000) and the current study (equal weights analysis) are detailed and contrasted. Clades of relevance to the evolution of the tracheal system and the loss of the paracymbium are also discussed. Additional notes on selected well-supported or otherwise significant nodes are also provided.

"Linyphioid" phylogeny: families and subfamilies. Evidence for "linyphioids" (Pimoidae plus Linyphiidae) in Hormiga (2000) was provided by three unambiguous synapomorphies: stridulatory striae on the male chelicerae (char. 55), autospasy at the patella-tibia joint (char. 60), and an enlarged base of the mesal cylindrical gland spigot on the PLS (char. 68). In addition to these three characters (Chars. 116, 133, and 164, respectively), new characters supporting the monophyly of "linyphioids" include a transition from a hirsute thorax to a thorax with setae in sparse rows restricted to the margins and segmental radii (Char. 111), the origin of ventral macrosetae on the tibia (Char. 146) and metatarsus

Appendix E

	49. Embolic basal lobe: abs; pres	51. Radix-embolus connection: continuous; membranous	52. Radical tail piece: abs; pres	53. Radical tailpiece: straight; spiral; recurved; mesal	55. Radical anterior process: abs; pres	56. Radical anterior process type: tooth-like; flagelliform	59. Radix distal lobe: abs; pres	66. Lamella characteristica: abs; pres
Tetragnatha	0	-	-	-	-	-	-	-
Theridiosoma	0	-	-	-	-	-	-	-
Steatoda	0	-	-	-	-	-	-	-
P. rupicola	0	-	-	-	-	-	-	-
P. altioculata	0	-	-	-	-	-	-	-
Stemonyphantes	0	0	1	4	1	0	0	0
Microlinyphia	0	0	0	-	0	-	0	1
Linyphia	0	0	0	-	0	-	0	1
Bolyphantes	0	0	0	-	0	-	0	1
Tenuiphantes	0	0	0	-	0	-	0	1
Haplinis	0	0	0	-	0	-	0	0
Novafroneta	0	0	0	-	0	-	0	0
Leptorhoptrum	0	0	1	0	0	-	0	0
Drepanotylus	0	0	0	-	0	-	0	0
Hilaira	0	0	0	-	0	-	0	1
Tibioploides	0	0	0	-	0	-	0	0
Triplogyna	0	0	1	0	1	0	0	0
Laminacauda	0	0	1	0	1	0	0	0
Scolecura	0	0	1	3	1	0	0	0
Ostearius	0	0	1	0	0	-	0	0
Neocautinella	0	0	1	0	0	-	0	0
Anodoration	0	0	1	0	0	-	0	0
Rhabdogyna	0	0	1	0	0	-	0	0
Ctenophysis	0	0	1	0	1	0	0	0
Valdiviella	0	0	1	0	0	-	0	0
Deichomma	0	0	1	0	1	0	0	0
Notiomaso	0	0	1	4	0	-	0	0
Pseudotyphistes	0	0	1	0	0	-	0	0
Sisicus	0	0	0	-	0	-	0	1
Onychembolus	0	0	1	0	1	0	0	0
Smermisia	0	0	1	0	0	-	0	0
Lygarina	0	0	1	0	1	0	0	0
Hypselocara	0	0	1	0	1	0	0	0
Neomaso	0	0	0	-	0	-	0	1
Gigapassus	0	0	0	-	0	-	0	1
Asthenargus	0	0	0	1	0	-	0	1
Gongylidiellum	0	0	0	-	0	-	0	1
Spanioplanus	0	0	0	1	0	-	0	1
Sciastes	0	0	1	0	1	0	0	0
Islandiana	0	0	1	2	1	0	0	0
Gravipalpus	0	0	1	0	0	-	0	0
M. dentiger	0	0	1	2	0	-	0	0
M. rapidulus	0	0	1	2	0	-	0	0
Paraletes	0	0	1	0	1	0	0	0
Erigone	0	0	1	2	1	0	0	0
Myrmecomelix	0	0	1	0	1	0	0	0
Microplanus	0	0	1	0	1	0	0	0
Toltecaria	0	0	1	0	0	-	0	0
Fissiscapus	0	0	1	1	1	0	0	0
Labicymbium	0	0	1	1	0	-	0	0
Diplocentria	0	0	1	0	1	0	0	0
Sisicottus	0	0	0	-	0	-	0	1
Oedothorax	0	0	0	-	0	-	0	1
Gongylidium	0	0	0	-	0	-	0	1
Hylyphantes	0	0	0	-	0	-	0	1
Tmeticus	0	0	1	0	1	0	0	0
Typhochrestus	0	0	1	1	1	0	0	0
Araeoncus	0	0	1	0	1	0	0	0
Diplocephalus	0	0	1	0	1	0	0	0
Savignia	0	0	1	0	1	0	0	0
Entelecara	0	0	1	0	0	-	0	1
Dismodicus	0	0	1	0	0	-	0	0
Hybocoptus	0	0	1	0	0	-	0	1
Lophomma	0	0	1	0	1	0	0	0
Walckenaeria	0	0	1	1	0	-	0	0
Gonatium	0	0	1	0	1	1	0	0
A. daedalus	0	0	0	-	1	1	0	0
A. janetae	0	0	0	-	1	1	0	0
Tapinocyba	0	0	1	0	0	-	0	0
Ceratinops	0	0	1	0	0	-	0	0
Parapelecopsis	0	0	1	1	0	-	0	0
Grammonota	0	0	1	1	1	0	0	0
Intecymbium	0	0	1	1	0	-	0	0
Psilocymbium	0	0	1	1	1	0	0	0
Dolabritor	0	1	1	1	0	-	0	0
Gonatoraphis	0	0	1	1	0	-	0	0
Ceratinopsis	0	1	1	1	1	0	0	0
Tutaibo	0	1	1	1	1	0	0	0
S. rubescens	0	1	1	0	1	0	0	0
S. bicolor	0	1	1	1	1	0	0	0
S. spadicaria	0	1	1	1	1	0	0	0
S. crassa	0	1	1	1	1	0	0	0

(Char. 150), and the origin of a trichobothriuim on metatarsus IV (Char. 152). Based on an analysis including a new pimoid genus, Hormiga (2003) suggests that a transition from integral to intersegmental paracymbium (Char. 11) may be synapomorphic for ''linyphioids'' with a reversal in *Pimoa*. This optimization cannot be shown given the taxon sample in the current analysis. ''Linyphioid'' monophyly was supported by 2 steps of Bremer support in Hormiga (2000); it is one of the best supported nodes on the current study with 5 steps of Bremer support.

Pimoid monophyly (clade 4) was unambiguously supported in Hormiga (2000) by the presence of a cymbial denticulate process (char. 1), a pimoid cymbial sclerite (char. 3), a pimoid embolic process (char. 19), anteriorly directed fertilization ducts (char. 40), the origin of a trichobothrium on metatarsus IV (char. 65), and by the loss of aciniform gland spigots on the PMS (char. 66). In the current study, several pimoid characters have been reevaluated. The cymbial denticulate process has been generalized to a cymbial retromedian process, a homoplasious structure found occasionally in several araneoid groups (Char. 1). In *Pimoa*, the retromedian process is covered in denticles, which provides ambiguous support for clade 4 (Char. 2). Hormiga (2003) found that the field of denticles may occur elsewhere on the cymbium. The presence of a pimoid cymbial sclerite (Char. 3), pimoid embolic process (Char. 37), and an anterior origin of the fertilization ducts (Char. 99) continue to provide unambiguous support for clade 4. The origin of the metatarsus IV trichobothrium (Char. 152) no longer supports clade 4 but instead supports the ''linyphioid'' clade (see above). The loss of aciniform gland spigots on the PMS (Char. 162) no longer provides support for clade 4 because the basal linyphiid *Stemonyphantes* also lacks these spigots. Additional unambiguous support for clade 4 comes from the loss of the column (Char. 38; but see below), the origin of a second retrolateral trichobothrium on the male palpal tibia (Char. 73), an increase in the number of ventromesal macrosetae on the female palpal tarsus (Char. 131), and the origin of dorsal (Char. 147), prolateral (Char. 148) and retrolateral (Char. 149) macrosetae on metatarsus I. The presence of an integral paracymbium (Char. 11) is optimized as giving ambiguous support to *Pimoa* following Hormiga (2003). Clade 4 is well supported in both Hormiga (2000; 5 steps of Bremer support) and the current analysis (7 steps of Bremer support).

According to Hormiga (2000), linyphiid monophyly was unambiguously supported by the origin of intersegmental paracymbium attachment (char. 4), the origin of the suprategulum (char. 11), radix (char. 20), and column (char. 24), and the loss of the median apophysis (char. 15) and conductor (char. 16). In the

current study, linyphiid monophyly is unambiguously supported by the origin of the suprategulum (Char. 24), the radix (Char. 50), and the loss of the median apophysis (Char. 35) and conductor (Char. 36); the retention of the aggregate-flagelliform triplet in the male (Char. 166) contributes ambiguous support for Linyphiidae. The origin of the column (a membranous articulation between the tegular and embolic divisions (Char. 38) no longer provides support for Linyphiidae because it was coded as present in *Steatoda* (Agnarsson, 2004; *contra* Griswold et al., 1998; Hormiga, 2000) as well as in *Tetragnatha*. However, this seems to be an artifact of taxon sampling. Based on the phylogeny of araneoid families in Griswold et al. (1998), embolus-tegulum membranes are independently derived in tetragnathids, theridiids, and linyphiids. The monophyly of Linyphiidae is well supported in Hormiga's (2000) analysis with 4 steps of Bremer support. In the current study, Linyphiidae is only weakly supported with a single step of Bremer support. This is probably due to several similarities shared between *Pimoa* and *Stemonyphantes*; such characters are also responsible for the non-monophyly of linyphiids with a *Pimoa-Stemonyphantes* clade found in some previous analyses (Hormiga, 1993, 1994a,b).

Monophyly of clade 6 (Linyphiidae exclusive of *Stemonyphantes*) is unambiguously supported by the origin of an embolic membrane (Char. 40), reduction in the thoracic furrow (Char. 114), fusion of the labium to the sternum (Char. 122), and the origin of aciniform gland spigots on the PMS (Char. 162). The origin of PMS aciniform gland spigots at this node would seem to suggest that linyphiid PMS aciniforms are not homologous with those of other araneoid spiders. However, given the level of homoplasy in character 162 (15 steps) and the widespread distribution of PMS aciniform gland spigots in araneoid spiders, it seems more likely that this is really a case of multiple independent losses, and not really a synapomorphy at this node. Also, the pimoid genus *Weintrauboa* has aciniform gland spigots on the PMS (Hormiga, 2003, fig. 8C), consistent with parallel losses in *Pimoa* and *Stemonyphantes*.

Hormiga (2000) argued for the monophyly of Linyphiinae (clade 7) based on four synapomorphies: the presence of a terminal apophysis (char. 26) and lamella characteristica (char. 27), and constructing (char. 72) and ejaculating (char. 73) into the spermweb from above; there was no unambiguous character support for Linyphiinae. Hormiga (2000) justified his selection of a preferred tree that included a monophyletic Linyphiinae by arguing that optimizations of some characters in alternative topologies were nonsensical. Both the terminal apophysis and lamella characteristica arise from the radix. Since non-linyphiid taxa lack a radix, they must be coded as inapplicable for both the terminal apophysis and lamella characteristica. Given the topologies found by Hormiga (2000), the optimization of these characters only provides ambiguous support for Linyphiinae. Behavioral characters (72 and 73) were coded for relatively few taxa and no non-linyphiid taxa, so they can only provide ambiguous support for Linyphiinae. Hormiga (2000, p. 13) noted that an unidentified tetragnathid had been filmed ejaculating into the spermweb from below, the condition observed in several non-linyphiine linyphiids, and at least ejaculating (and possibly also building) from above the spermweb might be synapomorphic for linyphiines. In the current analysis, Linyphiinae has unambiguous support from the origin of a terminal apophysis (Char. 65) and a lamella characteristica (Char. 66), consistent with Hormiga's argument. These characters can provide unambiguous support because *Stemonyphantes*, which has a radix but lacks both a terminal apophysis and a lamella characteristica, is sister to all other linyphiids. Additional unambiguous support for a monophyletic Linyphiinae comes from elongation of the spermathecae (Char. 98), origin of dorsal macrosetae on metatarsus I (Char. 147), and loss of the trichobothrium on metatarsus IV (Char. 152).

Unambiguous support for a sister-taxon relationship between Mynogleninae and Erigoninae (clade 10) comes from the reduction of the clypeal setae in the female from several to one (Char. 113), the loss of retrolateral (Char. 145) and ventral (Char. 146) macrosetae on Tibia I, and the loss of ventral macrosetae on metatarsus I (Char. 150).

Hormiga (2000) found unambiguous support for the monophyly of Erigoninae (clade 12) from the presence of a palpal tibial apophysis (char. 28) and loss of the claw on the female palpal tarsus (char. 59). In the current study, the presence of a palpal tibial apophysis (Char. 67, the prolateral apophysis) supports clade 13 (Erigoninae exclusive of *Leptorhoptrum*). Loss of the female tarsal claw (Char. 126) continues to support Erigoninae. Additional unambiguous character support comes from the origin of a retrolateral groove on the cymbium (Char. 7), loss of the distal dorsomesal macroseta on the female palpal tarsus (Char. 128), loss of prolateral macrosetae on femur I (Char. 135), branching of the median tracheal trunks (Char. 157) and their extension through the pedicel into the prosoma (Char. 160), and by the loss of the epiandrous gland spigots (Char. 169). We found strong support for the monophyly of Erigoninae (5 steps of Bremer support); Hormiga (2000) found only weak support for Erigoninae (1 step of Bremer support).

Linyphiid phylogeny: erigonine genera. Our erigonine phylogeny (Fig. 4) has a basal grade of four taxa with taenidia in their tracheoles. Above this grade are two large clades, one composed mostly of Haplotracheate

and transitional erigonines (clade 17), and the other composed of *Sciastes* and the "distal erigonines" (clade 38).

As noted above, clade 13 (Erigoninae exclusive of *Leptorhoptrum*) is supported by the origin of a prolateral tibial apophysis (Char. 67). Additional unambiguous character support for this clade comes from the presence of a spiral paracymbium (Char. 12), ventral extension of the distal suprategular apophysis from the suprategulum (Char. 31), reduction in the strength of the dorsal macroseta on the male palpal patella (Char. 78), and by the loss of the proximal dorsoectal macroseta on the female palpal tarsus (Char. 129).

Clade 16 is composed of the two major erigonine clades noted above: 17 and 38. Unambiguous support for this node comes from the origin of an anterior radical process (Char. 55), the transition from a dorsally oriented to a distally oriented prolateral tibial apophysis (Char. 68), the transition from compressed to widely spaced stridulatory striae (Char. 118), and reduction in the setal bases on the anteriolateral part of the chelicerae (Char. 120).

Clade 17 contains *Triplogyna*, *Laminacauda*, and the "haplotracheate erigonines." *Triplogyna* retains the primitive condition for erigonines, desmitracheate tracheae with taenidia in the tracheoles. The tracheal system in *Laminacauda* has been investigated for several species (Millidge, 1985; Hormiga, 2000). Branching of the median trunks is sparse compared to the typical desmitracheate condition. Clade 17 is supported by the origin of a retrolateral tibial apophysis (Char. 70), which initially coexists with the prolateral tibial apophysis, and by the origin of a proximal dorsoectal macroseta on the female palpal tarsus (Char. 129).

The "haplotracheate erigonine" clade (19) is unambiguously supported only by the character from which it derives its name: loss of branching in the median tracheal trunks (Char. 157). Reduction in the width of the median tracheal trunks (Char. 159) provides ambiguous support for clade 19. This seems credible because although our *Laminacauda* exemplar exhibits narrow trunks, other *Laminacauda* species are known to have wide trunks (e.g., *Laminacauda diffusa*, Hormiga, 2000, fig. 31G). We postulate parallel reductions in median trunk width in clade 19 and within *Laminacauda*.

Clade 29 contains several endemic Neotropical genera plus three taxa from Hormiga's (2000) original study: *Sisicus*, *Asthenargus*, and *Gongylidiellum*. Clade 29 is unambiguously supported by an articulated junction between the tegulum and the suprategulum (Char. 25), and by the presence of striations on the suprategulum (Char. 27). However, coding suprategular characters for *Sisicus* is controversial (see Appendix D, Char. 24). Clade 29 is supported by two steps of Bremer support. Relationships among *Sisicus*, *Asthenargus*, and *Gongylidiellum* in the current study are congruent with the results in Hormiga (2000). In Hormiga (2000), the *Sisicus–Asthenargus–Gongylidiellum* clade was supported by the origin of the protegulum (char. 8) and the lamella characteristica (char. 27); the *Asthenargus–Gongylidiellum* clade was supported by reductions in embolus length (char. 17) and the number of dorsal macrosetae on tibia IV (char. 64). In the current study, the origin of the protegulum (Char. 16) provides unambiguous support for a deeper clade of haplotracheate erigonines (clade 20; *Ostearius melanopygius* has been recoded from Hormiga, 2000 as having the protegulum present, pl. 52F). The origin of the lamella characteristica no longer supports the *Sisicus–Asthenargus–Gongylidiellum* clade. Although *Sisicus* retains a lamella characteristica in the current study (Char. 66), *Asthenargus* and *Gongylidiellum* have been recoded as having a membranous division between the embolus and radix (Char. 51; see Appendix D, Char. 52). Reduction in embolus length (Char. 43) and in the number of dorsal macrosetae on tibia IV (Char. 142) continue to support the *Asthenargus–Gongylidiellum* clade, optimizing at nodes 30 and 31, respectively.

Clade 38 is composed of *Sciastes* plus the "distal erigonines" clade. This clade appeared among the set of most parsimonious trees in Hormiga (2000) and in his preferred tree. Hormiga (2000) mapped the origin of protegular papillae (char. 9) as providing ambiguous support for this clade. In the current study, the origin of protegular papillae (Char. 17) provides unambiguous support for this clade. Additional unambiguous support for clade 38 comes from the origin of the protegulum (Char. 16), a shift in the relative orientation between the subtegulum and the tegulum (Char. 21) and a reduction in embolus length (Char. 43).

Hormiga (2000) found unambiguous support for the "distal erigonines" (clade 39) in the loss of taenidia in the tracheoles (char. 52), a shift from ridged to imbricated stridulatory striae (char. 56), and the loss of the distal macroseta on tibia IV (char. 64). All three characters continue to support this node (Chars. 161, 117, and 143, respectively). We found no new character support for this node. This node is supported by two steps of Bremer support in both Hormiga's (2000) analysis and in the current study.

Clade 52 is composed of *Sisicottus* sister to *Oedothorax*, *Gongylidium*, *Hylyphantes* and *Tmeticus*. Miller (1999) attempted to discover appropriate outgroups for a species level phylogeny of *Sisicottus* by adding *Sisicottus* to Hormiga's (2000) data matrix. That analysis indicated *Sisicottus* was sister either to *Oedothorax*, or to a clade consisting of *Oedothorax*, *Hylyphantes*, and *Gongylidium*. The current study yields results similar to the latter solution, except that *Tmeticus* is added sister to *Hylyphantes*. This clade is supported by the origin of a tegular sac (Char. 19) and a membranous connection between the embolus and radix (Char. 51).

Clade 53 contains four taxa from Hormiga's (2000) study, all of which are supported by 2 or more steps of Bremer support. Hormiga's study recovered a *Hylyphantes–Gongylidium–Oedothorax* clade. The current study adds *Tmeticus* as sister to *Hylyphantes*, disrupting the monophyly of this group. The loss of a *Gongylidium–Oedothorax* clade disrupts Millidge, 1977) "*Gongylidium* group", which was recovered by Hormiga (2000).

Unambiguous support for a sister-taxon relationship between *Savignia* and *Diplocephalus* (clade 56) was provided by the presence of a male PME cephalic lobe (char. 42) in Hormiga's study. In the current study, the PME lobe (Char. 102) supports the more inclusive clade 59. Unambiguous support for clade 56 comes from the elongate shape of the spermathecae (Char. 98). This clade had a single step of Bremer support in both Hormiga's (2000) analysis and the current study.

Clade 61 is composed of *Entelecara*, *Dismodicus* and *Hybocoptus*. Hormiga (2000) found unambiguous support for this clade in the elongation of the embolus (char. 17), reduction in the number of retromarginal teeth on the female chelicerae (char. 58), and the origin of a trichobothrium on metatarsus IV (char. 65). In the current analysis, reduction in the number of retromarginal teeth (Char. 123) and the origin of the fourth metatarsal trichobothrium (Char. 152) continue to provide support for this node. Additional support is provided by the loss of the anterior radical process (Char. 55) and the presence of lateral sulci (Char. 108) with pits (Char. 109) on the male prosoma. The elongate embolus (Char. 43) supports a much more inclusive clade (51) with several reversals and considerable homoplasy on the tree. Note that in Hormiga's phylogeny, internal relationships of this clade differ with *Entelecara* and *Hybocoptus* as sister taxa. The presence of an *Dismodicus–Hybocoptus* clade, rather than an *Entelecara–Hybocoptus* clade, disrupts Millidge's (1977) "*Entelecara* group", which was recovered by Hormiga (2000).

Clade 66 is comprised of the Holarctic genus *Gonatium* and two exemplars of the Neotropical genus *Asemostera*. This relationship is unambiguously supported by the extension of the cymbium well beyond the alveolus (Char. 6), the loss of the protegulum (Char. 16), the origin of papillae on the embolic membrane (Char. 41), the proximal origin of the embolus (Char. 42), the modification of the radical anterior process into a flagelliform structure (Char. 56), and the loss of copulatory duct encapsulation (Char. 95). The monophyly of *Asemostera* (clade 67) is the best supported group in the analysis with 10 steps of Bremer support.

Clade 69 contains three taxa from Hormiga's analysis, *Tapinocyba*, *Parapelecopsis*, and *Ceratinops*. These taxa formed a grade leading to the *Dismodicus–Entelecara–Hybocoptus* clade in Hormiga's phylogeny. Unambiguous support for clade 69 is provided by the loss of the anterior radical process (Char. 55) and the presence of lateral sulci (Char. 108) with pits (Char. 109) on the male prosoma.

Clade 71 contains *Grammonota* from Hormiga's taxon sample plus several Neotropical endemic genera. This clade is unambiguously supported by the origin of papillae on the tegulum (Char. 20), the origin of the embolus, which arises from the radix at a distinct angle (Char. 47), the modification of the radical tailpiece into a spiral shape (Char. 53), and the long path of the sperm duct through the radix (Char. 63).

Clade 72 is endemic to the Neotropics, except for a few species that can be found in northern Mexico and the southern margin of the United States. This clade is supported by the loss of papillae on the protegulum (Char. 17), the transition from a spiral to a curved embolus (Char. 44), the presence of a ridge on the radix (Char. 60), the loss of copulatory duct encapsulation (Char. 95), the reduction in the density of cuticular pores in the male (Char. 110), and a reduction in the number of clypeal setae (Char. 113). Clade 72 includes two independent losses of the paracymbium, once in *Psilocymbium*, and again in *Sphecozone* (see Appendix D, Char 12).

Clade 74 is unambiguously supported by the dorsal orientation of the prolateral tibial apophysis (Char. 68), the presence of a distal tooth on the tibial apophysis (Char. 69), the origin of an atrium (Char. 92), and the elongation of the spermathecae (Char. 98). Additional ambiguous support comes from the reduction of the paracymbium into a vestigial structure (Char. 12). A vestigial paracymbium is observed in *Gonatoraphis* and *Dolabritor*; *Psilocymbium* has completely lost the paracymbium.

Clade 76 is unambiguously supported by the transformation of the paracymbium from a spiral into a straight hook (Char. 12), the presence of a membranous connection between the radix and embolus (Char. 51), the compression of the stridulatory striae (Char. 118), and the presence of smooth booklung covers (Char. 154). Clade 76 contains *Ceratinopsis interpres* (type species for the genus) but not *Intecymbium* (formerly *Ceratinopsis*) *antarctica*. The non-monophyly of these taxa necessitated the placement of *Intecymbium antarctica* in a different genus or the synonymy of several genera. Wunderlich (1987) advocated the synonymy of several genera including *Ceratinopsis* under *Sphecozone*, but this has been rejected by subsequent workers (e.g., Millidge, 1991).

The monophyly of *Sphecozone* (clade 78) is supported by the loss of the paracymbium (Char. 10) and radical ridge (Char. 60), and the origin of an atrium (Char. 92). *Sphecozone rubescens* O. Pickard-Cambridge, 1870 is the type species for the genus. *Sphecozone bicolor* (Nicolet, 1849) is the type species of *Hypselistoides* Tullgren, 1901; which is considered a junior synonym of *Sphecozone* (Millidge, 1985). *Sphecozone spadicaria* (Simon, 1894) is

the type species of *Brattia* Simon, 1894. *Gymnocymbium* Millidge, 1991 is represented by *Sphecozone crassa*, which is the only species in Millidge's circumscription of the genus currently known from both males and females. As noted above, there are indications that *Sphecozone crassa* may not be very closely related to *Gymnocymbium grave* Millidge, 1991, the type species for the genus (Miller, in press a). The relationships among the four taxa in clade 78 necessitated nomenclatural changes. *Sphecozone* as circumscribed by Millidge was clearly paraphyletic, with *S. rubescens* and *S. bicolor* forming a grade leading to the exemplars representing *Brattia* and possibly *Gymnocymbium*. The genus *Clitolyna* Simon, 1894 probably belongs to the *Sphecozone* clade, but was represented by insufficient material to be included in the analysis. The synonymization of *Brattia*, *Gymnocymbium*, and *Clitolyna* (along with *Hypselistoides*) under *Sphecozone* produces a diagnosable group. It should be noted that *S. rubescens* is rather unusual for the genus. If future work supports the basal position of *S. rubescens*, it may be possible to segregate *S. rubescens* (and a few similar species) into a small genus sister to a resurrected *Hypselistoides*, containing the rest of the species currently under *Sphecozone*. The proper affinities of *Gymnocymbium* and *Clitolyna* will require further investigation and the acquisition of additional specimens.